

MATURATION OF INTRA-OVARIAN EGGS AND SPAWNING PERIODICITIES IN SOME FISHES*

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PREFACE

It is well known that, in the temperate as well as in the tropical waters, fishes exhibit various types of spawning tendencies which are closely connected with the development of the intra-ovarian eggs in batches. Examination of the periodicity in the production of ova in batches from the ovigerous

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lamellae in the ovaries of oviparous teleosts and a statistical study of the distribution of intra-ovarian eggs in the ovaries of various stages of maturity have been found to give reliable evidence on spawning habits of fishes. Such a study of the intra-ovarian eggs in the ripe and earlier stages of maturity is the basis of the present investigation which was initiated with a view to determining the duration of spawning period in some of the edible food fishes. The work was started in 1945 at the suggestion of Dr. N. K. Panikkar, the then Director of the Madras University Zoology Research Laboratory, and continued later in the Central Marine Fisheries Research Station, Mandapam Camp.

INTRODUCTION AND HISTORICAL

A series of changes are undergone by the intra-ovarian eggs before they become mature and attention has already been paid to their development and accounts have been given by various earlier authors. As early as in 1899, Fulton observed that the occurrence, in large numbers, of ova of intermediate size, between the small immature ova and the bigger yolky ones, in mature fishes, is closely associated with a prolonged spawning period. An attempt to study the maturity by the measurements of the ova was first made by Clark (1934) on the California sardine (*Sardina caerulea*). Later, Hickling and Rutenberg (1936) determined the spawning periods in hake, haddock, pilchard, herring and lepidogaster by the same method. Recently De Jong (1939) has investigated, on the same lines, the spawning habits of 13 species of teleostean fishes from the Java sea.

Thus, by studying the dimensions of eggs in the ovaries of fishes in the mature stage or in the penultimate stage of maturity, it is possible to study the duration of spawning periods. Even though spawning is not a continuous process after the attainment of maturity, still, in tropical places, adult individuals may be found throughout the year with ripe gonads. De Jong remarks that conditions in tropical seas make it probable that specimens, which contain ripe ovaries, will be found throughout the year, so that a periodicity in the individual may be obliterated in the species as a whole. However, the same author thinks that, although fishes with ripe ovaries may be found in every season, the species as a whole may show a rather definite periodicity.

As no work, on the lines suggested by Hickling and Rutenberg and De Jong, has yet been published by fishery workers on the different species occurring in the Indian waters, except on one species, namely, *Thrissoles purava* (Ham.) by Palekar and Karandikar (1952), it was thought that the present investigation would yield some useful information on the spawning habits of those fishes selected for the present study. Although an investigation on the spawning habits of a species of fish would normally

require observations on the gonadic condition of the particular species for at least twelve months, De Jong is of opinion that, by employing this method of a statistical study of the intra-ovarian eggs, it is possible to discuss, at least for some of the species, the spawning habits of a species as a whole.

MATERIAL AND METHODS

The material for the present investigation includes nine species, under six different families.†

Family	Species
Centropomidæ	<i>Psammoperca waigiensis</i> Cuvier
Theraponidæ	<i>Therapon puta</i> Cuvier
	<i>Therapon jarbua</i> (Forskål)
	<i>Pelates quadrilineatus</i> (Bleeker)
Carangidæ	<i>Caranx (Selaroides) leptolepis</i> Cuvier and Valenceinnes
Bagridæ	<i>Macrones vittatus</i> (Bloch)
Exocoetidæ	<i>Cypsilurus oligolepis</i> (Bleeker)
Clupeidæ	<i>Chirocentrus dorab</i> (Forskål)
Engraulinæ (Sub-family)	<i>Stolephorus indicus</i> (v. Hass.) [<i>Anchoviella indica</i> (v. Hass.)]

Among the nine species selected for the present investigation, all except *Macrones vittatus* and *Therapon jarbua* are marine forms. *T. jarbua* occurs both in the Adyar backwaters as well as in the sea; but the Adyar collections consisted mostly of young ones. *Macrones vittatus* is a brackishwater inhabitant, forming a major part of the catches in the fishing operations in the Adyar area. Specimens of *Psammoperca waigiensis* were mostly collected from the perch-trap catches in the Gulf of Mannar and Palk Bay and at times from the shore seine catches in the Palk Bay near Mandapam. *Caranx (Selaroides) leptolepis*, *Stolephorus indicus* and *Cypsilurus oligolepis* were collected from the shore seine catches only and all these three species were found to be shoaling forms, as is evident from the fact that, on those days when these species were caught, they constituted the majority of the catches from shore seines. Maturing and mature specimens of *Chirocentrus dorab* were available only from the gill-net catches from the offshore waters. *Therapon puta* and *Pelates quadrilineatus* were collected from the catches of the bag nets operated about 3 to 4 miles away from the shore and also from

† The classification adopted is from the *Fishes of Indo-Australian Archipelago* by Weber and Beaufort, except in the case of *Macrones vittatus* which was identified from Day's *Fishes of British India*. The author is aware that the correct taxonomic assessment of the latter species is not very easy at present.

the drag nets, operated along the coastal areas. In all cases, only specimens with ovaries in ripe or penultimate stage of maturity were selected for the present investigation.

Fishes were brought to the laboratory alive or just after death for dissecting out their ovaries which were fixed either in 5% Formaldehyde or in Bouin's fluid for sectioning. The diameters of about 1,000 ova from each fish were recorded from ovaries fixed in 5% Formaldehyde and from sections of ovaries fixed in Bouin's fluid. In the former case, a small portion of the ovary was teased out on a slide in the same medium and measurements made of all ova in the field of the microscope, until about 1,000 ova from each fish had been examined. In the latter case, sections of ovaries, 7 to 8 μ thick, were utilised for recording the measurements of eggs. Owing to lack of symmetry in the eggs due to preservation, the micrometer was placed in a horizontal position and the diameters were measured parallel to the graduations on the micrometer. Clark (1934) and De Jong (1939) have found this method to give satisfactory results, but the latter is of opinion that, as a consequence of following this method, in the frequency polygon of the diameters of the ova, the differences between two groups of eggs appear less than they are in reality. De Jong further says that in some cases the largest diameter of an egg of a younger group exceeds the smallest diameter of one in an older group. Hence, in considering the different graphs, the fact has to be borne in mind that if two groups of eggs are apparently connected by a few ova of intermediate size, this connection, as a rule, does not exist and both groups are clearly separated during life. The diameters of eggs were measured under the microscope with an ocular micrometer at a magnification which gave a value of 16.7 μ to each micrometer division (m.d. represents micrometer divisions in the text).

Measurements of ova were made from sections of ovaries of *Macrones vittatus* and *Therapon jarbua*. In all the other species, measurements of ova were made from ovaries fixed in 5% Formaldehyde. In each species, measurements of ova were made from the ovaries of three different specimens and a fourth set of measurements were also made from random samples, from ovaries of the same species from 6 to 8 different individuals, with a view to checking the results obtained from the measurements from the individual ovaries. Thus, about 4,000 eggs were measured from ovaries of each species and a total of about 36,000 eggs had to be measured during the course of this investigation. Although some of the earlier authors, namely, Clark (1934), De Jong (1939) and Arora (1951), who have followed this method for determining the spawning habits of fishes, have drawn conclusions from measurements of only 500 ova or even less, it was considered by the present

author that the measurements of at least 1,000 eggs were necessary to mitigate the probable error in the representation of various groups of eggs in different stages of maturity and represented by various modes in the graphs. However, it was not found necessary to record the diameters of the numerous ova measuring less than 5 m.d., as such ova were sufficiently well represented in the first batch of immature eggs in each species.

GENERAL

In all the teleostean fishes selected for investigation of their spawning habits, ovaries are of cystovarian type and they get distended towards the spawning season. The increase in volume and weight of the ovary in the maturing season is due to certain changes undergone in the contents of eggs, resulting in the formation of yolk. The intra-ovarian eggs vary not only in their size but also in their inclusions in ovaries which are fully ripe or in the penultimate stage of ripeness. There are several batches of oocytes which take their origin from the germ cells of the ovigerous lamellæ and, as the spawning process continues every season, these batches pass on from one stage to the other. Fulton (1899) states that, in the ovaries of different species, gradations in size may be detected between two groups, but the degree in which the transition exists varies very much in different species. The same author says that, if a comparison is made between the fully mature ovaries of a teleostean, whose eggs are pelagic, with those of one whose eggs are demersal, a striking difference will be perceived in that the eggs in the latter, to be shed, are developed equally, they grow gradually until they reach a certain size, practically uniform in a given species, they become more pellucid or semi-transparent and are then expelled, whereas in species with pelagic eggs, examination of the ovary reveals the presence of large, clear eggs of crystalline transparency, scattered throughout its substance, presenting a marked contrast both in size and appearance to those around them, which are whitish, opaque and smaller. Norman (1931) has mentioned that the actual rate at which the eggs are extruded varies a great deal in different species, in some cases all or a large proportion of the ova being ripe for fertilisation at more or less the same time, while in others the process is comparatively slow and only a certain number ripen and are extruded at one time. De Jong (1939) says, "in the ovary of the adult fish we find a stock of small yolkless eggs, the cytoplasm of which stains deeply with Hæmatoxylin. From this general egg stock, quota are withdrawn to be matured and finally spawned". Farran (1938) found that all the eggs, destined to ripen, are fixed from the time the storage of yolk has begun.

The intra-ovarian eggs in an immature ovary are developed from the ovigerous lamellæ and a microscopic examination reveals that the differences

in their sizes are rather negligible. The first batch of eggs to be spawned gets richer in their yolk content while the cytoplasm gets pushed to the periphery. In some species of fishes, when the first batch of eggs become fully ripe, a second or even a third batch of eggs may be seen to have been withdrawn from the general egg stock. As observed by Fulton, one may trace a pretty regular gradation from the small yolkless eggs to the largest yolked eggs, but in most forms the demarcation between the yolkless and the yolked eggs is pronounced, as maturity is approached.

It is thus quite possible that an examination of the ovary during the spawning season or just prior to spawning, may reveal the presence of eggs in various stages of development. Various workers have differed slightly in the classification of the intra-ovarian eggs, but the following convenient classification was adopted for the present study:—

- (1) Immature ova .. These include the minute transparent ova as they arise from the germ cells, from the time they could be distinctly recognised as possessing a nucleus and a protoplasmic layer.
- (2) Maturing ova .. These include all the small opaque ova in which the formation of yolk has just commenced, but which are not fully yolked.
- (3) Mature ova .. This group includes all the ova that are opaque, full of yolk and with distinct yolk spherules, but still contained within the follicle.
- (4) Ripe ova .. Include all those fully mature, large, free, fully or partly transparent eggs which have burst from the follicles.

The measurements of the diameters of ova were made without any size selection and represent, with fair accuracy, the numerical ratio of eggs in different size-groups. However, it was found that the number of immature eggs was always comparatively much more than that of eggs in all the other stages of maturity, but the equality in numbers of various maturing groups occurred with a fair consistency in the ova-diameter frequencies for the different individuals in each species.

MATURATION OF INTRA-OVARIAN EGGS AND SPAWNING HABITS

(1) *Psammoperca waigiensis* Cuvier.—Ovaries of this species in maturing condition were collected in the month of June from specimens varying in

length from 22.5 to 23.8 cm. This species is caught throughout the year and does not exhibit any seasonal abundance. Measurements of intra-ovarian eggs were made from ovaries of three individual specimens of 22.8, 23 and 23.5 cm. length and also from random samples made from eight other specimens varying in length from 22.5 to 23.8 cm. The ovaries were yellowish in colour and contained eggs, the diameters of which varied from 4 to 30 m.d. The bigger eggs were yolky and opaque, but none of the eggs were transparent, thereby indicating that the ovaries were only in the penultimate stage of maturity. The entire range in the diameters of ova has been grouped into 2 m.d. groups and the frequency of ova in such 2 m.d. groups are shown in Fig. 1.

It could be seen from Fig. 1 that, in the whole ovary, there are several batches of eggs, represented by modes *a*, *b*, *c*, *d* and *e*, indicating a clear periodicity in the development of ova in the ovary. Considering the degree of formation of yolk as an indication of the stages of maturity of the different batches of eggs, the ova represented by the modes *e* and *d* are the mature ones in Stage III. Mode *c* represents the ova in maturing condition in Stage II and all the rest of ova, under modes *b* and *a*, are immature in Stage I. All the eggs, ranging in diameter from 20 to 30 m.d., are fully yolked, whereas, in eggs of 15 m.d., the formation of yolk has only just commenced around the nucleus and a distinct peripheral zone of cytoplasm is visible. Eggs with a diameter of 10 m.d. and less are completely devoid of yolk. Thus, ova between 20 and 30 m.d. can be considered as mature, which are to be shed during the next spawning season. As this batch of mature eggs under modes *e* and *d* are sharply differentiated from the rest of the groups of eggs (Fig. 1) it is quite likely that the spawning period of this species is not a prolonged one, but restricted to a definite and short period. However, even before the commencement of the shedding of the mature group of eggs at modes *e* and *d*, there is an indication of the formation of the next group of eggs in maturing condition (Stage II) at the 13 to 15 m.d. These eggs, wherein the yolk formation has already commenced, probably represent the eggs to be shed in the succeeding spawning season. Owing to the fact that the maturing eggs in Stage II have already been differentiated into a definite batch of eggs from the general immature egg stock, it is possible that the interval between two spawning periods may not be a long one, as has been observed by Palekar and Karandikar (1952) in *Thrissoles purava*. As the mature stock of eggs at the modes *e* and *d* are not yet fully ripe and assuming that these yolky opaque eggs would take another month or more to attain full maturity, it is probable that the spawning period in this species may be in July-August. From the facts that the next batch of eggs, in which

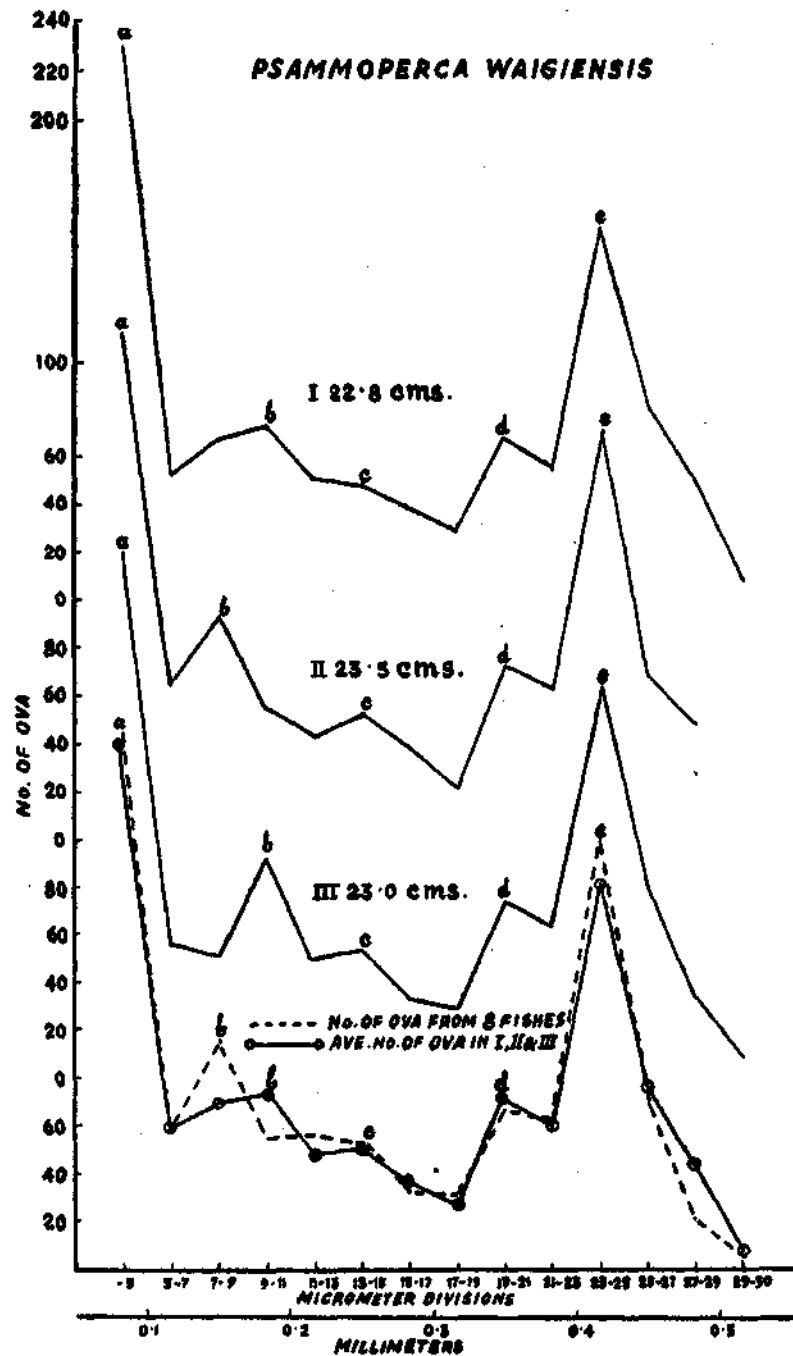


FIG. 1. Showing frequency of ova in the ovaries of *P. waigiensis*.

yolk formation has already commenced, has been differentiated into a definite group of eggs and that the spawning is restricted to a short and definite period,

it can be inferred that this species spawns more than once a year, probably once in July–August and a second time in January–February.

(2) *Therapon puta* Cuvier.—Mature ovaries of this species were collected during the months of February and March from specimens ranging in size from 12.4 to 14.3 cm. This species is also caught throughout the year and does not exhibit any seasonal abundance.

The measurements of intra-ovarian eggs from ovaries of three individuals, 13, 13.4 and 14 cm. in length, were made. The range in length of six other specimens, from which random samples of ovaries were taken, varied from 12.4 to 14.3 cm. The ovaries were light orange in colour and contained eggs in all four stages of maturity. The range in diameter of the intra-ovarian eggs varied from 4 to 30 m.d. The ova measuring 25 m.d. and above were found to be in an advanced stage of maturity, having a clear transparent zone along the periphery and a number of oil globules scattered in the central dark yolky region. The transparent peripheral zone (a characteristic of most of the pelagic fish eggs) is probably the area where the yolk has absorbed some amount of water prior to spawning. However, the presence of eggs in Stage IV in the ovaries of this species during February and March probably denotes that individuals of this species are likely to spawn during these months.

From Fig. 2 it could be seen that there are at least three distinct groups of ova represented by the modes *a*, *b* and *c*. All the ova under mode *a* are immature, under mode *b* maturing and under mode *c* mature and fully ripe. As all the eggs with a diameter of 20 m.d. have also been found to be yolked and since the eggs with a diameter of 25 m.d. and above are also in an advanced stage of maturity, it is likely that all ova ranging in diameter from 20 to 30 m.d. at mode *c* are to be shed during the approaching spawning season. Owing to the fact that the mature eggs, varying in diameter from 20 to 30 m.d., are sharply differentiated from the immature ones, the spawning in this species also may be restricted to a definite and short period. As in the case of *P. waigiensis* there is an indication of the maturing ova in Stage II forming a small mode *b*, thereby showing that, in this species also, there may be a secondary spawning. Hence it is likely that this species spawns more than once a year, probably once in February–March and a second time in August–September; mainly because the time required for the eggs at the mode *b* to attain maturity may be more or less half that of the time required for the ova at mode *a* to attain full maturity (Stage IV).

(3) *Therapon jarbua* (Forskål).—This species also occurs throughout the year in brackish waters as well as in the sea, but usually specimens collected from marine environment had mature gonads. Mature specimens of this

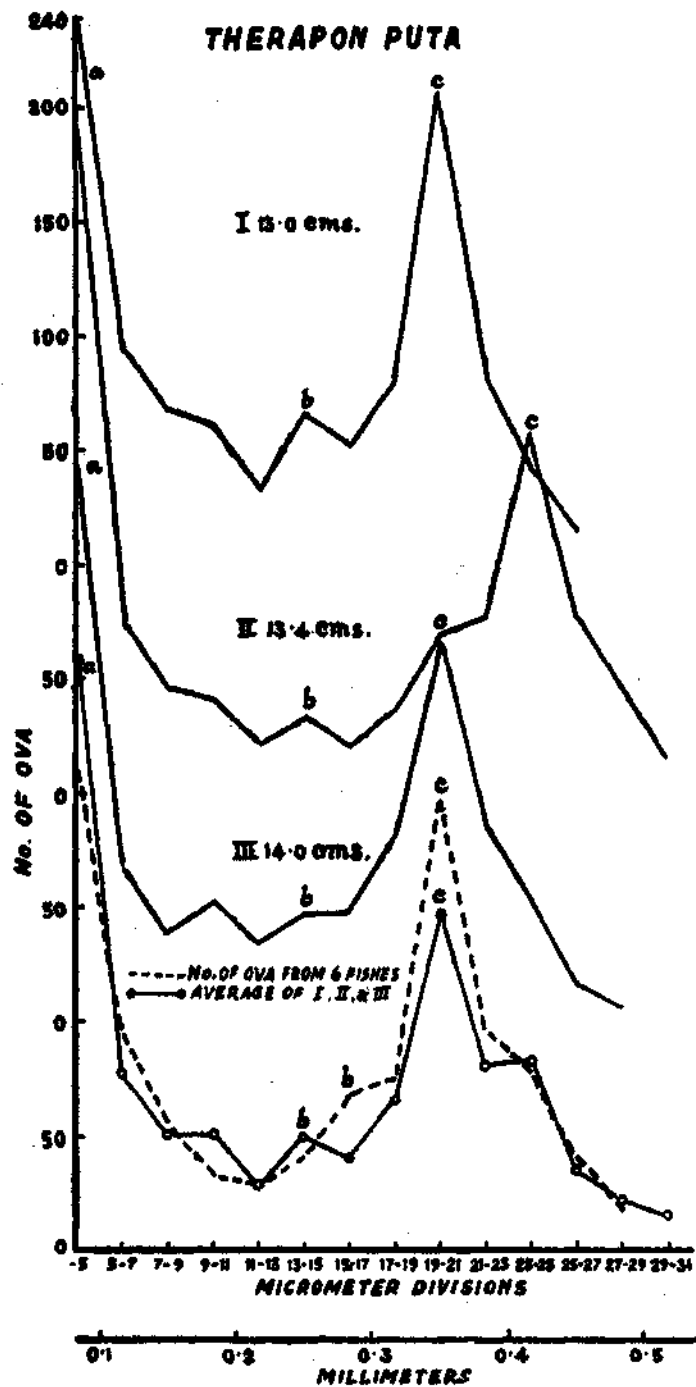
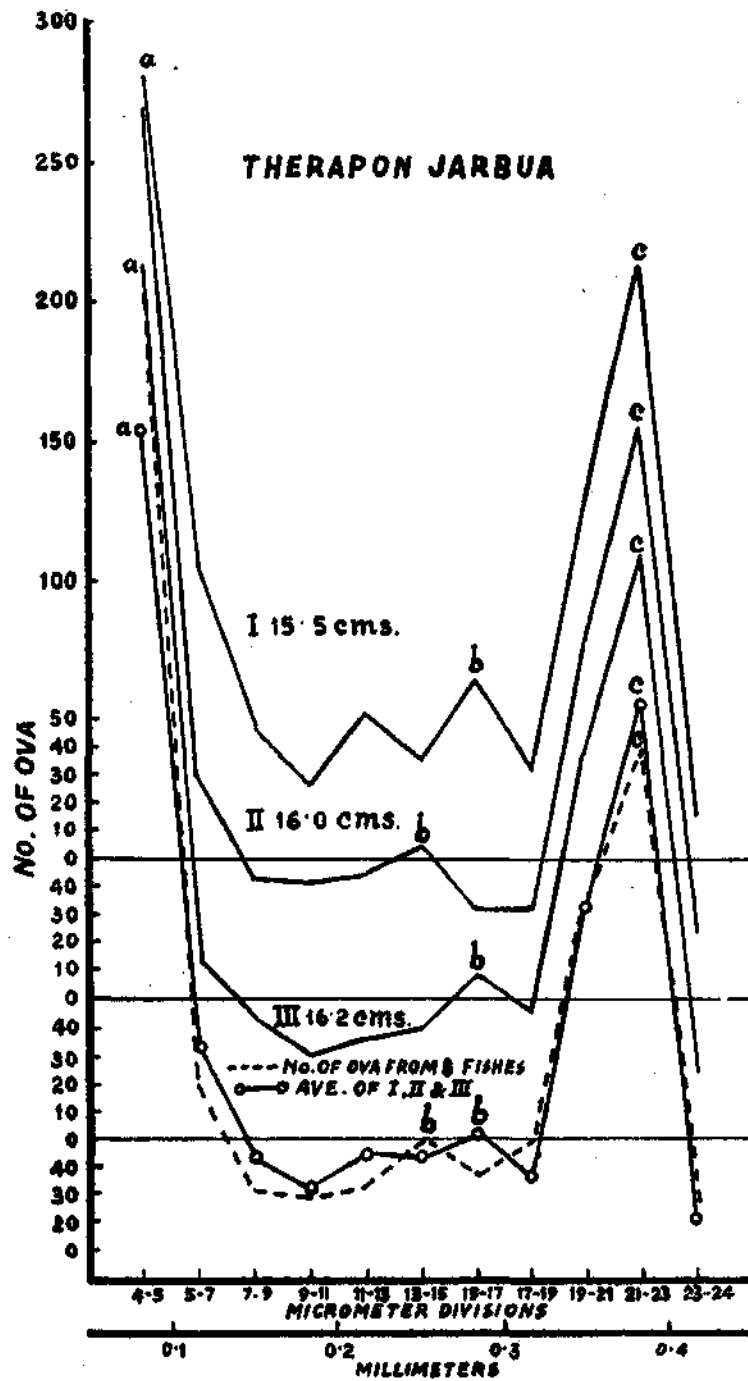


FIG. 2. Showing frequency of ova in the ovaries of *T. puta*.

species were collected during the months of January and February. The length of the individuals with mature ovaries examined for the present study varied from 14.5 to 16.2 cm. The colour of the mature ovaries was light yellow and the largest eggs were found to be in mature condition. Measurements of ova were made from sections of ovaries fixed in Bouin's fluid. In this species, eggs in only two stages of maturity, namely, immature and mature, were observed. Mature eggs, with diameter varying from 15 to 24 m.d., were fully yolked and the smaller ova did not show any indication of the development of yolk in them. From Fig. 3 it could be seen that there are three modes *a*, *b* and *c*, representing three batches of eggs in the ovaries of this species. Although eggs under modes *b* and *c* seem to be slightly separated from each other, most probably, in reality, they may not be separated at all, firstly because both the batches of eggs are in more or less the same stage of maturity, viz., Stage III, and secondly because the ova represented by mode *b* are relatively less in number than those represented by the mode *c*. However, it is quite probable that both these batches of eggs, under modes *b* and *c*, will be shed during the next spawning season. As these batches of mature eggs are sharply differentiated from the immature stock of eggs, represented by mode *a*, it can be concluded that the duration of spawning in this species is short and restricted to a definite period. Since there is no indication of the development of eggs in the intermediate stage of maturity in the mature ovaries of this species of fish, it is quite likely that this species spawns only once a year. Owing to the fact that the specimens collected in January–February had mature ovaries in Stage III, it is possible that this species may spawn within a short period. Therefore, the spawning period in *T. jarbua*, which migrate into the sea for breeding, is likely to be in February–March.

(4) *Pelates quadrilineatus* (Bleeker).—Specimens ranging in size from 12.1 to 13.2 cm. of this species, with gonads in ripe condition (Stage IV), were collected in the month of February. Measurements of ova from three individual fishes of 12.2, 12.4 and 13.2 cm. were made. The ovaries were light yellowish in colour, containing ova in all the four stages of maturity. The total range in size of the intra-ovarian eggs was 4 to 27 m.d. All the ova, measuring 25 m.d. and above, had transparent peripheral zone and these eggs could be pressed out of the ovaries by the slightest pressure on the abdomen of the fish indicating that they were in fully ripe condition ready to be shed. The next group of eggs, measuring 20 m.d., did not possess any transparent peripheral zone, but were fully yolked. The same stage of maturity was observed in the case of eggs measuring 15 m.d. These two groups, as judged from the formation of yolk in them, were thus found to be mature (Stage III). In the next group, measuring 10 m.d., the formation of yolk around the

FIG. 3. Showing frequency of ova in the ovaries of *T. jarbua*.

nucleus had just commenced and they showed all the characteristics of eggs in maturing condition (Stage II), whereas all the eggs smaller than 10 m.d. were found to be immature (Stage I).

Now that the presence of eggs in the ovaries of *P. quadrilineatus* in all four stages of maturity has been discussed, the determination of the spawning period and its duration, from the data on the frequency of eggs in different size-groups, becomes slightly complicated owing to the fact that there are only two distinct modes *a* and *b* in Fig. 4, representing the immature, the mature and the ripe ova. Moreover, the eggs under mode *b* seem to be sharply differentiated from the immature eggs. From the fact that the largest eggs were in fully ripe condition, or even in spawning condition, in the month of February, it is quite possible that this species spawns during this month. As the numerical ratio between the eggs in fully ripe condition measuring 25 m.d. and the next group of eggs in mature condition indicates that the former are comparatively less in number, it is quite probable that the individuals are already in spawning condition. Since the difference in diameter between the fully ripe ova and the mature ova is only 5 m.d.—less than 0.1 mm.—it is also quite possible that by the time the fully mature ova get shed, the latter batch of ova would have attained full maturity, to be spawned subsequently. Thus the same process might follow in the case of fully yolked, mature eggs measuring 15 m.d. From these observations it could be inferred that the spawning in this species takes place in the month of February and that its duration is not restricted to a short period but is a prolonged one. However, from the structure of eggs in Stage II, it was seen that the formation of yolk had only just commenced and hence it is likely that these ova might not attain maturity and be ready to be shed by the time the already present mature and ripe ova are shed. Thus the ova measuring 10 m.d. are the quota of eggs to be shed during the next spawning season.

The inference that the spawning period in this species is a prolonged one is further substantiated by the curve 1 showing the frequency of ova in the specimen of 13.2 cm. in length. In this curve, the mode *b* representing eggs in Stage III is roughly at the 15th m.d. and the occurrence of such an individual in February, with the mature eggs forming a mode only at the 15th m.d., probably signifies that this particular individual is one among those that must have spawned very late during its previous spawning season. The occurrence of such individuals, with ovaries in Stage III, in the month of February is still more evident from the curve showing the frequency of ova in the ovaries of eight different fishes. In this curve also there is a distinct

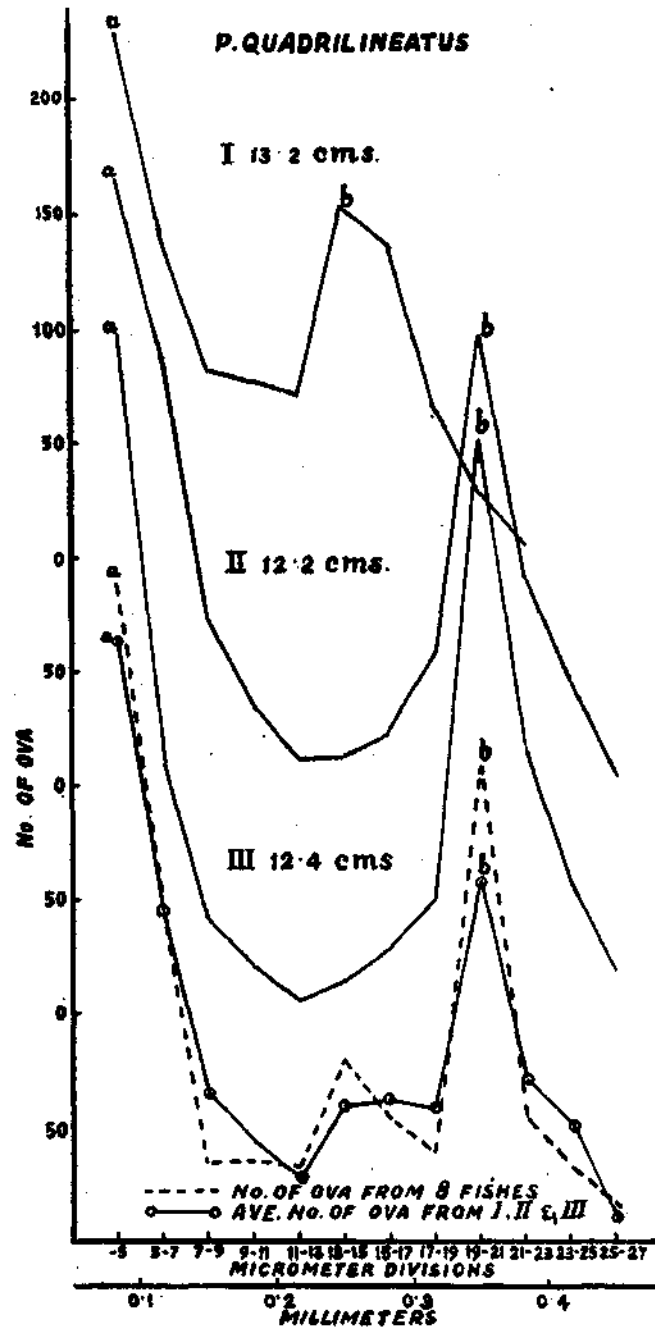


FIG. 4. Showing frequency of ova in the ovaries of *P. quadrilineatus*.

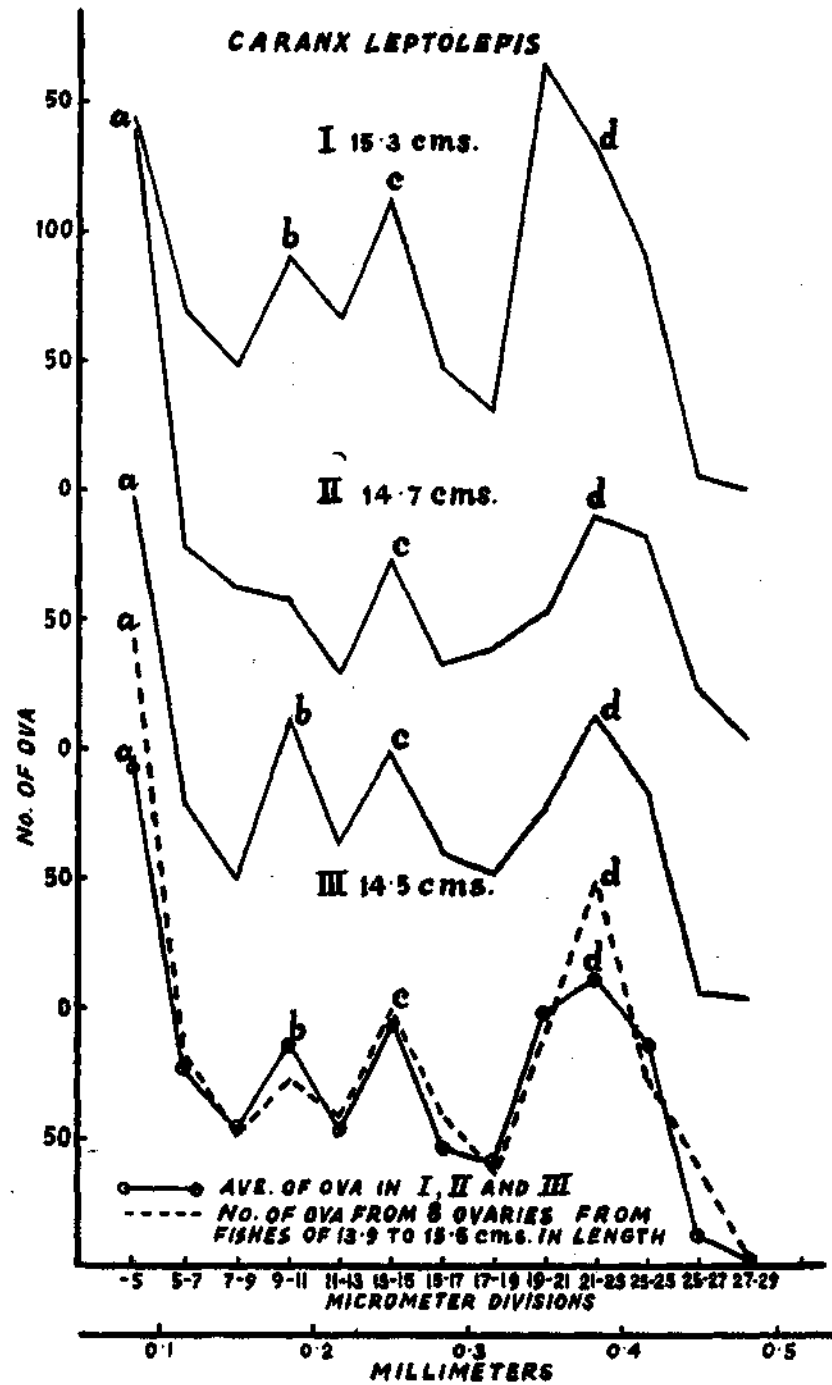
mode at about the 15th m.d. Since the duration of spawning in this species has been found to be a prolonged one and from the fact that specimens with

fully ripe ovaries have been observed in the month of February, it is quite likely that the spawning in this species commences in the month of February and extends over a period of two or three months, up to April.

(5) *Caranx (Selaroides) leptolepis* Cuvier and Valenciennes.—This pelagic shoaling species, exhibiting a seasonal abundance in the coastal waters, has been found to be caught in large numbers during the months of January, February and March in the shore seine operations. Specimens of this species, with ovaries in fully ripe condition, were collected in the month of February. Measurements of ova from three ovaries, of individuals of 14.5, 14.7 and 15.3 cm. in length, were made. In this species also the ovaries were light yellowish or light orange in colour and contained eggs in three stages of maturity, namely, immature, maturing and ripe (Stages I, II and III).

From Fig. 5 it could be seen that there are four modes *a*, *b*, *c* and *d* representing four batches of eggs. The eggs with a diameter of about 25 m.d. were found to be in ripe condition (Stage IV), showing all the characteristics of ripe pelagic ova. All the ova represented by mode *c* and *b* were found to be in the same stage of maturity, namely, maturing (Stage II), thereby indicating that although both the group of eggs at the two different modes *c* and *b* seem to be slightly differentiated between one another, in reality they may not be so. A microscopic examination of the eggs represented by modes *c* and *b* show that yolk formation has only just commenced in them. The ova at mode *a* are the immature stock of eggs.

Thus it is clear that in the ovaries of this species, mature ova in Stage III are conspicuously absent. As the ripe ova in Stage IV at the mode *d* are a distinct batch of eggs sharply separated from the ova in Stage II at the modes *c* and *b*, it is evident that the spawning in this species is restricted to a definite period and that the spawning period is not a prolonged one, as there are no eggs in Stage III to attain maturity subsequently and be spawned. Before the first batch of ripe ova at mode *d* is completely shed, the presence of a second batch of eggs in Stage II is evident from the modes *c* and *b* in Fig. 5. This batch of eggs in Stage II, half-way to maturity, constitute the quota of eggs to be shed in due course. Thus it is probable that, though the spawning is restricted to a definite period, there may be yet another spawning season as judged from the presence of ova in Stage II at modes *c* and *b* in which yolk formation has already commenced before the ripe eggs are shed. The spawning periodicity observed in this species is thus similar to that in the case of *Psammoperca waigiensis*. From the fact that specimens with ovaries in fully ripe condition are abundant in the month of February, it has been inferred that this species spawns once during this month; and

FIG. 5. Showing frequency of ova in the ovaries of *C. leptolepis*.

considering that the time required for the eggs in Stage II to attain full maturity is approximately half of that of the eggs in Stage I to become fully ripe, and that ova in Stage II are already differentiated into a distinct batch of eggs (modes *b* and *c*), it is quite probable that this species spawns for a second time somewhere in July-August.

(6) *Macrones vittatus* (Bloch).—Specimens, with mature ovaries, of this species, inhabiting brackish waters of Adyar, were collected in the month of July. Measurements of ova from ovaries of three individuals, 16.5, 16.8 and 17.5 cm. in length, and random samples from six different ovaries of fishes ranging in size from 16.8 to 18 cm. were taken. The ovaries, which were all in mature condition, were light orange in colour. The intra-ovarian eggs, in three different stages of maturity, were present in the ovaries.

The largest ova, measuring 24 m.d., were found to be in mature condition (Stage III), those measuring 15 m.d. in Stage II, and all the eggs with a diameter of 10 m.d. in Stage I. As the largest ova, measuring 12 m.d., were found to be only in Stage III of maturity, it was inferred that the ovaries were not fully ripe. From Fig. 6 it could be seen that there are only two modes *a* and *b*, the former representing only the immature stock of eggs and the latter mature ova, from which it is evident that the group of eggs in the intermediate stage of maturity are not at all differentiated into a separate batch of eggs to form a different mode. Since the mature stock of eggs at mode *b* are sharply differentiated from the immature stock of eggs at mode *a*, the spawning in this species is probably restricted to a short and definite period. In the month of November, all mature individuals of this species showed gonads in fully ripe condition. Thus the mature eggs in Stage III, in the ovaries of specimens examined in July, must have attained full maturity in the course of three months (August-September). As there is no indication at all, in any of the curves in Graph 6, as to the formation of a separate mode representing the ova in Stage II, it has to be inferred that there is no possibility of a secondary spawning taking place and hence it is probable that this species spawns only once a year during October-November, and that the duration of spawning is restricted to a short period.

(7) *Cypsilurus oligolepis* (Bleeker).—Fully ripe ovaries of this species, which exhibits a seasonal abundance along the coastal waters, were collected from shore seine catches in the months of February and March. Measurements of ova from three individual ovaries of specimens 20.0, 20.1 and 20.2 cm. in length and from random samples of ovaries taken from eight different individuals ranging in size from 18.7 to 20.5 cm. in length, were

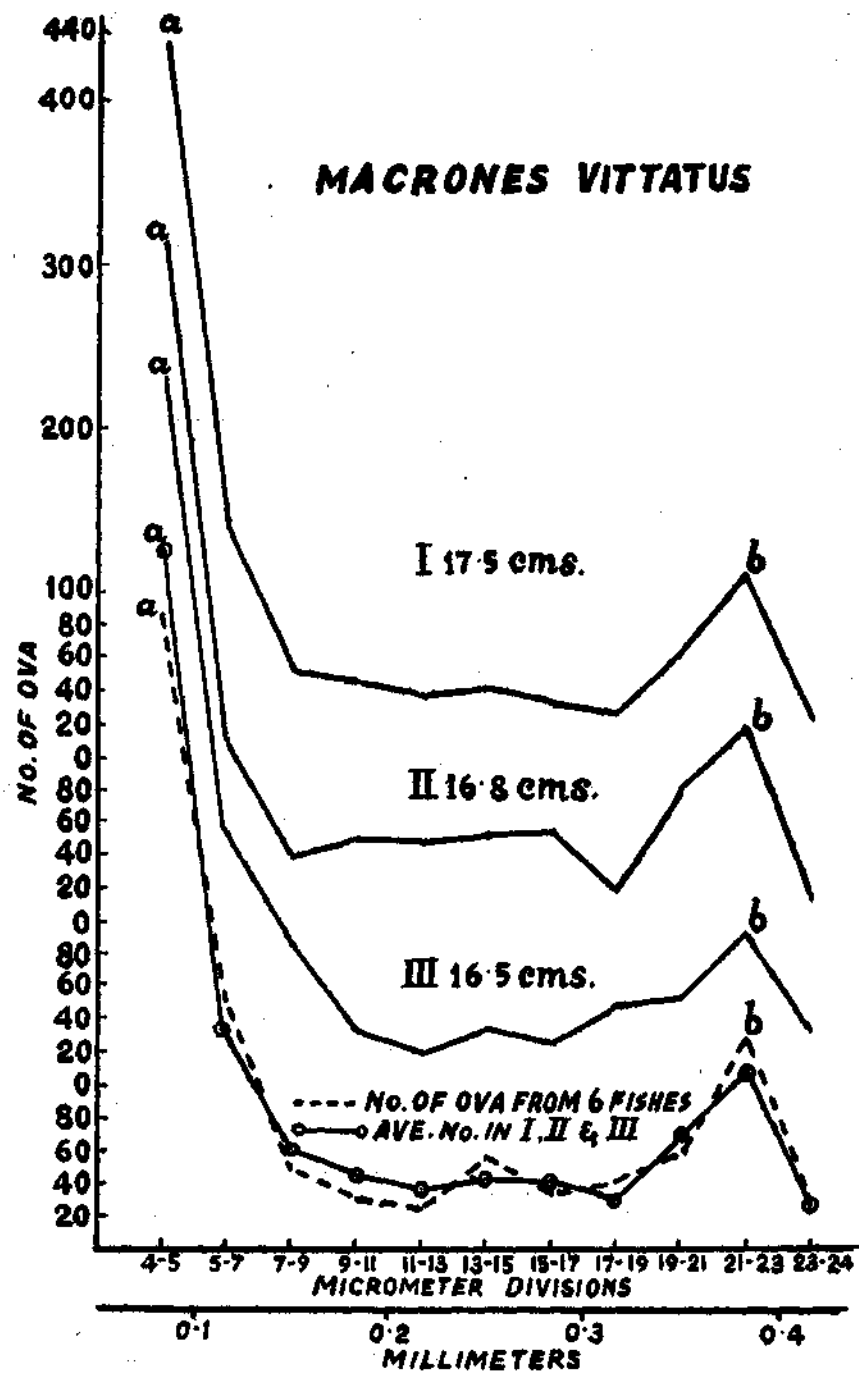


FIG. 6. Showing frequency of ova in the ovaries of *M. vittatus*.

made. Microscopic examination of the intra-ovarian eggs revealed that the ovaries contained eggs in all the four different stages of maturity.

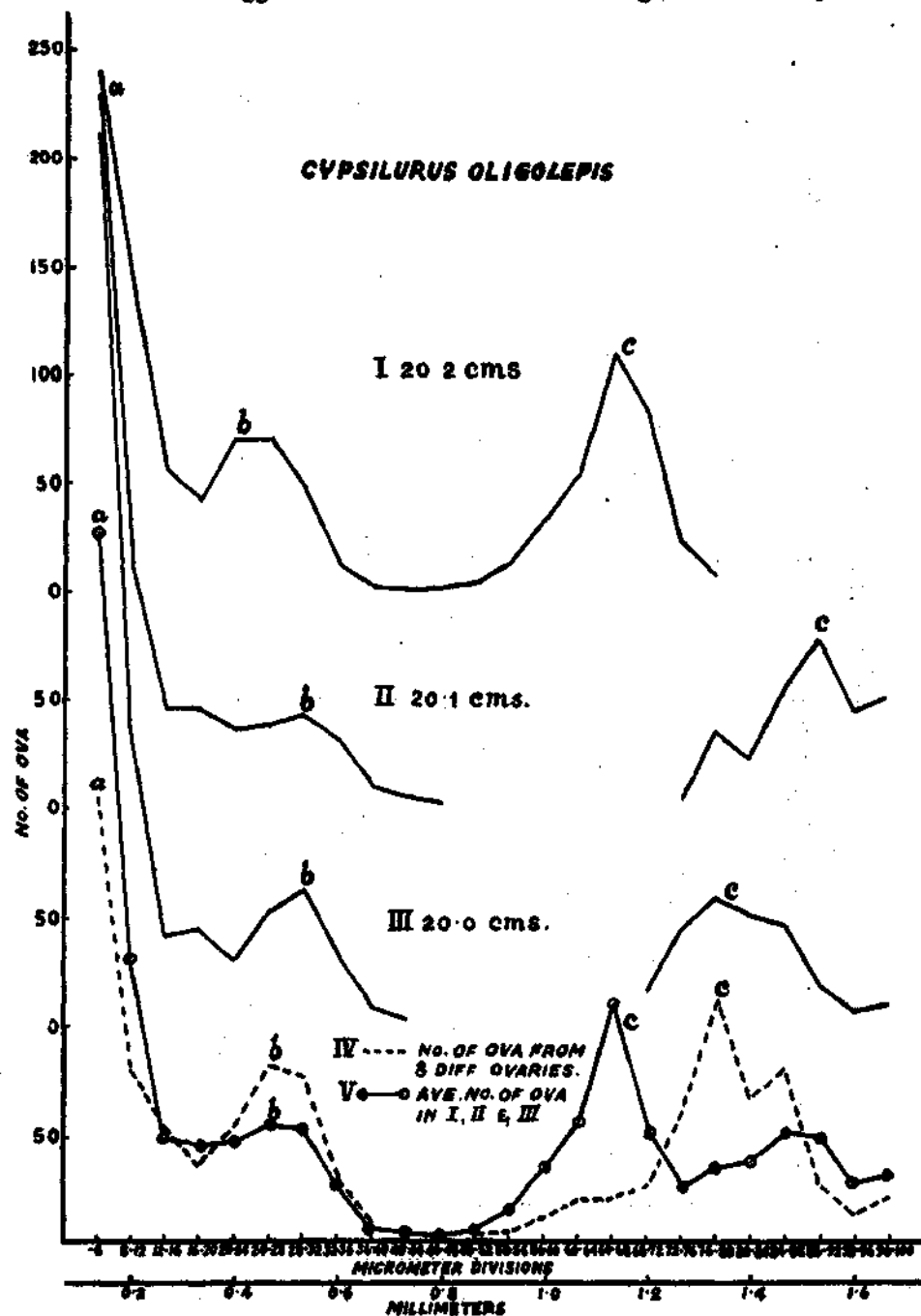


FIG. 7. Showing frequencies of ova in the ovaries of *C. oligolepis*.

From Fig. 7 it could be seen that the fully ripe ova are well represented by mode *c* and that all ova, ranging in size from 50 to 100 m.d., were in fully ripe condition (Stage IV). Similarly, ova in Stage III are also well represented by mode *b* in all the curves in Graph 7, whereas eggs in Stages II and I are represented by mode *a*, indicating that the differentiation of ova in Stage II from the general egg stock has not yet taken place. In the eggs measuring 15 m.d., it was observed that yolk formation has already commenced around the nucleus although they were not differentiated as a distinct batch of eggs from the immature ova.

Considering that the ova, ranging in size from 50 to 100 m.d., are the stock of eggs to be shed during the next spawning season and also the fact that they are sharply differentiated from the rest of the eggs in Stages I to III, it is quite probable that the spawning in this species is restricted to a definite period. Since the eggs in the mature stock vary in diameter from 50 to 100 m.d., it is also quite likely that the actual process of shedding of the ova may not be limited to a very short period, but extended over a longer period than in *Macrones vittatus*. This point is evident from Curve 1 in Fig. 7, representing the frequency of eggs in the ovary of a specimen of 20.2 cm. length. In Curve 1 the mode *c* is somewhere at 60–65 m.d., whereas in Curves 2, 3 and 4 the mode is between 70 and 90 m.d., indicating that the specimen of 20.2 cm. is probably one that might have spawned very late during the previous spawning season. If such a disparity in the diameters of mature ova, all of which are in the same stage of maturity, in different specimens of the same species should occur, it is quite likely that it must be due to the early and late spawning of different individuals during the previous spawning period. However, the presence of ova in Stage III at mode *b* in the different curves in Graph 7 suggests that another batch of eggs has already been differentiated from the general egg stock to be spent during the next spawning season, but owing to the fact that they are only 30 m.d. in diameter and secondly because there is a significant difference between the number of eggs in modes *b* and *c*, it is not likely that they will attain a size of 100 m.d.—the maximum size observed in the fully ripe ovary—by the commencement of the next spawning season during the succeeding year. Therefore, it is not likely that this species spawns more than once a year. As individuals with ripe ovaries in spawning condition were observed in March, it is quite possible that, in this species, spawning commences from the month of March and extends over one or two months, up to May.

(8) *Chirocentrus dorab* (Forskål).—Mature specimens of this species, with ovaries in ripe condition, were collected from gill-net and shore seine

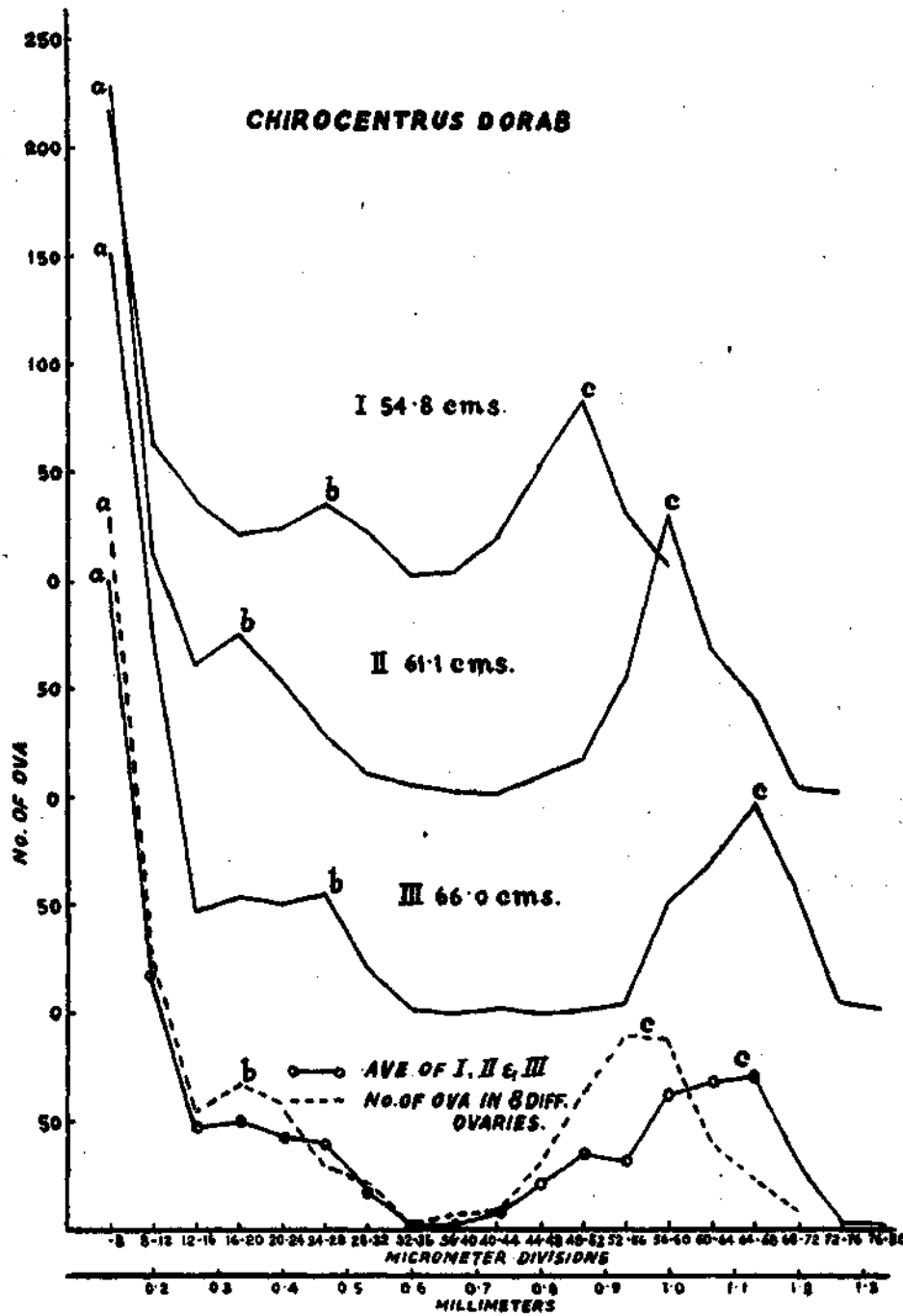


FIG. 8. Showing frequency of ova in the ovaries of *C. dorab*.

catches in the month of January. Measurements of ova from mature ovaries of three different individuals of 54.8, 61.1 and 66.0 cm. and from eight random samples of ovaries from eight different specimens varying in length from 54.8 to 66.5 cm., were made.

From Fig. 8 it could be seen that there are three distinct batches of eggs represented by the modes *a*, *b* and *c*. All the ova between 50 and 65 m.d. were found to be in fully ripe condition, the peripheral zone of the ova being transparent. Ova, measuring 35 m.d. in diameter, were fully yolked but they were not in fully ripe condition. In the ova of 20 m.d. diameter yolk formation had just commenced. Thus all the ova above 50 m.d. in diameter were observed to be in Stage IV, those between 35 and 50 m.d. in diameter in Stage III, those above 20 m.d. up to 35 m.d. in Stage II and all the ova less than 20 m.d. in Stage I. In Fig. 8, however, the ova in Stage III are not at all represented by any significant mode, whereas immature ova in Stage I, mature ova in Stage II and ripe ova in Stage IV, are well represented by modes *a*, *b* and *c* respectively. As the stock of ova in Stage IV are sharply differentiated from the general egg stock, the spawning in this species is restricted to a short and definite period. Owing to the fact that specimens of this species, with ovaries containing ova in more or less the same stage of maturity, have been observed in the month of March also, it has been inferred that the rate of growth of the ova in this species is very slow and so it is quite probable that the ripe ova, with a narrow peripheral transparent zone, might take some more time to become fully transparent and be shed. This inference is supported by the fact that spent ovaries were observed in the month of September. Hence, it has been inferred that spawning in this species takes place in July–August. As the ova in Stage III are not at all well represented by any distinct mode in any of the curves in Fig. 8, it has also been inferred that this species spawns only once a year.

(9) *Stolephorus indicus* (v. Hass.).—Specimens of this species, with gonads in ripe condition, were collected in the month of February. Measurements of ova from ovaries of three individuals of 8.3, 7.7 and 7.4 cm. in length and from eight random samples of ovaries from eight different individuals ranging in size from 6.2 to 7.5 cm. were made. In this particular species the ova were found to be elliptical and hence, while measuring the ova, only the longest diameter of each ova was recorded.

A microscopic examination of the intra-ovarian eggs revealed that all the ova, measuring 18 m.d. and above, were in fully ripe condition. Ova measuring less than 18 m.d. were found to be immature in Stage I. Thus, mature ovaries of this species were found to contain ova in only two stages

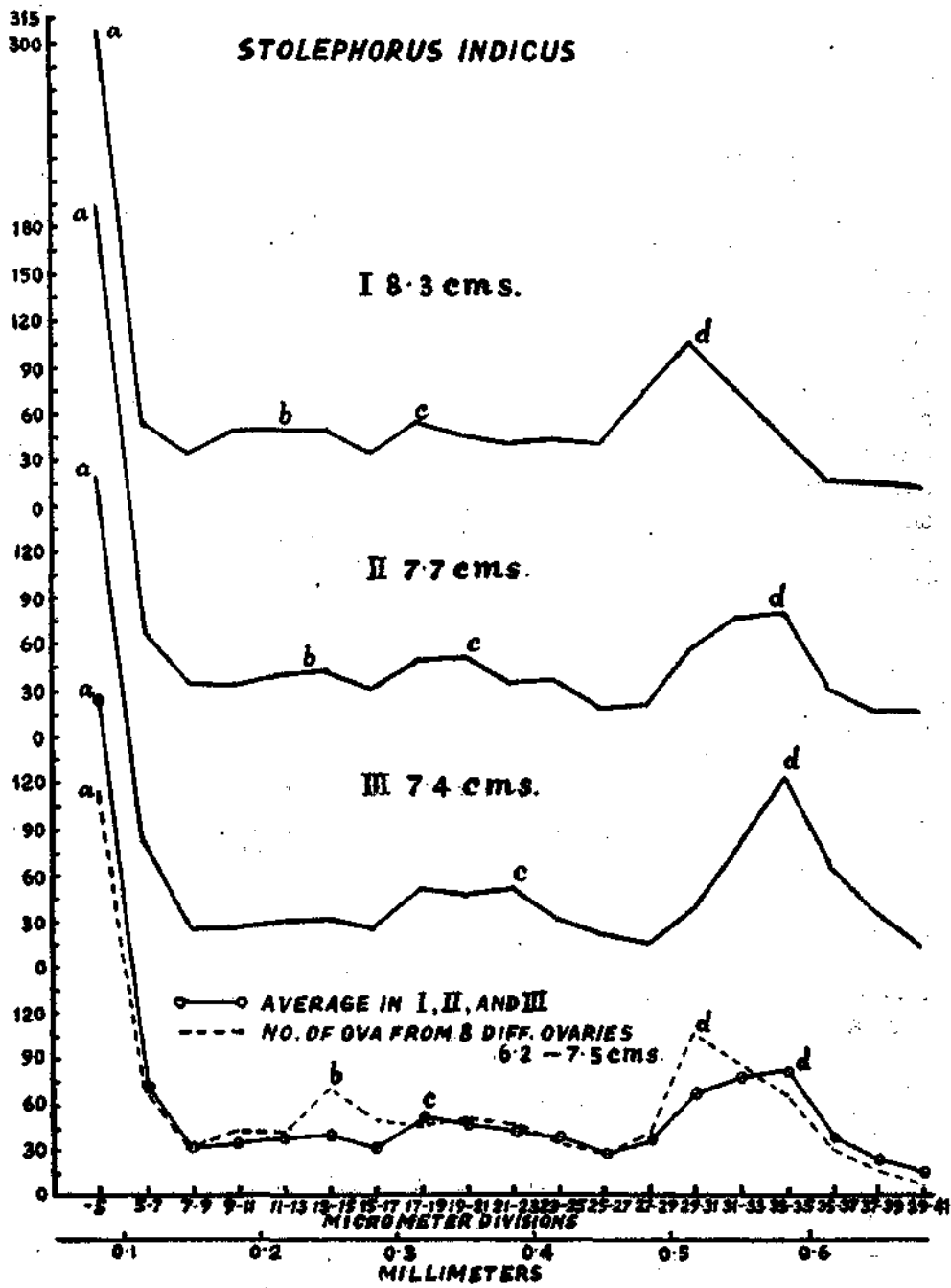


FIG. 9. Showing frequency of ova in the ovaries of *S. indicus*.

of maturity, namely, Stages I and IV and secondly, only those ova measuring 10 m.d. and more were observed to be elliptical whereas the smaller ones were more or less round. From Fig. 9 it could be seen that the mature ova, ranging in diameter between 26 and 40 m.d., are well represented by a significant mode. As stated already, eggs measuring even 18 m.d. were found to be in Stage IV, but in Fig. 9 it could be seen that the ova ranging in diameter from 18 to 26 m.d. are not represented at all by any significant mode except by a small mode *c*. Moreover, it could be seen from the different curves in Fig. 9 that except the minute immature ova and the ripe ones, all the intermediate ova are not at all sharply differentiated from each other. Thus it is possible that a well marked differentiation of the ova, represented by mode *c*, from the immature stock of ova may take place only after the ova at mode *d* are shed; in which case, the ova at mode *b* might develop and attain maturity by the time ova at mode *c* shift to mode *d* before they are shed finally. Therefore, it is evident that the ripe eggs at mode *c* will be shed subsequent to the shedding of the stock of eggs at mode *d* and in the meantime, the mode *d* also might shift to mode *c*. From these observations it could thus be inferred that the spawning periodicity in this species differs from that of the other species. The fact that there are two modes *c* and *d*, far apart from each other, representing ova in the same stage of maturity, namely, Stage IV, shows that soon after the shedding of the ova at mode *d*, another batch of eggs at mode *c* will also be almost ready to be shed. When the ova at mode *c* develop and attain the maximum size prior to spawning, another batch of ova from mode *b* will also be developing to replace the stock of eggs at mode *c* again. Thus, different batches of eggs will be passing on from one stage to the other continuously. Therefore, specimens of this species with mature gonads may probably be found throughout the year, but from the observations made on the frequency of ova in different individuals, it can be inferred that the spawning in this species takes place intermittently throughout the year. Though the present observation corroborates the statement of Hardenberg (1934) that *S. indicus* spawns throughout the year, it is likely—in spite of the fact that specimens with mature gonads may be found throughout the year—that this species has a definite spawning periodicity.

TYPES OF SPAWNING IN DIFFERENT SPECIES

The inferences made, on the periodicity of spawning in the different species, from the foregoing observations on the intra-ovarian eggs in various stages of development show clearly that the spawning in the different species is strictly periodic. Certain typical differences in the development of intra-

ovarian eggs encountered among the different species have enabled in distinguishing four distinct types of spawning.

Type A: Spawning taking place only once a year during a definite short period.—This type of spawning is represented by species like *T. jarbua*, *M. vittatus* and *C. dorab*. In the ovaries of fishes which spawn only once a year and in which the duration of spawning is restricted to a definite and short period, the mature stock of ova will be found to have differentiated from the general egg stock (Fig. 8) and, in the whole ovary, there will be only one batch of mature eggs to be shed during the succeeding spawning season.

Type B: Spawning taking place only once a year, but with a longer duration.—This type of spawning is represented by *P. quadrilineatus* and *C. oligolepis* in which, even though the spawning is restricted to a definite period, its duration may be longer than in Type A. It could be seen from Fig. 7 that, though the mature ova in *C. oligolepis* vary in size from 50 to 100 m.d., they are all in the same stage of maturity. Sometimes there may be two modes representing ova in the same stage of maturity, as in *P. quadrilineatus*, where the range in size of mature ova was found to be from 15 to 27 m.d. In species exhibiting this type of spawning, the range in size of the mature ova, irrespective of the number of modes representing them, has been found to be nearly half of the total range in size of the entire intra-ovarian eggs in the whole ovary.

Type C: Spawning twice a year.—This type of spawning is represented by three species, namely, *P. waigiensis*, *T. puta* and *C. leptolepis*. In the ovaries of fishes exhibiting this type of spawning, in addition to the batch of eggs in ripe condition, another batch of eggs in which yolk formation has already commenced will distinctly be represented in the curve showing the frequency of intra-ovarian eggs. Such modes, representing ova half-way to maturity, have been found more or less in the middle of the total range in size of the intra-ovarian eggs in the whole ovary. Although such ova, in which yolk formation has commenced, may be found in the ovaries of fishes exhibiting other types of spawning, they have not been observed to form distinct modes.

Type D: Spawning throughout the year, but intermittently.—In *S. indicus*, which spawns throughout the year, it has been observed that the mature eggs are represented by more than one mode, which may be far apart from one another, and that their range in size is very wide. Moreover, the different batches of eggs in the whole ovary, except the minute immature ova and the fully ripe ones, are not sharply differentiated from one another, thereby indicating that the passing of one batch of eggs into the next stage is more or less a continuous process.

CORRELATION BETWEEN SPAWNING AND THE RELATIVE SIZE OF OVA
IN DIFFERENT SPECIES

According to the size to which individuals of different species grow at the attainment of maturity, the nine species, taken up for the present study, have been classified into (1) small, (2) medium and (3) large-sized fishes. Thus *S. indicus* has been classified as small-sized, *P. waigiensis*, *T. puta*, *T. jarbua*, *P. quadrilineatus*, *C. leptolepis*, *M. vittatus* and *C. oligolepis* as medium-sized and *C. dorab* as large-sized fishes. A study of the relative size of ova in individuals of different species has shown that, though *S. indicus* is a small-sized fish, mature eggs were found to attain a size of 0.63 mm. (Table I). The largest ova of *C. oligolepis*, a medium-sized fish which is

TABLE I

Table showing the minimum sizes with mature gonads, largest size of eggs in ovaries, types of spawning and spawning periods in different species

Species		Minimum size with mature gonads (cm.)	Size of largest egg (mm.)	Type of spawning	Spawning period
1. <i>P. waigiensis</i>	..	22.8	0.50	C	July-Aug. Jan.-Feb.
2. <i>T. puta</i>	12.4	0.50	C	Feb.-Mar. Aug.-Sep.
3. <i>T. jarbua</i>	14.5	0.40	A	Feb.-Mar.
4. <i>P. quadrilineatus</i>	..	12.0	0.45	B	Feb.-Apr.
5. <i>C. leptolepis</i>	..	13.9	0.50	C	July-Aug. Feb.-Mar.
6. <i>M. vittatus</i>	16.5	0.40	A	Oct.-Nov.
7. <i>C. oligolepis</i>	..	18.7	1.65	B	Mar.-May
8. <i>C. dorab</i>	54.8	1.32	A	July-Aug.
9. <i>S. indicus</i>	6.2	0.63	D	Jan.-Dec.

comparatively much smaller than *C. dorab*, measured 1.65 mm. whereas the largest ova of *C. dorab*, a large-sized fish, measured only 1.32 mm. In all the other medium-sized fishes the diameter of the largest ova varied from 0.4 to 0.5 mm. Now, if the ova are classified according to the largest size to which they grow in the individuals of different species, it could be seen that in the small-sized species, *S. indicus*, the eggs are medium-sized, in all the medium-sized species, except *C. oligolepis*, the ova are small-sized, in *C. oligolepis*, a medium-sized fish, and in *C. dorab*, a large-sized species, the ova are large-sized. Hence it has been observed that the size of the individuals in different species and the size of their respective mature ova have no correlation between each other. However, an attempt was made to see whether the size of ova in different species exercised any influence on the spawning habits of individuals in different species. From Table I it could be seen that (a) the small-sized fish *S. indicus*, producing medium-sized ova, spawns throughout the year, (b) the medium-sized species *P. waigiensis*, *T. puta* and *C. leptolepis*, producing small-sized ova, show a tendency to spawn twice a year, (c) the medium-sized fish *P. quadrilineatus* and *C. oligolepis*, producing small and large-sized ova respectively, have a single but prolonged spawning period and (d) the medium-sized species *T. jarbua* and *M. vittatus*, producing small-sized ova, and the large-sized species, *C. dorab*, producing large-sized ova, have a single spawning period of restricted duration. From these observations it could be inferred that even the relative sizes of ova in the individuals of different species, which vary considerably in their size at maturity, do not have any significant influence on the spawning of the individuals in different species. However, it is likely that the relative size of the mature ova in the ovaries of adult individuals of different species may have some influence on the fecundity of the particular species.

DISCUSSION

The present investigation, undertaken with a view to determining the duration of spawning periods in nine species of teleostean fishes by a study of the intra-ovarian eggs, has shown that the different species exhibit four types of spawning. As investigations on similar lines have not so far been carried out on other Indian species, except by Karandikar and Palekar (1950) on *Polynemus tetradactylus* and Palekar and Karandikar (1952) on *Thrissoles purava*, these results could only be compared with those that have been obtained in regard to foreign species.

Hickling and Rutenberg (1936), while investigating the duration of spawning periods of the hake, haddock, pilchard and herring, have found that the haddock and herring have short spawning periods, as indicated by

the distribution of the frequencies of the diameters of intra-ovarian eggs. They found, in respect of these two species, that there was sharp separation of the ripening eggs from the immature ones in the general egg stock. As has already been stated, the maturing eggs in *Therapon jarbua*, *Macrones vittatus* and *Chirocentrus dorab* differ considerably in size from the eggs of the immature batch in the general egg stock. Hence, as in the case of haddock and herring, the duration of spawning in *Therapon jarbua*, *Macrones vittatus* and *Chirocentrus dorab* is restricted to a short period. It was also inferred that probably *Therapon jarbua* spawns in February–March, *Macrones vittatus* in October–November and *Chirocentrus dorab* in July–August. Raj (1916) states that he observed specimens of *Macrones vittatus* in brackish water at Madras, with eggs in the month of March, but he did not mention the condition of the ovaries.

In the case of pilchard and hake, Hickling and Rutenberg found that their spawning periods were long and indefinite. Probably the type of spawning referred to by them is similar to the one observed in *Pelates quadrilineatus* and *Cypsilurus oligolepis* where the spawning has been found to be extended over a long period. However, these authors have remarked that even though pilchard and herring are clupeoids, a difference in the duration of spawning periods is indicated by the graphs showing the frequencies of the diameters of the intra-ovarian eggs. A similar difference in the duration of spawning periods has been made out from observations on the spawning habits of two species belonging to the family Clupeidae, namely, *Chirocentrus dorab* and *Stolephorus indicus* and three species belonging to the family Theraponidae, namely, *Therapon puta*, *Therapon jarbua* and *Pelates quadrilineatus*. Hence it can be concluded that the duration of spawning periods in different species belonging to the same family may vary considerably, which is in accord with the behaviour of many species from temperate waters.

De Jong (1939), while investigating the spawning habits of some fishes of Java Sea, found that in *Caranx crumenophthalmus*, there was only one batch of eggs undergoing maturation, whereas in *Caranx leptolepis* investigated by the present author, the graph indicated two batches of eggs, the first peak indicating the immature eggs and the second peak indicating the ripe eggs which have already got differentiated, to undergo maturation, from the general egg stock. Hence, he thinks that in *C. crumenophthalmus*, the differentiation of the eggs from the immature egg stock takes place only after the mature eggs have been spawned just as he found in the case of *Stromateus niger*. The type of curve referred to by him in the case of *Caranx crumenophthalmus* is thus similar to the curve indicating the frequency of ova in species exhibiting

Type A spawning and the curve in *Caranx leptolepis* resembles the curve found to be typical of the species exhibiting Type C spawning.

Clark (1934), in the course of her investigations on the maturity of the California Sardine by the measurements of ova, found that individual sardines spawn more than once during each spawning season which extends for about seven months from February to August. The type of curve in the California Sardine more or less resembles the curve found in the case of *Stolephorus indicus*, where mature ova in the same stage of maturity are represented by more than one mode.

Karandikar and Palekar (1950) found that mature specimens of *Polynemus tetradactylus* spawn only once a season owing to the fact that the ovaries in mature fish of this species contained only two types of ova, namely, mature and immature. Since mature and spent fish are found simultaneously in two consecutive seasons, they state that this species spawns twice a year. In *Thrissocles purava*, a small-sized edible fish occurring along the Bombay Coast, Palekar and Karandikar (1952) found the spawning season, as determined by the ova diameter measurements and the structure of the mature ovary, to be of short duration and that the minimum period required for the rematuration of the spent ovaries to be about six months. Therefore the spawning in this species is similar to that in the case of *Psammoperca waigiensis*, *Therapon puta* and *Caranx leptolepis*.

Though a periodic origin of the maturing class of ova from an intermediate group may be common in many species, the presence of several classes of ova in the ovaries during the spawning season has been demonstrated by several authors in many fishes. Calderwood (1892) has classified in general the intra-ovarian eggs into three groups, namely, 'minute', 'small' and 'great', and states that the great ova would be spawned at the present season, the 'small' ones a year later and the 'minute' in succeeding years. However, the classification of the ova in a mature ovary adopted for the present investigation slightly differs from that of Calderwood, but closely agrees with that of Thompson (1914) who classified ova in the Pacific Halibut into ripe ova, ova for next season and ova for the future seasons and further classified the ripe ova into opaque and translucent. This grouping corresponds to the 'fully ripe' (translucent ova), 'mature' (opaque), 'maturing' (ova for the next season) and 'immature' (ova for the future seasons) as classified for the present study. From these classifications of ova in mature ovaries into several groups in different species by various authors, it is evident that the number of generations of ova during the spawning season apparently varies in different species and, as stated by Clark (1925),

conclusions drawn from one form will not necessarily hold true for another. However, the observations made by Fulton (1899) that the presence of intermediate group of ova in large numbers is associated with a prolonged spawning season, probably has a general application and it has been found to hold good in the case of different species studied during the present investigation.

De Jong has concluded from observations on the frequency polygons of the ova in the ovaries of different species studied by him that the spawning of the individual fishes is strictly periodic. He further states that constant and typical differences encountered in the frequency polygons of ova enable in distinguishing three distinct types of spawning, namely, *a*, *b* and *c*. He found in the ovaries of fishes exhibiting *a* type of spawning, namely, *Stromateus niger*, *Decapterus russelli*, *Caranx crumenophthalmus*, *Caranx mate* and *Caranx malam*, only one batch of maturing eggs and, after the shedding of the eggs, the ovaries resembling empty sacs. The *b* type of spawning was represented by *Clupea fimbriata*, *Lactarius lactarius*, *Caranx leptolepis* and *Cesio erythrogaster*, in the ovaries of which he found a second batch of eggs getting differentiated from the general egg stock before the first quota of eggs had reached maturity. Therefore, he thinks that after spawning the ovary may contain, besides small eggs of the general egg stock, a batch of rather large eggs half-way to maturity, which may be spawned in due course. The third type of spawning is represented by *Scomberomorus* sp., in the nearly mature ovaries of which he found not less than three batches of developing eggs. Comparing the three types of spawning to those of the four types observed in fishes studied during the course of the present investigation, types *a*, *b* and *c*, according to De Jong's classification, were found to correspond to the Types A, C and D. Two species, namely, *P. quadrilineatus* and *C. oligolepis*, included in the present study, appear to be characterised by a single but prolonged spawning period, a type different from the three noted by De Jong in the fishes he studied.

While dealing with the various types of breeding in brackish water animals of Madras, Panikkar and Aiyar (1939) have contradicted an earlier belief that tropical marine species breed continuously. Their observations have shown that brackish water animals do exhibit certain definite breeding periodicities. The four types of breeding described by them are to some extent comparable with those presented in this paper.

It has been a common practice among the fishery biologists interested in determining the spawning period and its duration in different species of fishes, to draw conclusions from a statistical study of the intra-ovarian eggs in mature ovaries, but the present study has shown that when there are several

modes representing different groups of ova in a mature ovary, sometimes ova, represented by more than one mode adjacent to each other, actually may indicate ova in the same stage of maturity. The present study has shown that the observations on the spawning period and its duration, as determined by a study of the intra-ovarian eggs in fishes, would be more accurate if the ova represented by various modes are studied in relation to the different stages of maturity, represented by the respective modes in curves showing the distribution of frequencies of intra-ovarian eggs of varying diameters. It remains for future investigation to follow up the line of work presented here with observations on length frequencies of fishes, growth, stages of the gonads of the different species and the actual spawning periods determined by the occurrence of larvæ.

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SUMMARY

From a study of the intra-ovarian eggs, their stages of maturity and the frequencies of ova in various stages of development from ovaries in ripe or penultimate stages of ripeness, the spawning periods, their duration and seasons have been indicated in the case of nine species of edible teleostean fishes.

The intra-ovarian eggs in mature ovaries of different species of fishes have been classified into four stages of maturity and the range in size and structure of ova in different stages of development have been studied.

The nine species of fishes selected for the present study have been observed to exhibit four different types of spawning.

Therapon jarbua, *Macrones vittatus* and *Chirocentrus dorab* were found to spawn only once a year, the spawning period in each species being restricted to a definite and short period.

Though *Pelates quadrilineatus* and *Cypsilurus oligolepis* spawn only once a year, the duration of spawning was observed to extend over a long period.

The spawning in *Psammoperca waigiensis*, *Therapon puta* and *Caranx (Selaroides) leptolepis* was found to be restricted to a definite and short period but these species seem to spawn more than once a year.

In *Stolephorus indicus* though there is a definite periodicity in spawning, it has been observed that this species spawns throughout the year intermittently.

No correlation could be established between the sizes of individuals and mature eggs with the types of spawning exhibited by the different species.

The curves showing the frequencies of intra-ovarian eggs in various stages of maturity and the spawning periods and habits of the nine species have been compared with those of other species investigated elsewhere by other authors.

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