AN APPRAISAL OF THE STUDIES ON MATURATION AND SPAWNING IN MARINE TELEOSTS FROM THE INDIAN WATERS

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ABSTRACT

Maturation and spawing in many teleosts from the Indian waters have been studied by different authors using conventional methods. The most common among these methods are seasonal changes in the condition of gonads and the ova diameter frequency distribution. The latter is supposed to give an index of the progression of oocytes and their withdrawal from the ovaries. There are several drawbacks in these methods, as they were essentially developed for fishes from the temperate regions. It is therefore desirable that other methods should also be used for arriving at a realistic picture of the spawning process. Maturity is clearly linked with the growth rate of fishes and hence the two phases—pre-and post-maturity—should be clearly distinguished. Spawning in a population is possibly geared to external events, when conditions for the newly produced broods are most favourable. Fishes in the Indian waters spawn in all the months of the year, but along the east coast spawning largely seems to occur during the pre-monsoon months and along the west coast during the monsoon and post-monsoon months. Many species appear to be continuous breeders, and hence to develop a clear understanding of their maturation and spawning, it is necessary to make observations throughout the year.

INTRODUCTION

Maturation here refers to cyclic morphological changes which the male and female gonads undergo to attain full growth and ripeness. This definition does not include the complicated physiological changes involving endocrine control. Similarly, 'spawning' means the emission of male and female gametes from the body of the fish to the exterior, where fertilization occurs. Very often, these terms have been found confusing in the literature, and hence it seems desirable to define their usage more precisely. 'Breeding,' for instance, has frequently been used as a synonym to spawning, although breeding includes a sequence of events related to both pre-spawning and spawning phases. Thus 'breeding season' signifies the time of peak maturity and the period during which spawning occurs in a population. The phenomenon of breeding, therefore, simple as it may appear, is frequently accompanied with a complex behaviour pattern involving nest building, pairing, courtship, migration and shoaling. Thus the specialization in reproduction, which the teleosts have undergone as a group, is almost unique in the entire animal kingdom.

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PURPOSE OF STUDY

In fishery biology studies, it is important to determine the cycle of maturation and depletion of gonads. The purpose of this determination could be manifold; but it is basically aimed at understanding and perhaps predicting the changes which the population as a whole undergoes during the year. From these studies, inferences could be drawn on a variety of lines—the rate of regeneration of stocks to conservation and management of resources, or the determinations of ecological conditions which lead to synchronization of breeding activity. Similarly, studies on related aspects such as fecundity, size and age at first maturity, sex-ratio and so on, are pertinent to the main objective, and the information on any aspect could be used in a variety of scientific ways. However, all these studies are essentially meant for elucidating both short-term and long-term variations in the production of fish broods which are finally recruited in the population as exploitable stocks.

METHODS COMMONLY USED FOR STUDY

The arbitrary ways in which the studies on maturation of gonads have been undertaken, though imprecise, are probably aimed at dealing with a large number of specimens in the shortest possible time, generally in the field—ship-board, fish-landing-centres or fish-markets, where any sophistication in methodology could probably be impractical. Some of the common methods used by the fishery biologists are as follows :

(a) *Classification of gonads or quantification of maturity stages*

For the determination of the cycle of maturity of gonads, the most common method is to define the stages of sexual maturity and follow them at monthly, fortnightly or weekly intervals in a sample fairly representative of the population. The criteria used for the quantification of maturity are colour, shape and size of gonads in relation to body cavity, diameter of the unspawned eggs and so on (see Table 1). Ovaries have been used for the classification more readily than the testes, chiefly because the progress of maturity can be ascertained in the former with a greater ease. A large number of such classifications has been developed and different workers have adopted different maturity schemes, because it is neither possible to have uniformity in the criteria of quantification; nor would it be correct to propose a modified form of classification which is applicable to oviparous teleosts in general. Very often, a distinction of stages, if these are too numerous, is not easy. Essentially, this type of study was developed for fishes from the temperate waters which have a definite breeding season, either short or long. In such species, the gonads show a regular seasonal change and at any one time of the year, the stages of maturity are fairly uniform throughout the population. Thus the 8 maturity stages in herring (Hjort, 1910) which were further modified by the International Council for the Exploration of the Sea

(ICES) in 1962, and the multi-stage classification in cod or hake (see Graham, 1924; Hickling, 1930), can easily be distinguished according to the criteria on which these are based.

The species which have prolonged breeding seasons are those in which the ovaries include several batches of eggs destined to be matured and shed periodically (Qasim, 1956 a). In these species, the population consists of fishes of variable stages of maturity and hence utmost care should be exercised to determine the breeding season accurately. In perennial breeders, almost all conceivable stages of maturity occur in the population throughout the year; and hence any classification of maturity based on the models of temperate-water-forms will not give a correct picture of the breeding season. Qasim and Qayyum (1961), while studying the breeding habits of freshwater fishes of India, have already pointed out similar difficulties. Considering the overall implications of the problem related to quantification of maturity, the present author feels that in tropical and sub-tropical forms, the classification of gonads should only be limited to about 5 maturity stages as follows :

I. Immature virgins II. Maturing virgins or recovered spents III. Ripening IV. Ripe V. Spent.

Qasim (1957a & b) developed this classification for studying the spawning habits of two British species namely *Centronotus gunnellus* and *Blennius pholis*. The former species had a short breeding season, lasting about 3 months, whereas the latter had a long breeding season spread over 5 months. *C. gunnellus* had a single batch of ova in the ovaries, which was matured and shed during the breeding season. *B. pholis*, on the other hand, had 3 groups of eggs in its ovaries and spawned 3 times successively during the season. The periodicity in spawning was confirmed by making direct observations in the aquarium (Qasim, 1956 b).

The five maturity stages noted above were applied to several freshwater fishes of northern India at first by Qayyum and Qasim (1964a, b & c) and later on by Bhatt (1968; 1970; 1971a & b) with considerable success.

In the continuous breeders it may even be desirable to reduce the number of stages from 5 to about 3 such as:

I. Immature II. Maturing III. Ripening.

Since the spent gonads are not normally found in the population of continuous breeders, the inclusion of this stage in the classification would be superfluous and misleading. Similarly, the chances of getting a perfectly ripe fish would also be remote, as before the ovaries turn fully ripe, a part from these is spawned. However, whatever maturity stages an investigator may select or define for a particular fish, the choice should be based on careful considerations so that subsequent workers on the same fish may adopt the same classification.

It should also be kept in mind that the maturity stages should be simple and distinctive so that these could be applied in the field. This would perhaps be the simplest procedure for knowing the spawning season of a species in different areas of its geographical distribution and any marked differences may be reminiscent of different stocks or may lead to some other interesting findings. Such an information could also indicate the dependence of reproductive activity of a species on similar environmental factors in different areas.

(b) *Seasonal changes in gonad weight*

This is another method used widely (see Table 1), either singly or in conjunction with the other methods (see Qayyum and Qasim, 1964 a, b & c). If the gonads undergo a regular seasonal change during the year and when this is accompanied with large changes in weight, particularly in females, their seasonal analysis should be indicative of peak spawning activity. The overlap in gonad weight, as a result of size differences in a species can, to some extent, be overcome by using the gonad weight : body weight ratio (see Qasim, 1957a & b). Nevertheless, the individual variations of maturity in the population complicate this method. To counteract this difficulty, it is necessary to determine the range in the gonad weight : body weight ratio for the different stages of maturity. Perhaps in this way a correlation of the two methods may give a more precise information on spawning.

(c) *Ova-diameter frequency*

This method has been used very widely by the Indian workers (see Table 1), although its validity in tropical waters without adequate experimental evidence on marine fishes, is questionable. The anology between Indian forms showing several batches of eggs and similar fishes from higher latitudes, in which this condition indicates repeated spawnings, does not offer convincing evidence to arrive at a similar conclusion in tropical waters, in view of our knowledge of the resorption of unspawned eggs, if external conditions are not favourable. Qasim (1956a) deduced that in British waters a succession of spawnings is a feature characteristic of the Mediterranean-boreal forms which spawn during summer, when abundance of food provides a means to support the maturation of several batches of eggs. Winter spawners, on the other hand, are the Arctic-boreal species whose spawning occurs during the winter, when sea temperature and food supply are at their minimum. In fact, conditions during the winter are too adverse for prolonged spawnings and hence each individual puts all its reserves into a single spawning. Three spawnings, on the contrary, corresponding to three batches of eggs in the ovaries of a Mediterranean-boreal fish (*Blennius pholis*), were confirmed by making the fish breed in captivity. Although no such direct evidence is available on any marine species from the Indian waters, there are indications that the freshwater murrel (*Ophicephalus punctatus*), which has several batches of eggs in its ovaries, breeds more than once during the season (Qayyum and Qasim, 1962).

TABLE 1. *Methods adopted by different workers in determining the time and duration of spawning in some marine teleosts from the Indian waters*

Species	Methods followed	No. of stages	Duration of spawning	Reference
Anchoviella commersonii	Ova diameter and general appearance of ova	5 stages	...	Dharmamba, 1959
Anchoviella heterolobus	Ova diameter and general appearance of ova	5 stages	...	Dharmamba, 1959
Anodontostoma chacunda	Ova diameter	6 stages	November-March	Annigeri, 1963
Auxis thazard	Ova diameter, general appearance and coloration of gonads	7 stages	April-September	Rao Narayana, 1964
Caranx kalla	Ova diameter, general appearance and coloration of gonads	7 stages	December-January and May-June (Peak periods)	Kagwade, 1968
Chanos chanos	Ova diameter	4 stages	October-November and February-March	Tampi, 1957
Chirocentrus dorab	Ova diameter	4 stages	July-August	Prabhu, 1956
Chorinemus lysan	Ova diameter and size of gonads	4 stages	April-August	James, 1967
Coilia borneensis	Ova diameter and ponderal index	6 stages	March-July	Varghese, 1961
Coilia dussumieri	Development of intraovarian eggs	5 stages	September-March	Gadgil, 1967
Cynoglossus semifasciatus	General appearance of gonads	7 stages	October-May	Seshappa and Bhimachar, 1955
Cypsilurus oligolepis	Ova diameter	4 stages	March-May	Prabhu, 1956
Dussumieria hasselti	Ova diameter and general appearance of ova	5 stages	February-July	Dharmamba, 1959
Eleutheronema tetradactylum	Ova diameter	4 stages	January-April and July-September (Peak period)	Kagwade, 1970
Eupleurogrammus muticus	Ova diameter	7 stages	February-May	James, 1967
Eupleurogrammus intermedius	Ova diameter	7 stages	February-May	James, 1967
Euthynnus affinis	Ova diameter	7 stages	April-September	Rao Narayana, 1964
Harpodon nehereus	Ova diameter and condition factor	7 stages	April-July and November-December (Peak periods)	Bapat, 1970
Hemirhamphus marginatus	Ova diameter	7 stages	November-December	Talwar, 1967

Species	Methods followed	No. of stages	Duration of spawning	Reference
Hyporhamphus georgii	Ova diameter	7 stages	March-April	Talwar, 1962
Johnius dussumieri	Ova diameter and ponderal index	7 stages	January-February and June-September	Devadoss, 1969
Johnius carutta	Ova diameter	6 stages	January-April	Rao Appa, 1967
Katsuwonus pelamis	Ova diameter, gonad index and condition factor	8 stages	February-July (Peak periods)	Raju, 1964
Leiognathus bindus	Ova diameter and ponderal index	7 stages	December-February	Balan, 1963
Leiognathus splendens	Gonad index, liver index and lipid content	7 stages	January-February and June	Rao Satyanarayana, 1967
Lepturacanthus savala	Ova diameter	7 stages	February-May	James, 1967
Lethrinus lentjan	Ova diameter	7 stages	December-February and June-August	Toor, 1964
Liza macrolepis	Ova diameter	6 stages	June-February	Luther, 1963
Mugil cunnesius	Ova diameter and condition factor	...	May-August	Sarojini, 1958
Mugil parsia	Ova diameter	3 stages	December-March	Sarojini, 1957
Nematalosa nasus	Ova diameter and general appearance of eggs	6 stages	October-November	Annigeri, 1963
Opisthopterus tardoore	Ova diameter	7 stages	February-August	Radhakrishnan, 1963
Osteogeneiosus militaris	Condition factor and size of ovary	8 stages	March-May	Pantulu, 1963
Otolithus argenteus	Ova diameter	6 stages	October-January	Annigeri, 1963
Otolithus ruber	Ova diameter	7 stages	July-October	Devadoss, 1969
Pampus argenteus	Ova diameter	5 stages	January-February	Kuthalingam, 1963
Pelates quadrilineatus	Ova diameter	3 stages	February-April	Prabhu, 1956
Polydactylus indicus	Ova diameter	4 stages	April-June and October-December	Nayak, 1959
Polynemus heptadactylus	Ova diameter	4 stages	March-June and August-November	Kagwade, 1970
Polynemus paradiseus	Ova diameter	6 stages	...	Kagwade, 1970
Psammoperca waigiensis	Ova diameter	3 stages	July-August and January-February	Prabhu, 1956
Psettodes erumei	Ova diameter	7 stages	September-October	Pradhan, 1962
Pseudosciaena aneus	Ova diameter	6 stages	January-March	Rao Appa, 1964
Pseudosciaena aneus	Fat content	7 stages	December-March	Rao Appa, 1967

(*Cnotinued*)

TABLE 1. (*Continued*)

Species	Methods followed	No. of stages	Duration of spawning	Reference
Pseudosciaena bleekeri	Ova diameter	6 stages	February-May	Rao Appa, 1964
Pseudosciaena coibor	Gonads-Somatic index	...	May-August	Rajan, 1964
Pseudosciaena diacanthus	Ova diameter and condition factor	7 stages	June-September	Rao Venkatasubba, 1963
Raconda russelliana	Ova diameter	6 stages	December-February	Varghese, 1961
Rastrelliger kanagurta	Ova diameter	7 stages	March-May (east coast) November-December (east coast) June-August (west coast)	Nair and Virabhadra Rao, 1970
Sarda orientalis	Ova diameter	7 stages	April-September	Rao Narayana, 1964
Sardinella albella	Ova diameter	5 stages	...	Radhakrishnan, 1961
Sardinella fimbriata	Ova diameter	7 stages	January-April	Radhakrishnan, 1964
Sardinella gibbosa	Condition factor and seasonal occurrence of eggs	7 stages	February-May	Ganapati and Rao Srinivasa, 1957
Sardinella longiceps	Ova diameter	10 stages	July-September	Antony Raja, 1964
Sardinella longiceps	Ova diameter	6 stages	June-November or December	Annigeri, 1969
Sardinella longiceps	Ova diameter	7 stages	June-September	Dhulkhed, 1963
Saurida tumbil	Ova diameter and general appearance of gonads	6 stages	October-January	Annigeri, 1963
Scomberomorus guttatus	Ova diameter	3 stages	April-July	Krishnamoorthi, 1958
Selaroides leptolepis	Ova diamer and condition factor	6 stages	February-April and July-October	Tandon, 1961
Sillago sihama	Condition factor and ova diameter	5 stages	August-February	Radhakrishnan, 1957
Stolephorus indicus	Ova diameter	4 stages	Throughout the year	Prabhu, 1956
Therapon puta	Ova diameter	4 stages	February-March and August-September	Prabhu, 1956
Trichiurus lepturus	Ova diameter	....	May-June and November-December	Tampi *et al.*, 1968
Trichiurus haumela	Ova diameter	5 stages	June	Prabhu, 1955
Thrissocles dussumieri	Ova diameter	5 stages	February-September	Dharmamba, 1959
Thrissocles mystax	Appearance gonads	...	September-May	Venkataraman, 1956
Upeneus tragula	Ova diameter	7 stages	May-November	Thomas, 1969

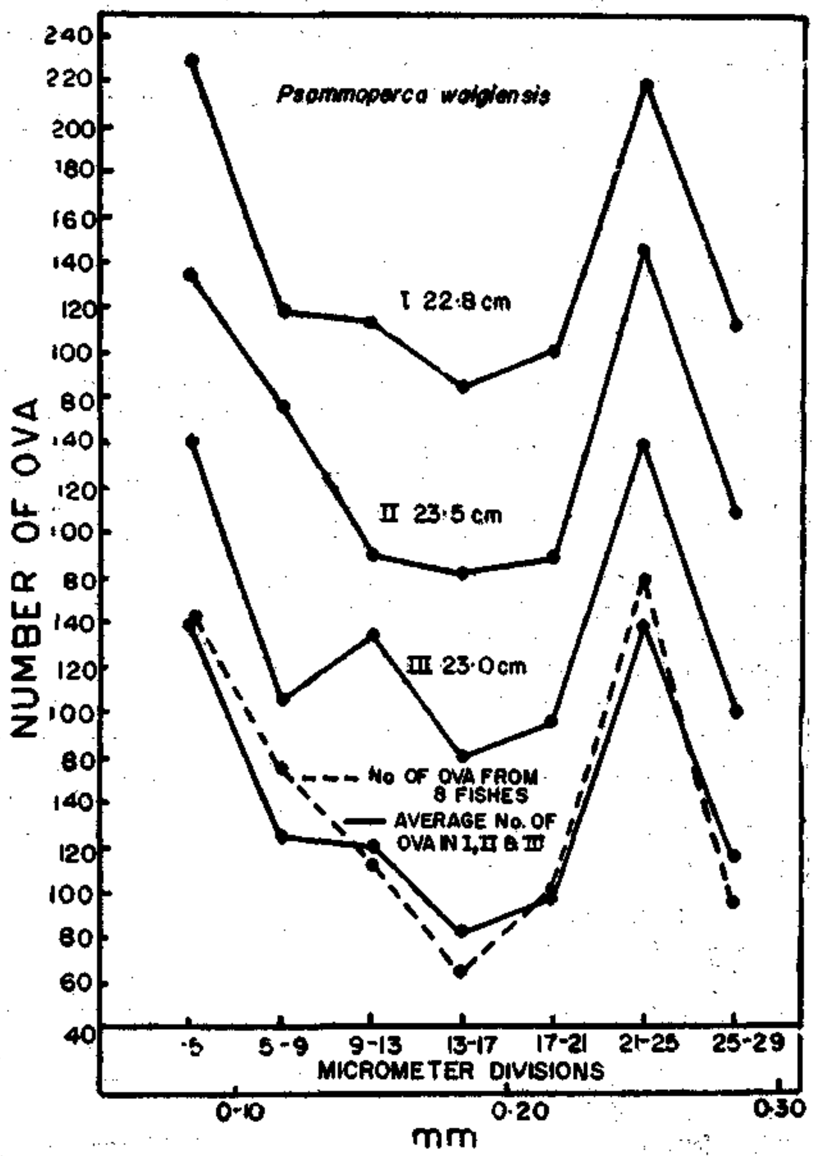

FIG. 1. Size frequency distribution of maturing ova in ovaries of *Psammoperca waigiensis*, after the figure was redrawn by doubling the size intervals given by Prabhu (1956).

The size of the eggs as a criterion for classifying them into distinct batches poses certain problems. For instance, in the ovaries of *Psammoperca waigiensis*, it has been shown that eggs of many size groups are present in various stages of development (Prabhu, 1956). The large-sized ova seem to dominate in all the stages of maturity. From this it is difficult to conclude that only the larger ones will be spawned first. The selection of the size-interval of the eggs is also important as the modes largely depend upon the way in which size-grouping is done arbitrarily. For example, when the size frequency polygon of ova in *Psammoperca waigiensis* is redrawn by doubling the size-intervals (see Fig. 1), it gives only two or three modes instead of five shown in the original figure of Prabhu (1956, p. 66). This illustrates the arbitrary nature of the modes and indicates that there has been far too much dependence on the size measurements of preserved eggs and very little effort has been made even to examine the characteristic features of the unspawned eggs in freshly collected specimens.

(d) *Condition factor or ponderal index*

Seasonal changes in the ratio of body weight and length provide information on the breeding of fish, for changes in the condition factor are associated with the rise and fall in gonad weight. Many Indian workers have used this method either singly or along with other methods, to determine the time of spawning and the onset of maturity (see Table 1). However, since the body weight of the fish is influenced by obesity, feeding or as a result of the overall well-being of the fish, too much reliance on this method, as an index of spawning in tropical fishes, does not seem a realistic approach, for in continuous breeders the body weight is seldom subjected to drastic changes and individual variations in weight make the study very inconsistent. Various formulae to smoothen the inconsistency and to make the method more sensitive have been developed (LeCren, 1951). However, it is important that the method is used with care and its applicability on fishes from the tropical waters is carefully re-evaluated in future studies. As a caution against hasty generalization, it must be added that the apparent similarities in an approach are not as important as the inherent dissimilarities, which put the method to a real test and make the whole problem really interesting.

(e) *Occurrence of eggs and larvae*

Although it is a direct method for determining the spawning season of a fish, few attempts have been made to study the eggs and larvae from the plankton, probably because of difficulties in their identification and lack of facilities for collection. The short incubation period of the eggs in tropical waters, often lasting a few hours only, makes their availability in the environment fairly restricted. Because of high temperature, the planktonic larval phase is also short-lived. Nevertheless, the atlas on the distribution of fish eggs and larvae in the Indian Ocean (IOBC, 1970) is perhaps the first systematic and praiseworthy approach and it is hoped that the data given in this atlas would form a basis for more intensive studies on fish eggs and larvae in the future.

(f) *Histological changes in gonads*

Maturation and spawning is a complicated process and, therefore, a reasonably correct picture can hardly be accomplished by the arbitrary classification of gonads. Similarly, the study of the progression of oocytes, by measuring their diameters, only gives evidence of an exploratory nature on spawning. Histological studies giving details of spermatogenesis and oogenesis have seldom been attempted on the Indian species and there is an urgent need for a variety of details indicating a coordination between histological changes in the gonads and those observed by an external examination. Gokhale (1957) studied the gametogenesis in the whiting and in the Norway pout of the Irish sea and found that the seven stages of maturity identified by microscopic examination had strict correlation with the seasonal histological changes in both male and female gonads.

MATURITY AND GROWTH

In fishes, growth is a continuous process and lasts throughout life. Thus the three phases—juvenile, adult and senile—are not easy to distinguish from the study of growth rate alone. However, since the two processes, maturity and growth introduce considerable metabolic demand upon body reserves, these are not normally concurrent. Food ingested by the fish is utilized as energy for growth and a part of this energy is transferred to the developing gonads. For this reason, maturation is normally delayed until the main growth period is virtually over. The post-maturity phase of growth generally becomes exceedingly slow and continues throughout life. Shortage of food or prolonged starvation retards both the processes. Similarly, nutritional excess is reflected from timely maturity and a rapid rate of growth.

SYNCHRONIZATION OF SPAWNING

The process of maturation is so adjusted amongst the individuals that a large number must mature at the same time, so that they may spawn together. The spawning of a population must be geared to external events when the environmental conditions are most favourable.

Two main factors seem to influence the synchronization of spawing: (a) internal factors (b) external factors.

(a) *Internal factors*

Reproduction in fishes, like other metabolic processes, is controlled by hormones. A series of hormone-controlled changes occur both in the testes and ovaries in such a way that peak maturation is attained at an appropriate time. In those species which spawn successively, perhaps an automatic sorting device is developed to ensure that only the ripe eggs are released from the ovaries. A considerable literature is available (see Liley, 1969) to show that endogenous factors are most important in determining the onset of maturation.

(b) *External factors*

In many fishes, coordination in spawning is achieved by shoaling behaviour. Very often, the spawning congregation involves migration over long distances and this is so adjusted that large numbers of individuals are available at the spawning ground. Both internal (endocrine) and environmental factors seem to be responsible for the behaviour leading to congregation. While the fish is shoaling, the contents of both male and female gonads are released to the exterior where fertilization occurs. The phenomenon of spawning is epidemic in nature, which means that spawning of one individual induces the others to follow. Often the males reach the spawning grounds earlier than the females and the presence of spermatozoa seem to induce the females to shed their eggs.

Spawning followed by hatching of eggs in temperate and Arctic-boreal fishes occurs during a period when there is an abundance of food in the environment (Qasim, 1956a). In higher latitudes, the existence of a favourable temperature threshold has been considered of much importance for favouring reproduction and this has been referred to earlier as Orton's rule (see Qasim, 1956a). In tropical waters, where variations in sea temperature and food supply are not so well-marked, these two factors do not seem to act as trigger stimuli for breeding. However, annual changes in salinity and temperature, associated with the monsoon rain, are in certain regions, especially along the south-west coast of India, fairly large. But these affect the coastal waters only (see Qasim *et al.*, 1972). If the breeding grounds of certain species happen to be within the coastal belt, the decline in salinity and temperature could perhaps provide the breeding stimuli. The failure of a fishery during the season has been attributed to poor rainfall during the monsoon period, which, in turn, has been related to unsuccessful spawning of the fish populations (Antony Raja, 1972). From tropical waters, we have practically no knowledge of the environmental stimulation of spawning.

FECUNDITY

The knowledge of the total number of eggs produced by a fish during a year is of much value in determining the spawning potential of fish stocks, although in most species where the eggs are destined to be withdrawn from the ovaries in batches, an accurate determination of fecundity is almost impossible. This difficulty has already been pointed out in freshwater fishes (Qasim and Qayyum, 1963). Further, the availability of ripe fishes for the determination of fecundity is also difficult in those species which have a prolonged spawning season (see p. 168). It should be remembered, however, that whenever such difficulties are encountered, they must be pointed out, for the knowledge of the limitation in the approach is the first step to provide modifications to overcome the difficulty. In Indian forms, the data on fecundity are too numerous, but these seem to be deceptive, for large-scale resorption and degeneration of oocytes under certain environmental conditions are quite common in our waters.

SPAWNING SEASONS IN INDIAN WATERS

The available information on the spawning season of teleosts in the Indian waters suggests that spawning in fishes goes on in all the months of the year. A survey of the literature indicates that the information available during the monsoon months is extremely meagre. The lack of data has led to a considerable degree of speculation whether spawning could occur in these months or not. In

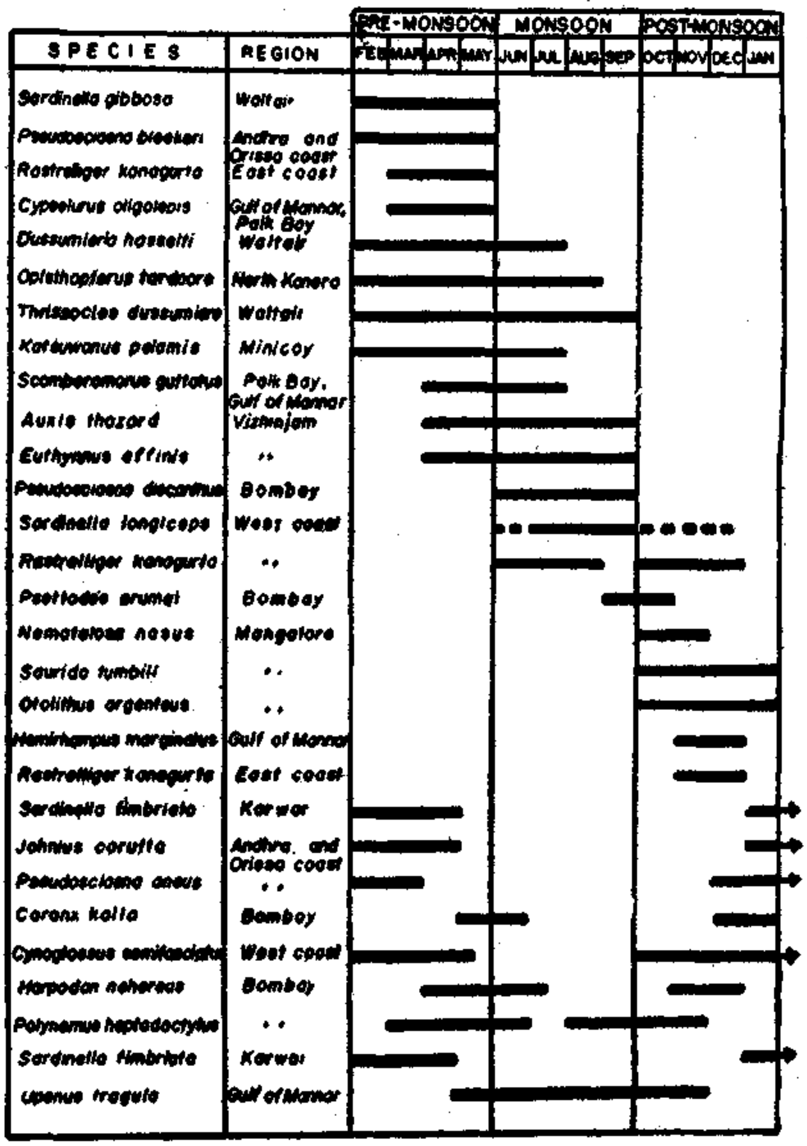

FIG. 2. Diagrammatic representation of time and duration of the spawning seasons in some marine teleosts from the Indian waters as deduced from the works of different authors. In determining the duration, the predominant view has been taken. The view held by some regarding the oil sardine has been shown by broken line.

some species, the gaps in the season have resulted because of the absence of material for the study during the monsoon months, when fishing is temporarily suspended.

Fig. 2 indicates the duration of spawning in different species. As can be seen from the figure, there is no definite pattern in the time and duration of spawning according to which the fishes could be grouped. Nevertheless, there are indications that along the east coast, spawning largely occurs during the pre-monsoon months (February to May). Fishes, along the west coast, on the other hand, largely seem to spawn during the monsoon (June to September) and post-monsoon months (October to January). Many species appear to be continuous breeders and prolonged spawning, lasting 7-9 months during the year, in many species, as has been reported in the literature (see Table 1 and Fig. 2), does not confer them to have seasonal spawning. The restriction imposed on the spawning in some months appears to be simply because of the lack of proper observation. The present author strongly feels that most species in the Indian waters, with the exception of a few in which seasonal breeding has been clearly established, are continuous breeders and future investigations should be carefully planned to determine whether seasonal rhythm in breeding is really an endogenous phenomenon or it arises as a result of environmental factors.

Conclusion

From numerous works it is clear that maturation and spawning in teleosts are highly variable in the Indian waters. We have little detailed information on the spawning of the same fish from different geographical regions. It is therefore suggested that future studies should not be restricted to sketchy observations on spawning, but should be planned to develop an understanding of the maturation process of the population in a particular area. A good deal of work of an exploratory nature is already available and there is a pressing need for resisting the temptation to accept whatever has been said, as proven.

Acknowledgements

I thank Miss G. K. Vinci, Mr. R. S. Lal Mohan, Mr. M. S. Rajagopalan and Mr. K. M. S. Ameer Hamsa for their help in finalising Table 1.

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