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Reproductive biology of the larvivorous fish *Macropodus cupanus* (Cuv. and Val.)

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Abstract. Investigations on the maturity stages, pattern of distribution of ova in the ovary, growth of the ova to maturity, minimum size at first maturity, sex ratio, growth rate of the ovary, spawning frequency, spawning season and fish-fecundity relationships of the larvivorous fish *Macropodus cupanus* indicate the extent to which breeding is geared to take maximum advantage of environmental and other factors which afford the greatest opportunity for survival and development of the new generation. The mode of development and growth of the ova reveal that the first maturation is normally delayed till the main period of body growth is over; further, the linear relationships derived between growth rate of the (female) gonads and fish size are a reflection of the symmetry of the gonads. Correlating data on egg size, fecundity and conditions for incubation, *M. cupanus* with its high fecundity and rapid development can be said to incline towards '*r*-selection' on the continuum between '*k*' and '*r*-selection'. Investigations on spawning frequency and season reveal the protracted spawning season from April to September and the shorter one in January and February. The distinct monsoon spawning peak leading to an increase of its population during this season coincides with the peak incidence of mosquito larvae, indicating the larvivorous potential of the fish.

Keywords. Reproductive biology; larvivorous fish; *Macropodus cupanus*.

1. Introduction

Indiscriminate releases of the exotic larvivorous fish *Gambusia affinis* and *Poecilia reticulata* into the aquatic environment for mosquito larval control have threatened the survival of valuable aquatic fauna (Myers 1965; Bay 1973; Menon 1977). This has renewed interest in the biocontrol potential of indigenous larvivorous fish such as *Macropodus cupanus* (Cuv. and Val.). An essential aspect of such investigations is the reproductive cycle and potential. Even though a biocontrol agent may have a high unit preference and feeding capacity for mosquito larvae, its effectiveness in reducing the larval population is a function of its population density (Bay 1972). However, although studies on the eggs and early development of *M. cupanus* have been conducted (Jones 1940; Padmanabhan 1955), detailed information on the gonadal cycle of fecundity and spawning is lacking, which prompted the present study.

2. Material and methods

Regular fortnightly samples of *M. cupanus* collected for one year (March 1977 to February 1978) from Veli lake, Chakai canal and surrounding paddy fields in Trivandrum, were utilised to record data on standard length, weight, stage of sexual maturity and length and weight of the gonad. The criteria used for quantification of maturity were colour, shape and size of the ovary, diameters of the unspawned eggs and their general appearance, particularly the extent of yolk formation, since male gonads could not be graded macroscopically. To eliminate sampling error resulting from regional differences in the ovary (the anterior region of the ovary of *M. cupanus* has a larger complement of immature ova than the middle and posterior regions, (Jacob 1981), a mixed sample of ova from the different regions was used for all ova diameter studies. Random samples of 1000 ova from ovaries in the different stages of maturity and mature/ripe ovaries were used to elucidate the progression of development of the ova to maturity and types of spawning tendencies following Hickling and Rutenberg (1936) and Prabhu (1956). Specimens were categorized into different length groups on the basis of their stages of maturity, to determine minimum size at first maturity; stages III, IV and V were treated as mature. To delineate the spawning season—through a study of the gonado-somatic index and percentage occurrence of gonads in the different stages of maturity during the different months—females alone were used since male gonads exhibited only microscopically discernible changes, apart from minor alterations in size. Fecundity estimates were based on sub-sampling of unbiased samples of ovaries from gravid fish collected during their peak spawning season (May) as recommended by Bagenal and Braum (1968).

3. Results

3.1 *Delineation of the maturity stages of the female gonads*

In *M. cupanus*, the ovaries have been classified into 5 stages, as suggested by Qasim (1973) for tropical fish.

3.1a *Stage I Immature virgins:* The small, thread-like, whitish, almost transparent ovaries occupy only a minute portion of the abdominal cavity. The ova are invisible to the naked eye, but under the microscope are transparent with a central nucleus. At this stage yolk formation has not yet commenced. The diameter of majority of ova in this stage ranges from 40-60 μ; the largest measuring 98 μ in diameter.

3.1b *Stage II Maturing virgins/recovered spents:* The semi-transparent, whitish ovaries are larger owing to lateral and anterio-posterior expansion. The shape and positioning are distinct; each ovary is triangular when viewed from the side with the apex directed backwards and the anterior extremity of the ovary forming the base of the triangle. The anterior extremities are close together and their ventral angles are united although the posterior two-thirds of each ovary are separated since they extend into the posterior part of the body cavity lying between the haemal processes of the vertebral column. The maturing ova with a mode at 110 μ and a maximum diameter of 165 μ are separated from the general immature stock and are opaque owing to the commencement of yolk formation.

3.1c *Stage III Ripening:* The opaque yellow ovaries are almost fully packed with the fully yolked ripening ova and occupy almost half the total space available posteriorly between the haemal processes of the vertebral column. Anteriorly, however, they extend only slightly into the abdominal cavity, unlike in most other fish. The spherical, fully yolked ova show a mode at 550 μ and a maximum diameter of 716 μ.

3.1d *Stage IV Ripe:* The massive yellowish-red ovaries with very thin distended ovarian walls, and numerous blood vessels ramifying over the surface, are fully packed with large opaque eggs showing a mode at 750 μ, but with a maximum diameter of 1002 μ. The ovaries now extend deep into the spaces on either side of the vertebral column, almost up to the caudal region posteriorly. The anterior basal portion is deeply concave; the concavities of the two ovaries form a shallow depression into which the intestinal coils fit.

3.1e *Stage V Spent:* The highly shrunken flaccid blood-shot ovaries bear a superficial resemblance to Stage II, but differ in the loosely-packed nature of the maturing ova, in the scattered transparent areas visible and in the general granular appearance of the ovary. In a recently spawned fish a few remnants of mature ova with a maximum diameter of 680 μ are present as resorbing and disintegrating structures, but the majority of the ova are small, transparent and invisible to the naked eye.

3.2 *Development of the ova to maturity*

Data from frequency polygons of ova diameter measurements taken from ovaries of different maturity stages (figure 1) reveal the progression of development of ova in *M. cupanus.* In stage I, there are only immature ova, ranging from 23 to 98 μ in diameter with a distinct mode at 50 μ. As maturation progresses, this batch of eggs is separated from the immature stock and represented by a mode at 110 μ in stage II; the maximum ovarian size at this stage is 165 μ. In stage III, this maturing group of ova with a mode at 550 μ shows an increase in size and yolk deposition. A second group of maturing ova with a mode at 350 μ, distinct from the immature stock, is visible at this stage. As development progresses, the second group of maturing ova shows only a slight increase of 100 μ, vide stage IV. The first distinctly separate group

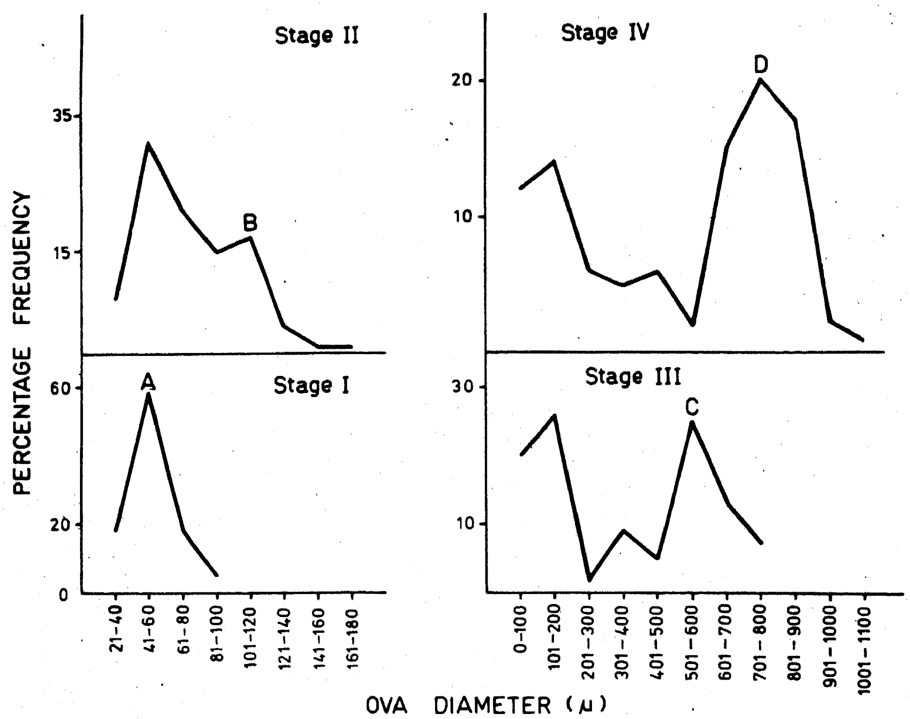


Figure 1. Ova diameter measurements from ovaries of different stages of maturity, showing the progression of development of the ova in *M. cupanus*.

with a mode at 750 μ and a maximum ova diameter of 1002 μ evidently constitutes the mature group of eggs which would be spawned in the ensuing spawning season. It should also be noted that the rate of development of ova is maximum between stages II and III.

3.3 *Minimum size at first maturity*

The results presented in table 1 show that all specimens below 18 mm are immature; maturity sets in from the 19 mm stage onwards. The length at which 50% of the specimens attain maturity, considered the length at first maturity (Kagwade 1968), lies between 22 and 24 mm.

Table 1. Occurrence of female *M. cupanus* in different stages of maturity in the various size groups.

Standard length (mm)	Immatures (%)	Maturing virgins (%)	Matures (%)
13–15	100.00	—	—
16–18	100.00	—	—
19–21	74.29	20.00	5.71
22–24	51.16	37.21	11.63
25–27	15.22	47.83	36.96
28–30	4.17	16.67	79.17
31–33	3.33	10.00	86.67
34–36	—	7.69	92.31
37–39	—	—	100.00

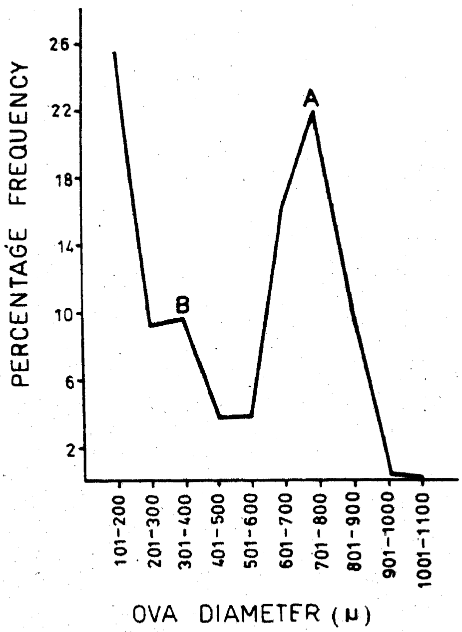


Figure 2. Diameter measurements of 1000 ova from stage IV ovary of *M. cupanus*.

3.4 *Spawning frequency*

Data (figure 2) indicate that within the ovary, apart from the general immature stock, there are two distinct batches of eggs, represented by the modes *A* and *B*. The group of eggs under mode *A* is in the ripe condition and ready to be spawned, while the second group of eggs at mode *B* is the maturing batch in which yolk formation has already advanced. It is likely to be shed subsequent to the first batch, indicating the possibility of a second spawning. Again, as the time required for the second batch to attain maturity is less than that required for the first batch (de Jong 1939) and as the two batches are not clearly and sharply demarcated, it is likely that this species spawns twice during the spawning season.

3.5 *Spawning season*

The percentage occurrence of female fish with gonads in various stages of maturity (table 2) reveals that although ripe females are present during all the months except October, November, December and March, a distinct periodicity in breeding is discernible. A major peak in gravid female number is recorded in April/May which then gradually falls, reaching a minimum in August. The spent fish number is high in these months with a maximum in June, after spawning. The number of recovered spents is high in July and August, indicating the conversion of at least a part of the spents into the recovering stage. In September, a second rise in ripe female number is visible. In October and November, after spawning, the number of spents and recovered spents is high; no ripening and ripe fish are obtained during these months.

Table 2. Monthly percentage occurrence of female *M. cupanus* in the different stages of maturity (females 28 mm and above alone are considered).

Months	Stages of maturity				
	I Immature	II Maturing/ recovered spent	III Ripening	IV Ripe	V Spent
March '77	—	80.00	20.00	—	—
April	—	7.14	58.57	34.29	—
May	8.33	—	13.00	51.67	27.00
June	—	—	6.00	30.00	64.00
July	—	17.65	—	29.41	52.94
August	—	9.09	18.18	18.18	54.55
September	—	5.88	5.88	76.47	11.76
October	12.50	57.50	—	—	30.00
November	—	66.67	—	—	33.33
December	—	100.00	—	—	—
January '78	—	38.89	11.11	38.89	11.11
February	—	—	—	30.00	70.00

By December, all specimens collected are in the recovered spent stage. In January, the number of ripe and ripening females begins to increase and another spawning takes place. The number of ripe fish declines in February while the number of spents increases, amounting to 70% of the total collection. In March almost 80% of the population is in the recovered spent stage while a few have gone into the ripening stage. From April the number of ripening and ripe specimens increases until peak spawning in May.

The gonado-somatic indices (figure 3) confirm the pattern described above. There is a long spawning period between April/May and September, with a major peak in May and a smaller one in September. In January the gonado-somatic index peaks again, and then declines till the peak in April/May.

3.6 *Sex ratio*

The sex composition of random samples examined each month (table 3) shows that the two sex are present in more or less equal numbers since the variation in the number of males and females is negligible during most months.

3.7 *Growth rate of the ovaries*

The relationships between the parameters of length and weight of the fish and ovary was utilised for following the growth rate of the ovary (table 4). It is evident that the

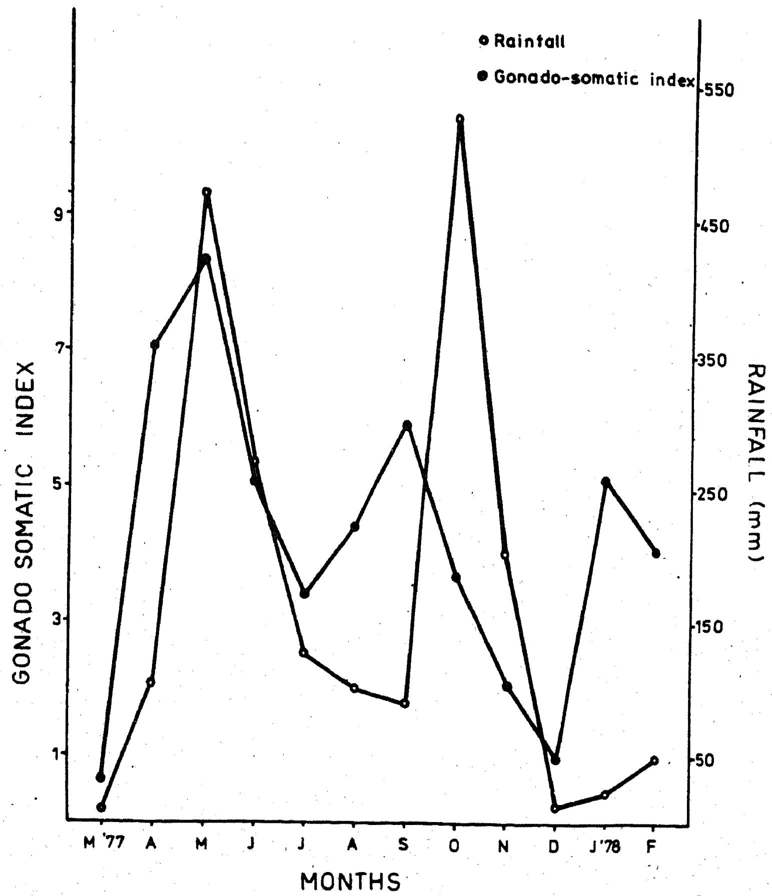


Figure 3. The breeding of *M. cupanus* in relation to rainfall.

Table 3. Sex ratio in *M. cupanus*.

Months	No. of fish examined	Males (%)	Females (%)
March '77	30	46.67	53.35
April	25	36.00	64.00
May	37	48.65	51.35
June	25	44.00	56.00
July	53	45.28	54.72
August	54	50.00	50.00
September	49	38.78	61.22
October	49	48.98	51.02
November	49	55.10	44.90
December	54	55.56	44.44
January '78	58	50.0	50.00
February	65	40.00	60.00

Table 4. Relationship between body growth and ovary growth in *M. Cupanus*.

Variables	Equation	Correlation coefficient
Length of the fish, L Length of the ovary, LO	LO = 0.4456 L − 3.0080	0.8504
Weight of the fish, W Weight of the ovary, WO	WO = 0.1288 W − 23.8846	0.8699

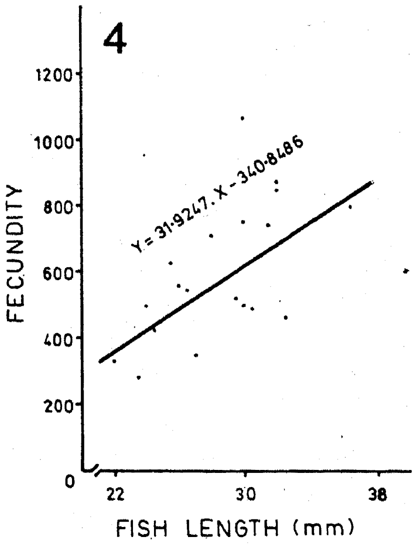
All correlation coefficients are significant at the 1% level

rate of growth is linear, the ovaries increasing in length and weight in proportion to the increase in length and weight of the fish.

3.8 *Fecundity*

Figures 4-7 indicate the relationships between fecundity and the variables—length of the fish, weight of the fish, ovary length and ovary weight (a slight asymmetry was noted in certain specimens between the right and left ovaries, but this feature was neither consistent nor significant). The regression equation obtained from relating fecundity and fish length is linear and the correlation coefficient is significant at the 5% level indicating that as fish length increases, fecundity also increases proportionately. However, the relationships between fecundity and fish weight, ovary length and ovary weight are exponential. The coefficient of correlation is significant at the 1% level, indicating that the rate of increase of fecundity, proportionate to these 3 variables is initially fast, but decreases with time.

The relationships between relative fecundity (*i.e.*, the number of eggs per gram body weight of the fish) and the various variables is shown in table 5. *M. cupanus* has a mean relative fecundity of 841. The relationship between this value and standard length and weight is linear, suggesting that relative fecundity increases with increase in these variables. When ovary length and weight are related to relative fecundity, the coefficient of correlation is not significant in both cases, suggesting that these variables do not affect relative fecundity.



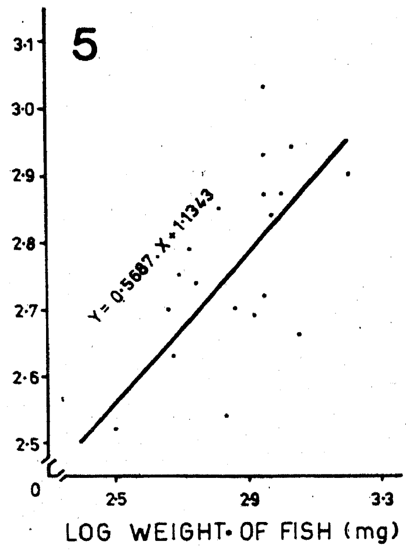
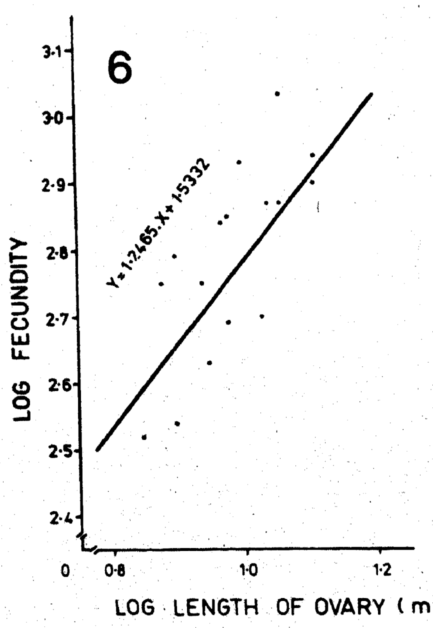


Figure 4. The relationship between fish length and fecundity in *M. cupanus*.

Figure 5. The relationship between fish weight and fecundity in *M. cupanus*.



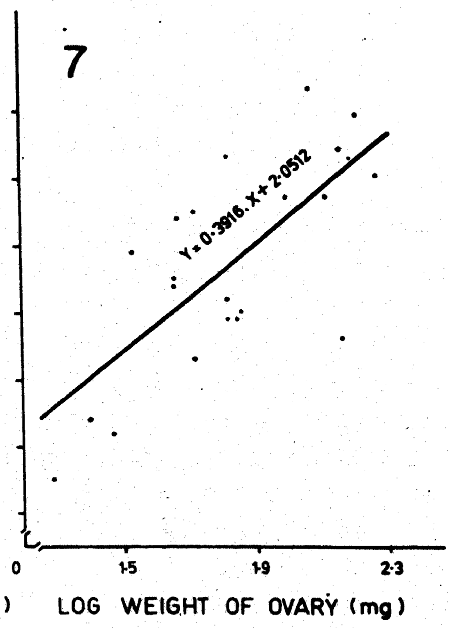


Figure 6. The relationship between ovary length and fecundity in *M. cupanus*.

Figure 7. The relationship between ovary weight and fecundity in *M. cupanus*.

Table 5. Relationship between relative fecundity and the different variables in *M. cupanus*.

Variable	Equation	Correlation coefficient
Length of the fish, L	F = 1.3110 L + 4.8098	−0.5394*
Weight of the fish, W	F = 0.4299 W + 4.1304	−0.5797**
Length of the ovary	Relationships not worked out since correlation coefficients are not	−0.3453
Weight of the ovary	significant	−0.3789

**Significant at the 1% level; *Significant at the 5% level. Other correlation coefficients not significant.

4. Discussion

That a cycle of gonadal maturation, imposed by the energy demands of maturing a batch of eggs/young ones exists, even in regions where environmental conditions are relatively stable and offsprings are produced throughout the year, is undisputed (Peter and Hontela 1978). However, in this study, considering the overall implications of the problems relating to the quantification of maturity, the multi-stage classifications commonly used (Bagenal and Braum 1968) were discarded, and the suggestion of Qasim (1973), that in tropical forms the classification should be limited to 5 maturity stages was followed. Data reveal that as stated by Hoar (1969), gonadal maturity and body growth are linked since the analysis of the body length-gonad length relationships reveals that increase in female gonad length is proportional to fish length; this is partially supported by the work of Rao (1967) in other fish.

Considering the sex ratio, the situation in *M. cupanus* is in contrast to that in other larvivorous fish, specifically *G. affinis* where more females are encountered in the environment (Mallars and Fowler 1970).

Earlier data on the spawning season and frequency are contradictory. Thomas (1870) reported that the fish breeds in May and June but Jones (1940) could collect eggs in January, February, May and from September to November. Padmanabhan (1955) stated that the fish is a perennial spawner with a noticeable increase in the frequency of spawning during the monsoon months. The available data from this investigation indicate that the fish exhibits a protracted spawning from April to September and then a shorter one in January and February. This corresponds to data available for a large number of West coast species (Qasim 1973). It must be mentioned that females alone were considered for the demarcation of the spawning season since male gonads did not show clear cut maturity stages. Bennet (1967) claims that the sexual cycle is adjusted in both sexes so that the spawning acts coincide. A knowledge of the seasonal gonadal cycle of one sex should therefore, be quite sufficient to indicate the general pattern. Further, although *M. cupanus* fits into category *C* of the classification of fish on the basis of spawning activity by Prabhu (1956) and Karekar and Bal (1960), and into category II of the classification of Qasim and Qayyum (1961), Qasim's (1973) opinion that there is no definite pattern in time and duration of spawning according to which fish can be grouped seems applicable here, since neither categorization covers all contingencies in breeding.

In so far as the onset of maturation and the synchronization of spawning are concerned, although considerable literature is available to show that endogenous factors are most important (Liley 1969), in tropical waters, as stated by Antony Raja (1972), Qasim (1973) and Peter and Hontela (1978), climatic changes associated with the monsoon rains may also stimulate spawning as shown by the relation between gonado-somatic index and rainfall (figure 3). The inundation of low lying areas consequent on the monsoon floods which interconnect adjoining stretches of water and bring together large numbers of breeding pairs may also be responsible. Whatever the reason, the monsoon spawning peak leads to an increase in fish population during this season, coinciding with the peak incidence of mosquito larvae (National Filariasis Control Prevention Unit—personal communication). This indicates the larvivorous potential of the fish.

Considering fecundity, although work on Indian marine fish is voluminous, those on freshwater fish are comparatively few. Absolute fecundity has been usually related to fish or gonad length and weight (Bagenal 1966). Length has an advantage over other factors in that the fish does not shrink significantly though it can lose weight during the spawning season (Bagenal 1967). The close relationship between absolute fecundity and length demonstrated here is supported by Jhingran (1961), Mathur (1964) and Bhatt *et al* (1977), among others. Nevertheless, a variability in fecundity even in fish of the same length is noted, as stated by Le Cren (1951), Rao (1967) and Thomas (1969). This has been attributed to atresia by Henderson (1963). Winters (1971) suggests that fish, previously spawned, have a greater fecundity than fish of the same age and size spawning for the first time.

Analysis of the fecundity-weight relationships reveals that both gonad weight and body weight are exponentially related to fecundity. This could be explained by Bagenal's (1967) contention that either larger ovaries produce larger and fewer eggs or the connective tissue increases disproportionately in the ovaries of the larger fish. However, these relationships must be qualified by the fact that in many fish, somatic weight changes significantly towards the spawning period (Wootton 1973) resulting in an alteration of the relation between fecundity and weight as the season progresses. Further, a spurious correlation may be obtained when total weight is utilised since the greater number of eggs in the more fecund fish will weigh more than those in less fecund fish (Bagenal 1978).

For a better comparison of fecundities and to eliminate the alteration in (absolute) fecundity with fish age and size, the relative fecundity was calculated. The negatively linear relationships worked out in *M. cupanus* conform in some degree, to the findings of Bhatt *et al* (1977).

Connecting egg size and fecundity with the conditions for incubation, *M. cupanus* with its relatively high fecundity and rapid development exhibits parental care until the young attain a certain size (Jacob 1981). Although inclining towards '*r*-selection' (Mac Arthur and Wilson 1967), the fish could be considered as a compromise on the continuum between the two extremes of '*r*-' and '*t*-selection'.

Thus the reproductive behaviour is geared to take advantage of environmental and other factors which offer the greatest opportunities for survival and development of the new generation.

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