Cey. J. Sci. (Bio. Sci.) Vol. 23, No. 1, 1994

REPRODUCTIVE ECOLOGY OF TWO CO-OCCURRING, STREAM-DWELLING, ENDEMIC CARPLETS (PISCES, CYPRINIDAE) OF SRI LANKA

K. H. G. M. DE SILVA and R. M. D. SOMARATHNA

Department of Zoology, University of Peradeniya, Peradeniya, Sri Lanka.

Correspondence: Dr. K. H. G. M. de Silva, Department of Zoology, University of Peradeniya, Peradeniya, Sri Lanka

ABSTRACT

The reproductive ecology of *Barbus cumingi* and *B. nigrofasciatus* was studied in two head-streams of the river Mahaweli. Both species bred throughout the year but breeding was enhanced during the months in which the rainfall was low. *B. nigrofasciatus* spawned predominantly among submerged aquatic macrophytes, whereas *B. cumingi* spawned at the edge of the stream in very shallow areas at locations which are sheltered from the main current. *B. cumingi* showed territorial behaviour but *B. nigrofasciatus* formed loose aggregations of males and females for breeding. Males of both species showed aggressive behaviour towards potential rivals. Spawning of both species occurred in well-lit areas usually between 0900 and 1600 hrs.

Sex ratio of *B. cumingi* was 0.67 favouring females whereas that of *B. nigrofasciatus* was 0.78. Sex ratio did not fluctuate significantly over the months. A higher proportion of females occurred in higher size classes of *B. cumingi* and lower size classes of *B. nigrofasciatus*. The mean size at maturity was 33.0 mm in *B. cumingi* and 31.5 mm in *B. nigrofasciatus*. The fecundity of both species increased with increase in both body size and body weight. The size-frequency distribution of eggs in the ovaries of both species showed multiple peaks indicating multiple spawning. The number of mature eggs of the females of the same size class varied over a wide range which is suggestive of serial spawning.

INTRODUCTION

Cyprinids are the commonest and the most diverse of the 69 indigenous fish species recorded in the freshwaters of Sri Lanka and include 30 indigenous species of which 16 are *Barbus* species. The latter species are mostly of small size usually not exceeding 10 cm. They inhabit a variety of both lotic and lentic habitats.

Of the indigenous cyprinids, only a few larger species such as *B. sarana, Labeo dussumieri* and *Tor khudree* are of commercial importance. Many of the endemic species are of small size and are in danger of extinction because of the changes in their habitats brought about by man's direct or indirect interference and also because even the few existing natural populations are rapidly being depleted for aquarium trade. *B. cumingi* Günther and *B. nigrofasciatus* Günther are rare and are listed as vulnerable species by the IUCN (1988). The former species occurs in two colour varieties (De Silva & Kortmulder, 1977) of which the "orange fin" variety was studied in the present investigation. The present study was carried out on co-occurring populations of the two species in a montane stream in the central part of the island.

Reproductive ecology of some Sri Lankan cyprinid species has been closely studied by several workers. De Silva and Kortmulder (1977) studied the reproductive ecology of three *Barbus* species and De Silva *et al.* (1985) studied that of six *Barbus* species in the head waters of two rivers. Chandrasoma and De Silva (1981) studied the reproductive ecology of *B. sarana* and De Silva (1983) examined the reproductive strategies of five commercially important cyprinid species in a reservoir.

MATERIALS AND METHODS

Habitat

Reproductive biology of the two fish species was studied in a perennial stream, called "Kahawaturu oya", which joins the river Mahaweli in its upper reaches at an elevation of 585 m. The study area (7° 1'N, 80° 29'E) was situated on the lower part of the stream below the flood water level of the main river. The stream was 10-15 m wide and the substratum was mostly stony and sandy. The water flow was moderate (5-15 cm sec-1). The stream was 1.0-1.5 m deep in the sampling region, and contained several dense patches of the exotic submerged aquatic weed *Elodea canadensis*. Aufwuchs were common on the substratum in the areas of slow flow.

The reproductive behaviour of the two species was studied also in another perennial stream, called "Sarasavi Oya", that flows through the campus of the University of Peradeniya. The habitat in this stream was different as it was devoid of submerged macrophytes. During the non-rainy months, the stream became narrower and shallower to only about 1-3 m wide and less than 20 cm deep in most places. The two species were present only in the lower part to a distance of about 0.5 km from the stream mouth. The substratum of this area consisted mainly of pebbles and sand. This part of the stream was subjected to floods during heavy rains.

Sampling

Monthly samples were obtained during the period of September 1986 to November 1987 from five sites, which were randomly selected, at the beginning of the sampling programme, along a length of about 100 m of the stream. The same sites were sampled each month. A cast net of 1 cm stretched mesh size and a pond net on 1 mm mesh size were used for sampling. A monthly sample contained 25-50 individuals of each species. Fish were injected with formol calcium into the body cavity immediately after capture, and the entire sample was preserved in 5% formalin.

The reproductive behaviour of the two species was studied from about 0600 hrs to 1800 hrs on several days in different months.

During each sampling session, the temperature, pH, conductivity and concentration of dissolved oxygen of water were measured using calibrated portable electronic meters. The speed of water flow was estimated by noting the time taken by a floating cord to travel a specified distance along the middle of the stream. Monthly mean depth of water was calculated by measuring the depth at 1 m intervals along a line transect at each site. The rainfall data were obtained from the Meteorological Station at Blackwater Tea Estate, which is situated at the same elevation about 2 km away from the sampling site.

Analyses

The total and standard lengths of each fish were measured to the nearest 1 mm and each fish was weighed to the nearest 1 mg. The gonads were dissected out, weighed to the nearest 1 mg and the stage of development noted. Gonads, especially ovaries, were categorised into six stages, which were more or less similar to the stages described by Nikolskii (1963). These developmental stages in ovaries can be briefly described as follows:

Stage I (indifferent) gonads - these are the thread-like gonads of the juveniles at early stages of differentiation that cannot be identified by unaided eye as ovaries or testes.

Stage II (developing) ovaries - These can just be distinguished by unaided eye as ovaries because of the slightly granular appearance given to it by developing eggs.

Stage III (maturing) ovaries - These contain yolky eggs and have a clear granular appearance. The size of the eggs can be of a wide range depending on the state of maturity but they have not yet attained the maximum size.

Stage IV (gravid) ovaries - These contain large yellow eggs and those that are mature are at their maximum size. However, the eggs are not extruded under slight pressure on the abdomen.

Stage V ovaries (ovaries of spawners) - In these, mature eggs are extruded under slight pressure on the abdomen;

Stage VI ovaries (ovaries of post-spawners) - These have a collapsed sac-like appearance as the mature eggs had been shed, but, the next batch of maturing eggs can sometimes be seen developing at stage III. A few unovulated eggs now degenerating, may also be present.

The fecundity was estimated using ovaries of stages IV and V. These were placed in Gilson's fluid in order to separate ova. All eggs in one egg sac were counted. The diameter of mature as well as immature eggs in one egg sac were counted. The diameter of mature as well as immature eggs were measured using stage V ovaries. Gonado-somatic index (GSI) (i.e. the weight of gonad as a percentage of the body weight) was estimated for each fish and the mean of the monthly sample was taken as the monthly GSI.

RESULTS

Limnological characteristics of habitat

Temperature, pH, conductivity and dissolved oxygen concentration in stream water at "Kahawaturu oya", measured during sampling period, varied from 19.0-26.5 °C, 6.2-7.1, 26-58 μS^{25} and 7.8-9.8 mg l^{-1}, respectively; water flow and mean depth varied from 4.0-14.4 cm sec^{-1} and 45-140 cm. Monthly rainfall varied from 30-1189 mm.

Reproductive behaviour

Adult males of *B. nigrofasciatus* assumed the breeding coloration of dark red colour developing into an almost uniform black within 2-3 hours of sunrise. Spawning usually took place in well-lit areas, in contrast to the feeding, which usually took place in shady areas. The courting males chased away others of the breeding coloration but were not usually aggressive towards males of paler, non-breeding coloration. Males did not protect definite localized territories but moved from one region to the other within the spawning area. However, they chased away other males that came too close to the females that they were courting. There appeared to be some degree of dominance among males of breeding coloration that were not courting, since some males always chased away other males even when a female was not in the vicinity. However, these "dominant" or more aggressive males were chased away by the courting males. Females of either species did not display any aggressive behaviour.

Males and females of *B. nigrofasciatus* aggregated for spawning in patches of submerged vegetation. Courting was observed just above the surface of the mat of *Elodea canadensis* and spawning was observed among the fronds of the macrophyte. Courtship and spawning were also observed in some areas devoid of aquatic macrophytes. In such areas, they moved around other submerged objects such as pieces of sticks, stones, etc. The aggregations in these areas were small, often less than 10, whereas those in *E. canadensis* mats numbered over 50.

Such breeding aggregations were not observed in *B. cumingi*, which showed territorial behaviour. The courting and spawning of *B. cumingi* were observed in shallow water, which was often not more than a few centimetres in depth. They rarely ventured into the deeper waters or among the fronds of *E. canadensis*. The males attained a bright yellow to orange breeding coloration. Courting pairs were observed to swim around submerged objects, such as stems of emergent plants, sticks or stones, within an area of about 30 cm in diameter. They rarely moved out of this area. Strangers were allowed to enter this area, but were chased away by the male if came too close to the courting pair.

The observations in Sarasavi oya were similar, except that *B. nigrofasciatus* spawned in very shallow areas at the edge of the stream.

Sex ratio

Overall male to female sex ratio of the pooled samples of 15 months was 0.67 (n=374) in *B. cumingi* and 0.78 (n=487) in *B. nigrofasciatus*. The overall sex ratio was found to deviate significantly ($P<0.01$) from the expected ratio of 1.0 in *B. cumingi* ($\chi2=14.64$, d.f.=1, n=374) as well as in *B. nigrofasciatus* ($\chi2=7.64$, d.f.=1, n=487). Monthly sex ratio varied from 0.30 (n=39) to 1.00 (n=24) in *B. cumingi* and from 0.47 (n=22) to 1.06 (n=33) in *B. nigrofasciatus* (Fig. 1), but these did not vary significantly from the respective overall ratios of either species. The sex ratio of individual length classes changed from class to class in both species (Fig 2). $\chi2$ test for goodness of fit indicates that the ratio in *B. cumingi* was significantly lower than the expected ratio of 1.0 ($P<0.05$) in length classes above 40 ($\chi2=7.00$-19.33, n=7-140, d.f.=1), and also in the length class 21-25 mm ($\chi2=5.56$, n=18, d.f.=1). In *B. nigrofasciatus*, the ratio differed significantly ($P<0.05$) from 1.0 in length classes less than 40 mm ($\chi2=4.26$-5.16, n=19-65).

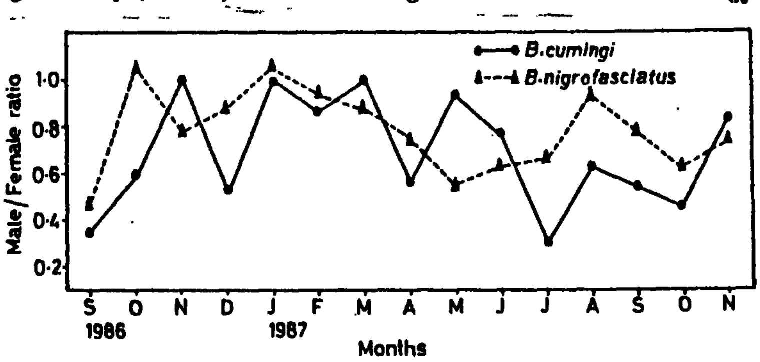

Fig. 1 Monthly male: female sex ratio of the two species.

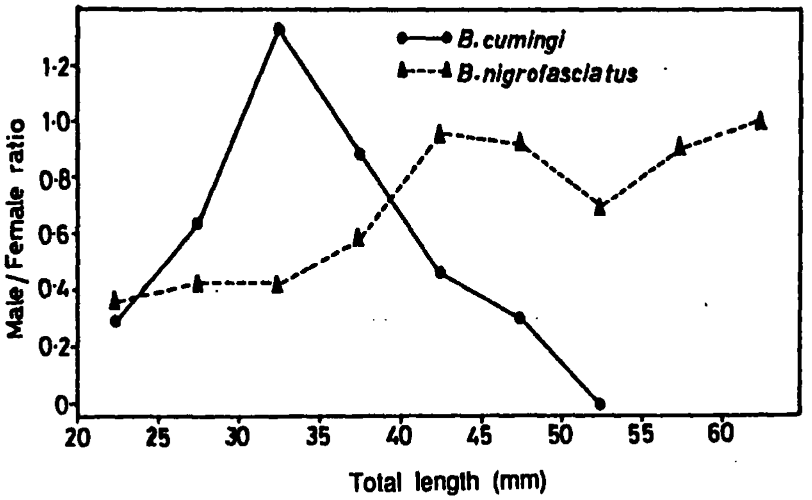

Fig. 2. Sex ratio in different size classes.

Gonad development and Spawning cycle

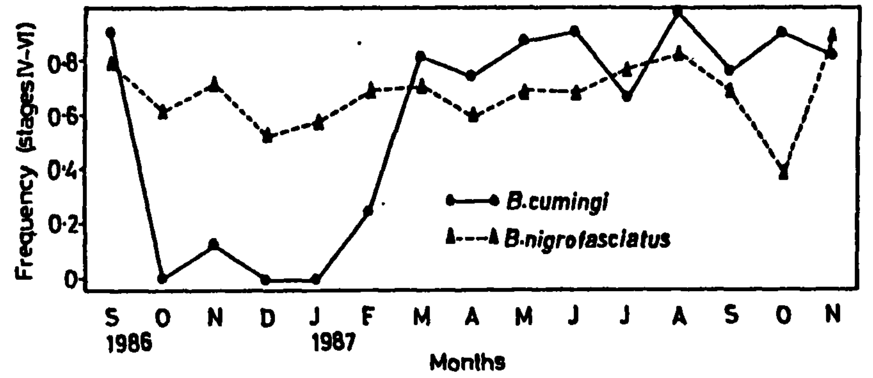

Fig. 3. Monthly frequency of gravid, spawning and post-spawning (Stages IV, V & VI) females.

In *B. cumingi*, females of the maturity stage IV-VI occurred during all months except during October and December 1986 and January 1987 (Fig. 3). This suggests that breeding occurs during most of the months, if not throughout the year. *B. nigrofasciatus* females of developmental stages V-VI were observed during all months (Fig. 3) indicating that the species spawned throughout the year. Small juveniles were also observed during all months. The monthly gonadosomatic index (GSI) of *B. cumingi* was high during the period of January to August 1987, but was generally low after the onset of the main rainy period (September to December) (Fig. 4). In *B. nigrofasciatus* also, the GSI of females was generally high during the period of January to August (Fig. 4). Thus, it appears that the breeding of both species is enhanced during the periods of low flow.

The highest values of monthly GSI in males and females of *B. cumingi were* 1.6 and 6.7 respectively, and occurred in January and April 1987, whereas those in males and females of *B. nigrofasciatus* were

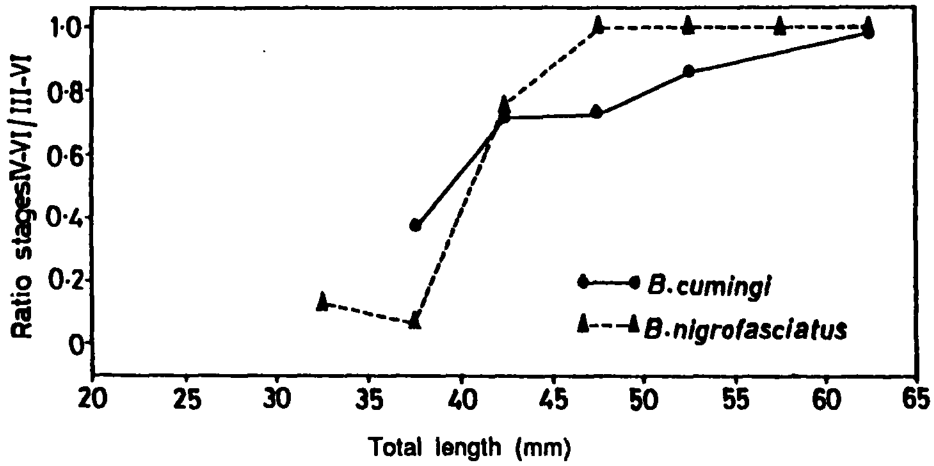

Fig. 4. Monthly gonado-somatic index of females.

1.6 and 5.4, respectively, and these too were observed in January and April.

The proportion of Stages IV-VI (gravid, spawning and recently spawned) females of each size class increased with increasing size and was above 70% in the size classes 45 mm and above (Fig. 5).

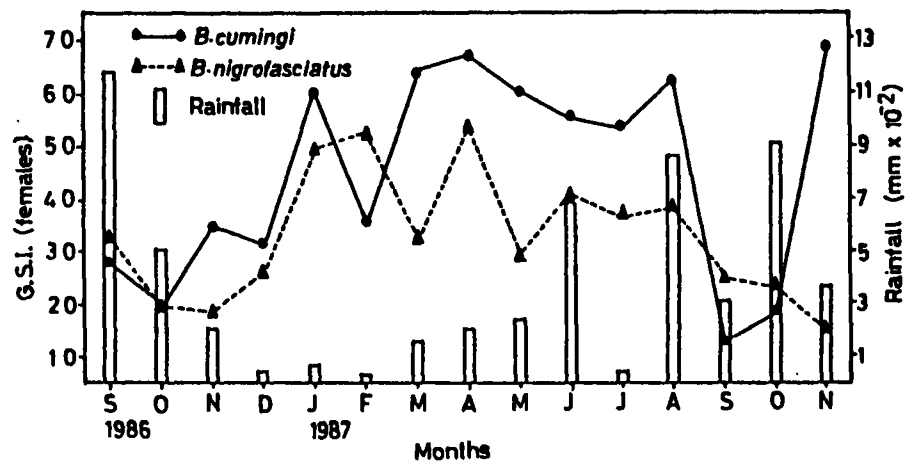

Fig. 5. Variation of the proportion of gravid, spawning and spawned (Stages IV-VI) females among the mature (Stage III-VI) females.

Mean size at Maturity

The mean length at maturity (Stage III and above) was 33.0 mm in *C. cumingi* and 31.5 mm in *B. nigrofasciatus* (Fig. 6). Mean maturity was reached at about 60% of the maximum length in *B. cumingi* and 54% of the maximum length in *B. nigrofasciatus*. The mean size at which the ovaries were at Stage IV (gravid ovaries) and higher was about 36 mm in both species (Fig. 6).

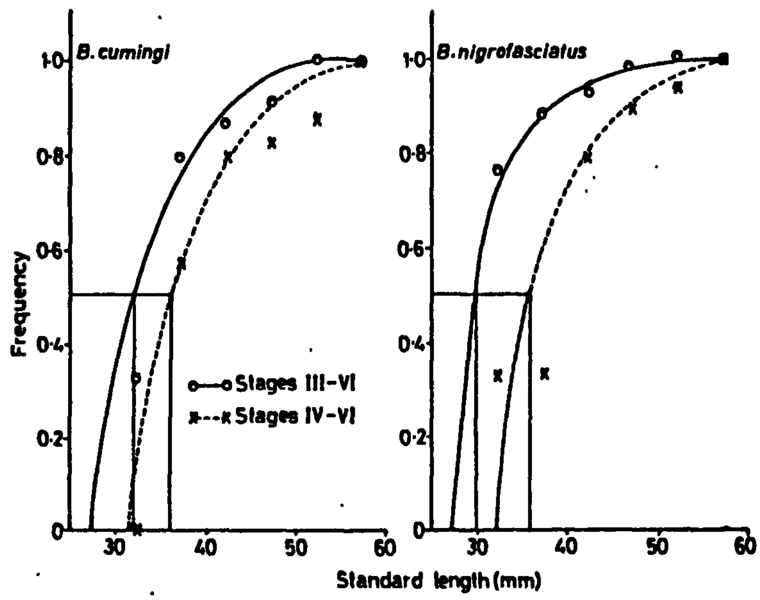

Fig. 6. The mean size at maturity of females and the mean size at which the ovaries reach the gravid stage.

Egg diameter distribution

Egg diameter distribution of Stage V ovaries of both species (Fig. 7) shows the presence of more than one mode. Since the batches of eggs continuously mature, it is difficult to estimate the range of diameter of the mature eggs. However, Fig. 7 shows that the mature eggs probably ranged in diameter from 600-950 µm.

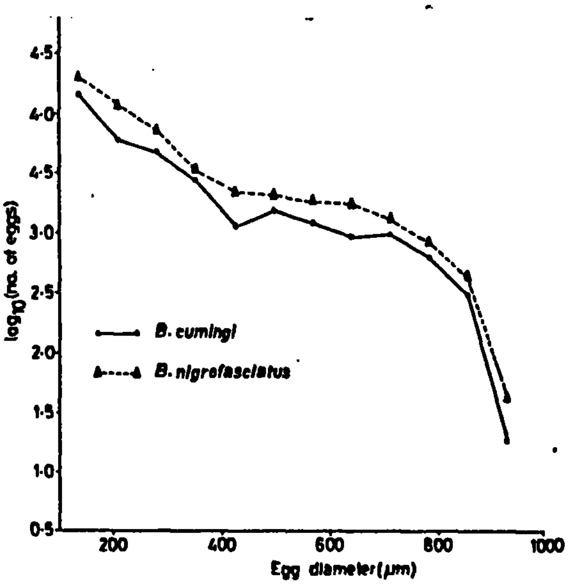

Fig. 7. diameter-frequency distribution of mature eggs.

Fecundity

Fecundity was estimated to vary from 120 to 766 in *B. cumingi* and from 126 to 894 in *B. nigrofasciatus*. (The lower limit of the fecundity was difficult to estimate because both species appear to lay eggs over a period of several days and it was sometimes difficult to distinguish between ovaries at Stage V (ready to spawn) and those at Stage V/VI (partially spawned)).

The relationships between the fecundity (F) and the total length (L) and fecundity and body weight (W) of the two species were calculated to be as:

B. cumingi $F=1.49\times10^{-3}L^{3.29}$ ($r^2=0.18$, $n=46$, $P<0.01$)
$F=276.73W^{1.18}$ ($r^2=0.34$ $n=46$, $P<0.01$)

B. nigrofasciatus $F=2.46\times10^{-3}L^{3.10}$ ($r^2=0.24$, $n=50$, $P<0.01$)
$F=271.38W^{0.78}$ ($r^2=0.18$, $n=50$, $P<0.01$)

These show that the relationship between the fecundity and body weight is more significant than that between the fecundity and the body length.

DISCUSSION

Reproductive Behaviour

The reproductive behaviour of both species agrees in general with what has been described by Kortmulder *et al.* (1978) and Kortmulder (1982) in populations of the river Gin. The habitats of the two streams in the present study differed from each other in that *Elodea canadensis* grew profusely in "Kahawaturu oya", whereas such submerged macrophytes were absent in "Sarasavi oya". Submerged macrophytes were also scarce in the habitats studied by Kortmulder *et al.* (1978) and Kortmulder (1982). *B. cumingi* spawned in very shallow water at the edge in all these streams. *B. nigrofasciatus*, however, displayed, courted and spawned mainly among the fronds of *E. canadensis* in Kahawaturu oya, although some courtship and spawning were observed in shallow water devoid of macrophytes. The top layers of *E. canadensis*, however, always remained only a few centimetres below the surface giving an apparent depth of only 5-10 cm. In Sarasavi oya, *B. nigrofasciatus* spawned in very shallow water at the edge of the stream, similar to the population in river Gin. Thus, it is apparent from the present study that *B. nigrofasciatus* prefers for spawning aquatic macrophytes to areas devoid of submerged macrophytes, whereas *B. cumingi* spawns at the edge of the stream in areas devoid of submerged macrophytes. Such habitat segregation for spawning of the two species have not been described earlier.

The spawning grounds of *B. nigrofasciatus* in rivers Gin and Kalu are reported as shallow water at stream bank screened from the main current, and that of *B. cumingi* as lateral waters and flooded banks (Schut *et al.*, 1984). It was also reported that *B. cumingi* is found below the flood level whereas *B. nigrofasciatus* is found above the flood level, thus achieving complete spatial segregation. Thus the observations of the present study are somewhat different to those of Schut *et al.* (1984).

Since *B. nigrofasciatus* fed in the shallow areas near the edge of the stream, and spawned in the mid stream among *E. canadensis*, and since the spawning activity was mostly limited to a time interval of a few hours of bright sunlight, there was a daily movement of the adult males and females from the feeding areas to the spawning areas and *vice versa*. Such movements involved, at the most, only a few meters. Juveniles and non-breeding adults seldom ventured into the breeding areas. Kortmulder *et al.* (1978) also observed daily movements of adults between feeding and spawning areas in the populations in rivers Gin and Kalu.

Reproductive Ecology

Breeding of tropical freshwater fish species could be seasonal, or continuous with or without peak activities in certain months (Welcomme, 1965; Lowe-McConnell, 1987). However, all indigenous carplets studied in Sri Lanka appear to breed throughout the year although, in most species, there appear to be breeding peaks in some months (de Silva & Kortmulder, 1977; Chandrasoma & de Silva, 1981; de Silva, Schut & Kortmulder, 1985).

Monthly fluctuations of the mean GSI and the non-seasonal occurrence of individuals with mature gonads as well as the small juveniles in the habitat indicate that both *B. cumingi* and *B. nigrofasciatus* breed throughout the year. These observations are somewhat different from those of Kortmulder (1987), who considers *B. cumingi* as a seasonal spawner but *B. nigrofasciatus* as a continuous spawner.

The general lowering of the GSI during rainy months, which is especially clear in *B. cumingi* (Fig. 4), indicates increased breeding of both species during that period. This agrees well with the observations of De Silva *et al.* (1985), according to which the peak breeding activities of both species, especially that of *B. cumingi*, in rivers Kalu and Gin are related to the rainy season.

Spawning cycles of fish are adapted to climatic and environmental conditions (Billard et al. 1981). In tropical countries such as Sri Lanka, the temperature and the photoperiod remain high throughout the year (except at high elevations) with only minor seasonal changes. On the other hand, rainfall could change widely over the months. Breeding of many tropical freshwater fish species are known to be related to rainfall (Welcomme, 1965; Lowe-McConnell, 1987).

It has also been shown that different species inhabiting the same stream may have seasonal differences in spawning, some spawning in the dry season, some in the rainy season and some throughout the year (Kramer, 1978). However, all the carplets studied in Sri Lanka appear to breed throughout the year although, in most species, well marked breeding peaks occur during the rainy season(s) (De Silva & Kortmulder, 1977; Chandrasoma & De Silva, 1981; De Silva *et al.* 1985).

During the rainy season, a water body could expand and inundate the nearby low-lying areas providing shallow areas with vegetation suitable for nest-building, egg-laying and the development of eggs and larvae. This is specially so in shallow lakes and irrigation reservoirs. For instance, Chandrasoma & De Silva (1981) showed that although *B. Sarana* spawns throughout the year in Parakrama Samudra reservoir, it has a clearly marked breeding peak during the rainy season. Similarly, the spawning of reservoir-dwelling snakeheads such as *Channa marulius*, *C. punctatus*, and *C. striata* in Sri Lanka is associated with rainy season (K. H. G. M. de Silva, unpublished data). However, for small fish species living in hill streams, there are several disadvantages for breeding during the rainy season. These include the damage to eggs and loss of eggs and larvae owing to the high flow conditions, high turbidity of water and damage to the habitat vegetation. On the other hand, when the rains were low, water flow is moderate, water remains clear and the aquatic vegetation shows luxuriant growth. Thus, spawning during the less-rainy season has more advantages for spawning. Therefore, it is difficult to explain why the two species show enhanced breeding during the rainy season. It may be that they move into sheltered areas during high flow. It is also noteworthy the view that the two species have recently been introduced into the streams of Mahaweli (Wikramanayake, 1990), in which case one may speculate that the two species are not yet adapted fully to the conditions of the streams.

The deviation of the sex ratio from the expected ratio of 1.0, as has been observed in the present work in both *B. cumingi* and *B. nigrofasciatus*, has also been observed in populations of several other cyprinids.

Preponderance of females was observed in *B. sarana* in the Parakrama Samudra reservoir (Chandrasoma & De Silva, 1981) but males predominated in *B. vittatus* in the river Kalu (De Silva, Schut & Kortmulder, 1985). However, De Silva *et al.* (1985) reported a male to female ratio was closer to 1.0 in *B. bimaculatus*, *B. titteya* and *B. dorsalis* as well as in *B. cumingi* and *B. nigrofasciatus*.

Change of sex ratio with length is known in several species and has been attributed to differential growth and/or maturity of males and females (Nikolskii, 1965; De Silva, Schut & Kortmulder, 1985). The higher percentage of females indicates either a higher mortality rate or lower growth rate or both of males since the sex ratios of initial size classes are not significantly different from 1.0. The increase of the proportion of females in the higher size classes of *B. cumingi* could be explained if the mortality of males are higher than that of females or the growth rate of males are lower (or both). The sex ratio of less than 1.0 of the size class of 21-25 mm of *B. nigrofasciatus* is difficult to explain. It may be that the males have a higher mortality rate and a higher growth rate so that the proportion of males in the lower size classes was less than that of females. De Silva *et al.* (1985) also found preponderance of females in the higher length classes of *B. cumingi* similar to the observations reported here. However, in *B. nigrofasciatus*, contrary to the observation in the present study, they observed a sex ratio closer to 1.0 in lower length classes with a preponderance of males in the higher classes. Such deviations in different populations of the same species could be due to prevailing environmental conditions. Among *Barbus* species, preponderance of females in higher size classes has been observed in populations of *B. bimaculatus*, *B. dorsalis*, *B. vittatus* (De Silva, Schut & Kortmulder, 1985), *B. sarana* (Chandrasoma & De Silva, 1981) and *B. stigma* (Qayyum & Qasim, 1964), but in *B. titteya*, there were more males than females in the higher size classes (De Silva et al. 1985).

Multiple peaks in the egg diameter-frequency distribution suggest that both species are multiple (or batch) spawners in which successive batches of eggs become mature as the previous ones are released. When one batch of eggs is at Stage V and ready to be ovulated the next batch is already at Stage III or higher so that batches of eggs can be released at frequent intervals. High percentage of females at Stage IV-VI (Fig. 3) and the high numbers of individuals observed in spawning grounds also indicate that adult individuals come to spawn frequently. Stage V females of similar length showed widely varying fecundities. This may be because all mature eggs are not released at a single occasion but are released over a several days. Therefore, both species are serial spawners.

ACKNOWLEDGEMENTS

We are very grateful to Prof. H. H. Costa of Department of Zoology, University of Kelaniya for his careful reading of the manuscript and very valuable suggestions. We are also thankful to Mr T.S.B. Alagoda of Department of Zoology, University of Peradeniya, for preparing the figures.

REFERENCES

BILLARD, R., BRY, C. & GILLET, C. 1981. Stress, environment and reproduction in teleost fish. In: A. D. Pickering (ed.) Stress and Fish, Academic Press, London. 185-208.

CHANDRASOMA, C. & DE SILVA, S. S. 1981. Reproductive biology of *Puntius sarana*, an indigenous species, and *Tilapia rendalli*, an exotic, in an ancient man-made lake in Sri Lanka. Fish Manage., 12: 17-28.

DE SILVA, S. S. 1983. Reproductive strategies of some major fish species in Parakrama Samudra reservoir and their possible impact on the ecosystem - a theoretical consideration. In: Schiemer, F. (ed.) Limnology of Parakrama Samudra - Sri Lanka. W. Junk, The Hague. 185-191.

DE SILVA, S.S. & KORTMULDER, K. 1977. Some aspects of the biology of three species of Puntius *(=Barbus)* (Pisces, Cyprinidae), endemic to Sri Lanka. Neth. J. Zool., 27 (2): 182-194.

DE SILVA, S.S., SCHUT, J. & KORTMULDER, K. 1985. Reproductive biology of six *Barbus* species indigenous to Sri Lanka. Environmental Biology of Fishes, 112 (3): 201-218.

IUCN, 1988. 1988 IUCN red list of threatened animals. IUCN Conservation Monitoring Centre, Gland. 72-83.

KORTMULDER, K. 1987. Ecology and behaviour in tropical freshwater fish communities. Arch. Hydrobiol. Ergebn. Limnol. 28: 503-513.

KORTMULDER, K. FELDBRUGGE, E.J. & DE SILVA, S.S. 1978. A combined field study of *Barbus (=Puntius) nigrofasciatus* Günther (Pisces; Cyprinidae) and water chemistry of its habitat in Sri Lanka. Neth. J. Zool., 28: 111-131.

KRAMER, D.L. 1978. Reproductive seasonality in the fishes of a tropical stream. Ecology 59: 976-985.

LOWE-McCONNELL, R.H. 1987. Ecological studies in tropical fish communities. Cambridge University Press, Cambridge. 381 pp.

NIKOLSKII, G.V. 1963. The Ecology of fishes. (Translated from Russian) Academic Press, London. 352 pp.

NIKOLSKII, G.V. 1965. Theory of fish population dynamics, as the background for rational explanation and management of fishery resources. (Translated from Russian). Oliver & Boyd, Edinburgh. 320 pp.

QAYYUM, A. & QASIM, S.Z. 1964. Studies on the biology of some freshwater fishes. II. *Barbus stigma* (Cuv. & Val.). J. Bombay Nat. Hist. Soc., 61: 330-344.

SCHUT, J., DE SILVA, S.S. & KORTMULDER, K. 1984. Habitat associations and competitions of eight *Barbus (=Puntius)* species (Pisces, Cyprinidae) indigenous to Sri Lanka. Neth. J. Zool., 34 (2): 159-181.

WELCOMME, R.L. 1985. River fisheries. FAO Fisheries technical paper 262. 330 pp.

WIKRAMANAYAKE, E.D. 1990. Conservation of endemic rain forest fishes of Sri Lanka: Results of a translocation experiment. Conserv. Biol., 4: 32-37.