Habitat preference, reproduction and diet of the earthworm eel, *Chendol keelini* (Teleostei: Chaudhuriidae)

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Synopsis

The ecology of the earthworm eel, *Chendol keelini*, was studied in the field over a period of nine months. In addition this information was supplemented by aquarium observations. The species was most abundant in pools where it was associated with leaf litter and mats of fine tree roots along the banks. It fed on benthic invertebrates, especially chironomid and ephemeropteran larvae. *C. keelini* is sexually dimorphic; adult males develop a headhump and grow to a larger size than females. Reproduction was seasonal; the reproductive phase coincided with the wet season and lasted for several months. Fecundity was around 40 eggs per clutch. The eggs were spherical, between 1.2 and 1.5 mm in diameter, and possessed a pair of long filaments for adhesion to the substrate. Females probably spawned more than once during the breeding season. The length frequency distributions and juvenile growth suggest that *C. keelini* is a short-lived species that matures during the first year with few individuals surviving to the second breeding season.

Introduction

Earthworm eels (Synbranchiformes, Mastacembeloidei, Chaudhuriidae) are tiny, eel-like fishes endemic to the freshwaters of Southeast Asia. The family currently contains seven species in five genera: *Chaudhuria*, *Pillaia*, *Nagaichthys*, *Chendol* and *Bihunichthys* (Kottelat & Lim 1994). Chaudhuriids are known to occur in northeastern India, Burma, Thailand, Cambodia, Laos, Vietnam, Malaysia, and western Indonesia (Annandale 1918, Prashad & Mukerji 1929, Roberts 1971, 1980, Yazdani 1972, 1975, Talwar et al. 1977, Kottelat 1985, 1991, Rainboth & Kottelat 1987, Kottelat et al. 1993, Kottelat & Lim 1994, Tan & Tan 1994). In the Sundaic region, the family was not discovered until 1985, indicating that earthworm eels are both

rare and easily overlooked in ichthyological surveys. To date, work on this group has been restricted to taxonomic descriptions and phylogenetic studies (Regan 1919, Annandale & Hora 1923, Yazdani 1978, Travers 1984). What is known about the ecology of chaudhuriid fishes mainly comes from short comments made in the original descriptions or in faunal surveys. Most specimens have been collected from small forest creeks and swamps, common habitats are shallow standing or slow flowing waters. At least one species, *Bihunichthys monopteroides*, seems to be restricted to the highly acidic black waters in peat swamp forests (Ng et al. 1994). Earthworm eels are typically found in the bottom substrate, like leaf litter, or among dense aquatic vegetation (Kottelat & Lim 1994). Yazdani (1975) kept specimens of *Pillaia indica* in the aquarium for a short
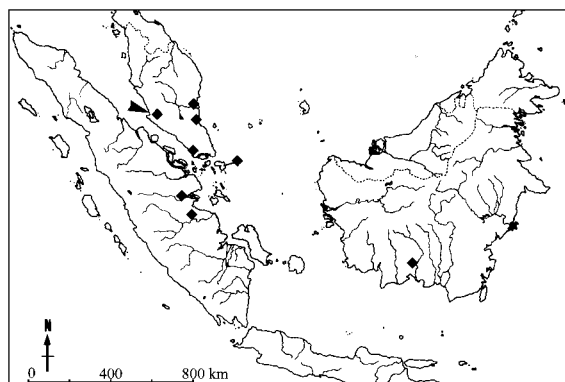
Figure 1. Distribution of *C. keelini* in Sundaic Southeast Asia. Arrow head indicates the location of the study site (for coordinates see material and methods) in the state of Selangor, Malaysia.

while and commented that the fish were very inactive and mostly spent their time lying on the bottom either buried in mud or clinging to submerged vegetation.

Annandale (1918) reported that the stomach of a specimen of *Chaudhuria caudata* was full of small crustaceans. The diet of *Pillaia indica* has been found to consist of aquatic insect larvae, especially chironomids and ephemeropterans (Yazdani 1978, Majhi & Dasgupta 1989).

Freshwater swamps and peat swamp forests, the prime habitats of earthworm eels, are among the most threatened ecosystems in Southeast Asia (Ng et al. 1994, Dudgeon 1995). Habitat loss combined with the lack of knowledge about the distribution and biology of chaudhuriids raises concern about the conservation of this little known family. The good accessibility of the type locality of *Chendol keelini* provided an opportunity to study the ecology of a member of the Chaudhuriidae. *C. keelini* is one of four species of chaudhuriid fishes described from Malaysia, Sumatra, and Borneo in the 90s (Kottelat 1991, Kottelat & Lim 1994). It is known from the south of the Malay peninsula, the east coast of Sumatra; and a single specimen was recorded from Borneo (Figure 1). The objectives of the present study are to describe aspects of the ecology and outline the life cycle of *C. keelini*.

Materials and methods

The study site

Field work was performed at the type locality of *C. keelini* in the state of Selangor on the Malay Peninsula, approximately 30 km north-west of the Malaysian capital Kuala Lumpur (3°20'N, 101°29'E). The area lays within the drainage system of the Selangor River, which drains into the straits of Malacca. The wet season on the west coast of the Malay Peninsula typically lasts from October through December with a second shorter peak of rainfalls around April (Dobby 1964). The region used to be characterised by extensive lowland swamps, but industrial and agricultural development (oilpalm and rubber tree plantations) have changed it significantly in recent years. The study site is a small, low gradient stream inundating a remnant pocket of freshwater swamp forest with dense vegetation. *Gynotroches axillaris* (Rhizophoraceae) is the most abundant tree in the swamp forest.

Fish collections were made along a 1.5 km transect close to the source of the creek. The slow flowing creek is approximately 1 m wide and 20 cm deep, except for several deeper pools. Numerous small backwaters and shallow isolated pools make for an extremely heterogenous aquatic habitat. The ground is covered by a layer of leaf litter and peat with the substrate below consisting of very soft mud.

Field methods

Nine sampling trips were made in approximately monthly intervals from August 1997 to April 1998. Fish were collected with a hand-held dip net (62 × 52 cm square frame) with a double layer of fine mesh (2 mm mesh size). The net was either held at an angle to the bank while the vegetation was disturbed by trampling, or the leaf litter and soft substrate was scooped into the net. The organic matter in the net was then washed and searched carefully.

Immediately after capture, the total length (TL) of specimens was measured with a ruler. The presence of ripe ovaries in females was noted. The girth of such females is significantly increased and the oocytes can be seen through the abdominal wall. The habitat type was recorded (e.g. run, pool, backwater or off-channel), and the dominant cover substrate was noted (e.g. leaf litter, tree roots, woody debris, aquatic vegetation, submerged grass). An effort was made to sample all habitat types according to their abundance at the site.

On the first three field trips, specimens were kept alive and returned to aquarium facilities at the National University of Singapore to establish a captive stock. Fish caught at each sampling trip were kept in separate

glass tanks. The maximum stocking density was 24 specimens in a 50 l tank.

From October onwards fish were preserved in 10% formalin immediately after capture for dietary studies. Fish were transferred to 70% ethanol solution after 2 days. Water temperature, pH and conductivity were measured at the same location between 9:00 and 10:30 h on each sampling day.

Laboratory methods

Length-frequency histograms were constructed for each sampling trip. The formalin preserved fish were dissected and the sex was determined by gonad inspection. Large gonads were readily distinguishable as ovaries or testes. For small gonads, tissue samples were examined under a microscope with $100\times$ magnification. The diameter of all oocytes in ripe ovaries was measured under a stereomicroscope with $20\times$ magnification. Fecundity was recorded by direct counting of vitellogenic oocytes in the entire ripe ovaries of females. Ripe ovarian eggs were also observed and photographed using a scanning electron microscope following the procedure described in Britz et al. (1995).

The stomach contents of 88 animals were analysed. The alimentary canals were removed and the contents squeezed onto a convex microscopic slide. A semipermanent glycerine mount was prepared. The gut contents were examined under a stereomicroscope with variable magnification up to $20\times$. The food items were identified to the lowest possible taxon level and counted. Head capsules were used to count the number of insect specimens. Analysis was performed by size groups using two methods: (1) numerical occurrence, where the number of each food type is expressed as a percentage of the total number of food items in all examined stomachs; and (2) frequency of occurrence, where the number of stomachs in which each item occurred is expressed as a percentage of all non-empty stomachs (Hyslop 1980).

Results

Habitat

Physico-chemical conditions and water levels at the study site fluctuated only slightly between the dry and wet season. Extensive flooding did not occur over a prolonged period. Water temperature in the creek varied between 24° and 27°C, pH between 5.8 and 6.8 and conductivity between 17.0 and 24.0 μS cm^{-1}, respectively. Rainfall and temperature data from the meteorological station in Subang, 25 km south of the study site, are presented in Figure 2.

C. keelini typically occurred in pools, where the fish where found among mats of tree roots along the banks or inside the layer of leaf litter. Habitat preferences and preferred cover substrates are shown in Tables 1 and 2.

Pools were the preferred habitat type in all size classes, 72.6% of all animals were collected from pools.
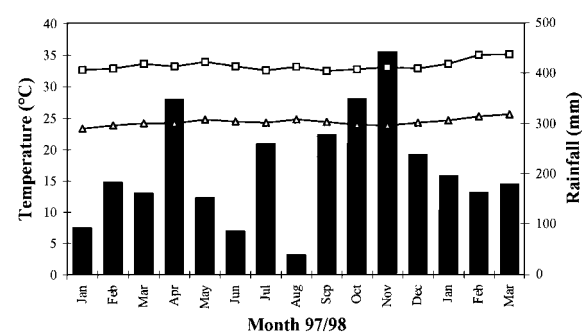
Figure 2. Monthly rainfall (bars) and mean minimum and maximum air temperatures (lines) at the meteorological station in Subang, 25 km south of the study site.

Table 1. Percentage utilisation of different habitats by *C. keelini* at the study site in Selangor.

Habitat type	Size group (mm)					Total
	≤22	23–32	33–42	43–52	≥53	
Pool	60.0	72.7	71.8	77.8	75.9	72.6
Run	15.0	21.2	23.1	16.7	17.2	19.1
Backwater	25.0	6.1	5.1	5.6	6.9	8.3
Off-channel	—	—	—	—	—	—
No. specimens	20	33	39	36	29	157

Table 2. Percentage utilisation of different cover substrates by *C. keelini* at the study site in Selangor.

Cover type	Size group (mm)					Total
	≤22	23–32	33–42	43–52	≥53	
Leaf litter	50.0	30.3	35.9	30.6	34.5	35.0
Tree roots	40.0	66.7	56.4	63.9	58.6	58.6
Woody debris	5.0	—	7.7	2.8	6.9	4.5
Aquatic vegetation	5.0	3.0	—	—	—	1.3
Submerged grass	—	—	—	2.8	—	0.6
No. specimens	20	33	39	36	29	157

In all but the smallest size class significantly more animals were found in pools than in all other habitats combined ($\chi^2 = 5.9$; 6.6; 6.6; 10.0; 6.7 for the four largest size classes respectively; 1 df; $p < 0.05$ in all classes).

The fish were less abundant in the faster flowing areas of the creek and in backwater habitats. The percentage utilisation of backwater habitats by the smallest size class was significantly higher compared to the rest of the animals ($\chi^2 = 5.8$; 1 df; $p < 0.05$).

No specimen of *C. keelini* was ever found in an off-channel habitat, whereas other species, namely some small cyprinids and fighting fishes were common in these shallow stagnant ponds without connection to the main channel.

Over 90% of all animals were found associated with either tree roots or leaf litter as the dominant cover substrate (Table 2). Fine tree roots were the preferred cover for all size classes except the smallest. Other types of cover were rarely used.

Bundles of fine tree roots, which were brought back from the field, were offered as hiding substrates in the aquarium and were readily accepted. The fishes were usually so closely associated with them that the bundles could be lifted out of the water with the animals remaining inside. Hidden among the roots, the fishes stayed motionless throughout most of the day.

Reproduction

A total of 181 fish was collected during the study, measuring between 12 and 57 mm in standard length. The sex of 127 specimens was determined by gonad inspection. The sex ratio of males : females was 1 : 1.27. The observed sex ratio showed no statistically significant deviation from an expected 1 : 1 ratio ($\chi^2 = 1.54$, 1 df; $p > 0.05$).

Chendol keelini is a sexually dimorphic species. The majority of adult males had a conspicuous hump on the forehead (Figure 3). No such hump was ever observed in females. Dissection showed that the feature is caused by an enlargement of the adductor mandibulae muscle. The headhump was found in all males exceeding a standard length of 47 mm, with the exception of two specimens collected on the last trip in April, in which it was missing. Of the aquarium specimens, only one animal had a headhump when it was collected in the field, but 6 out of 12 males developed a hump in captivity between September and November.

Males also grew to a larger size than females. The mean standard length (SL) of the ten largest males and females from the field was 53.6 mm (± 3.0 mm) and 50.5 mm (± 2.4 mm), respectively (T-test: t = 8.907, 9 df; $p < 0.01$). The largest male specimen measured 57 mm SL, the largest female 55 mm SL.

In the field, females reached maturity at 43 mm SL. Ripe ovaries were found in three specimens of this size, but no smaller females were found with ripe ovaries. Well developed male gonads were not found in specimens smaller than 47 mm SL.

Mature ovaries of *C. keelini* are large, unpaired structures occupying the greater part of the body cavity. Two distinct populations of oocytes are present in the ovaries at this stage (Figure 4). Oocyte development
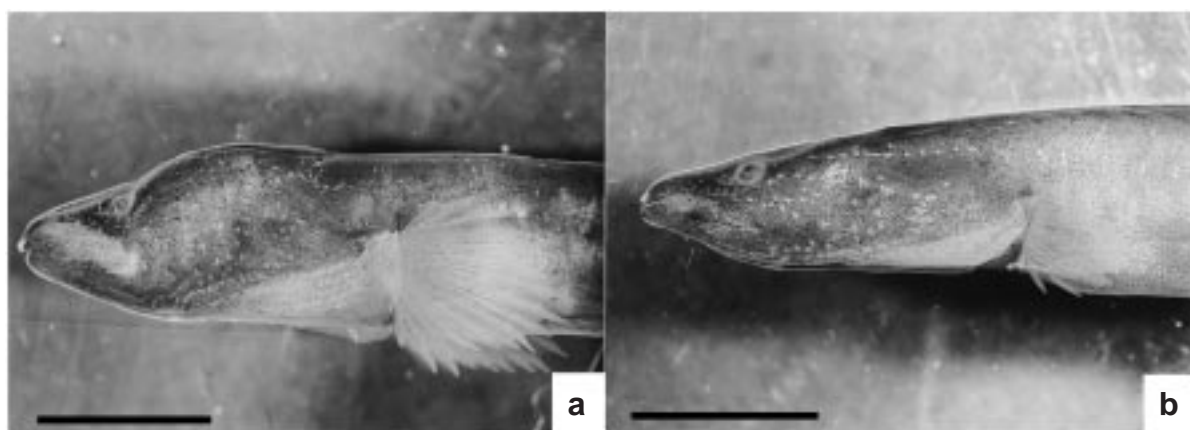

Figure 3. Head profiles of an adult male (a) and female (b) of *C. keelini*, showing the sexual dimorphism. A hump is developed on the forehead of the male (scale bars = 4 mm).

is thus following the group synchronous mode (de Vlaming 1984). The large (ca. 0.8–1.5 mm diameter), vitellogenic oocytes are almost spherical, translucent, yellow in colour, and seem well supplied with yolk. A second group of white, non-vitellogenic and smaller
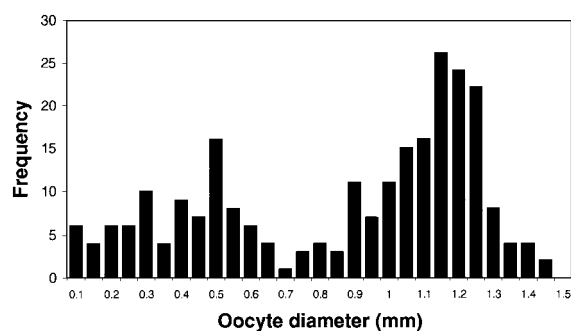

Figure 4. Oocyte size distribution in ripe ovaries of *C. keelini* (N = 6).

(ca. 0.1–0.6 mm diameter) oocytes lies interspersed between the larger eggs and probably presents the next clutch. The number of vitellogenic oocytes in ripe ovaries ranged from 20 to 58. The mean clutch size of 14 ripe ovaries was 41.4 ± 13.6. Standard length of fish and clutch size were positively correlated (r = 0.67; p < 0.05).

The surface of ripe eggs is covered by a pair of long filaments originating with anchor-shaped bases in close proximity to each other on the vegetal pole (Figure 5). These filaments get entangled in the substrate upon spawning and thereby attach the eggs to the substrate. The micropyle on the opposite pole belongs to type II of Riehl & Götting's (1974) classification, which is characterised by a shallow micropylar pit (Figure 5c). The entire egg surface is covered by granular structures about 1–1.5 μm in diameter.

A female in the aquarium spawned in early November. A total of 42 eggs were laid in a loose
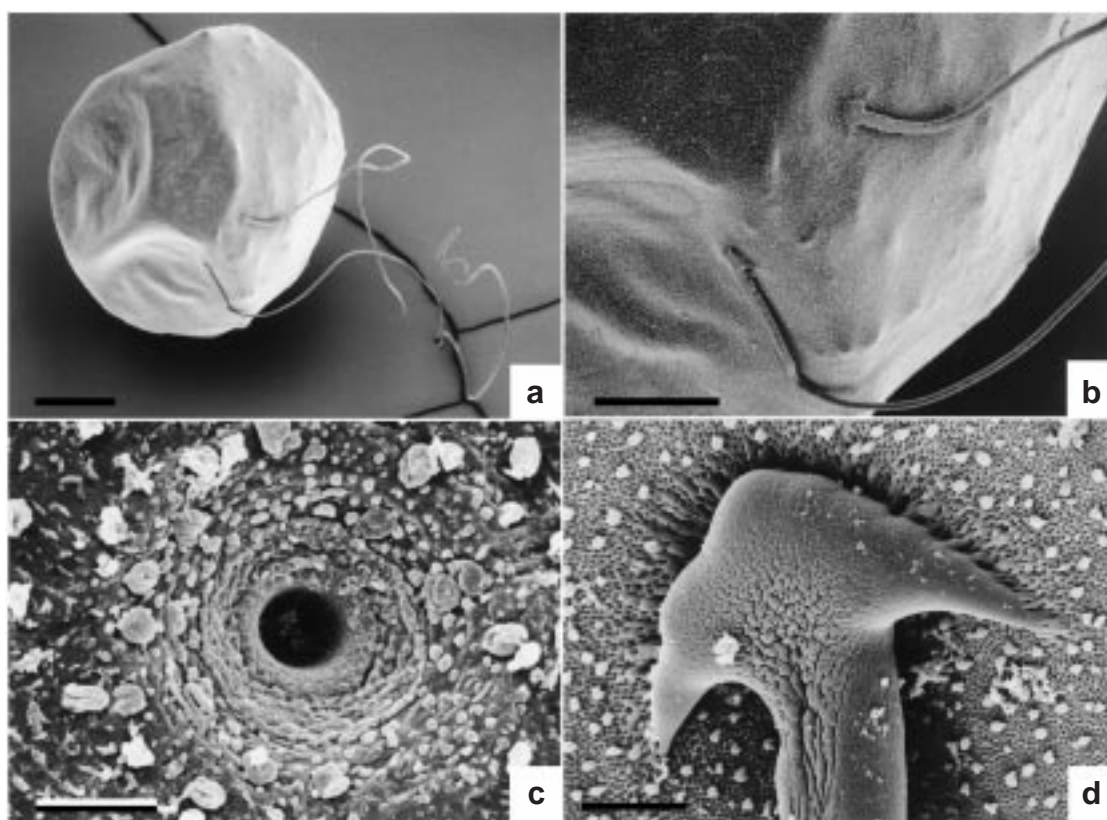

Figure 5. SEMs of ripe eggs from the ovary of *C. keelini*: a – whole egg showing the insertion of the two filaments in close proximity to each other, b – proximal part of filaments, c – micropyle, d – anchor-shaped base of filament on egg surface (scale bars: a = 200 μm, b = 100 μm, c = 4 μm, d = 10 μm).

clump attached to a leaf and some woody debris on the bottom of the tank. Eggs ranged in diameter between 1.2 and 1.5 mm with a mean of 1.38 ± 0.08 mm. None of the eggs showed any signs of development, and this remained the only spawning event noticed in the aquarium. No sign of parental care of the egg clutch was observed. Several other females developed ripe ovaries during September and October, but they did not spawn and dissections later showed that the eggs had become atretic or were absorbed.

Reproduction in the field coincided with the wet season from October to December. Females with ripe ovaries were present from September to December with the addition of a single ripe female collected in April. The length-frequency distributions revealed a pronounced temporal aspect in the structure of the population (Figure 6). During the first half of the study until December the population was dominated by animals in the 35 mm size class or larger, except for a single juvenile specimen in the 25 mm class collected in August. In December two juveniles were collected, and in January a large number of juveniles was suddenly present. After January two distinct cohorts were recognisable. After it appeared, the cohort of juveniles dominated the population while adult animals were less abundant from January onwards. Besides the difference in size, the two cohorts could also be distinguished in the pigmentation and general condition of the skin. In large specimens the skin was lighter, often covered with numerous scratches of abraded epidermal areas. These were supposedly effects of senescence.

Figure 7 shows the growth in the cohort of juveniles from January to April. Juvenile growth during this time was adequately described by a linear regression line ($r^2 = 0.999$). When time is plotted in days starting from the 1st of December on the X-axis, the equation for the regression line is given as $y = 0.1139x + 18.967$. Thus, if it is assumed that growth continues at the same rate, adult size would be reached during the first year of life.

Diet

All except one of the stomachs analysed contained at least one prey item. A total of 264 items were identified and assigned to seven different prey groups.

C. keelini is a carnivorous species feeding on aquatic invertebrates. Chironomid larvae were the major prey source, followed by ephemeropteran larvae. These two groups comprised the bulk of the diet. Remains of chironomid and ephemeropteran larvae were found in 79.3% and 43.7% of all non empty stomachs, respectively. The numerical occurrences of the different food types are shown in Table 3. Size related shifts in diet were not apparent, animals in all size groups predominantly fed on the two prey sources mentioned above. However, both chironomids and ephemeropterans were found in a considerable range of different sizes, and the stomachs of fish in the smallest size class contained only small insect larvae. Less important groups of prey included culicid larvae, aquatic coleopterans and their larvae, ostracods and cladocerans.

In captivity *C. keelini* readily accepted live and frozen chironomid larvae (blood worms). When food was placed in a tank, the fish slowly appeared from their shelters and started to search the bottom of the aquarium. Upon locating a prey item they stopped and remained motionless for a short while, then quickly sucked in the worm and shook their heads or whole bodies vigorously. A fish normally took about two to four worms at a time before retreating to a shelter.

Discussion

Chenol keelini is a fossorial species. At the study site, it was most common in the deep pools of the stream, where mats of fine tree roots hung into the water and thick layers of leaf litter had formed. Conditions seemed to be less optimal in run and backwater habitats, and animals completely avoided off-channel habitats with shallow stagnant water. Large scale shifts in the utilisation of habitats between different phases of the life cycle seemed not to occur, although the proportion of animals found in backwater habitats was larger in the smallest size class.

While the lower abundance of animals in areas with swift current might be primarily due to the lack of a suitable cover substrate, backwaters and isolated ponds may be less optimal habitats due to oxygen deficiency and strong temperature fluctuations. Air breathing is known to occur in other synbranchiform fishes and was suggested for *P. indica* by Pardhasaradhi & Alfred (1981), but it was not observed for *C. keelini* during the present study, neither in the field nor in the aquarium.

Aquarium observations of *C. keelini* were very similar to those made by Yazdani (1975) for *P. indica*, both species seem to be very inactive animals that remain almost motionless for long periods. Such a behaviour seems to be common for small cryptic teleosts. Studies on fish communities in Amazonian blackwaters
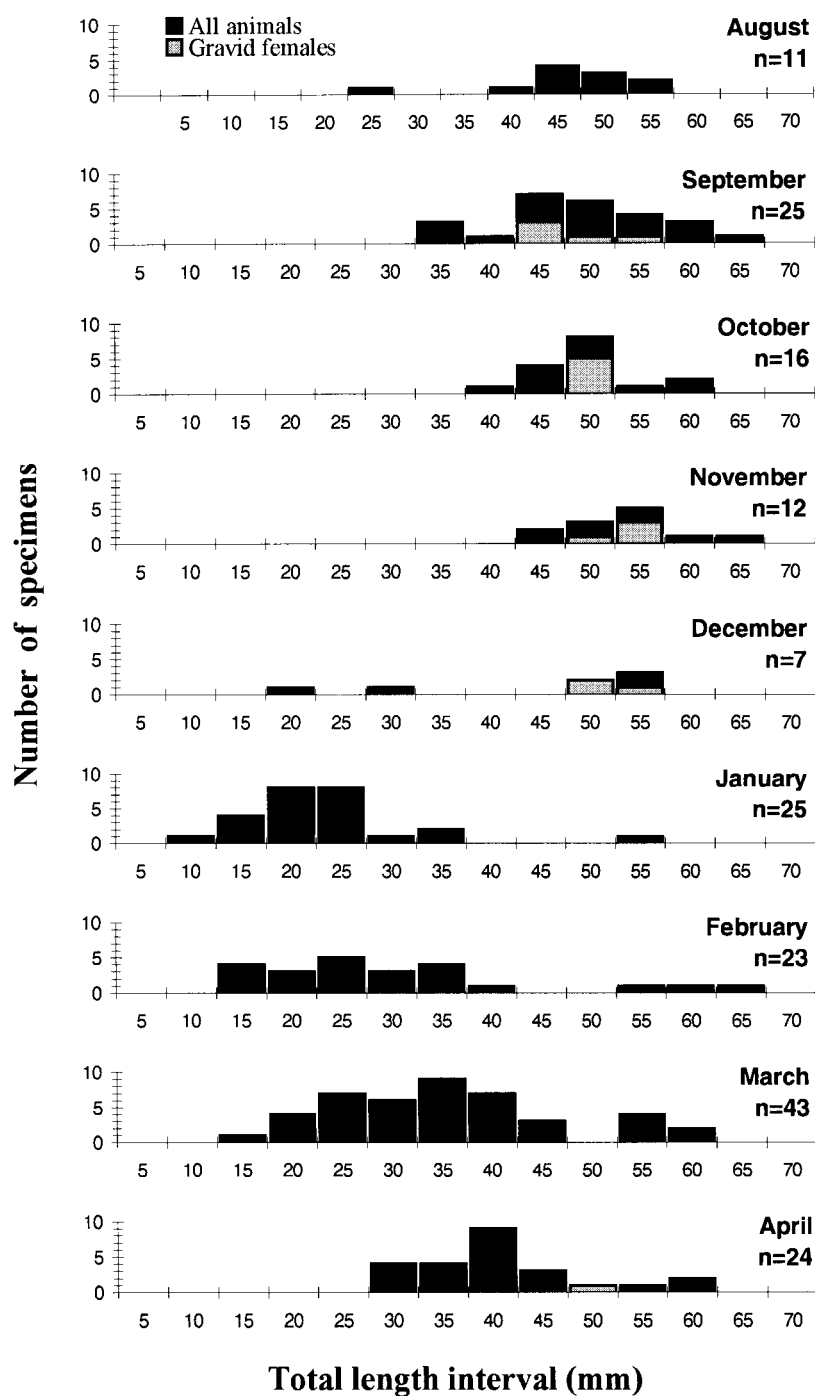
Figure 6. Length-frequency histograms for *C. keelini* during nine months in 1997/1998 at the study site in Selangor.
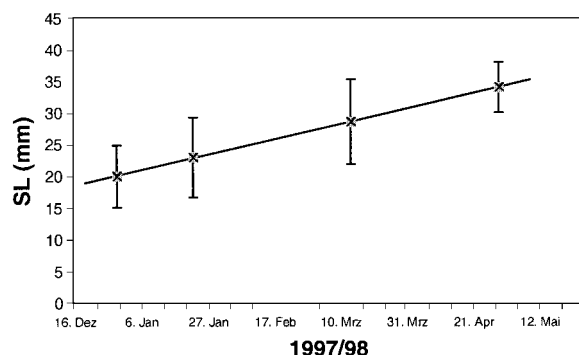
Figure 7. Mean standard lengths of juvenile *C. keelini* emerged during the wet season showing the growth of the new cohort during four months (linear regression $R^2 = 0.99$).

Table 3. Percentage numerical occurence of different prey items in the diet of *C. keelini* at the study site in Selangor.

Food type	Size group (mm)					Total
	≤ 22	23–32	33–42	43–52	≥ 53	
Chironomidae	58.1	79.7	86.4	53.1	57.9	67.8
Culicidae	—	—	—	3.1	3.5	1.1
Ephemeroptera	27.4	13.0	11.4	34.4	22.8	20.8
Coleoptera	3.2	—	—	—	7.0	2.3
Unid. insects	1.6	1.4	—	—	7.0	2.3
Ostracoda	9.7	5.8	2.3	—	1.8	4.5
Cladocera	—	—	—	9.4	—	1.1
No. stomachs	22	24	14	9	18	87

showed that the majority of the small benthic fishes living inside the leaf litter were static and remained within a one meter radius for several weeks (Henderson & Walker 1990).

Chendol keelini is a predatory species. The diet consisted almost entirely of benthic invertebrates with the cover substrates providing not only shelter but food.

Juveniles and adults share the same prey and the species seems to exhibit little feeding specialisation. Chironomid and ephemeropteran larvae, the main prey of *C. keelini*, belong to the most abundant macroinvertebrates in small tropical streams (Bishop 1973, Angermeier & Karr 1983). Benthic invertebrates seem to constitute a vast food resource for small fishes in tropical streams. Henderson & Walker (1986) reported that almost all of the 20 small species living in the leaf litter of a South American blackwater stream fed on benthic invertebrates. Mizuno & Furtado (1982) studied the food habits of 21 species of fish from Tasek Bera, a freshwater swamp forest in Peninsular Malaysia. They found that a large group consisting of 11 small species fed on aquatic insects, especially chironomid larvae. Competition for this resource seems to be limited.

The spawning season of *C. keelini* coincided with the period of highest rainfall from October to December. The presence of ripe females just prior to and during the wet season was followed by the emergence of a new cohort of juveniles from December onwards. Some spawning also seemed to occur outside the main season, interestingly coinciding with the second peak of rainfall in April. Spawning during the wet season is found in a large number of freshwater fish in the tropics. The adaptive advantages of different reproductive styles in tropical freshwater fishes have been discussed by several authors (Kramer 1978, Winemiller 1989, Lowe-McConnell 1979, 1987, Munro 1990). Seasonal reproduction is generally considered as an adaptation to seasonal variations in habitat quality and food availability for the offspring, but the importance of biotic pressures such as predation, may also be important. The long period during which ripe females were found, the group synchronous oocyte development, and the large size differences in the cohort of juveniles are indications that each female spawns more than once during the reproductive season. Without further knowledge about the periodicity of spawning, fecundity estimates are difficult. Compared to many other flood spawning teleosts, the number of ripe eggs in the ovaries is relatively low (Lowe-McConnell 1987). Such a low clutch fecundity is considered a general constraint of small size in teleosts (Roff 1992). The fact that in many small fishes individuals tend to spawn several times in a season might be interpreted as an attempt to maximise overall female fecundity. Another advantage of this style is probably that, by breeding over a prolonged period, each individual also maximises the chance that at least one spawning occurs when conditions for the offspring are optimal (Munro 1990).

Spawning in seasonally breeding teleosts is often dependent on certain environmental cues. In tropical species which reproduce during the wet season, changes in flood regime and water chemistry are the most important factors inducing spawning (Kirschbaum 1984, Munro 1990). The lack of such cues in the aquarium might have prevented the majority of fish from spawning.

Chendol keelini is a substrate spawner with large demersal eggs that are attached to the substrate with

a pair of long filaments. Whether it exhibits any form of parental care is currently not known. Eggs of other chaudhuriids, namely those of *Chaudhuria caudata* and *Bihunichthys monopteroides*, also posses two long filaments (personal observation), and this character may constitute an autapomorphy of the Chaudhuriidae.

The biological role of the enlarged adductor mandibulae muscle causing a head hump in males is unclear. A strong jaw musculature could obviously be advantageous during territorial and courtship fights. Further aquarium observations on the reproductive behaviour are necessary to reveal its actual role.

Measures of absolute abundance were beyond the scope of this study. However, the relative abundance of adult animals quite drastically declined during the latter part of the study. Juvenile growth data further indicate that *C. keelini* reaches mature size within the first year of life. A likely interpretation of these findings is that *C. keelini* is a short-lived species that reproduces only during one season. Most individuals do not survive to the breeding season of the following year. If our interpretation is correct, *C. keelini* has a simple life cycle. Animals use the same habitat and food resources throughout life, start reproducing soon after maturity is reached and then continue to reproduce for a short while before they die. Such a pattern would correspond well with that described by Munro (1990), who found that many small-sized freshwater fishes in the tropics are short-lived, partial or small brood spawners with a prolonged breeding season or aseasonal reproduction.

Along with its dependence on special habitats, the short life cycle, absence of dispersal stages like floating eggs or free swimming embryos and larvae, could all be causes for the rarity and patchy distribution of *C. keelini*, and make this species susceptible to extinction.

Acknowledgements

References cited

Angermeier, P.L. & J.R. Karr. 1983. Fish communities along environmental gradients in a system of tropical streams. Env. Biol. Fish. 9: 117–135.

Annandale, N. 1918. Fish and fisheries of the Inle Lake. Rec. Indian Mus. 14: 33–64.

Annandale, N. & S.L. Hora. 1923. The systematic position of the Burmese fish *Chaudhuria*. Ann. Mag. Nat. Hist. 11: 327–333.

Bishop, J.E. 1973. Limnology of a small Malayan river, Sungai Gombak. Dr W. Junk Publishers, The Hague. 485 pp.

Britz, R., M. Kokoscha & R. Riehl. 1995. The anabantoid genera *Ctenops*, *Luciocephalus*, *Parasphaerichthys*, and *Sphaerichthys* (Teleostei: Perciformes) as a monophyletic group: evidence from egg surface structure and reproductive behaviour. Japan. J. Ichthyol. 42: 71–79.

De Vlaming, V. 1983. Oocyte development patterns and hormonal involvements among teleosts. pp. 177–199. *In:* J.C. Rankin, T.J. Pitcher & R.T. Duggan (ed.) Control Processes in Fish Physiology, Croom Helm, London.

Dobby, E.H.G. 1964: Southeast Asia, 8th Edition. University of London Press, London. 415 pp.

Dudgeon, D. 1995. The ecology of rivers and streams in tropical Asia. pp. 615–657. *In:* C.E. Cushing, K.W. Cummins & G.W. Minshall (ed.) Ecosystems of the World, Vol. 22, River and Stream Ecosystems, Elsevier Science, Amsterdam.

Henderson, P.A. & I. Walker. 1986. On the leaf litter community of the Amazonian blackwater stream Tarumazinho. J. Trop. Ecol. 2: 1–17.

Henderson, P.A. & I. Walker. 1990. Spatial organization and population density of the fish community of the litter banks within a central Amazonian blackwater stream. J. Fish Biol. 37: 401–411.

Hyslop, E.J. 1980. Stomach content analysis – a review of methods and their application. J. Fish Biol. 17: 411–429.

Kirschbaum, F. 1984. Reproduction of weakly electric teleosts: just another example of convergent development? Env. Biol. Fish. 10: 3–14.

Kottelat, M. 1985. Fresh-water fishes of Kampuchea. A provisory annotated check-list. Hydrobiologia 121: 249–279.

Kottelat, M. 1991. Notes on the taxonomy and distribution of some Western Indonesian freshwater fishes, with diagnoses of a new genus and six new species (Pisces: Cyprinidae, Belontiidae, and Chaudhuriidae). Ichthyol. Explor. Freshwaters 2: 273–287.

Kottelat, M., P.K.L. Ng & K. Lim. 1993. Recent collections of freshwater fish from Terengganu, Peninsular Malaysia. Malay. Naturalist 46: 7–12.

Kottelat, M. & K. Lim. 1994. Diagnosis of two new genera and three new species of earthworm eels from the Malay Peninsula and Borneo (Teleostei: Chaudhuriidae). Ichthyol. Explor. Freshwaters 5: 181–190.

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

Lowe-McConnell, R. 1979. Ecological aspects of seasonality in fishes of tropical waters. Symp. Zool. Soc. Lond. 44: 219–241.

Lowe-McConnell, R. 1987. Ecological studies in tropical fish communities. Cambridge University Press, London. 382 pp.

Majhi, A. & M. Dasgupta. 1989. A study on the food and feeding habits of *Pillia* [sic!] *indica* Yazdani. Arquivos de Museu Bocage 1: 353–359.

Mizuno, N. & J.I. Furtado. 1982. Ecological notes on fishes. pp. 321–354. *In:* J.J. Furtado & S. Mori (ed.) Tasek Bera, the Ecology of a Freshwater Swamp, Dr W. Junk Publishers, The Hague.

Munro, A.D. 1990. Tropical freshwater fish. pp. 145–239. *In:* A.D. Munro, A.P. Scott & T.J. Lam (ed.) Reproductive Seasonality in Teleosts: Environmental Influences, CRC Press, Boca Raton.

Ng, P.K.L., J.B. Tay & K. Lim. 1994. Diversity and conservation of blackwater fishes in Peninsular Malaysia, particularly in the North Selangor peat swamp forest. Hydrobiologia 285: 203–218.

Pardhasaradhi, A. & J.R.B. Alfred. 1981. A note on the biogeographical relictness of *Pillaia indica* Yazdani (Pillaidae: Mastacembeloidei). J. Bombay Nat. Hist. Soc. 78: 175–177.

Prashad, B. & D.D. Mukerji. 1929. The fish of the Indawgyi Lake and the streams of the Myitkyina district (Upper Burma). Rec. Indian Mus. 31: 161–223.

Rainboth, W.J. & M. Kottelat. 1987. *Rasbora spilocerca*, a new cyprinid from the Mekong River. Copeia 1987: 417–423.

Regan, C.T. 1919. Note on *Chaudhuria*, a teleostean fish of the order Opisthomi. Ann. Mag. Nat. Hist. 3: 198–199.

Riehl, R. & K.J. Götting. 1974. Zu Struktur und Vorkommen der Mikropyle an Eizellen und Eiern von Knochenfischen (Teleostei). Arch. Hydrobiol. 393–402.

Roberts, T.R. 1971. The fishes of the Malaysian family Phallostethidae (Atheriniformes). Breviora 374: 1–27.

Roberts, T.R. 1980. A revision of the African mastacembelid fish genus *Macrognathus*. Copeia 1980: 385–391.

Roff, D.A. 1992. The evolution of life histories. Chapman and Hall, London. 536 pp.

Talwar, P.K., G.M. Yazdani & D.K. Kundu. 1977. On a new eel-like fish of the genus *Pillaia* Yazdani (Pisces: Mastacembeloidei) from India. Proc. Indian. Acad. Sci. 85: 53–56.

Tan, S.H. & H.H. Tan. 1994. The freshwater fishes of Pulau Bintan, Riau Archipelago, Sumatra, Indonesia. Tropical Biodiversity 2: 351–368.

Travers, R.A. 1984. A review of the Mastacembeloidei, a suborder of synbranchiform teleost fishes. Part II: phylogenetic analysis. Bull. Br. Mus. Nat. Hist. Zool. 47: 83–150.

Winemiller, K.O. 1989. Patterns of variation in life history among South American fishes in seasonal environments. Oecologia 81: 225–241.

Yazdani, G.M. 1972. A new genus and species of fish from India. J. Bombay Nat. Hist. Soc. 69: 134–135.

Yazdani, G.M. 1975. Fishes of the Khasi Hills, Meghalaya (India), with observations on their distributional pattern. J. Bombay Nat. Hist. Soc. 74: 17–28.

Yazdani, G.M. 1978. Adaptive radiation in mastacembeloid fishes. Bull. zool. Surv. India 1: 279–290.

Yazdani, G.M. & P.K. Talwar. 1981. On the generic relationship of the eel-like fish, *Pillaia khajuriai* Talwar, Yazdani & Kundu (Perciformes, Mastacembeloidei). Bull. Zool. Surv. India 4: 287–288.