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Reproductive and feeding biology of the Natal mountain catfish, *Amphilius natalensis* (Siluriformes: Amphiliidae)

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Synopsis

Aspects of the biology of the Natal mountain catfish, *Amphilius natalensis*, including gametogenesis, spawning season, size-at-maturity, sex ratio, diet and feeding morphology were determined from fish collected in the Songimvelo Game Reserve, South Africa, between 1989 and 1990. Female sexual maturity was established at 63 mm total length. *A. natalensis* is an asynchronous, iteroparous spawner, breeding throughout summer from August to February. Sex ratio of females to males was 2.2:1, with females attaining a significantly larger size than males. Gametogenesis followed a pattern similar to that of other freshwater teleosts peaking over the spawning period. Stomach content analysis and observations on feeding morphology revealed that *A. natalensis* was an opportunistic predator with large fish consuming larger prey from a greater variety of taxonomic groups. The most abundant prey items eaten were dipteran (particularly Chironomidae) and ephemeropteran (particularly Baetidae) larvae.

Introduction

The family Amphiliidae comprises nine genera and about 60 species. Only five species are found in southern Africa, three of which belong to the genus *Amphilius* (Skelton 1993). These soft-bodied catlets inhabit clear, fast flowing mountain streams where they live amongst cobbles, feeding predominantly on benthic invertebrates (Crass 1964, Skelton 1993). The Natal mountain catfish, *A. natalensis* Boulenger, 1917, is a small, nocturnal species with a restricted distribution along the eastern seaboard of southern Africa. It occurs in mountain streams from the Umkomaas River north to the Limpopo system in South Africa. It is also present in the Marozi River, a tributary of the Zambezi River in Zimbabwe and in the Ruo River, Malawi (Skelton 1984, 1993).

Skelton (1993) suggested that predation by introduced trout species has led to scarcity of *A. natalensis* in many streams. In spite of this, no studies on the biology of this catfish species have been published. This study presents the first quantitative information on the biology of an amphiliid catfish, *A. natalensis* including gametogenesis, spawning seasonality, size-at-maturity, adult sex ratio and diet.

Materials and methods

Samples were collected monthly from Louws

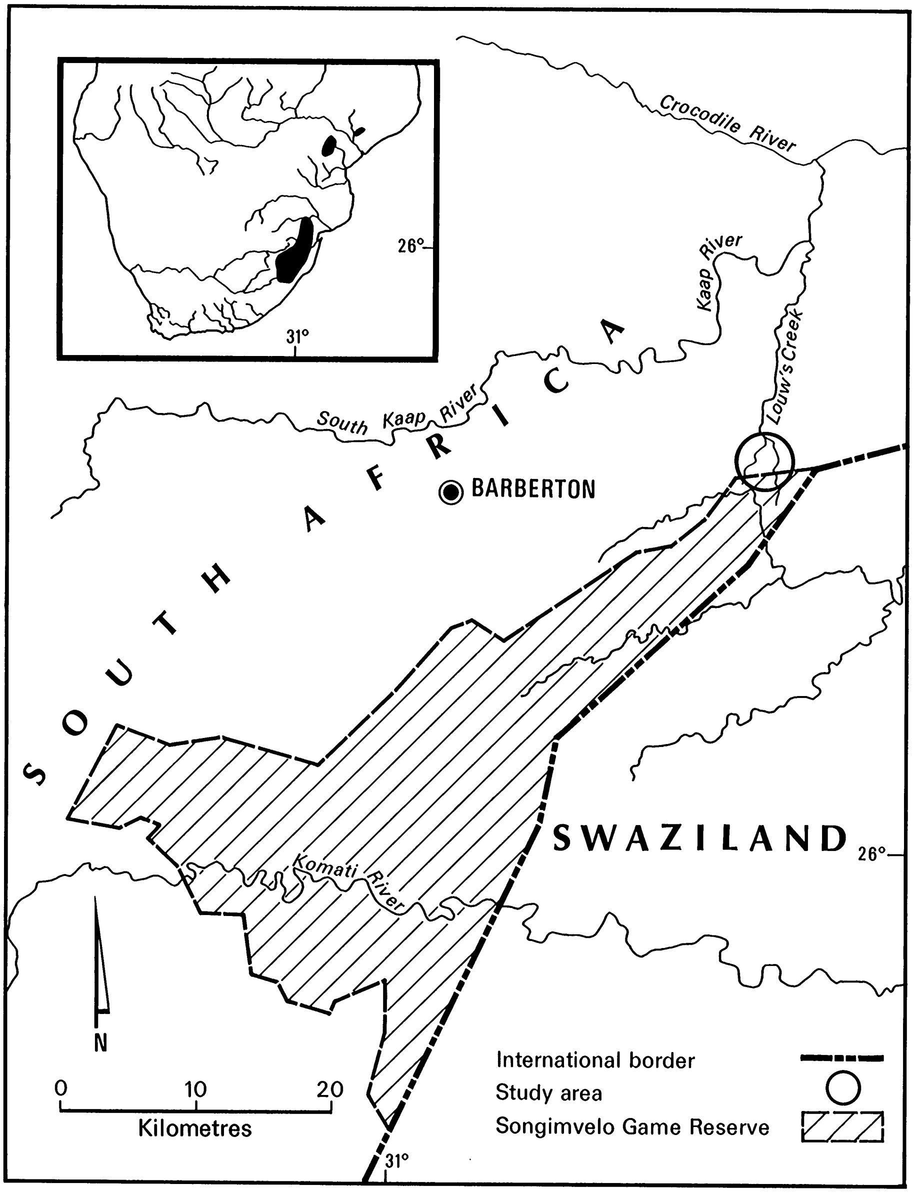

Figure 1. Map of the study area showing the position of Louws Creek in the Songimvelo Game Reserve, South Africa. The distribution range of *Amphilius natalensis* is indicated as the black area on the inset map of southern Africa.

Creek, Songimvelo Game Reserve, South Africa (Figure 1) between March 1989 and March 1990, using AC electrofishing gear. A total of 193 fish were collected. Specimens were preserved in 10% formalin before transferring to 60% propyl-alcohol for storage. Individual fish were weighed after blotting off excess liquid to the nearest 0.01 g, and measured [total (TL), standard and fork lengths] to the nearest 0.1 mm. The dissected gonads were blotted dry and weighed to the nearest 0.001 g. Stomach contents and gonad samples were retained for dietary analysis and histological examination of gametogenesis respectively. Due to the advanced stage of prey digestion, the hindgut was not examined.

Gonad samples were routinely embedded in paraffin wax and sectioned to 5–7 μm, before staining with Gill's haematoxylin and Papanicoloau's eosin A. Maturity was determined for female fish sampled during the breeding season with female fish considered mature if they contained oocytes from the primary yolk vesicle stage. Size at sexual maturity was calculated by fitting a logistic ogive to the proportion of mature fish in 4 mm TL size classes. The 2 parameter logistic ogive used can be decribed by the equation:

$$P(l) = \frac{1}{1 + \exp^{-(l-l_{50})/\delta}},$$

where $P(l)$ is the percentage of mature fish at length l, l_{50} the length at sexual maturity and δ the width of the ogive. Gonado-somatic indices for males and females were calculated using mature fish, by expressing gonad mass as a percentage of eviscerated body mass.

Stomach contents were identified to the lowest possible taxon. Visual estimates of percentage volume (% V), the number of individuals of each prey item (% N) and the frequency of occurrence (% FO) of each prey item to the diet was determined. An index of relative importance (IRI) was calculated for each prey item according to Hyslop (1980) where:

$$IRI = (\%N + \%V) \times \%FO.$$

The pharyngeal, maxillary and dentary tooth pads were removed and prepared for examination by scanning electron microscopy using methodology described by Cross[1] to elucidate any ontogenetic changes in feeding habits. To determine whether prey selectivity was gape dependent, the means of the 20 largest prey items in the stomachs of the largest fish (such as head capsule diameter for dipteran larvae or thorax diameter for ephemeropteran nymphs) and gape width of the 20 smallest fish were compared using a student's t-test. Measurements were made to the nearest 0.1 mm. To investigate seasonal changes in diet, a percentage IRI for large fish (> 40 mm TL) was calculated for four principle prey groups (Chironomidae, Ephemeroptera, other insects and other invertebrates) during each season and compared using a one-way analysis of variance.

[1] Cross, R.H.M. 1987. A handbook on the preparation of biological material for electron microscopy. Electron Microscopy Unit, Rhodes University, Grahamstown. 71 pp.

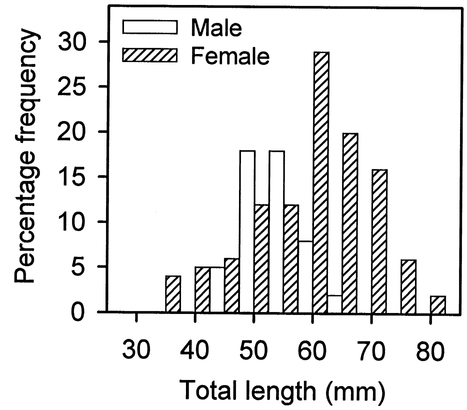

Figure 2. Size frequency distributions of male and female *Amphilius natalensis,* sampled from Louws Creek, South Africa, between March 1989 and March 1990.

Results

Morphometrics and population structure

Morphometric relationships between length and mass of preserved fish are summarized in Table 1. The length frequency distributions for males and fe-

Table 1. Morphometric relationships between length and mass of *Amphilius natalensis,* sampled from Louws Creek, South Africa, between March 1989 and March 1990. Measurements are based on samples stored in 60% propanol.

Equation		r^2	n
Total mass (g)	= 0.0113 total length$^{2.8521}$ (mm)	0.944	193
Eviscerated mass (g)	= 0.0095 total length$^{2.8307}$ (mm)	0.943	193
Total length (mm)	= 1.0194 fork length (mm) + 0.0341	0.992	193
Total length (mm)	= 1.0774 standard length (mm) + 0.2983	0.983	193

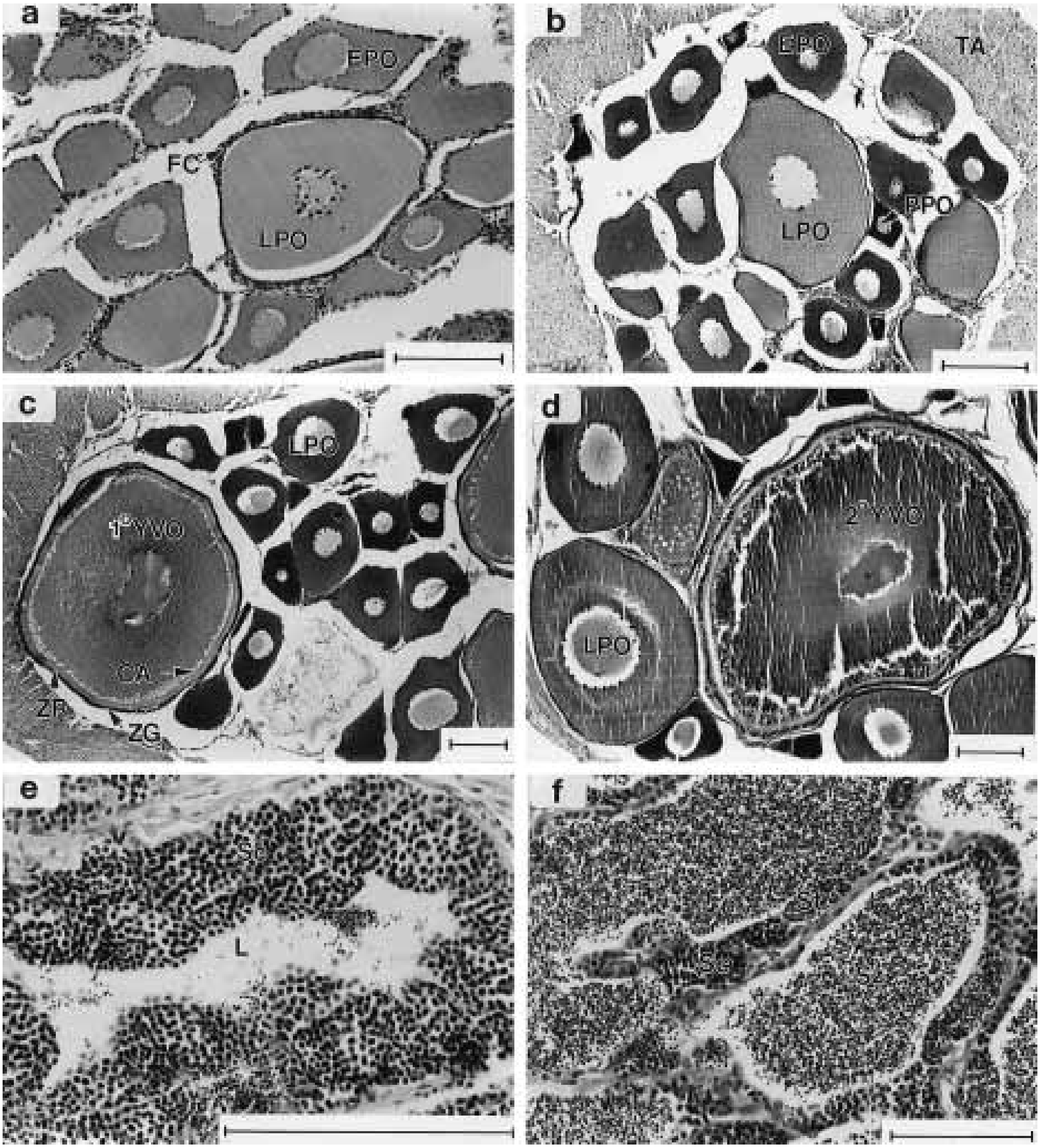

Figure 3. Transverse sections through gonads of *Amphilius natalensis* illustrating gametogenesis: a – Immature ovary containing early (EPO) and late perinuclear oocytes (LPO) surrounded by follicle cells. b – Immature ovary containing all stages of perinuclear oocytes (PPO = pre-perinuclear oocyte). c – The onset of maturation begins with the appearance of primary yolk vesicle oocytes (1°YVO) (note the development of the zona radiata (ZR) and zona granulosa (ZG) with cortical alveoli (CA) forming in the periphery of the cytoplasm). d – Secondary yolk vesicle oocytes (2°YVO) appear with the sequestration of vitellogenic yolk. e – Testes between breeding seasons contain predominantly spermatocytes (Sc) with little sperm visible in the lumen (L). f – During the breeding season spermatozoa (Sz) fill the lumen (St = spermatids). All scale bars = 200 μm. Stained using Gill's haematoxylin and Papanicoloau's eosin A.

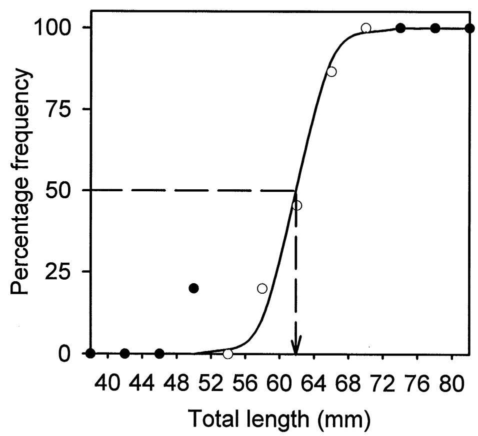

Figure 4. Percentage frequency of mature female *Amphilius natalensis* in different size classes, sampled from Louws Creek, South Africa, between March 1989 and March 1990. The curve was fitted to the open dots using a 2-parameter logistic ogive.

males in the sample are described in Figure 2. Modal lengths of the sexes were found to be significantly different (T = 2904.5, $p < 0.05$), with females attaining a larger size than males. Female to male sex ratio was 2.2:1, significantly different from unity ($\chi^2_{[0.05,9]} = 45.7$, $p < 0.05$). Despite the bimodal distribution of the sexes, there was no histological evidence for protandry (Sadovy & Shapiro 1987).

Oogenesis

The ovaries of *A. natalensis* are large, paired, saclike organs suspended in the body cavity by mesovaria. Each ovary contained up to 300 eggs at various stages of development. Oogenesis commenced with the multiplication of oogonia on the ovarian lamellae, forming early pre-perinuclear oocytes (Figure 3b). With increased cytoplasmic growth, there was an increase in the number and decrease in size of the nucleoli, as they moved to the periphery of the nucleus becoming basophilic and less angular. Late perinuclear oocytes were greatly enlarged and rounded with the formation of the zona radiata and zona granulosa. Following the perinuclear oocyte stage, cortical alveoli, characteristic of the primary yolk vesicle stage, formed around the inside of the cell periphery (Figure 3c). These increased in size and number as they moved within the cytoplasm. At this stage the zona radiata and zona granulosa are well developed. The last phase of oogenesis involved the sequestration of secondary yolk with the cell cytoplasm becoming strongly acidophilic (Figure 3d). Due to their large size (1.15 mm ± 0.02, n = 30) and high yolk volume, mature eggs sectioned with difficulty. Mature ovaries showed various oocyte stages including pre-perinuclear oocytes to mature eggs indicating that this species is iteroparous with an unknown periodicity of spawnings.

Spermatogenesis

The testes of *A. natalensis* are large, grey-white, paired, convoluted organs, suspended in the body cavity by mesorchia. They were found to be similar in structure to those of bagrids (Loir et al. 1989). Spermatogenesis was initiated with the proliferation and growth of spermatogonia, forming primary spermatocytes (Figure 3e). These later gave rise to secondary spermatocytes and then to spermatids. The spermatids were similar in size to spermatozoa, yet were associated with the interstitial tissue. They

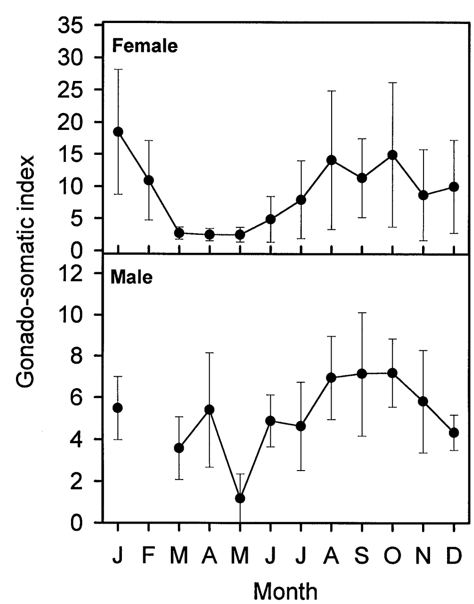

Figure 5. Variation in mean (± standard deviation) gonado-somatic indices for both male and female *Amphilius natalensis*, sampled from Louws Creek, South Africa, between March 1989 and March 1990.

were later released into the lobule lumen where they matured as spermatozoa (Figure 3f).

Spermatogenesis occurred at low levels during the winter months with the testes containing predominantly spermatocytes (Figure 3e). Spermatogenesis peaked during spring and summer where large numbers of spermatozoa filled the entire lumen with few spermatocytes and spermatids visible (Figure 3f).

Sexual maturity and spawning seasonality

Female median length-at-maturity was estimated at 62 mm TL with total maturity at 70 mm TL (Figure 4). Seasonal variation in the mean gonado-somatic indices suggested that *A. natalensis* breeds throughout spring and summer. Although not as marked as the females, male gonado-somatic indices followed a similar trend (Figure 5). This was confirmed by the presence of mature stages of oocyte development in the ovaries and the abundance of sperm in the testes during the proposed breeding season.

Feeding biology

Based on observed dietary differences in fish greater and less than 40 mm TL, fish were divided into two size classes for the purposes of feeding analysis. Stomach content analysis of *A. natalensis* revealed that they are opportunistic predators, feeding on a wide variety of aquatic and terrestrial prey items. Food items are summarised in Tables 2 and 3. In both large and small size classes, aquatic insects were the dominant dietary items, contributing 91% and 90% of the volume, respectively. Within the Insecta, dipterans contributed 86% of the volume in the smaller size class, with chironomids, in particular *Cricotopus* spp., constituting the dominant prey. In the larger fish, dipteran and ephemeropteran larvae contributed almost equally in volume (44% and 45%) to the diet. Ephemeropterans were assigned a lower index of relative importance due to a smaller number and frequency of occurrence. Although within the two major prey orders there was greater diversity in the larger class, *Cricotopus* spp. and baetid larvae, in particular *Baetis harrisoni*, were the dominant prey eaten. Small amounts of sand and plant material were present but are considered incidental.

Caniniform teeth of a uniform size were found in rows on the tooth pads of all size classes of fish examined (Figure 6). The only observed difference related to fish size was in the number and spacing of the tooth rows, where those of smaller fish were fewer and more widely distributed. Mean gape size of the smallest fish was found to be significantly

Table 2. Stomach content analysis of small *Amphilius natalensis* (< 40 mm total length) sampled from Louws Creek, South Africa, between March 1989 and March 1990. The group 'miscellaneous insects' consists of small quantities of ephemeropteran, trichopteran and hemipteran prey each comprising < 1% by the volume and number (n = 14).

Food item	% volume	% numbers	% frequency of occurrence	IRI
Insecta	**89.8**	**95.1**	**85.7**	**15843**
Diptera	86.2	93.1	85.7	15364
Chironomidae	85.7	92.1	85.7	15240
Cricotopus dibalteatus	5.8	6.4	6.0	73
Cricotopus spp.	61.7	68.7	64.3	8385
Limnophyes natalensis	2.9	3.2	2.9	18
Rheotanytarsus fuscus	2.9	3.2	3.1	19
Thienemanniella sp.	9.0	10.1	9.4	101
Orthocladiinae (adult)	3.5	< 1	7.1	28
Micellaneous insects	**4.1**	**2.0**	**56.8**	**346**
Isopoda	**3.7**	**3.9**	**7.1**	**83**
Sand	**< 1**	**< 1**	**7.1**	**8**
Amorphous material	**1.92**	**< 1**	**7.1**	**17**

larger than the mean size of the largest prey consumed by the largest fish (T = 9.20; $p < 0.05$). No significant difference was found between diets of large fish (> 40 mm TL) sampled during different seasons (F = 0.59, $p > 0.05$).

Discussion

Reproductive activity in *A. natalensis* is well correlated to both an increase in temperature and photoperiod. This is similar to other small catfish species which tend to have a variable length breeding season over the warm, summer period (Zholdasova & Guseva 1987, De Villiers 1991, Baker & Heins 1994). The breeding period for *A. natalensis* is long, extending from August to February. This protracted spawning period allows for reproduction to coincide with favourable environmental conditions producing favourable food availability and nursery areas (Bruton 1979, Rinne & Wanjala 1983). The proximate causes for the initiation of spawning have been well studied in catfishes most of which have related to rainfall patterns or flooding (Van der Waal 1974, Bruton 1979, Owiti & Dadzie 1989). As the breeding season of *A. natalensis* also coincides with the rainy season it is possible that spawning is initiated in response to increased water flow rate or changes in water quality, following periods of rainfall.

Gametogenesis in *A. natalensis* was shown to be typical of the pattern found in other small catfish (De Villiers 1991) and freshwater teleosts in general (Yamamoto & Yamazaki 1961, Wallace & Selman 1981, Hibiya 1982, Zholdasova & Guseva 1987, Makayeva & Yemel'yanova 1989). The presence of various oocyte developmental stages indicate that *A. natalensis* is an asynchronous, iteroparous spawner producing more than one egg clutch in a single reproductive season (Zholdasova & Guseva 1987, Baker & Heins 1994).

Results on the population structure of *A. natalensis* from Louw's Creek suggest a skewed sex ratio dominated by large female fish. Given that the fish

Table 3. Stomach content analysis of large *Amphilius natalensis* (> 40 mm total length) sampled from Louws Creek, South Africa, between March 1989 and March 1990. The group 'miscellaneous' consists of small quantities of coleopteran, hemipteran and odonatan insect prey together with nematode, isopod, oligochaete and crustacean prey each comprising < 1% by both volume and number.

Food item	% volume	% numbers	% frequency of occurrence	IRI
Insecta	**90.9**	**88.6**	**87.2**	**15626**
Diptera	40.4	72.2	82.7	9308
Chironomidae	36.5	70.2	82.7	8816
Orthocladiinae (larvae)	36.2	69.8	82.1	8701
Cricotopus dibalteatus	2.5	4.9	5.7	42
Cricotopus spp.	27.2	52.3	61.2	4865
Limnophyes natalensis	1.3	2.4	2.8	10
Rheotanytarsus fuscus	1.4	2.5	3.0	12
Thienemanniella sp.	3.9	7.7	9.0	104
Orthocladiinae (adult)	< 1	< 1	5.6	4
Ephemeroptera	40.7	13.9	51.9	2834
Baetidae	40.4	13.8	51.9	2816
Baetis harrisoni	37.3	12.9	50.3	2526
Baetis sp.	< 1	< 1	4.5	6
Pseudopannota sp.	2.2	< 1	4.5	12
Trichoptera	8.3	2.5	14.5	158
Cheumatopsyche afra	8.3	2.5	14.5	158
Miscellaneous	**9.5**	**7.3**	**15.0**	**252**
Sand	**5.6**	**2.4**	**36.3**	**290**
Plant material	**< 1**	**1.2**	**2.9**	**5**
Amorphous material	**1.6**	**< 1**	**3.9**	**7**

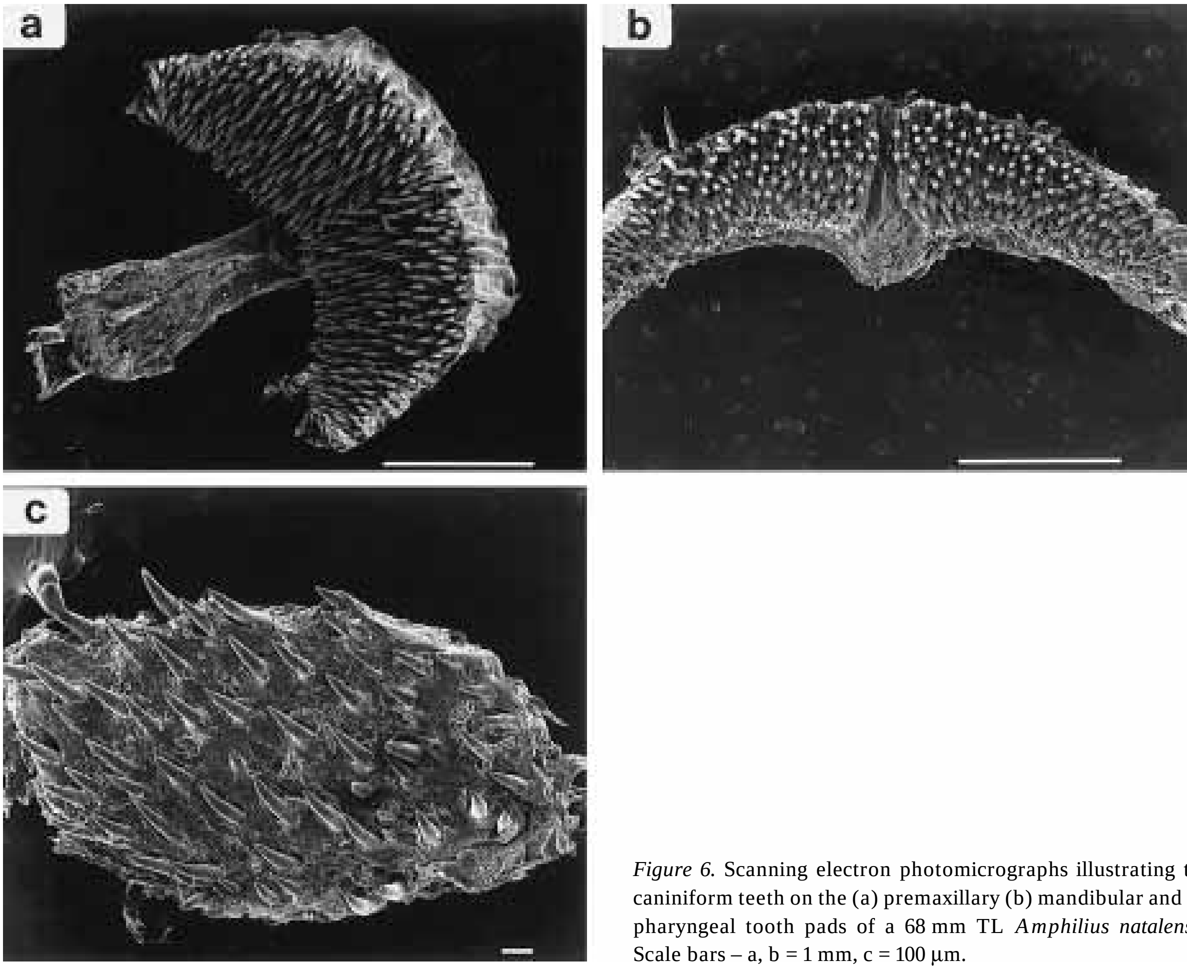

Figure 6. Scanning electron photomicrographs illustrating the caniniform teeth on the (a) premaxillary (b) mandibular and (c) pharyngeal tooth pads of a 68 mm TL *Amphilius natalensis.* Scale bars – a, b = 1 mm, c = 100 µm.

were sampled using electrofishing gear in a high gradient stream environment and that female fish were on average twice the size of male fish, these changes could merely represent differences in sampling selectivity. Alternatively, as little is known about the reproductive behaviour of this species with the observed differences arising from females becoming vulnerable to the sampling gear due to sexual behaviour. On the contrary, as all male fish sampled were sexually mature with advanced stages of spermatogenesis occuring in the testes (female sexual maturity occurred at a size larger than the larger males observed), no large males were sampled during this study; that small immature female fish were sampled, these results suggest that the samples taken during this study do possibly represent the true structure of the population. If this is the case, territoriality or aggression during courtship between males would possibly be reduced due to their small size and low ratio to available females. With male fitness not necessarily a function of body size due to the reduced competiveness in securing mates or reduced sperm competition due to the lower ratio of males to females (Choat & Robertson 1975), energy would rather be directed into gonadal development resulting in a smaller body size, earlier reproductive maturity and extended reproductive activity (Gross 1984).

The diet of *A. natalensis* is similar to that of other South African and North American catfish species (Vives 1987, De Villiers 1991). The high diversity and small quantities of prey eaten implied that *A. natalensis* is an opportunist predator, feeding nocturnally on the most available prey items using the large concentrations of tastebuds on its barbels and skin to locate it's prey (Booth 1997). This is supported by the occasional presence of terrestrial organisms, such as earthworms in the diet. Allochthonous material often forms an important component in the diet of many freshwater species (Garman 1991, Daniels & Wisniewski 1994) where the fish acts as an important link between the terrestrial and aquatic food webs (Merron & Mann 1995). In *A. natalensis,* terrestrial organisms, though present, were in small quantities, indicating that energy is utilised and retained within the aquatic system.

There were differences in the diversity and relative importance of prey organisms in the diets of the two size classes examined despite similarities in their feeding morphology. The caniniform teeth appeared to primarily have a holding function as prey, which although sometimes broken, were generally ingested whole with little evidence of mastication. If smaller fish were able to exploit a food resouce which was not available to the larger size classes possibly due to their ability in utilising smaller spaces, different prey species to those of the larger size class would dominate the diet. Alternatively, prey which were not found in the diet of smaller fish may have escape responses allowing them to avoid smaller fish or that larger fish might hold better feeding positions due to dominance or by the ability to withstand stronger currents, allowing for the consumption of larger prey. Though most of the prey species were similar, those prey species that were unique to larger fish were larger than chironomid larvae, particularly the ephemeropteran nymphs. With dietary difference found not to be determined by gape size as the prey size of large fish was found to be significantly smaller than the gape size of small fish, the occupation of different feeding positions or the ability to pursue larger prey might explain why larger fish consumed larger prey items from a larger variety of taxa. Prey items found in both size classes were generally characteristic of fast flowing, clear streams (Scholtz & Holm 1989), typical habitat for *A. natalensis.*

Assuming that the prey of *A. natalensis* are spatially and temporally invariant, the results showing no significant temporal differences in the diets of larger fish suggest that *A. natalensis* remains resident in localised areas where they both feed and reproduce. This has implications with regards to developing a management strategy to ensure the conservation of species. Skelton (1993) suggests that the introduction of alien species, such as trout (*Oncorhynchus mykiss* and *Salmo trutta*), have already affected the distributional range of *A. natalensis.* It is therefore imperative that strict control measures regarding the introduction and monitoring of alien species be implemented in mountain streams which provide a habitat for this fish species.

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