

Redescription of *Amphilius jacksonii* (Siluriformes: Amphiliidae) with habitat and life-history notes

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Amphilius jacksonii is a medium-sized (<120 mm SL) benthic catfish with a limited range in western river tributaries of lakes George and Edward, southwestern Uganda and northeastern Democratic Republic of Congo (= Zaire), and possibly occurring in some Lake Tanganyika tributaries as far south as Zambia. We redescribe the species based on recently collected specimens. *Amphilius jacksonii* is rheophilic, occurs in streams and rivers with moderate current and gradient, and is generally associated with large rocks or mixed cobble and rock substrates. Individuals may reach 2+ years of age and feed almost entirely on autochthonous benthic invertebrates, especially larval trichopterans, ephemeropterans, and dipterans.

Introduction

The catfish family Amphiliidae includes nine genera and about 60 species, with the largest number of species (22) placed in the genus *Amphilius* (Teugels, 1996). The family is broadly distributed throughout west equatorial, southcentral, and sub-Saharan east Africa. Most amphiliid species are found in clear upland streams and larger rivers with moderate gradient or flow, and are often associated with rocky habitats. Amphiliids exhibit morphological features that reflect their benthic habits and adaptation to flowing waters; they are dorsoventrally flattened fishes with broad, pectinate pectoral and pelvic fins, upwardly directed eyes, and reduced gas bladders. Very little is known about the natural his-

tory of most amphiliids (Teugels et al., 1992), and the systematic relationships among species are obscure (Skelton, 1984). Marriott et al. (1997) provided quantitative data on reproductive biology and diet of *A. natalensis* Boulenger from South Africa, representing the most detailed ecological study of any species of the genus.

The Ugandan fauna includes a single recorded species of amphiliid catfish, *A. jacksonii* Boulenger, that has a limited distribution along the eastern escarpment of the Ruwenzori mountains (Greenwood, 1966). *Amphilius jacksonii* was described by Boulenger (1912) from a single specimen collected in the Hima River, tributary of Lake George, western Uganda. Subsequent explorations expanded the known distribution of this species to the Aduka, Agoye, and Rutshuru

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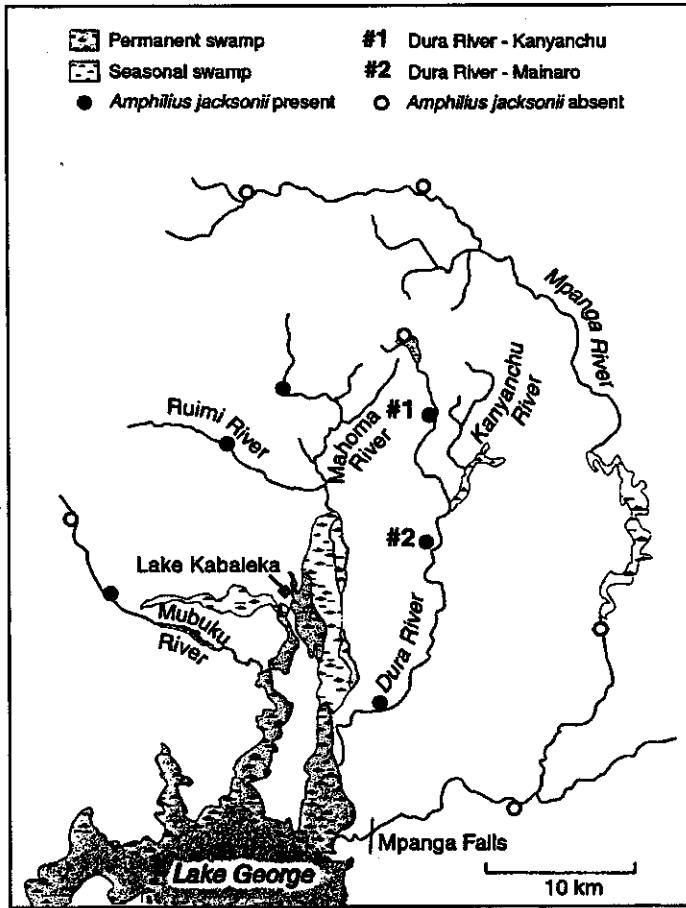


Fig. 1. Sites where *Amphilius jacksonii* were captured (closed circles) and not captured (open circles) in four western Ugandan tributaries. The two sites used for studies of habitat use are indicated: 1, Dura River-Kanyanchu, and 2, Dura River-Mainaro.

tributaries draining into lakes George and Edward, upper Nile River basin (Skelton & Teugels, 1986). This species or a closely related one also occurs in affluent drainages of Lake Tanganyika, including tributaries in Zambia (anonymous reviewer, in litt.). Very little published information exists on morphological variation and the ecology of *A. jacksonii* due to a paucity of available material and limited study by previous authors. Greenwood (1966) provided a brief summary of external morphology, coloration, general habitat, and distribution. Chardon (1968) described and illustrated the Weberian complex of the species and Corbet (1961) provided cursory data on food habits. Skelton & Teugels (1986) summarized literature references and distributional records. We are aware of no other published

biological information for this species. Herein we redescribe *A. jacksonii* and provide new distribution records, habitat data, and other natural-history notes.

Methods

Survey and fish collections. As part of an ongoing ecological investigation of the ichthyofauna of the tributaries and satellite lakes of Lake George and to determine distribution of *A. jacksonii* and other fish species, we intermittently surveyed several sites in the Dura and Mpanga rivers and at one or two sites each in the Mahoma, Mbuku, and Ruimi rivers between 1990 and 1996 (Fig. 1). At each site, fish were captured with minnow traps, seines, and an electroshocker when logis-



Fig. 2. Habitat of *Amphilius jacksonii* at Dura River-Mainaro, 23 July 1996.

tics permitted. Most specimens used for morphological studies and life-history data were collected by seine during July 1996 from the Dura and Ruimi rivers (Figs. 1-2). Fish to be examined in the laboratory were fixed in paraformaldehyde, rinsed in water, transported to our laboratory in Gainesville, Florida, and transferred to 70 % ethanol. Museum symbolic codes are: BMNH, British Museum (Natural History); UF, Florida Museum of Natural History (formerly Florida State Museum), University of Florida.

Morphology and life-history aspects. Most counts and measurements followed the methods of Skelton (1984). Specimens were measured with needle-point dial calipers to the nearest 0.1 mm standard length (SL). We followed Cailliet et al. (1986) in using the terms "origin" and "insertion" to designate, respectively, anterior and posterior base of all fins. Head length was measured as the distance from tip of snout to dorsal edge of opercular cavity. Fin lengths and body measurements were obtained as linear distances between respective landmarks as indicated in Table 1. Fin-ray and vertebral counts were determined from radiographs of 31 specimens. Rays of unpaired

median fins split to the base were counted as one. A small splint of bone at the anterior base of the anal fin, variably present, was excluded from anal fin-ray counts. Vertebral counts exclude 1-5 Weberian vertebrae and the fused preural and ural (PU1+U1) centra. Preanal vertebrae are those with hemal spines anterior to the first proximal anal pterygiophore. Description of caudal fin morphology follows the terminology of Lundberg & Baskin (1969). Gill-raker counts were made on the first arch of the left side. Four specimens were cleared and stained following the methods of Potthoff (1984) to confirm osteological details observed in radiographs.

Specimens were dissected to remove internal organs for examination of reproductive condition and identification of gut contents. Following dissection, eviscerated specimens and gonads were blotted dry and weighed to the nearest 0.1 mg to determine adjusted (eviscerated) body weight (BW) and wet gonad weight (GW). Regressions of BW on SL were calculated from log-transformed data to examine weight-length relationships by sex. Population size structure was estimated from length-frequency distributions by 5-mm size groups. The relationship between GW

and BW was examined among representative samples by calculating the regression of log GW on log BW as recommended by deVlaming et al. (1982).

Diets were determined from 118 preserved specimens. Stomachs and intestinal tracts of fish were removed whole and the contents examined under a stereomicroscope where food items were identified, counted, and a relative volume determined. Invertebrates were identified to lowest practical taxonomic category, generally order or

family, indicative of functional prey group (e.g., benthic, terrestrial, etc.). Prey items were quantified by calculating percent frequency of occurrence (% FO) and the number (mean and range) of individual prey items of each taxon. A relative index of volume of prey items per stomach was determined by estimating approximate volume of individual prey taxa as percentages of volume of all taxa combined, using categories of 0-25%, 26-50%, 51-75%, and 76-100%. The percent frequency by volume categories (% FV) for individ-

Table 1. Morphometric proportions of *Amphilius jacksonii* (n=20; UF 110746-110748).

| measurement | range | mean (± 1 SD) |
|---|------------|--------------------|
| Standard length (mm) | 35.4-102.5 | - |
| Percentage of standard length | | |
| Predorsal length | 32.4-38.5 | 36.2 (1.5) |
| Dorsal fin base length | 9.2-13.2 | 10.4 (1.1) |
| Dorsal fin insertion to adipose fin origin | 18.4-26.7 | 22.9 (2.7) |
| Adipose fin base length | 15.1-21.8 | 19.5 (2.0) |
| Adipose fin insertion to hypural plate | 8.4-14.2 | 11.1 (1.5) |
| Least caudal peduncle depth | 6.9- 9.1 | 7.9 (0.6) |
| Anal fin insertion to hypural plate | 14.0-20.1 | 16.4 (1.4) |
| Anal fin base length | 9.2-12.9 | 11.0 (1.0) |
| Pelvic fin origin to anal fin origin | 20.7-25.5 | 23.7 (1.3) |
| Pectoral fin origin to pelvic fin origin | 28.7-36.0 | 31.7 (1.5) |
| Pectoral fin origin to snout tip | 15.5-25.1 | 19.5 (2.5) |
| Dorsal fin origin to pectoral fin origin | 16.4-25.8 | 22.6 (2.3) |
| Dorsal fin origin to pelvic fin origin | 16.7-23.1 | 20.4 (1.5) |
| Pectoral fin origin to dorsal fin insertion | 27.1-33.5 | 30.6 (1.5) |
| Body width at pectoral fin origin | 19.0-22.0 | 20.1 (0.9) |
| Maximum body depth | 12.0-17.7 | 14.3 (1.5) |
| Dorsal fin insertion to pelvic fin origin | 26.5-33.9 | 30.4 (2.3) |
| Dorsal fin insertion to anal fin origin | 22.0-33.4 | 25.5 (2.3) |
| Adipose fin origin to pelvic fin origin | 10.6-16.1 | 13.3 (1.5) |
| Adipose fin origin to anal fin origin | 13.7-19.9 | 16.5 (1.7) |
| Adipose fin origin to anal fin insertion | 7.7-16.4 | 10.5 (1.7) |
| Adipose fin insertion to anal fin origin | 9.7-13.1 | 11.6 (1.0) |
| Adipose fin insertion to anal fin insertion | 15.2-22.6 | 19.3 (1.6) |
| Preisthmus length | 6.6-11.0 | 9.0 (1.3) |
| First pectoral-fin ray length | 14.2-21.8 | 18.5 (2.1) |
| First dorsal-fin ray length | 15.9-22.0 | 19.1 (1.9) |
| Pelvic fin length | 15.1-19.8 | 17.4 (1.4) |
| Head length | 21.0-26.4 | 23.4 (1.3) |
| Percentage of head length | | |
| Head depth | 39.6-61.5 | 49.6 (4.9) |
| Head width | 74.5-88.2 | 81.1 (4.2) |
| Gape width | 33.3-55.5 | 45.8 (6.2) |
| Interocular width | 24.5-33.7 | 29.2 (2.4) |
| Eye diameter | 7.6-13.7 | 11.3 (1.5) |
| Anterior internarial width | 9.8-16.4 | 12.3 (1.8) |
| Upper jaw length | 17.5-33.7 | 25.5 (3.8) |
| Maxillary barbel length | 57.7-101.0 | 67.0 (10.1) |

ual taxa was then calculated for all stomachs examined (i.e., % FV is the percentage of stomachs out of all combined in which the taxon fell within each of the above ranges). Parasites in the lower intestinal tract were counted and identified to order during examination of specimens for stomach contents.

Habitat use. Two study sites on the Dura River (Kanyanchu, Mainaro; Figs. 1-2) were selected for examination of habitat use by *A. jacksonii*. The Dura River drainage lies largely within Kibale National Park, western Uganda (0°13'-0°41' N 30°19'-30°32' E). Moist evergreen forest accounts for 57 % of land cover of the 766 km² Kibale NP, and the remainder is comprised of a mosaic of colonizing forest (19 %), grassland (15 %), wetland (45 %), woodland (4 %), and plantations (1 %) (Chapman & Lambert, in press). Mean annual rainfall in the park (1977-1996) has averaged 1678 mm (range = 1205 to 2139 mm) (Chapman et al., 1999). There are distinct wet and dry seasons which are bimodal in distribution. May through August and December through February tend to be drier than other months, with the May-August dry period of a longer duration than the second dry season.

At both study sites, the river consists of open water with no aquatic macrophytes flowing through primary forest. Six stations were set up at 50-m intervals along a 250-m reach of each river site. Dry season observations at each station were used to describe the two reaches. At Dura River-Kanyanchu, the river is fast flowing and averages 10.6 m in width and 50 cm in depth during the dry season, having a substrate that consists largely of rock and cobble (78 %) with marginal areas of sand (6 %) and mud (16 %). At Dura River-Mainaro, the river widens and deepens, averaging about 11.5 m in width and 73 cm in depth during the dry season. The bottom at Dura River-Mainaro is comprised largely of mud (50 %) with smaller areas of rock and cobble substrate (30 %) and sand (20 %).

As part of a more encompassing study of habitat use by fishes, minnow traps were set once per month between July 1995 and April 1997. On each occasion, three minnow traps were set overnight across the stream at each station, one within 2 m of each side, and one in the faster flowing main channel. For each minnow trap we recorded the following information: trap depth, water temperature, dissolved oxygen concentra-

tion, and current. Water current was ranked from 0 to 3 using 0.5 gradations (0=no current, 1=visible but low flow, 2=fast flow with little water perturbation, 3=white water). Although seining produced much larger numbers of *A. jacksonii* than minnow traps, we used traps to permit higher resolution in our assessment of microhabitat use. In the first year of study we observed that high-water periods during the rainy season produce areas of inundated forest in the Dura River floodplain which are exploited by main river fishes. We therefore established a flooded-forest station at each site in the second year which consisted of a large forest pool (50 m by 65 m) at Dura River-Kanyanchu, and a smaller forest pool (30 m by 30 m) at Dura River-Mainaro. An average of six traps were set in the pools each month that they maintained water.

Captured *A. jacksonii* were measured (total length) and individuals were marked with indelible tattoo ink on one of three sites on the body. Different sites and colors were used to indicate the station of capture (0 m, 50 m, etc.). The ink was injected into the muscle using a fine gauge hypodermic needle (Thresher & Gronell, 1978; Chapman et al., 1991).

Amphilius jacksonii Boulenger (Fig. 3)

Amphilius jacksonii Boulenger, 1912: 602 (original description; type locality: Uganda: Hima River, eastern foothills of Ruwenzori mountains, flowing into Lake George (Ruisamba), elev. 3500 ft; holotype: BMNH 1912.10.15:47). Additional citations in Skelton & Teugels (1986).

Material examined. UF 110743, 12, 48.6-104.3 mm SL; Uganda, Burahya-Kibale Province, Lake George drainage: Dura River-Kanyanchu; 5 July 1996. – UF 110744, 21, 23.6-115.9 mm SL (2 stained and cleared); same locality; 8 July 1996. – UF 110745, 5, 54.6-88.6 mm SL; same locality; 9 July 1996. – UF 110746, 40, 34.1-102.0 mm SL; same locality; 9 July 1997. – UF 110747, 54.4-111.1 mm SL (2 stained and cleared); Uganda, Burahya-Kibale Province, Lake George drainage: Dura River-Mainaro; 23 July 1996. – UF 110748, 41, 42.7-92.8 mm SL; Uganda, Bunyangabu Province, Lake George-Mahoma River drainage: Ruimi River at bridge on road between Fort Portal and Hima; 21 July 1996. – UF 110749, 1, 47.6; same

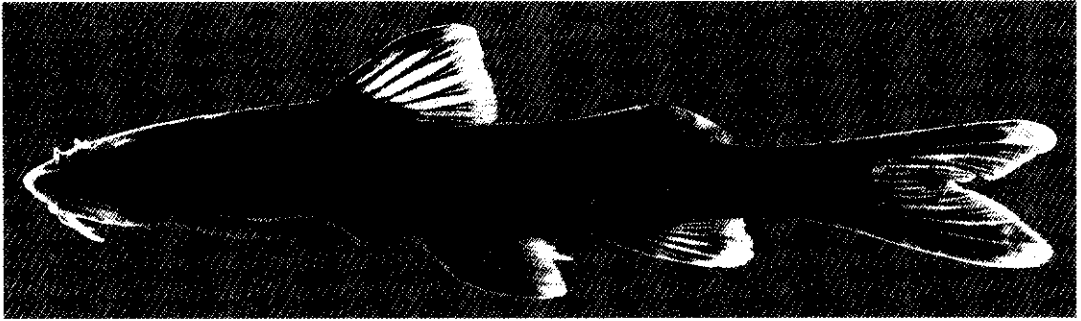


Fig. 3. *Amphilius jacksonii*, UF 110750, female, 56 mm SL; Uganda, Mbuku River.

locality; 28 July 1996 – UF 110750, 7, 52.8–85.1 mm SL; Uganda, Bunyangabu Province, Lake George-Mahoma River drainage: Mubuku River at bridge on road between Fort Portal and Kasese; 28 July 1996.

Diagnosis. *Amphilius jacksonii* differs from other east and southern African species of *Amphilius*, including the wide-ranging *A. uranoscopus* Pfeffer 1889, in having fewer total vertebrae, a mode of 6+7 principal caudal rays, and a crenulated epidermal fold at the base of the caudal fin; the latter character is shared with *A. platyichir* (Günther, 1864) and at least some other west African *Amphilius* species (Skelton, 1984). *Amphilius jacksonii* is further characterized by the following combination of characters (those designated by an asterisk common to most other *Amphilius* species): dorsal and pectoral spines absent*; dorsal fin with 7 soft rays; short adipose fin not adnate with caudal fin*; pectoral fin with 8–10 soft rays; anal-fin rays 7–10; forked caudal fin with rounded lobes*; 31–33 free vertebrae; and, variable, heavily mottled pigmentation*. With the exception of *A. angustifrons* Boulenger 1902 and *A. notatus* Nicols & Griscom 1917 (known only from type material, Ubangui River), *A. jacksonii* differs from other congeners in the Congo (=Zaire) River by having fewer total free vertebrae (31–33 versus 33–40). *Amphilius jacksonii* is distinguished from the latter two species by fewer pectoral rays (8–11, mode of 10, versus 8–9, mode of 9), anal-fin rays (mode of 10 versus 9), and mensural characters based on Skelton's (1986) data.

Description. Morphometric data for 20 specimens are presented in Table 1. Body elongate, terete, flattened ventrally from head to anal-fin

origin. Head and snout depressed. Tip of snout rounded, dorsal profile of head sloping straight to supraoccipital, profile of supraoccipital slightly convex to dorsal-fin origin. Body posterior to dorsal fin gradually tapered laterally and dorsoventrally. Caudal peduncle laterally compressed. Greatest body depth at dorsal-fin origin. Snout margin broadly parabolic in dorsal view. Lips fleshy, weakly papillose. Large, fleshy, flattened maxillary barbels extending posterolaterally at corners of mouth and continuous with thick upper lip. Bases of mandibular (lateral pair) and mental (medial pair) barbels displaced toward lateral edges of chin. Mouth small, inferior. Premaxillary tooth patch forming a small, rasping, trapezoidal-shaped wedge at midline. Branchiostegal fold deeply notched and V-shaped, connected by small frenum to isthmus at midline, but with shallow groove at posterior margin. Eyes small (horizontal diameter 8–14% head length), directed upward on top of head. Gill rakers on first epibranchial (number of specimens in parentheses): 1 (1), 2 (10), or 3 (9); rakers on first ceratobranchial 3 (1), 4 (1), 5 (8) or 6 (10); total gill rakers on first arch 5 (1), 6 (2), 7 (5), 8 (5) or 9 (7). Lateral line complete, nearly straight from upper margin of opercular cavity to base of caudal fin.

Pectoral and pelvic fins large, falcate, horizontal, with first lepidotrichium thickened at midsection, fleshy, unbranched. Pectoral-fin rays 8–11, modally 10. Pelvic-fin rays 6. Dorsal-fin rays 7. First ray of dorsal fin unbranched, stiffened basally, segmented distally and lacking serrae. Pterygiophore of first dorsal-fin ray in contact with first post-Weberian vertebra. First ray of pectoral fins enlarged, asymmetrically expanded near middle, unbranched, segmented distally, with minute fleshy serrations basally along ante-

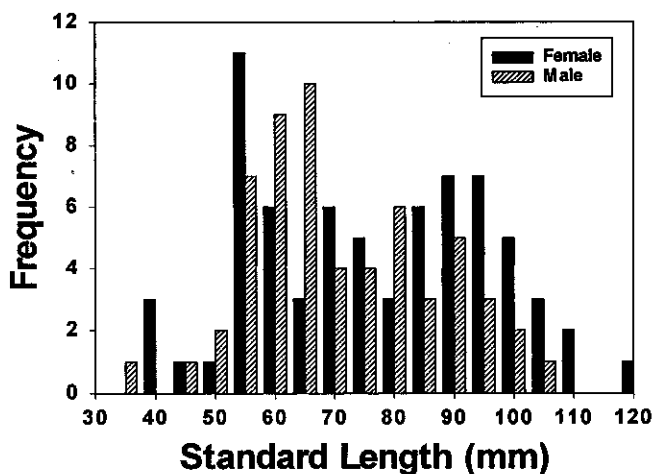


Fig. 4. Length-frequency distribution by 5-mm intervals of specimens of *Amphilius jacksonii* collected July 1996 (n = 128).

rior margin. Anal-fin rays 7-10, modally 10, first 2-3 unbranched; anal pterygiophores 8-10, modally 9 (2 lepidotrichia articulating on last pterygiophore). Adipose fin originating anteriorly to anal-fin origin, low-crowned, without posterior free flap and inserting on dorsum of caudal peduncle well in advance of caudal-fin base. Caudal fin moderately forked, tips of lobes slightly rounded. Principal caudal rays variable, modally 6+7, ranging from 5+6 to 7+7. Caudal fin with 7-10 (modally 8) upper and 6-10 (modally 9) lower procurent rays. Caudal hypural fusion pattern PH+1+2;3+4,5+6. Epidermis at base of caudal fin with a weakly crenulated free flap (see Skelton 1984: Fig. 2a). Preanal vertebrae 17-19 (modally 18); total vertebrae 31-33 (modally 32), both counts excluding first five of Weberian complex. Pleural ribs 8-10 pairs (modally 9). Gas bladder consisting of paired spherical vesicles, each partially encased by thin laminar outgrowths of bone (osteology of Weberian complex of *A. jacksonii* illustrated and described in detail by Chardon, 1968).

Coloration in life and alcohol similar, variable, heavily mottled. Background coloration pale yellowish, most noticeable on venter. Black or chocolate-brown pigmentation over entire dorsum and sides, broken into large contiguous blotches interspersed with smaller aggregations of chromatophores, especially in smaller specimens. Top of head nearly uniform dark brown. Top of barbels darkest, undersides and tips dusky. Most individuals exhibit 3-5 prominent, irregu-

lar bands or blotches laterally between pectoral and caudal fins, extending dorsally as saddles and often obscured by additional heavy pigmentation. Top of pectoral and pelvic fins dark brown, more lightly pigmented toward posterior margin. Dorsal fin with dense black pigmentation over rays, interradial membranes hyaline or lightly speckled. Adipose fin uniformly dark except for thin area along posterior margin. Caudal fin variably pigmented, usually with prominent large, irregular spots. Posterior edge of caudal peduncle with a prominent black or dark brown crescentic bar at base of caudal-fin rays.

Life-history aspects. Length-frequency analysis by 5-mm intervals of specimens collected in July 1996 suggest that three or more recruitment classes may have been represented (Fig. 4). Fish ranged in SL from 24 to 116 mm and putative recruitment classes corresponded to the following approximate size ranges: <24-50 mm (class 0; n = 10); 51-75 mm (class I; n = 69); >75 mm (class II+; n = 56). Females ranged in SL from 35-116 mm (n = 70) and males ranged in SL from 34-102 mm (n = 58); overall size-distribution between sexes was similar. Regression of log-transformed BW on log-transformed SL for females was $\log BW = -4.95 + 3.00 \log SL$ ($r^2 = 0.99$; n = 70), and for males was $\log BW = -5.06 + 3.08 \log SL$ ($r^2 = 0.99$; n = 60); the slope of each equation at or near a value of 3.0 indicates isometric growth in weight and length across the size range examined.

The female to male sex ratio of specimens

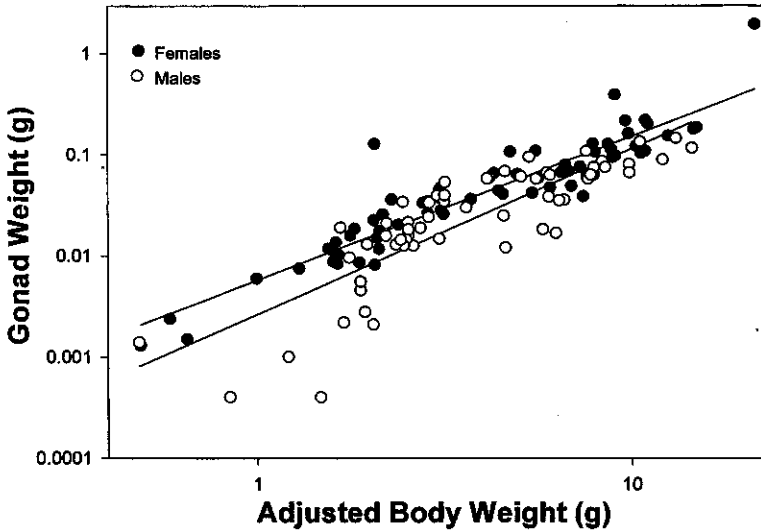


Fig. 5. Relationship between log gonad weight (g) and log adjusted body weight (g) in samples of *Amphilius jacksonii* collected July 1996.

examined internally was 1.15 to 1. Most specimens collected in the Dura River during July 1996 did not appear to be reproductively recrudescing, based on gross examination of gonads. The relationship between gonad weight and adjusted body weight was similar among females ($\log GW = -2.23 + 1.41 \log BW$; $r^2 = 0.93$, $n = 70$) and males ($\log GW = -2.56 + 1.58 \log BW$; $r^2 = 0.82$, $n = 60$) (Fig. 5). Three females had enlarged ovaries with previtellogenic, vitellogenic, or atretic oocytes.

Corbet (1961) examined gut contents of four specimens and reported that *A. jacksonii* fed on lithophilic insects, including ephemeropterans (species of Baetidae and *Afronurus*, family Heptageniidae), and trichopterans of the family Hydropsychidae. Our results confirm Corbet's observations, although we did not attempt to identify ephemeropterans or trichopterans below ordinal level. *Amphilius jacksonii* preys heavily on aquatic insects and has a limited diet relative to the total taxonomic diversity of benthic invertebrates in the Dura River. Larval trichopterans, ephemeropterans, and dipterans were the most commonly consumed prey items and made up the bulk of the diet in numbers as well as volume (Table 2). Relatively few species of these taxa were represented; trichopterans appeared to be dominated by one or two case-dwelling species, ephemeropterans may have been limited to only two species, and dipterans consisted mainly of a

few species of simuliids and chironomids or related families. Sand grains were common in stomachs as a result of the ingestion of whole trichopteran cases containing detritus and inorganic debris. A small number of terrestrial or winged invertebrates, including dipterans, hymenopterans, coleopterans, and thysanopterans were rarely eaten. Many stomachs were empty (31%) or had significant amounts of unidentifiable digested organic matter (37%), indicating that *A. jacksonii* probably feeds nocturnally, since all of the fish were collected by seine during daylight hours. *Amphilius jacksonii* feeds heavily on benthic aufwuchs as a result of this species' close microhabitat association with the substrate. Our limited sample precluded comparisons in diet among seasons or age and size classes.

Specimens of *A. jacksonii* were moderately internally parasitized. Of 130 fish examined, 44.6% had intact, unidentified nematodes and/or trematodes in the lower gastrointestinal tract. Nematodes occurred in 35.4% of the fish examined and numbered from 1-26 (mean = 3.2 ± 4.3 SD) per fish. Intact nematodes found in the muscular stomach of a small number of fish were assumed to be parasites that migrated from the intestine, but are included in the stomach contents (Table 2). An apparent single species of minute trematode occurred in 12.3% of the fish and numbered from 1-10 (mean = 2.6 ± 2.5 SD) per fish. Parasites were unattached within the gut or,

in the case of a few nematodes, embedded in the gastrointestinal epithelium. No other endo- or ectoparasites were observed. Skelton (1986) reported large nematodes (*Contracaecum* sp.) coiled in the mesenteries of *A. cryptobullatus* Skelton 1986.

Predators of *A. jacksonii* are unknown. Within the Dura River, fish diversity is low and the most likely vertebrate predators would be *Clarias* spp., otters, and aquatic snakes. In larger river systems where *A. jacksonii* occurs, large cichlids, bagrids, cyprinids, and wading birds could be potential predators.

Distribution and habitat use

Amphilius jacksonii was captured at all open-water sites sampled in the Dura River. However, we did not capture it in the Dura Swamp, a papyrus swamp at the headwaters of the system. It was also found in the Ruimi River, Mbuku River, and the lower reach of the Mahoma River, but was never recorded from any sites in the Mpanga drainage.

During our 2-year study of habitat use of fishes within the Dura River a total of 72 *A. jack-*

sonii were captured in minnow traps (32 at Dura River-Mainaro and 40 at Dura River-Kanyanchu); the number of specimens and timing of capture was inadequate to provide seasonal life-history information. Trapped fish appeared to be relatively solitary. In most cases (81%) only one fish was captured in a trap. In 9% of the traps, we captured two specimens, and in 4% and 6% of the traps, we captured three and four specimens, respectively.

Water temperature differed little between the main river channels of the two sites, but did vary over the months of study. Mean monthly values of water temperature averaged 18.8°C at Dura River-Kanyanchu ($\pm 1.5^\circ\text{C}$, SD, mean monthly range = 15.3-20.3°C) and 18.8°C at Dura River-Mainaro ($\pm 0.9^\circ\text{C}$, SD, range = 15.5-29.5°C). Average monthly oxygen values were higher at Dura River-Kanyanchu ($7.2 \pm 0.6 \text{ mg}\cdot\text{l}^{-1}$, range = 5.1-8.0 $\text{mg}\cdot\text{l}^{-1}$) than at the Dura River-Mainaro site ($6.4 \pm 1.4 \text{ mg}\cdot\text{l}^{-1}$, range = 4.6-9.9 $\text{mg}\cdot\text{l}^{-1}$). This may be associated with the shallower depth and faster current at Dura River-Kanyanchu (mean monthly depth = $49.1 \pm 14.9 \text{ cm}$, range = 33.5-90.7 cm; current rank = 1.23 ± 0.30 , range = 0.56-1.72) than at the Dura River-Mainaro site (depth = $76.3 \pm 24.3 \text{ cm}$, range = 40.5-122.8 cm; current rank

Table 2. Stomach contents of *Amphilius jacksonii* (n = 118). Abbreviations: % FO, percent frequency of occurrence; n, mean number of individuals per taxa (range in parentheses if greater than n = 1); % FV, percent frequency by relative volume (i.e., percentages of stomachs in which respective taxon fell within the indicated range as a percentage of total volume of all stomach contents).

| taxon | % FO | n | % FV | | | |
|-------------------------|------|------------|--------|---------|---------|----------|
| | | | 0-25 % | 26-50 % | 51-75 % | 76-100 % |
| Trichoptera | 37.3 | 3.3 (1-24) | 65 | 12 | 9 | 14 |
| Diptera (larval) | 37.3 | 6.3 (1-57) | 88 | - | 4 | 8 |
| Diptera (adult) | 3.4 | 2.3 (1-6) | 25 | 25 | 25 | 25 |
| Ephemeroptera | 34.8 | 4.0 (1-13) | 35 | 20 | 20 | 25 |
| Anisoptera | 5.1 | 1.3 (1-3) | 67 | 17 | - | 17 |
| Coleoptera (larval) | 4.2 | 1.6 (1-4) | 80 | - | 20 | - |
| Coleoptera (adult) | 3.4 | 1 | 50 | - | - | 50 |
| Hymenoptera | 0.8 | 1 | 100 | - | - | - |
| Insecta (unidentified) | 5.1 | 1 | 67 | - | 17 | 17 |
| Nematoda | 4.2 | 1 | 100 | - | - | - |
| Thysanoptera | 0.8 | 1 | 100 | - | - | - |
| Acari | 0.8 | 1 | 100 | - | - | - |
| Hydrozoa | 1.7 | 1.5 (1-2) | 100 | - | - | - |
| fish eggs | 0.8 | - | - | 100 | - | - |
| filamentous algae | 0.8 | - | - | 100 | - | - |
| seeds, sand grains | 16.9 | - | 71 | 24 | - | 5 |
| digested organic matter | 37.3 | - | 40 | 27 | 13 | 20 |
| empty stomach | 31.0 | - | - | - | - | - |

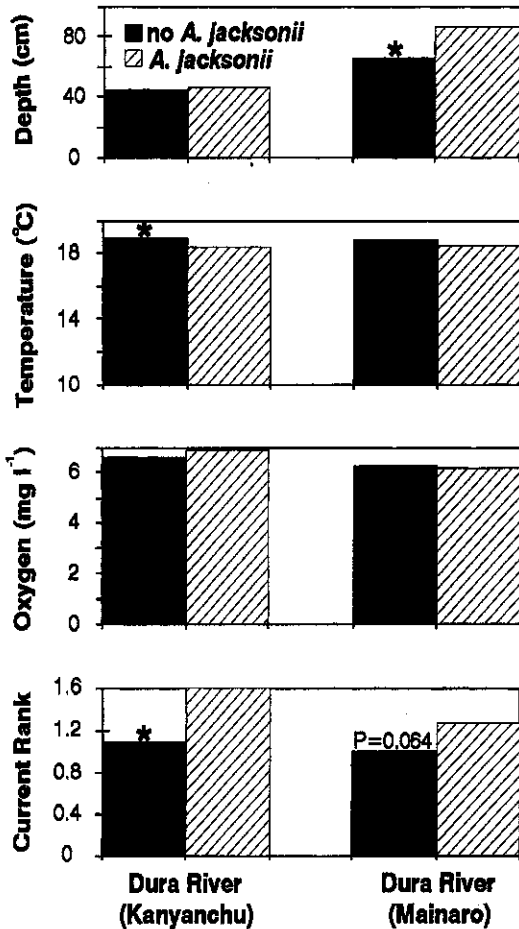


Fig. 6. Mean water depth (cm), water temperature ($^{\circ}\text{C}$), dissolved oxygen concentration ($\text{mg}\cdot\text{l}^{-1}$), and rank of water current for traps that captured *Amphilius jacksonii* and traps that did not capture *A. jacksonii* for two sites in the Dura River of western Uganda. Asterisks indicate significant differences ($P < 0.01$) in habitat variable between trap samples.

$= 1.16 \pm 0.21$, range = 0.73-1.53). At both sites the environmental characters of inundated forest pools differed markedly from main channel conditions with the exception of water temperature (Dura River-Kanyanchu forest pool: mean monthly temperature = $19.3 \pm 1.5^{\circ}\text{C}$, range = 17.9 - 21.5°C ; Dura River-Mainaro forest pool: mean = 19.0 ± 0.5 , range = 18.5 - 19.7°C). At Dura River-Kanyanchu, the forest pool averaged only 20.3 cm in depth (± 4.1 cm, range = 14.7 - 26.3 cm), and both dissolved oxygen and current were much lower than in the main river (mean monthly oxygen = $1.0 \pm 1.3 \text{ mg}\cdot\text{l}^{-1}$, range = 0.2 - $3.8 \text{ mg}\cdot\text{l}^{-1}$; current rank =

0.03 ± 0.07 , range = 0 - 0.2). At Dura River-Mainaro, the forest pool averaged 38.9 in depth (± 20.9 cm, range = 11.9 - 62.5 cm). Oxygen levels were higher than the forest pool at Dura-River-Kanyanchu but still much lower than the main river at Dura River-Mainaro, averaging $3.7 \text{ mg}\cdot\text{l}^{-1}$ ($\pm 0.8 \text{ mg}\cdot\text{l}^{-1}$, range = 2.8 - $4.5 \text{ mg}\cdot\text{l}^{-1}$). Current was negligible in the forest pool (mean monthly current rank = 0.01 ± 0.03 , range = 0 - 0.07).

None of the 72 fish that were marked during the study were recaptured. We therefore assumed that each capture period was independent of the previous one and combined our trap samples across months to evaluate environmental correlates of habitat use. *Amphilius jacksonii* were never captured in the forest pools over the course of the study. Two other species in the river system (*Clarias liocephalus*, *Barbus neumayeri*) were captured frequently in the inundated forest pools during the high flood periods, demonstrating that these areas are connected to the main river and available for colonization.

Because of the low degree of variation in the numbers of *A. jacksonii* captured in individual traps, we used the presence or absence of the species to detect environmental correlates of habitat use. We compared mean water temperature, dissolved oxygen concentration, current rank, and water depth between traps where *A. jacksonii* were captured and traps where they were not captured. Both the main river and flooded forest sites were included in the analysis. At Dura-River-Kanyanchu, traps with *A. jacksonii* were characterized by significantly cooler water temperature ($t = 2.02$, $P = 0.044$) and faster current ($t = 3.63$, $P < 0.001$) than traps that did not capture *A. jacksonii* (Fig. 6). At Dura River-Mainaro, traps with *A. jacksonii* were found in significantly deeper water ($t = 2.72$, $P = 0.007$) and marginally faster current ($t = 1.86$, $P = 0.064$) than traps that did not capture *A. jacksonii* (Fig. 6).

To examine the relationship between water current and habitat use in more detail, we calculated the expected number of fish in each current category (0, 0.5, 1.0, etc.) based on the availability of habitat in each current category, and compared expected to observed habitat use using a Chi-squared Goodness of Fit test. At both sites, *A. jacksonii* were never found in backwaters of the main river channels or inundated forest areas where flow was absent. At Dura River-Kanyanchu, *A. jacksonii* were found in fast flowing current more than would be expected if habitats

were used randomly ($\chi^2=32.4$, $P<0.005$), while at Dura River-Mainaro, *A. jacksonii* were found in moderately flowing current more than would be expected, but fast-flowing current less than would be expected if habitats were chosen at random ($\chi^2=10.89$, $P<0.05$).

Discussion

Amphilius jacksonii exhibits relatively little variation in meristic characters and caudal fin morphology, unlike the widespread *A. uranoscopus* from southeastern Africa (Skelton, 1984). It does, however, vary widely in pigmentation similar to both *A. uranoscopus* and *A. natalensis* (Jubb, 1967; Skelton, 1984), and, presumably, additional species. We interpret the reduced number of principal caudal fin rays and the presence of a thin epidermal fold at the base of the caudal fin as derived character states that may be synapomorphic among at least some west African species of *Amphilius* (including *A. platychir* and *A. jacksonii*). However, current available information precludes any hypotheses about phylogenetic relationships of *A. jacksonii* at the species level.

Our limited data do not provide the necessary seasonal information to determine reproductive period, age and size at maturity, fecundity, and other phenological aspects of reproduction in *A. jacksonii*. In southern Africa, *Amphilius* spp. breed during summer months (Skelton, 1993; Marriott et al., 1997), and, based on limited data, Teugels et al. (1992) noted that some other siluriforms in western Africa may breed year-round but mostly during the rainy season. As determined from gonosomatic indices and histological study, Marriott et al. (1997) found that *A. natalensis* was reproductively active for a protracted period from August to February in South Africa, coinciding with the rainy season. Marriott et al. (1997) also concluded that female *A. natalensis* were asynchronous, iteroparous spawners capable of producing more than one clutch in a single reproductive season. In the streams and rivers of Kibale NP the cyprinid *Barbus neumayeri* shows two peaks of reproductive activity per year associated with bimodal rainy periods (Chapman & Frankl, in press). Additional data are needed to determine if *A. jacksonii* conforms to this pattern. Because of the possibility of two breeding periods per year, we are unable to differentiate year classes from

our size frequency analysis. Our data suggest that fish may live 2+ years depending on whether recruitment occurs annually or twice a year. Marriott et al. (1997) observed a skewed sex ratio dominated by larger females in their samples of *A. natalensis*. We found no difference in distribution of size classes between males and females and no skewed sex ratio in samples of *A. jacksonii*.

In the Dura River, *A. jacksonii* feeds predominantly on benthic aquatic insects. We were unable to determine if there are seasonal or age- or size-class differences in diet. However, qualitative dip-net samples of benthic invertebrates from the Dura River substrate exhibit low seasonal variation in diversity and relative abundance of individual taxa (L. J. Chapman, unpubl. data). Marriott et al. (1997) did not examine possible seasonal variation in the diet of *A. natalensis*, but they did find differences among size classes, with larger fish consuming a greater variety of prey items. Like this study, Marriott et al. (1997) found that larval dipterans and ephemeropterans were important prey items in *A. natalensis*, with trichopterans appearing commonly in stomach contents but contributing less by volume or index of relative importance. Thus, *A. jacksonii* exhibits a diet very similar to that of *A. natalensis* and feeds on invertebrates that are characteristic of fast flowing, clear streams.

Like other members of the genus, *A. jacksonii* is a rheophilic species that inhabits flowing, well-oxygenated waters (Skelton, 1993). At Dura River-Kanyanchu, *A. jacksonii* selected areas of fast-flowing current, while areas of moderate current were selected at Dura River-Mainaro. The moderately flowing areas at Dura River-Mainaro were often the deeper main channel sites. We noticed at both sites that *A. jacksonii* was commonly associated with structurally complex bottom habitat (e.g., rocks, deadfall). At Dura River-Mainaro, much of the bottom of the central deeper channel is covered by mud and sand, with much less rocky habitat and submergent structural complexity than at Dura River-Kanyanchu. Areas of high current at Dura River-Mainaro may not be selected by *A. jacksonii* as frequently as areas of moderate flow because of the low availability of structure.

Our survey work in western Uganda expands the previously known distribution of *A. jacksonii* to include an additional four river tributaries of the Lake Edward-George system. The absence of

A. jacksonii in the Mpanga River (upstream of the Mpanga Falls) has been corroborated by a year-long study of the ichthyofauna at two sites using minnow traps, seines, and gill nets on a monthly basis (Chapman & Chapman, unpubl. data). The Mpanga Falls (Fig. 1), approximately 75 m in height, may pose a formidable upstream barrier to the dispersal of *A. jacksonii*, but we have yet to sample beneath the falls. *Amphilius jacksonii* is common in suitable habitats within its range in western Uganda, and currently faces no widespread ecological threats to its existence.

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