Notes on the electric organ discharges (EODs) of four *Mormyrus*-species (Osteoglossomorpha: Mormyridae) from the Nilo-Sahelo-Sudan ichthyofaunal province of Africa

by

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Abstract. – Field studies on the electric organ discharges (EODs) of *Mormyrus* species are rare, likely due to their biology hindering live capture in large numbers. Here the EODs of four Nilo-Sahelo-Sudanic species, *Mormyrus caschive* Linnaeus, 1758, *M. kannume* Forsskål, 1775, *M. hasselquistii* Valenciennes, 1847 and *M. rume* Valenciennes, 1847, are compared and discussed. Their discharges are largely equal to each other, mainly showing differences in length and peak of Fourier transformation with less pronounced differences in the relative amplitude of phases within an EOD. The discharge properties allow species discrimination, at least within eco-regions, and thus likely play a role in species recognition.

Résumé. – Notes sur les décharges de l'organe électrique (DOEs) de quatre espèces de *Mormyrus* (Osteoglossomorpha: Mormyridae) de la région nilo-soudanienne de l'Afrique.

Il y a peu d'enregistrements de décharges de l'organe électrique (DOEs) des mormyres en milieu naturel, probablement en raison de leur biologie les rendant difficiles à capturer en grand nombre. Ici, les DOEs de quatre espèces nilo-soudaniennes, *Mormyrus caschive* Linnaeus, 1758, *M. kannume* Forsskål, 1775, *M. hasselquistii* Valenciennes, 1847 et *M. rume* Valenciennes, 1847, sont comparées et discutées. Les décharges sont très similaires les unes aux autres, et ne diffèrent entres elles que dans la longueur et les pics de la Transformée de Fourier et, dans une moindre mesure, dans l'amplitude relative de chacune de leurs phases. Les différences entre les propriétés de ces décharges permettent d'identifier les espèces, au moins dans chaque éco-région, et jouent probablement un rôle dans la reconnaissance interspécifique.

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Within the family Mormyridae the genus *Mormyrus* Linnaeus, 1758 is easily recognizable by its long dorsal fin. So far there is no indication from genetic studies that the genus may not be monophyletic (Sullivan *et al.*, 2000; Lavoué *et al.*, 2003). Taxonomy within the genus on the other hand is less clear, due to some synonymisations and the uncertain status of sub-species (Lévêque and Bigorne, 1985). A systematic revision of the approximately 20 species is necessary. The genus *Mormyrus* is widely distributed throughout Africa with *M. caschive* Linnaeus, 1858 and *M. kannume* Forsskål, 1775 from the Nile basin in the North, *M. longirostris* Peters, 1852 from the Zambezi basin in the South, *M. rume* Valenciennes, 1847 and *M. hasselquistii* Valenciennes, 1847 from the Senegal basin in the West and *M. casalis* Vinciguerra, 1922 from Somalia in the East. The Congo basin seems to be a centre of diversity with 7 of 22 presently recognized species occurring here (Gosse, 1984; Eschmeyer, 2014; Froese and Pauly, 2014). In comparison with other members of the family Mormyridae they reach considerable sizes with many species surpassing 30 cm standard length (SL) and some even reaching 1 m SL. Therefore the genus also has a certain importance for fisheries.

Like all members of the Mormyridae, *Mormyrus* produces electric organ discharges (EODs) for communication (Khait *et al.*, 2009; Gebhardt *et al.*, 2012), orientation and object detection (general reviews for mormyrids by e.g. Moller, 1995; Kramer, 1996; von der Emde, 1999, 2004, 2006; von der Emde and Schwarz, 2002; Caputi and Budelli, 2006). EODs seem important for species recognition and are species-specific with a certain degree of intraspecific variability (e.g. Moritz *et al.*, 2008, 2009). EOD waveform, i.e. voltage alteration over time, primarily depends on the anatomy of the electric organ positioned in the caudal peduncle (Bass, 1986; Alves-Gomes and Hopkins, 1997; Hopkins, 1999). Changes of EOD waveform may occur, e.g. during growth (Kirschbaum, 1995) or depending on hormonal status (Carlson *et al.*, 2000). But such changes require time and cannot be applied within an on-going communication.

Data on the biology on *Mormyrus* species is limited. All species are most likely predominantly nocturnal and seem to prefer larger bodies of water which are in most cases main

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channels of rivers, often close to rocks (Crawford and Hopkins, 1989). Spawning behaviour seems to be closely related to the seasons taking place at the beginning of the rainy season. At least *M. rume* Boulenger, 1898 was successfully reproduced in captivity (Kirschbaum and Schugardt, 2002). During the reproductive phase external sexual dimorphism is expressed by an indentation of the body wall on the anal-fin base of males (Moller *et al*., 2004).

The limitation of biological field data from *Mormyrus* species probably arose from their life history, in which they prefer deeper bodies of water with many structures, such as rocks. Catching these species alive and in good condition is almost impossible, especially in high numbers. Water transparency in typical African river systems is very low to virtually absent. Therefore direct observations with EOD recordings, e.g. by scuba-diving as done for *Mormyrops* in Lake Malawi (Arnegard and Carlson, 2005), does not seem feasible.

The study presented here is based on the EODs of 47 *Mormyrus* specimens of four species from several different locations in West and Northeast Africa. The rarity of the available data of field recorded EODs from the genus justifies the present study.

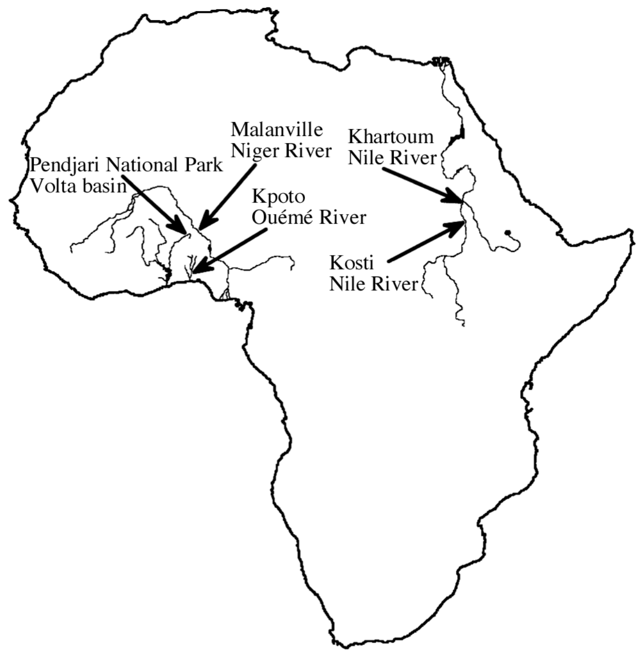

Figure 1. - Outline of the African continent showing sampling sites of the study. Only sampled river systems are displayed.

MATERIAL AND METHODS

Collecting specimens

Sampling took place during two field trips to Burkina Faso and Benin from February to May 2005 and January to April 2007 as well as during a two week field trip to Sudan in January 2006. Sampling sites are displayed in figure 1. All together EODs of 47 specimens of four different species could be recorded. These were eight specimens of *Mormyrus caschive* from the White Nile at Kosti, Sudan (68-112 mm SL), three specimens of *M. kannume* from the White Nile at Khartoum, Sudan (169-193 mm SL), 30 specimens of *M. hasselquistii* from different locations within the Pendjari National Park, Volta basin, Benin (138-249 mm SL) and six specimens of *M. rume*: three from different locations within the Pendjari National Park, Benin (156-187 mm SL), two from the Niger River at Malanville, Benin (159 and 174 mm SL), and one from the Ouémé River at Kpoto, Benin (230 mm SL). Sampling took place using a small seine (2.0 x 1.2 m) with 5 mm mesh size at all locations and traps of 30 cm diameter with 20 mm mesh size and 8 m leading net for the locations in the Volta basin. Mormyrids were sometimes located before capture using an acoustic mormyrid detector (custom built by the electronics shop of the University Bonn). Captured specimens were kept in buckets with water from the collecting location and were equipped with aeration in the case of longer transports or very high temperatures. Although a single specimen of the rare *M. niloticus* (Bloch & Schneider, 1801) was collected at the White Nile in Kosti, it did not survive until EOD measuring; apparently the species is sensitive to stress or low oxygen concentrations. Also two specimens of *M. macrophthalmus* Günther, 1866 collected by fishermen in the Niger River at Malanville using gill nets were too damaged to allow EOD recording.

EOD recording

EODs of collected specimens were recorded shortly after sampling in a 12-litre plastic tank with water from the collection site. A SDS 200 digital oscilloscope (200 MHz bandwidth, 100 MS/s using one channel; softDSP) was equipped with an amplifier and connected to a laptop. The amplifier was disabled for most *Mormyrus* specimens (amplification: 1x) due to their strong discharges, but for a few small specimens it was used at 10-times amplification. EODs were recorded by placing the positive electrode close to the head and the negative electrode close to the tail. All signals were recorded with the same settings to allow for comparison. Since all signals were recorded using AC coupling on the oscilloscope input, long duration EODs show a small peak, p-POS, as an artefact of the high-pass filtering. Therefore records do not show 'real' EODs, but are measurements of EODs under the condition of filtering effects by AC coupling. For the long signals of *Mormyrus* species these settings result in the alteration of the very long negative phase into a short negative phase followed by a small positive phase. Comparisons between recorded signals and studies using the same technique (e.g. Kramer, 2013) are neverthe-

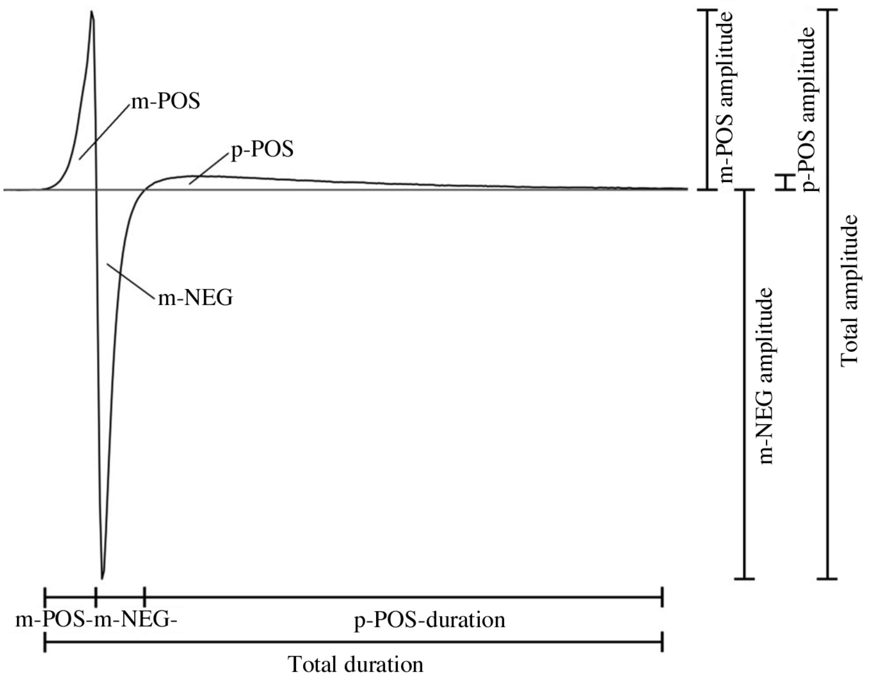

Figure 2. - AC coupled measurement of electric organ discharge (EOD) of *Mormyrus caschive* (97 mm SL; White Nile at Kosti, Sudan) showing nomenclature of waveform characteristics as used in this study. m-POS = main positive phase; m-NEG = main negative phase; p-POS = posterior positive phase. Beginning and end of the signal is given by exceeding 1.5% of the total amplitude; beginning and end of phases within the signal by zero-crossings.

Table I. - Characters of AC coupled signal measurement from *Mormyrus* species in this study. EOD-Dur = total EOD duration in μs; m-POS Dur = duration of main positive phase in μs; m-NEG Dur = duration of main negative phase in μs; p-POS Dur = duration of posterior positive phase; m-POS Amp = amplitude of main positive phase as percentage of total amplitude; P1 amp = amplitude of main positive phase as percentage of main negative phase as given in Kramer (2013) for equal comparisons; p-POS amp = amplitude of posterior positive phase as percentage of total amplitude; FFT-peak = peak of fast Fourier transformation in Hz.

Species, location and number	EOD-Dur (μs)	m-POS Dur (μs)	m-NEG Dur (μs)	p-POS Dur (μs)	m-POS Amp	P1 amp	p-POS Amp	FFT-peak (Hz)
M. caschive, White Nile; N = 8								
Mean	2510.00	353.00	468.00	1690.00	31.40	0.460	2.40	1398.00
Min.	2080.00	320.00	400.00	1320.00	29.20	0.413	2.10	1184.00
Max.	2940.00	400.00	520.00	2020.00	35.80	0.559	2.60	1642.00
S.D.	112.50	10.65	18.10	88.96	0.87	0.019	0.06	61.83
M. kannume, White Nile; N = 3								
Mean	7920.00	533.00	1067.00	6320.00	44.60	0.807	4.10	354.00
Min.	7280.00	480.00	1040.00	5680.00	43.60	0.773	3.80	266.00
Max.	8800.00	560.00	1120.00	7120.00	46.00	0.853	4.60	439.00
S.D.	454.90	26.67	26.67	423.32	0.72	0.024	0.25	50.24
M. hasselquisti, Pendjari; N = 30								
Mean	13756.00	1137.00	2252.00	10367.00	34.30	0.529	4.50	93.00
Min.	6600.00	680.00	1360.00	4100.00	23.30	0.304	1.20	39.00
Max.	24400.00	1800.00	4400.00	18200.00	42.00	0.723	9.00	180.00
S.D.	850.21	60.74	149.88	661.30	0.76	0.017	0.29	7.84
M. rume, several locations; N = 6								
Mean	2567.00	340.00	517.00	1710.00	32.20	0.477	2.00	1137.00
Min.	1600.00	280.00	360.00	960.00	28.20	0.393	1.50	342.00
Max.	3840.00	520.00	760.00	2940.00	35.00	0.538	3.10	1819.00
S.D.	356.30	37.95	58.52	295.92	1.10	0.024	0.24	207.45

less granted. After EOD recording for all specimen standard length (SL) and total length (TL) were measured. Selected voucher specimens were anaesthetized using benzocaine and were fixed in 4% formalin. The specimens were later transferred into 70% ethanol and are partly registered at the Deutsches Meeresmuseum Stralsund (DMM).

Data analysis

Naming EODs (Fig. 2) followed Moritz *et al.* (2008, 2009). The beginning and end of a signal was defined in this study to be 1.5% deviation from the average zero line in relation to the overall peak-to-peak amplitude range. For analysis a custom-made measuring programme for 'R' (R-project: http://www.R-project.org) was used. As a result length, relative amplitude and area for each phase were given, as well as total signal length and peak of Fourier transformation (FFT-peak). Knowing that many parameters within an EOD are dependent on each other (Westby, 1984) and therefore the use of principal component analyses is limited, such an analysis was performed using PAST version 2.71 (http://folk.uio.no/ohammer/past/index_old.html). The same program was used for descriptive statistics as given in table I.

For a better comparison within the regions the species are not presented alphabetically in graphs and tables. The purely Nilotic species (*M. caschive* and *M. kannume*) are presented first, followed by *M. hasselquistii* which occurs in the Nile system and West Africa, and finally *M. rume,* which is widely distributed in West African but absent from the Nile basin.

RESULTS

The measurements of the EODs of the four investigated *Mormyrus* species exhibited the same general pattern (Fig. 3): a head-positive phase (mposP) followed by a slightly larger head-negative phase (mnegP) and completed by a small, but relatively long second head-positive phase (pposP). The amplitude of mnegP is roughly double that of the absolute value of mposP, except for *M. kannume* where the mposP-amplitude is expressed as approximately 80% and the mnegP-amplitude is expressed as 45% of the total amplitude (Fig. 3, Tab. I). The second head-positive phase (pposP) has to be regarded as a filtering effect of the recording device. Parameters of pposP nevertheless depend on the characteristics of the original signal. An overview of the characteristics of the signal records is given in table I. Direct comparison of three characters, EOD duration, amplitudes of main positive phase and peak of Fourier transformation (FFT-peak), as boxplots (Fig. 4), show the importance of total EOD duration and FFT-peak for discrimination of the species. For sympatric species there is no overlap in FFT-peak and only some overlap in EOD duration for *M. kannume* and *M. hasselquistii*. Differences in waveform shape by relative amplitudes of phases are only expressed in the purely Nilotic species, which can thus be distinguished by

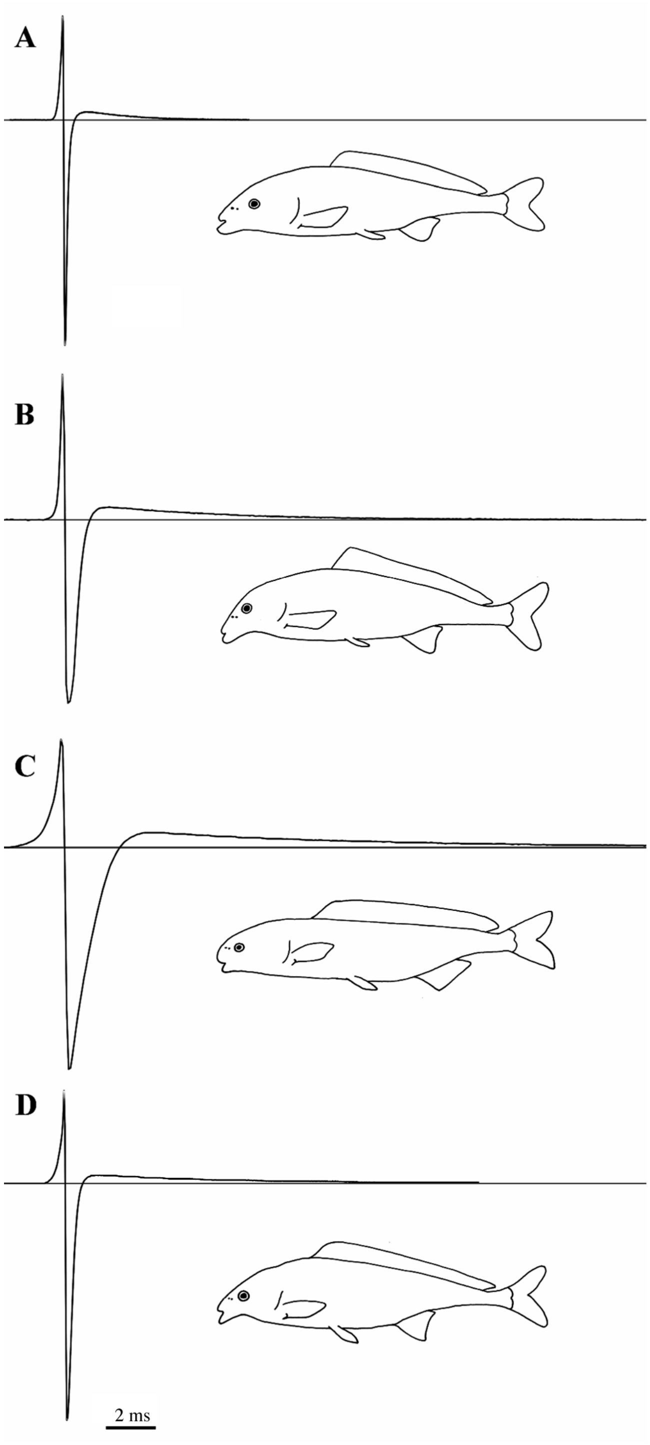

Figure 3. - Exemplary AC coupled measurements of electric organ discharges (EODs) of *Mormyrus* species. **A**: *M. caschive*, 97 mm SL, White Nile at Kosti, Sudan. **B**: *M. kannume*, 169 mm SL, White Nile at Khartoum, Sudan. **C**: *M. hasselquistii*, 188 mm SL, Mare Diwouni, Pendjari National Park, Benin. **D**: *M. rume*, 230 mm SL, Ouémé at Kpoto, Benin.

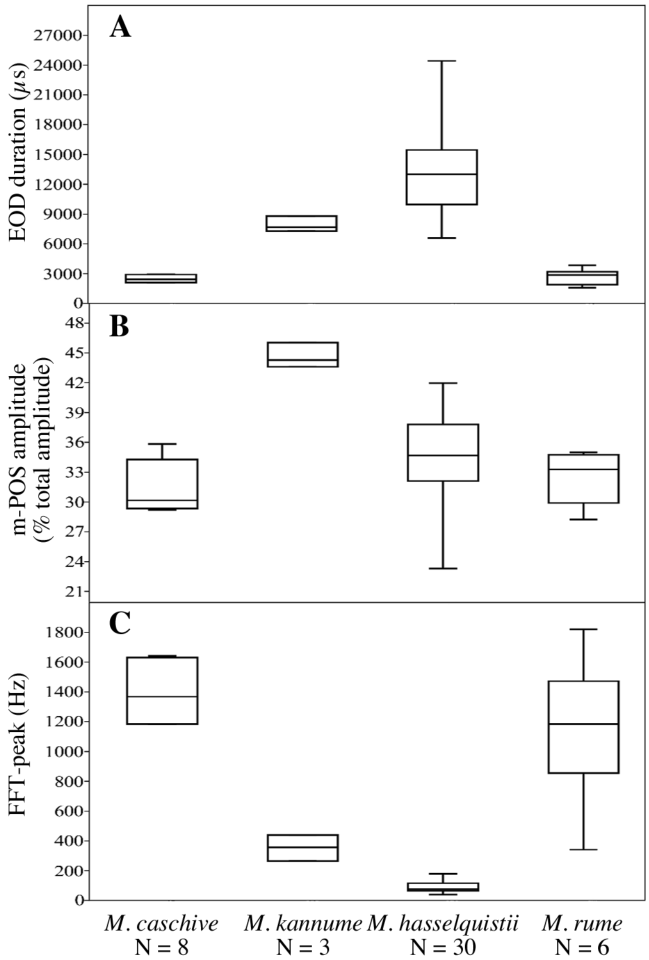

Figure 4. - Boxplots of selected signal characteristics. **A**: Total EOD duration in μs; **B**: Relative amplitude of main positive phase; **C**: Peak frequency of fast Fourier transformation in Hz.

such characters (Fig. 4). Apparent inverse differences in the variability of EOD length and FFT-peak between *M. hasselquistii* and *M. rume* are partly due to the logarithmic nature of frequency calculations. In a logarithmic scatterplot of these two characters, the correlation of both becomes visible and variability within and between the species is not remarkable (Fig. 5). The scatterplot, however, shows no strict correlation of these two parameters, e.g. EODs of the same length have different FFT-peaks in *M. kannume* and *M. hasselquistii*. It seems, as though there would be two correlation lines within *M. hasselquistii*: five specimens show a much higher peak frequency than conspecifics with EODs of the same length (Fig. 5). This finding cannot be explained by different sampling localities or by the size of the specimens. There may be a relation to the sex of the specimens, which cannot be tested with the present dataset. Similar correlation lines may be present in *M. rume*, but there is much too little data for such a statement.

An evaluation of the EOD waveform characteristics using a principal component analyses (PCA), confirmed the prominent importance of absolute duration of the signal and even more important it's FFT-peak. The first factor of the PCA explained 99.90% of the variance and is almost exclusively loaded (0.9993) by the FFT-peak. The second factor of the PCA explained 0.08% of the variance and is loaded to 98.84% by total EOD duration.

DISCUSSION

EOD characteristics in *Mormyrus* species

The general EOD waveform for the genus *Mormyrus* seems quite uniform with a head positive main phase, followed by a large, long lasting negative main phase (e.g. Moller *et al.*, 1979; Crawford and Hopkins, 1989; Gebhardt *et al.*, 2012). Depending on filtering of the measuring device signal records can transform the long negative main phase into a short negative main phase followed by a second small positive phase (Kramer, 2013; this study). Only *M. tenuirostris* Peters, 1882 from East Africa strongly deviates from this pattern by expressing a simple monophasic head positive pulse (Kramer, 2013). More variation by irregular slope of the phases or higher variability of phase duration seems to be present in *Mormyrus* species from the Congo basin (Lavoué *et al.*, 2012 [Fig.2]), but detailed studies are not yet available. The rather simple EOD waveform shape likely originates from a relatively simple morphology of the electrocytes receiving their innervation via non-penetrating stalks (Sullivan *et al.*, 2000; Lavoué *et al.*, 2003).

EOD-waveform and species recognition

The investigated Nilo-Sahelo-Sudanic *Mormyrus* species can easily be recognized on their EOD-waveform characteristics. Although the use of FFT-peak may have limits in some mormyrid species with highly variable multiphase EOD, e.g. *Pollimyrus isidori* (Valenciennes, 1847) (Moritz *et al.*, 2008), this is not the case for *Mormyrus* species, as they show a generally uniform EOD-waveform. It is possible that these waveform characteristics are also used for species recognition in the wild. At least for some mormyrids it was shown that they are able to recognize the EODs of their own species (Hopkins and Bass, 1981; Graff and Kramer, 1992) and it seems evident that EODs are used in species recognition (Sullivan *et al.*, 2002; Arnegard and Hopkins, 2003; Arnegard *et al.*, 2006). Mormyrids are, however, anatomically limited in EOD waveform shape alteration by the anatomy of their electrocytes (Bass, 1986; Alves-Gomes and Hopkins, 1997; Hopkins, 1999). Therefore variability of EOD waveform shapes within a genus is usually limited to some parameters. These are mostly total EOD duration, relative size of phases (but usually not amount of phases) and, somehow at least partly correlated, FFT-peak. Accord-

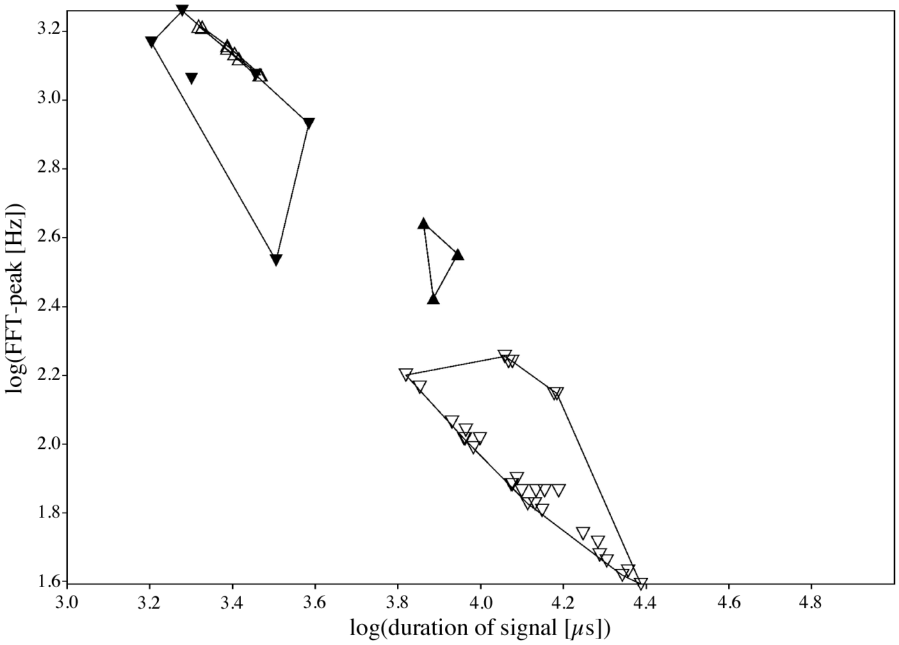

Figure 5. - Scatterplot of logarithmic total signal duration in µs versus logarithmic peak of fast Fourier transformation in Hz. Each symbol represents a single EOD from *M. caschive* (open triangle, n = 8), *M. hasselquistii* (open inverse triangle, n = 31), *M. kannume* (filled triangle, n = 3) and *M. rume* (filled inverse triangle, n = 7).

ingly it seems that congeners of different mormyrid genera have co-evolved species-specific waveforms within river basins in similar ways. Such apparent convergent waveform alterations were reported for *Petrocephalus*-species of the Ogooué basin (Lavoué *et al.*, 2004) the Volta basin (Moritz *et al.*, 2009) and the Northern Congo basin (Lavoué *et al.*, 2010). Species recognition by EOD-characteristics may also be an important mechanism for reproductive isolation and thus driving force in the evolution of weakly electric fish (Moller and Serrier, 1986; Crawford and Hopkins, 1989; Alves-Gomes and Hopkins, 1997; Arnegard *et al.*, 2005). The present study on *Mormyrus* species from the Nilo-Sudanic region cannot assure these hypotheses due to its limitations. However, findings do not contradict any of these assumptions and the following statements seem to apply also for *Mormyrus* species: 1, within river basins species use species-specific EODs; 2, EOD waveforms likely serve in species recognition; 3, the evolutionary mechanisms to form specifiable EODs between closely related sympatric species may be very similar in different genera of mormyrids.

Limitation of the study

This study deals with recorded signals altered by the settings of the measuring devices and not with original EODs. Comparisons between signal records are nevertheless permitted. Using filtering by AC coupling can decrease background noise and may facilitate species discrimination by displaying the signal waveform on a screen for a human observer. All together the number of specimens per species in this study is quite limited. Furthermore specimens originate from different locations and it has been shown, that location may have a high influence on EOD expression (Moritz *et al.*, 2008). Also the species sampling for the regions is incomplete, as the EODs of *M. niloticus* and *M. macrophthalmus* could not be recorded and for *M. hasselquistii* only specimens from West Africa, but not from the Nile basin were available. Finally, the study deals with rather small individuals of less than 20 cm SL for the three species reaching up to 100 cm in SL, *M. caschive*, *M. kannume* and *M. rume*. As explained above, these species are difficult to sample alive and in high numbers. Therefore, the discussion of the results presented here is justified and reasonable, if conclusions are drawn with an awareness of the previously mentioned limitations.

Conclusions

Species specificity of EODs in the genus *Mormyrus* allows species discrimination and likely also serves in species recognition within an eco-region. However, for definitive statements more data are needed: more specimens per river basins as well as all species of the genus for a respective area.

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