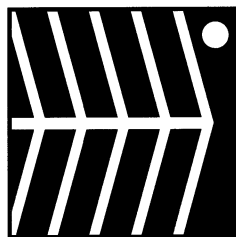# A field study of African elephantfish (Mormyridae, Teleostei): Electric organ discharges in *Marcusenius macrolepidotus* (Peters, 1852) and *Petrocephalus catostoma* (Günther, 1866) as related to sex

JAZ

Bernd KRAMER

B. Kramer
Zoological Institute of the University,
D–93040 Regensburg, Germany
E-mail: bernd.kramer@biologie.uni-regensburg.de

The question was studied of whether the waveforms of the electric organ discharges (EODs) of mormyrid fish differ between the sexes, as required for the hypothesis of mate recognition by EOD waveform. Two sympatric species, *Marcusenius macrolepidotus* (*N* = 84) and *Petrocephalus catostoma* (*N* = 37), were collected in the Upper Zambezi System (East Caprivi, Namibia). The EOD of *M. macrolepidotus*, as recorded in the field, is a biphasic pulse resembling a single–cycle sinusoid; it is of short and almost constant duration in immatures (416.4 ± S.E. 13.71 μs; 25°C) and females (519.6 ± 34.3 μs), whereas in the population of males (2980 ± 330.3 μs), EOD duration increased dramatically with the onset of sexual maturity (up to 11.5fold: 4779 μs). The increase of male EOD duration occurred in an abrupt, almost step–like fashion at 12.3–12.4 cm standard length. At that size, all males had sexually mature testes; there was a positive correlation of EOD duration with histological testis maturity stage. The EOD of *P. catostoma*, as also recorded in the field, is a triphasic pulse (head–positive, –negative, –positive) of a duration between 291 and 760 μs (average in adult females, 419.3 ± 25.6 μs; males, 395.3 ± 17.4 μs; 25°C). Exclusively in adults (that is, fish >40% of the maximum species size) the amplitude of the second head–positive (P2–) phase of the EOD decreased with standard length; in spite of considerable overlap, males showed significantly higher P2 amplitudes than females of the same size. Therefore, in *M. macrolepidotus* a sexual dimorphism with two distinct forms of EOD is present, whereas in *P. catostoma* a small, but statistically significant "sex difference" with wide overlap was found that one would not detect in an individual pair of fish.

Résumé français au verso.

Key words: electric organ discharge, sexual dimorphism, waveform analysis

Étude de Mormyridés (poissons téléostéens) en milieu naturel: Décharges électriques de Marcusenius macrolepidotus *(Peters, 1852) et de* Petrocephalus catostoma *(Günther, 1866) en relation avec le sexe* - On a étudié la question de savoir si la forme de la décharge de l'organe électrique d'un mormyridé dépendait du sexe ainsi que le prévoit l'hypothèse selon laquelle ces poissons nocturnes reconnaîtraient l'autre sexe par la forme de la décharge. Deux espèces sympatriques, *Marcusenius macrolepidotus* (*N* = 84) et *Petrocephalus catostoma* (*N* = 37) du système du Zambezi Supérieur (Est–Caprivi, Namibie) ont été étudiées. La décharge de *M. macrolepidotus*, telle qu'elle a été enregistrée sur le terrain, est une impulsion biphasique ressemblant à une sinusoïde à cycle unique; elle est d'une durée brève et presque constante chez les poissons juvéniles (416.4 ± 13.71 µs; 25°C) et chez les femelles adultes (519.6 ± 34.3 µs), tandis que, dans la population des mâles (2980 ± 330.3 µs), la durée de la décharge augmente de façon spectaculaire lors de la puberté (jusqu'à 11.5 fois: 4779 µs). Cette augmentation de durée de la décharge mâle s'effectue de manière abrupte à 12.3–12.4 cm de longueur standard. Les testicules des mâles de cette taille sont tous matures; plus le testicule est mature d'un point de vue histologique, plus la décharge d'un certain mâle est longue. La décharge de *P. catostoma*, également enregistrée sur le terrain, est une impulsion triphasique (tête-positive, –négative, –positive) d'une durée de 291 à 760 µs (moyenne pour les femelles adultes, 419.3 ± 25.6 µs; mâles, 395.3 ± 17.4 µs; 25°C). Ce n'est que chez les adultes (longueur supérieure à 40% de la taille maximum pour cette espèce) que l'amplitude de la deuxième phase positive (P2) de la décharge décroît avec la taille du poisson. Pour les poissons adultes de même taille et en dépit d'un chevauchement considérable d'amplitude, la phase P2 est plus forte chez les mâles que chez les femelles. En conclusion, la décharge de *M. macrolepidotus* révèle un dimorphisme sexuel parce qu'elle se présente sous deux formes distinctes; par contre, chez *P. catostoma*, la différence est moins importante bien qu'elle soit statistiquement significative. Contrairement à *M. macrolepidotus*, il n'est pas possible de reconnaître le sexe d'un *P. catostoma* uniquement par la forme de sa décharge.

INTRODUCTION

Fishes of the African freshwater family Mormyridae are active during night when their electric organ discharges (EODs) serve in active electrolocation (reviews, Bastian 1990, 1994) and communication (reviews, Hopkins, 1988; Moller, 1995; Kramer, 1990, 1994, 1996). Whereas the sequence of inter–discharge time intervals, or IDI pattern of EOD pulses, carries information in intraspecific (Kramer, 1979) and inter–specific communication (Kramer & Kuhn, 1994), it is not clear what kind of information is carried by the waveform of a (single) EOD pulse that varies widely between species (Hopkins, 1980; Kramer, 1996). Although the EOD waveform is constant for an individual there is some variation between individuals of the same species (Westby & Kirschbaum, 1982; Bratton & Kramer, 1988), and these differences are recognized by trained, food–rewarded *Pollimyrus isidori* even if only slight (Graff & Kramer, 1992). Thus mate selection by EOD waveform would be possible if the EOD waveform was a good indicator of sex.

The present paper addresses the question of whether the waveform of EOD pulses varies in a way that would allow mate selection, that is, whether or not there are sexually dimorphic EODs in two mormyrid species. In spite of a number of attempts this question is still open (see also Kramer, 1994).

Sexually dimorphic EODs have been proposed in the *Brienomyrus brachyistius* complex of, perhaps, three species that has not yet been worked out systematically (Hopkins & Bass, 1981), and mates would find or select each other on the basis of this cue, although experimental verification has remained elusive (no confirmation of initial observations that were only presented in short form yet). Landsman (1995) in his review, concludes

that "the species identification of *Brienomyrus* is not clear"; he even distinguishes five forms. This author also concludes that "... EOD sex differences have yet to be fully substantiated...", and that "... the term sexual dimorphism will not be used ... " in his review (Landsman, 1995), except for *Gnathonemus petersii* commercially imported from Africa and studied on the very day of their arrival in New York (Landsman, 1993). These findings are in contrast to those of Kramer & Westby (1985) who did not see a difference between the sexes in the same species. According to Kramer (1994), Landsman's (1993) findings could result from undue stress associated with inter–continental air travel (for this reason, importers usually keep and watch their fish for a while before selling them). Stress is known to affect both the EOD waveform (Landsman *et al.*, 1987; Landsman, 1991; Landsman & Moller, 1993; Kramer & Kuhn, 1993) as well as reproductive physiology and behaviour; often to a different extent for the two sexes (von Holst, 1987; Rankin & Jensen, 1993; Nelson, 1995).

In captive *P. isidori* a sexual dimorphism in EOD waveform was seen by Westby & Kirschbaum (1982). Bratton & Kramer (1988) confirmed that one waveform character differed statistically between the two sexes, but also demon-strated a very wide overlap. Therefore, these authors suggested the term "sex difference" for *P. isidori* rather than dimorphism which requires "two distinct forms" (Oxford Dictionary); sexual dimorphisms are thought to be brought about by a special form of evolution, sexual selection (review by Maynard Smith, 1991). The discussion seems academic in *P. isidori* because a waveform cue – seen by Crawford (1992) but disputed by Kramer (1994) – is not used for mate selection in this species (Crawford, 1991; Bratton & Kramer, 1989), and a physiological, more parsimonious explanation of the sex difference as a hormonal side–effect (anabolic action) rather than a result from sexual selection seems sufficient (Bratton & Kramer, 1988).

Because in previous studies of a sexual dimorphism in EOD waveform, factors that are important for their validity could not be sufficiently controlled (for example, taxonomy, statistics, zoogeo-graphy, recording procedure, prior history, and method of sexing), the present study was conducted in the field in order to start from the best possible conditions. Field data on mormyrid EOD waveforms are rare (Hopkins, 1980; Crawford & Hopkins, 1989; Moller & Brown, 1990), and EOD waveform analysis – where present – usually was performed on tape–recorded EODs. For the present study, EODs were digitized immediately after capture of the fish from their natural home waters, and numerically stored so that waveform distortions as introduced by magnetic tape (see Kramer & Weymann, 1987) were excluded.

The two sympatric species from southern Africa chosen in the present paper appear to have not been studied for their EOD waveforms before (a pre-liminary description is given in a phylogenetical study; Van der Bank & Kramer, 1996). Graff (1989) studied inter–EOD interval distributions in *M. macrolepidotus* that had been imported commercially to Europe from Tanzania; he did not address EOD waveform variation, nor taxonomically or geo-graphically relevant details. Part of the present data were reported in short form (Kramer, 1997).

MATERIALS AND METHODS

Fish were collected during field trips to East–Caprivi, Namibia, from 7–13 September 1993 and 5–15 March 1994.

All *Petrocephalus catostoma* (Günther, 1866) (*N* = 37), or churchill, are from the Upper Zambezi River near the town of Katima Mulilo, East Caprivi (17°29'S, 24°18'E; September 1993), except two fish. These two and the *Marcusenius macrolepidotus* (Peters, 1852) (*N* = 83), or bulldog, were caught in March 1994 at two places 130 km apart: 36 *M. macrolepidotus* and one *P. catostoma* were caught about 30 km downstream of Katima Mulilo in a Zambezi side–channel called Lisikili (17°29'S, 24°26'E), the other 47 *M. macrolepidotus* and a single *P. catostoma* were caught at Nakatwa in Mudumu National Park (18°06'S, 23°23'E; elevation, 950 m) in a side channel formed by the Kwando River draining (through sections called Linyandi River, Liambezi Lake, and Chobe River) to the Zambezi River downstream of Katima Mulilo. Two additional *M. macrolepidotus* (of 7.2 and 19.5 cm standard length) were caught in September 1993 at Nkasa Island (18°27'S, 23°42'E) in Mamili National Park, bordered by the Kwando River in the West and the Linyandi River in the South and East. All these water bodies are interconnected and form part of the Upper Zambezi System. The fish are deposited in a museum (see Table 1).

In March 1994 both temperature (26–28°C) and water level of the Zambezi were high whereas water conductivity was low (55–56 µS/cm) and continued to fall to 43 µS/cm within two weeks. At Nakatwa, conditions were similar except that water conductivity was very high and constant within 6 days for an almost stagnant water (129–133 µS/cm). In September 1993 the Zambezi was cooler (22°C), water level low, and water conductivity high (81 µS/cm) while at Nkasa Island the Kwando River had 108 µS/cm and only 18–19°C in the morning.

Immediately after capture, fish were placed in a 37–litre plastic aquarium between two carbon–rod electrodes for EOD measurement in the field using battery–powered equipment (fish were unrestrained). Head–to–tail potential differences were amplified (1 Hz ... 100 kHz, –3 dB per octave, gain variable up to x10) by a differential amplifier, and EODs captured by a digital storage oscilloscope (8 bit vertical resolution, up to 10 MHz sampling rate, 512 points per sweep). Digitized EODs were logged onto the hard disk of a computer via digital interface. Water was fresh from the river (conductivity as given above); when necessary, EOD duration was temperature–corrected to 25°C using a Q_{10} of 1.5 (Kramer & Westby, 1985). Temperature was recorded to within ±0.1°C; for both temperature and water conductivity measurements an electronic meter manufactured by WTW Weilheim, model LF92 was used. Because the river water the fish were adapted to was used, conductivity compensation was both unnecessary and not possible (Kramer & Kuhn, 1993).

Twelve *P. catostoma* not included in the present study and 19 mormyrids of two other species were not killed but sent to Frankfurt/Main airport, swimming in Regensburg aquaria after about 30 h of transport by road, plane and again road. All *P. catostoma* and all individuals of a second species have survived for 2 years at present; five specimens of the third species died within three days after arrival. Individual EOD waveforms "drifted" for several days after arrival in Regensburg before stabilizing; the stabilized waveforms were within the range of that species' EOD as recorded in the field in other individuals (Scheffel & Kramer, unpubl.). These observations show (1) that stress, such as associated with long–distance air transport, may indeed affect EOD waveform in the short term, in agreement with Landsman *et al.* (1987) but not Landsman (1993); (2) there is eventual stabilization to the form of EOD that is recorded in the field.

Custom–designed programs written in Famos (a software package for signal analysis by IMC Co.) analyzed the EODs for waveform parameters, such as amplitude and duration of certain phases. Fourier analysis of EODs was performed using waveforms with a maximum number of points, that is, 2^{14}, for best frequency resolution; without weighting function. However, Fourier amplitude spectra were not extensively used in the present study (there would have been a few more significant correlations). The reasons for refraining from this were (1) redundancy: the same data would have been shown in just another way (frequency-domain, see physics textbooks); (2) mormyrids have been shown to be exceedingly sensitive for slight variations in EOD waveform (that would go undetected by an amplitude spectrum and show up only in the phase spectrum), as occurring in intraspecific communication both in adults (adult EOD; Graff & Kramer, 1992) and larvae (larval EOD; Postner & Kramer, 1995), and active electrolocation (von der Emde & Zelick, 1995). Regression analysis was performed on the results, as indicated in the text. Standard errors are given except where indicated otherwise.

After EOD recording all fish were given an overdose of the anaesthetic 2–phenoxyethanol, tagged for individual identification, and preserved in 10% formalin. The sex of an individual was verified by gonad histology, and gonadal recrudescence assessed. Slices from Paraplast embedded gonads of 7 μm were stained according to the Azan method, as detailed in Romeis (1989). Although in many mormyrid species (including the two species of the present study) the sex of an individual can be told from the shape of the anal fin base (which is straight in females and shows a kink in males; Fig. 1), the kink character is absent in juveniles of both sexes and may still be difficult to see in subadult or small adults, especially in captivity (Lücker & Kramer, 1981; Bratton & Kramer, 1988; see also below).

RESULTS

On the preserved specimens 17 anatomical characters were measured or counted (Table 1; Fig. 1) and the species identified using the keys by Skelton (1993) and Bell-Cross & Minshull (1988). The *P. catostoma* did not present any taxonomic problems except that one fish had one dorsal fin ray more than the upper range limit which is 24 according to Bell-Cross & Minshull (1988) and Skelton (1993). A small and rare difference such as this one probably is of no concern because species descriptions in this fish group are sometimes based on few individuals, in addition, from a distant region (first described from the Ruvuma River on the Tanzanian/Moçambique border, some 1400 km away; Bell-Cross & Minshull, 1988).

In contrast, in *M. macrolepidotus* some of the counts were more consistently below the ranges given by Skelton (1993) and Bell-Cross & Minshull (1988) as follows (Table 1): The literature range for the pericaudal scale number is 14–16 which was only 12–14 in the present *M. macrolepidotus*, with the majority of fish possessing only 12 scales (only 3 fish had 14). The lower range limit for the number of dorsal fin rays in the above literature is 23, whereas in the present sample 15 fish had only 22, and two as few as 21. For the number of rays of the anal fin, the lower limit of 28 from the literature was not reached in four fish that had only 27. These differences probably reveal a population isolated genetically from that of the type locality which is the Lower Zambezi in Moçambique (Bell-Cross & Minshull, 1988). The Victoria Falls (of 110 m height) are a well–known distribution barrier for many fish species, including mormyrids. For a genetical

Fig. 1. — Photographs of preserved *M. macrolepidotus* (left), and of live *P. catostoma* (right). Females, top; males, below. Scale is in cm.

Table 1. — Anatomical characters of the study species.

	PDL	PAL	LD	LA	pD	CPL	CPD	LS	HL	N	SL	BD	nD	nA	SPc	Ch
Marcusenius macrolepidotus (1)																
Minimum	2.2	2.15	0.45	0.55	1.3	0.8	0.25	0.25	1	0.09	3.5	0.9	21	27	12	0.1
Maximum	12.5	12.3	3.5	3.8	7.3	3.45	1.9	1.15	4.4	0.3	19.5	6.6	25	31	14	0.64
Mean	7.81	7.5	2.03	2.49	4.54	2.33	0.98	0.78	3.04	0.18	12.31	3.49	23.06	28.77	12.12	0.37
± S. E.	0.16	0.15	0.05	0.06	0.09	0.04	0.03	0.02	0.05	0.01	0.24	0.08	0.1	0.1	0.05	0.01
N	84	84	84	84	84	84	84	84	84	84	84	84	84	84	84	84
Petrocephalus catostoma (2)																
Minimum	1.83	1.72	0.4	0.51	1	0.6	0.17	0.27	0.99	0.04	2.83	0.76	21	25	12	-
Maximum	6.6	6.45	1.55	2	3.9	2.05	0.75	0.8	3	0.1	10.5	3.4	25	30	13	-
Mean	4.13	3.93	1.06	1.39	2.62	1.4	0.47	0.55	2.03	0.07	6.74	2.03	22.59	28.27	12.05	-
± S. E.	0.2	0.2	0.05	0.07	0.12	0.06	0.03	0.03	0.09	0.01	0.32	0.12	0.14	0.18	0.04	-
N	37	37	37	37	37	37	37	37	37	37	37	37	37	37	37	37

All measures in cm, except nD, nA and SPc which are counts. PDL, predorsal length: distance tip of snout—dorsal fin origin. PAL, distance tip of snout anal fin origin. LD, dorsal fin length. LA, anal fin length. pD, distance dorsal fin origin—end of caudal peduncle. CPL, length of caudal peduncle. CPD, depth of caudal peduncle: the least vertical distance across the caudal peduncle. LS, length of snout: distance tip of snout—centre of eye. HL, head length: distance tip of the snout—furthest bony edge of the operculum. N, distance between the pair of nares of one side. SL, standard length: distance tip of the snout (disregarding any mental swelling, if present)—midbase caudal fin. BD, body depth: the greatest vertical distance across the body. nD, number of dorsal fin rays. nA, number of anal fin rays. SPc, number of scales around caudal peduncle. Ch, chin (mental swelling) length (distance tip of upper jaw—tip of chin). For more detail, see Skelton (1993).
(1) SNF 28264, 69 specimens, and (2) SMF 28265, 27 specimens, stored in the Senckenberg Museum, Frankfurt (Main), Germany.
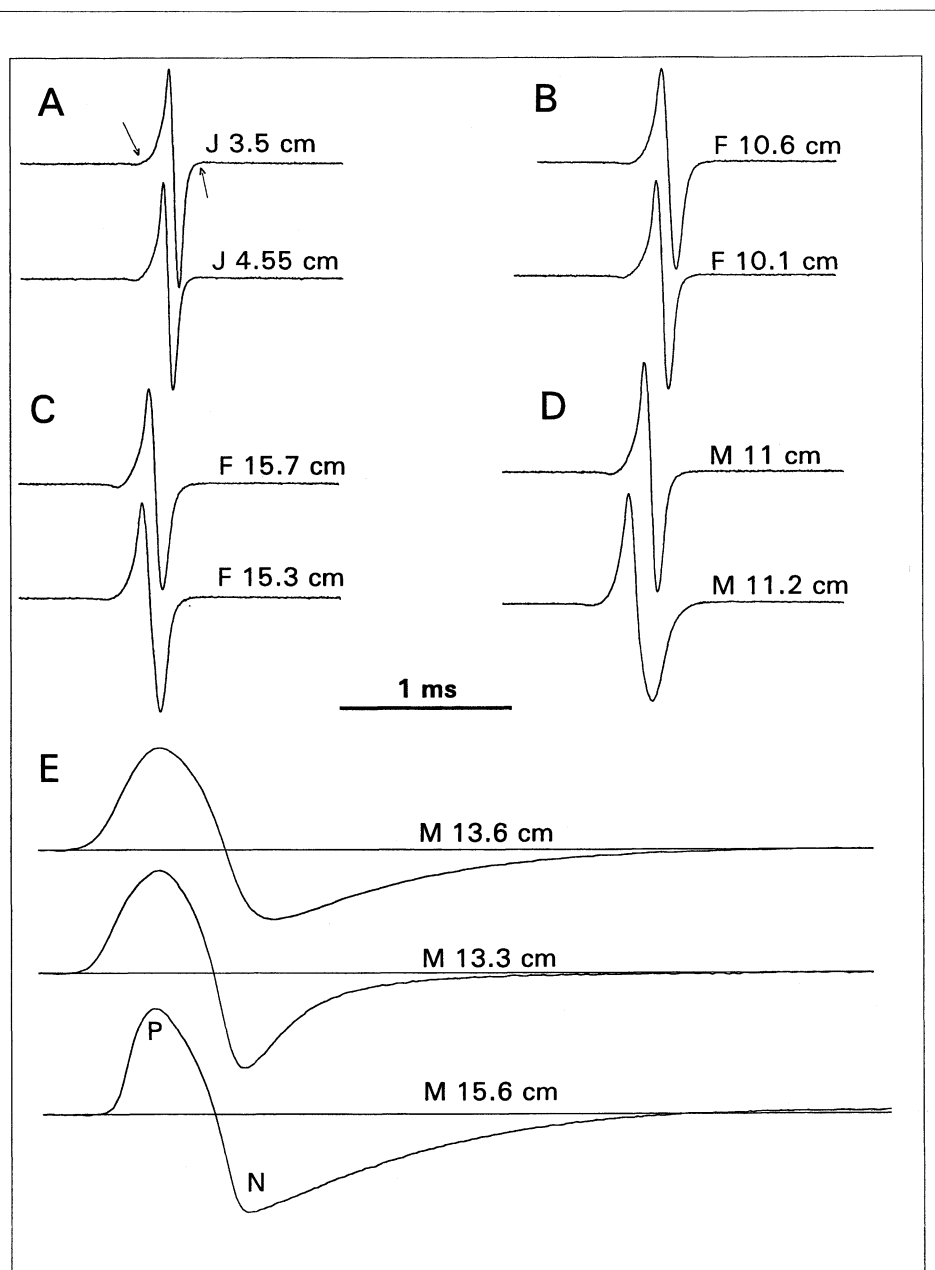
Marcusenius macrolepidotus (25 °C)

Fig. 2. — Oscillograms of electric organ discharges of *M. macrolepidotus*. Ordinate, voltage with the baseline scaled to zero and the positive peak to 1. Abscissa, time (see time bar). J, juveniles; M, males; F, females; standard length in cm. (A) "babies" (arrows, pre– and post–potentials); (B) sexually immature females; (C) mature females; (D) immature males; (E) mature males with a zero–line added. P, head-positive P phase; N, head-negative N phase. All EODs normalised to 25°C.

study of the present population of *M. macrolepidotus* from the Upper Zambezi, see Van der Bank & Van der Bank (1995), and Van der Bank & Kramer (1996). The fish of these studies are a sub-sample of the present sample (same individuals).

The EODs of the present two species differ in waveform, duration, and the degree of differences among the sexes.

EOD waveform variability

Marcusenius macrolepidotus

The EOD waveform of immature and female *M. macrolepidotus* (Fig. 2) is similar to that of other members of the genus (for example, those found in West Africa such as *M. senegalensis, M. tomasi,*

M. ussheri or *M. furcidens*; Scheffel & Kramer, in press; Kramer, in prep.): a head–positive P phase is followed by a head–negative N phase of similar amplitude and duration (pre– and post–potentials of very weak amplitude as shown in Fig. 2 are not further considered in the present paper). Males exceeding about 11.5 cm, however, developed an EOD of greatly increased duration (Fig. 2).

The change in EOD waveform seemed to go parallel with the development of a morphological kink character of the anal fin base (Fig. 1): of our 30 histologically confirmed males, only 2 had no kink, and 5 a "questionable" kink so indistinct that the sex of this fish became known only after gonad dissection and histology. All
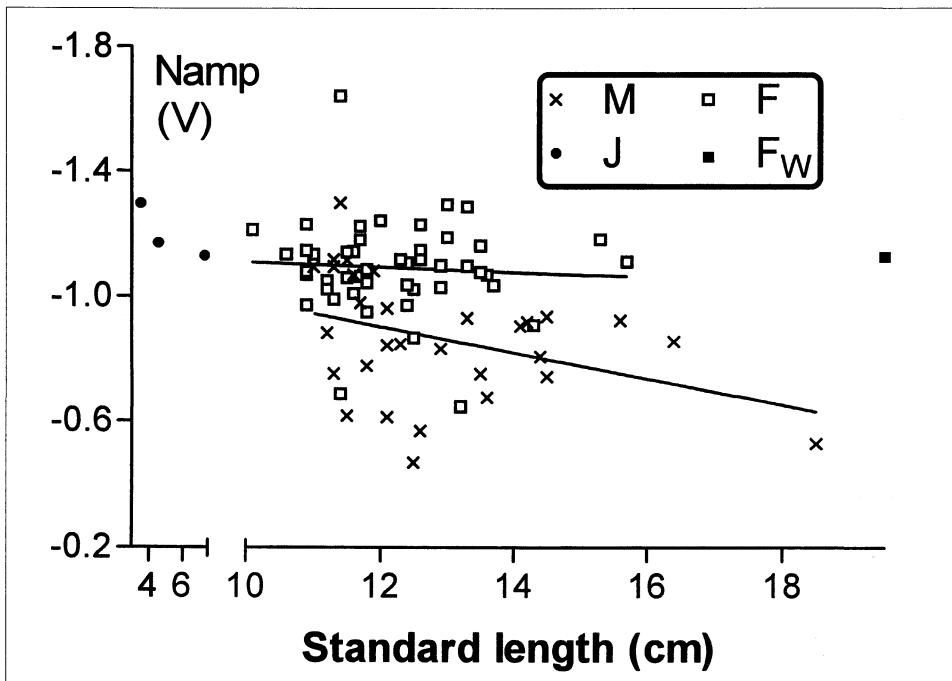

Fig. 3. — Linear regression of an EOD waveform parameter, amplitude of the head–negative N phase (Namp), with standard length in male and female *M. macrolepidotus*. The amplitude of the N phase is relative to the P phase=1 (Volts, not to scale). □, Females (N = 47); x, males (N = 30; both collected during summer); ■, one female collected in winter; •, juveniles of indeterminate sex (N = 3). Note compressed segment of abscissa for juveniles in order to better show the range of main interest. A decrease of N phase with size was statistically significant only in males.

of these 7 males except one (of 14.1 cm) were small, from 11–12.3 cm standard length. In none of the females $(N = 47)$ was the presence of a clear kink noted; only one female (13.0 cm) received a question mark for the kink character because the observer was in doubt.

The mean standard lengths of 30 males (12.89 ± 0.33 cm) and 47 females (12.23 ± 0.18 cm) of the present sample did not differ significantly between the sexes $(D. F. = 45$; two–tailed, unpaired Welch's t–test) although the associated standard deviations did $(P=0.007)$. The smallest female that was included in the regression analyses of EOD waveform (see below) had a standard length of 10.1 cm, the smallest male 11 cm; maximum values were 15.7 and 18.5 cm, respectively. The maximum standard length ever reported for *M. macrolepidotus* is 30 cm (Skelton, 1993).

EODs were normalised by scaling the baseline to zero and the peak of the P phase to 1 (examples shown in Fig. 2). Under this definition, for all fish beyond 10.1 cm standard length, the N–phase amplitude of female EODs varied between individuals, from 0.65–1.64 ($\bar{x} = 1.1 ± 0.03$; $N = 47$), whereas in males N–phase amplitude was significantly smaller (range, 0.47–1.3; $\bar{x} = 0.87 ± 0.04$; $N = 30$; $P<0.0001$, Welch's t–test). A more useful data analysis than the comparison of mean values for fish of all sizes was found to be regression analysis of the dependency of N–phase amplitude on fish standard length. In males, a correlation coefficient of $r = -0.377$ showed that with increasing standard length, N–peak amplitude decreased ($P = 0.0401$) according to $y = -0.042x + 1.41$. N–peak amplitude was unrelated to standard length in females; the slope of a least–squares regression–line was not significantly different from zero (no correlation; $P = 0.688$; Fig. 3). In both males and females a runs test confirmed that the data followed a straight line (nonlinearity was not significant; $P = 0.96$ and 0.19, respectively).

Three small juveniles and a very big female (that had been caught in September) were not included in the regression analysis, but are also shown on Fig. 3. Their N amplitudes agree well with the predictions from the regression lines for females when extrapolated.

For females only, the same result applied for all other EOD waveform measures analyzed: there was no correlation of their EODs with standard length, and a straight, horizontal line is a good description of all data (nonlinearity not significant; Fig. 4). The values for the three small juveniles and the single, very big "September" female were again close to the regression lines for females extrapolated to either side (Fig. 4). Although in a strict sense only shown for females of the size range from 10.1–15.7 cm standard length $(N = 47)$, there is probably no correlation of EOD waveform (as measured by seven parameters) for the whole size range from 3.5–19.5 cm in females.

The opposite is true for males (11–18.5 cm; $N = 30$) which did show a strong and highly significant correlation with size in all EOD parameters studied. This was already shown by the simplest model, linear regression: all EOD waveform parameters studied were positively and significantly correlated with size (N–phase amplitude, negatively). However, runs tests also showed that, except for N–phase amplitude, linear regression was not a good model because the data were significantly nonlinear. A sigmoidal curve of the type

$$y = A + \frac{B - A}{1 + k e^{a(B-A)t}}$$

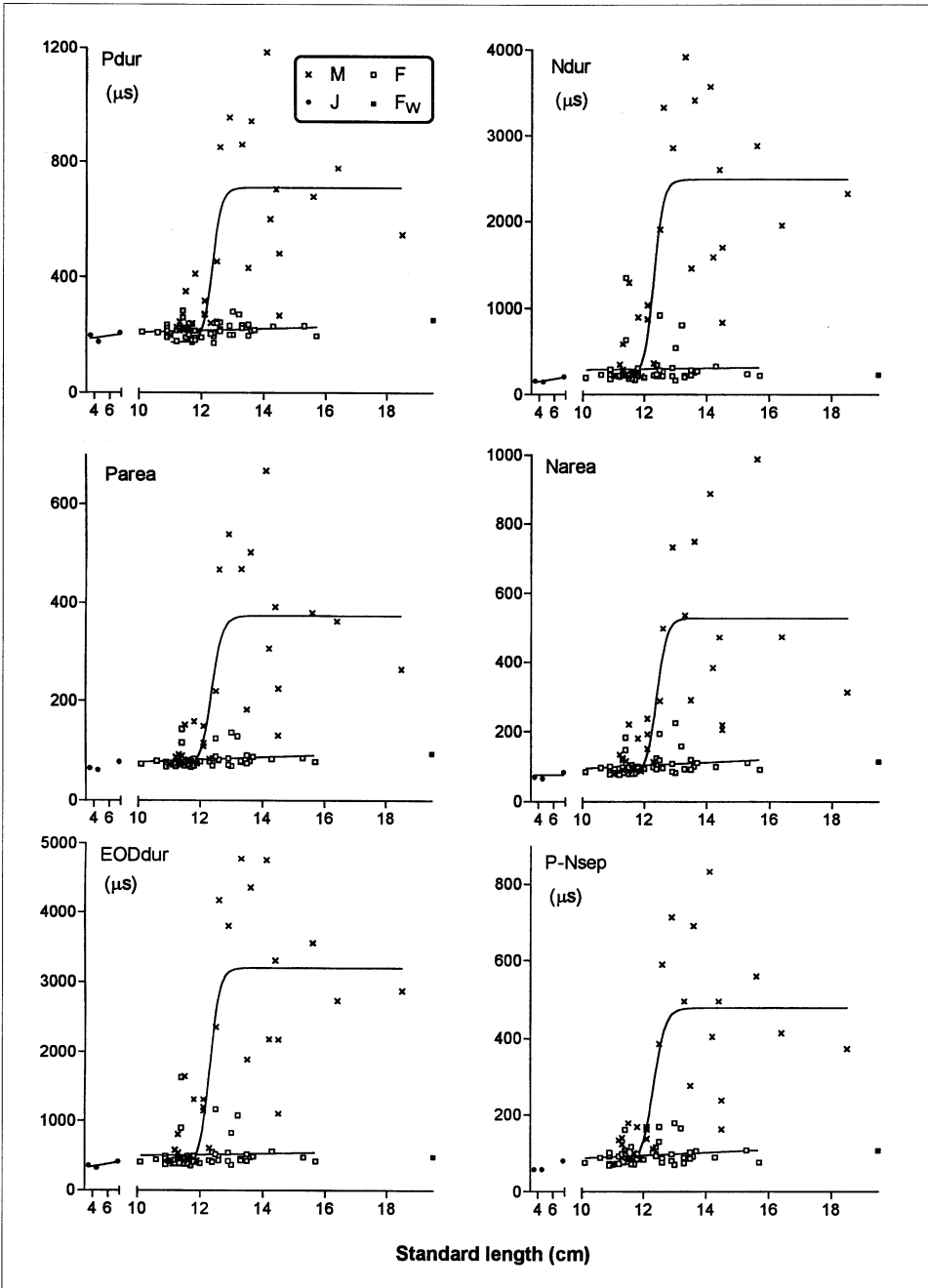(where A = the bottom, B = the top of the sigmoid, and k and a constants; Batschelet,

Fig. 4. — Regression of EOD waveform parameters with size (standard length in cm) in *M. macrolepidotus*. The duration measures Pdur, Ndur, EODdur, P–Nsep are all in μs; the area–under–curve measures Parea and Narea in [V x μs]. □, Females (*N* = 47); x, males (*N* = 30; both collected during summer); ■, one female collected in winter; •, juveniles of indeterminate sex (*N* = 3). Note compressed segment of abscissa for juveniles. Whereas in females (including juveniles) none of the EOD waveform parameters studied correlated with size (least–squares regression–lines are horizontal), in males greater than about 12 cm standard length parameters did correlate significantly with size according to a sigmoidal curve.

Table 2. — *Marcusenius macrolepidotus* males. Regression of various EOD parameters with standard length.

	Pdur	Ndur	EODdur	P-Nsep	Parea	Narea
Correlation coefficient r*	0.784	0.809	0.807	0.781	0.78	0.74
D. F.	28	28	28	28	28	28
Inflexion point of sigmoidal curve (cm)	12.4	12.3	12.3	12.3	12.4	12.4

Pdur, P-phase duration [µs]; Ndur, N-phase duration [µs]; EODdur, P- plus N-phase durations [µs]; P-Nsep, separation of, or time interval between, P- and N-peaks [µs]; Parea, Narea, areas under P- and N-phases from baseline, respectively (dimension, V x s).
*) Nonlinear regression according to a sigmoidal curve (Fig. 4).

1975, p. 353) is suggested by the data that first follow a horizontal regression line (similar to females) but begin to deviate by a steep increase at about 12 cm standard length. The increase ends already at around 14 cm standard length (if not earlier), that is, the transition occurs in an almost step–like fashion. A sigmoid seems the simplest model that follows the data.

Curve–fitting of the male data with a sigmoidal model proved successful, and, given the high scatter of data with increasing X, very good results were obtained by fine–tuning the variables (Table 2; Fig. 4). Whereas the "bottom" of the function was clear from the data (similar to females and juveniles), no such certainty could be obtained for the exact value of the "top", and rather conservative values were chosen (only two males of the sample were bigger than 16 cm). Rather steep slopes had to be selected for all data sets before satisfactory agreement of the model with the data was achieved. For a curve to be adopted for Fig. 4, a runs test had to be negative, showing that there was no significant deviation from the model. Also considered were r² that had to increase when optimizing the variables, the sum of squares, and the standard deviation of the residuals that both had to decrease. Further improvement beyond the level achieved (Table 2; Fig. 4) seems only possible with additional data for big males that would allow a better estimate for the "top".

The sigmoidal model fitted the data significantly better than a linear one, as shown by an F–test ($P < 0.0001$ for each of the six parameters in Fig. 4 and Table 2). For example, linear regression showed that N–phase duration of male EODs (Ndur) was positively and highly significantly correlated with standard length ($P = 0.0006$); yet this type of regression explained only 35% of the Y variance in the data, whereas the sigmoidal curve as shown in Fig. 4 explained 65% (as measured by r^2).

Up to a standard length of about 11.5 cm, most male EODs were inconspicuous, similar to those of juveniles and females (note, however, the male of 11.2 cm standard length in Fig. 2 where an increase of N duration can already be seen). Males of somewhat greater standard lengths showed a steep increase in the duration of their P– and N–phases, P–to–N separation, and areas under the N– and P–phases of their EODs. The steepest part of the regression curves, or inflection point, occurred at 12.3–12.4 cm where further increase began to taper off; at about 14 cm standard length the curve was again parallel to the x–axis. There seemed to be no further correlation of EOD waveform with body size beyond about 14 cm; the top part of the curve should, however, be confirmed by additional data (as proposed above).

The change that occurred in the male sex between about 11.5–13 cm standard length was dramatic. For example, total EOD duration (= duration of P–plus N–phases) of females was, on average, 519.6 ± 34.3 μs ($N = 47$) and 416.4 ± 13.71 μs ($N = 12$) in immatures (fish of both sexes up to 11 cm standard length), whereas males larger than 12.3 cm averaged at 2980 ± 330.3 μs ($N = 15$; difference compared to females: $P < 0.0001$, two–tailed t–test with Welch's correction for significantly different variances). A maximum EOD duration of 4779 μs was recorded in a male, corresponding to an increase by a factor of 11.5 compared to the average value in immatures. For N–phase duration alone, the mean value in female EODs was 301 ± 32 μs compared with the maximum value found in males of 3918 μs (an increase by a factor of 13). Members of the same species, M. m*acrolepidotus*, may differ by a factor of 26 in their N–phase duration (lowest value as found in a juvenile, 148.3 μs).

A few females of medium size seemed to follow the sigmoidal increase in N–phase duration as found in males, up to about half–way of the top of the sigmoid; they were clearly outside the rest of the female population. No such phenomenon was observed for the duration of the P phase. On the other hand, the biggest males of the present sample (up to 18.5 cm) had substantially shorter EODs (although clearly beyond the female population) than some smaller males around 12.5–14.5 cm. This may represent a statistical phenomenon well–known in studies of regression (outriders are extreme only on one parameter) but here selective predation is presumed (see Discussion).
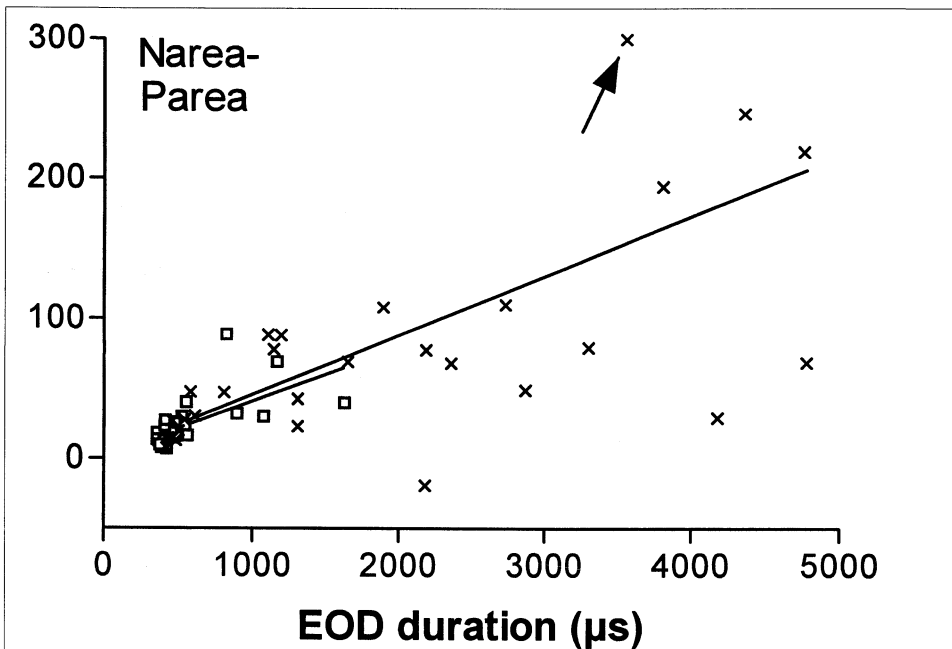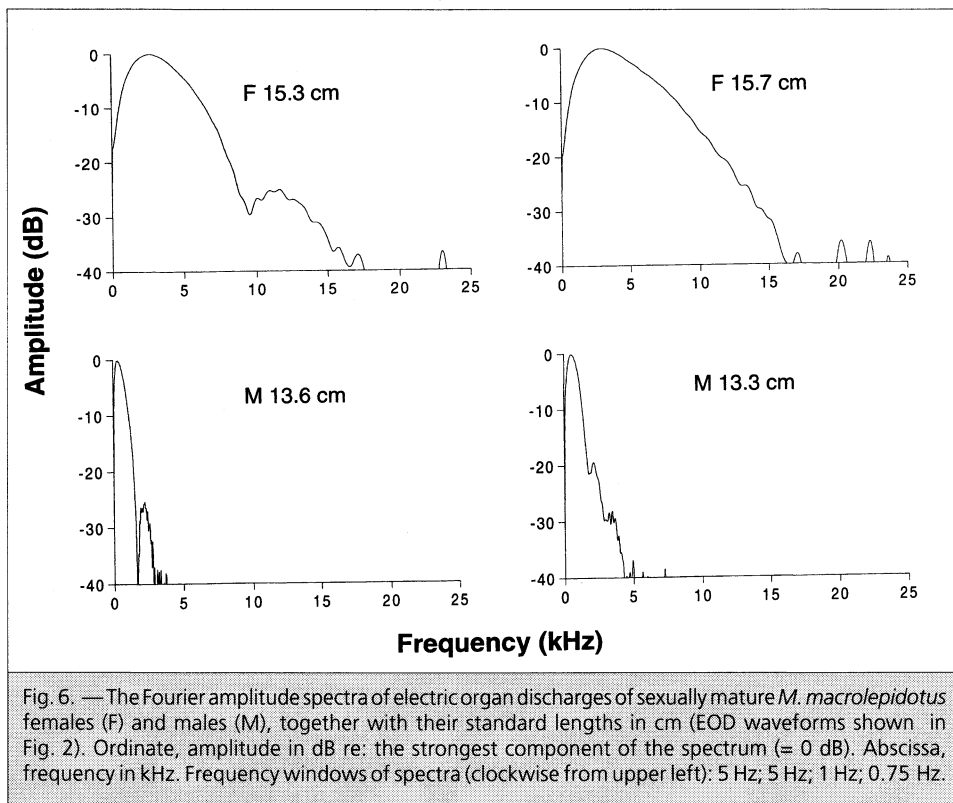

Fig. 5. — D.C. component of the EOD of *Marcusenius macrolepidotus* as a function of EOD duration. Ordinate, D.C. component measured as the difference between the areas of the two half–waves of an EOD, N and P (dimension, V x μs). □, females (N = 47); x, males (N = 30). Arrow, off–scale value (608). Note that least–squares regression lines are the same for females and males although a strong D.C. component was found only in males.

Fig. 6. — The Fourier amplitude spectra of electric organ discharges of sexually mature *M. macrolepidotus* females (F) and males (M), together with their standard lengths in cm (EOD waveforms shown in Fig. 2). Ordinate, amplitude in dB re: the strongest component of the spectrum (= 0 dB). Abscissa, frequency in kHz. Frequency windows of spectra (clockwise from upper left): 5 Hz; 5 Hz; 1 Hz; 0.75 Hz.

The values for the N–phase area exceeded those for the P–phase in all but one fish, resulting in a D.C. component to the EOD that was close to zero in all immature fish and most females. In both sexes the D.C. component (of head–negative polarity) increased significantly with EOD duration (Fig. 5); the common regression line (for both sexes) was $y = 0.0425x + 1.06$, with slopes and Y–intercepts being not significantly different between males (m) and females (f), and nonlinearity not significant (correlation coefficients, $r_m = 0.5326$ with $P = 0.0024$, $D. F. = 28$; $r_f = 0.6346$ with $P < 0.0001$, $D. F. = 45$). By far the highest D.C. components were observed in males with long–duration EODs.

The difference between male and female EODs was also apparent from Fourier analysis. For example, EOD amplitude spectra for four sexually mature males and females of Fig. 2 showed that the spectral frequency content of male EODs was much more low–frequency than that of females (Fig. 6). The two female EODs had their peak–amplitude frequencies at 2925 Hz and 2660 Hz, and 20 dB attenuation occurred at 11 407 and 8160 Hz, respectively. In the two male EODs the peak–amplitude frequencies were only 334 Hz and 514 Hz; 20 dB attenuation occurred already at 1397 and 2193 Hz, respectively, in these spectra of narrow bandwidth.

Petrocephalus catostoma

In all *P. catostoma* of at least 7.1 cm the gonads could be found and the sex determined ("adults"). A conspicuous size gap from 5.45 to 7.1 cm where no fish were collected divided the fish into two

groups. The group of smaller fish whose sex could not be determined ("juveniles"; 2.83–5.45 cm; $N = 15$) were probably young–of–the–year from the preceding spawning season, whereas the fish larger than 7.1 cm might be older than one year.

Among the 13 fish determined as males, 10 had a clear kink in the anal fin base (see Fig. 1), only three small males had a "questionable" kink (as determined before gonad dissection). None of the 12 fish classified as females, nor any of the juveniles, showed a kink (not even a "questionable" one). On average, the males (7.9 cm) of the present sample were smaller than the females (8.6 cm, difference not significant; Table 3) with the biggest female of 10.5 cm, and the biggest male of 8.8 cm standard length. Most individuals were far from the maximum species size of 13 cm (Bell–Cross & Minshull, 1988; Skelton, 1993); 15 cm according to Bell–Cross (1974).

P. catostoma displays a brief EOD of triphasic waveform: a head–positive P1 phase is followed by a sharp, head–negative N phase of considerable amplitude that gives way to a P2 phase much weaker in amplitude than the P1 phase (Fig. 7). A conspicuous and consistent difference in EOD waveform between the sexes, like that shown in *M. macrolepidotus*, was clearly not present in *P. catostoma* (Fig. 7). However, significant correlations of EOD waveform with size and sex that are difficult to see by eye were revealed by statistical analyses.

Among 12 EOD waveform parameters studied, four showed significant differences between the three groups of fish (that is, females, males and juveniles); of these four differences, three were linked with each other (P1–phase area, P1–phase duration, and total EOD duration; Table 3). For each of these three parameters, the three groups of fish shared common regression lines with negative slopes (Fig.

8); individual regression lines for the same parameter did not differ significantly among the three groups of fish (and were, therefore, pooled). P1–phase duration, P1–phase area and EOD duration all decreased with fish size; P1–phase duration following the equation $y = -8.67x + 215$; the correlation coefficient $r = -0.572$; the slope differed significantly from zero ($P = 0.0001$; $D. F. = 38$). For P1–phase area, the equation was $y = -1.88x + 59.6$; $r = -0.652$; the slope differed significantly from zero with $P < 0.0001$ ($D. F. = 38$). Total EOD duration decreased with size according to $y = -17.9x + 560$; $r = -0.36$; slope significant at $P = 0.0224$ ($D. F. = 38$).

For P2–phase amplitude, however, each group of fish behaved differently. The amplitude of the P2 phase varied greatly between individuals: from 19% to 55% of that of the P1 phase (Table 3). There was a significant decrease of P2–phase amplitude with size in both males and females, whereas in juveniles no such trend (nor any significant correlation) was found (Fig. 8; Table 4). The slopes of the regression lines for the two sexes were the same (not significantly different according to an F–test, $F = 0.7$; $P = 0.412$, $D. F. = 21$); however, in spite of the lines being parallel they were not identical because their elevations were different ($F = 6.7$; $P = 0.017$; $D. F. = 22$): at equal size, males showed significantly stronger P2–phase amplitudes than females. The regression line for males was $y = -0.0859x + 1.15$; $r = -0.727$; $P = 0.0049$; $D. F. = 11$; for females, these data were $y = -0.0556x + 0.84$; $r = -0.638$; $P = 0.0255$; $D. F. = 10$. The standard errors for the slopes were ± 0.025 for males and ± 0.022 in females, and the pooled regression slope for males and females combined was -0.063. All three data sets can best be described by straight lines and do not deviate significantly from such a linear model (Table 4).
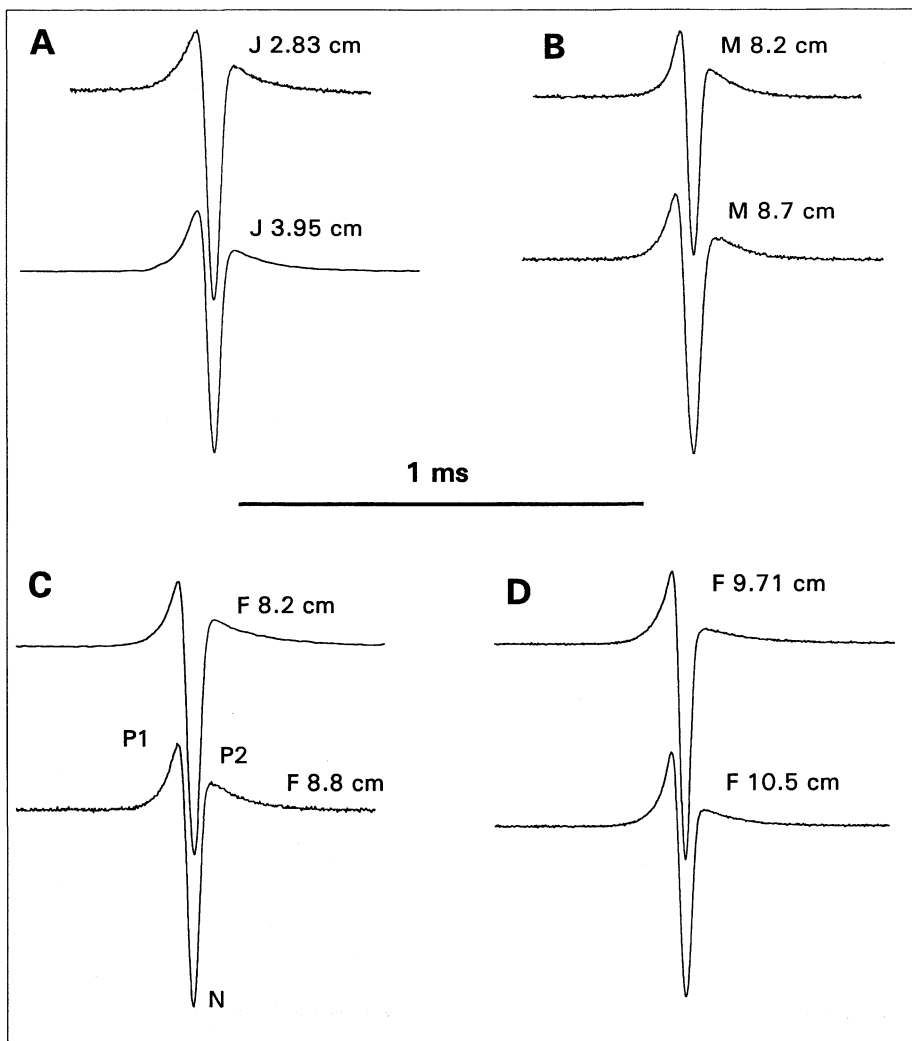
Petrocephalus catostoma (25 °C)

Fig. 7. — Oscillograms of electric organ discharges of *Petrocephalus catostoma*. Ordinate, voltage; with the baseline scaled to zero and the first positive peak (P1) to 1. Abscissa, time (see time bar). M, males; F, females; J, juveniles; with standard length in cm. (A) juveniles; (B) big males; (C) big females; (D) big females from the spawning season (all others from the non–spawning season). P2, second positive phase; N, negative phase. All EODs normalised to 25°C.

Table 3. — EOD waveform parameters in *Petrocephalus catostoma* as related to sex and size.

	SL (cm)	Namp (V)	P2amp (V)	EODdur (µs)	P1dur (µs)	Ndur (µs)	P2dur (µs)	P1Nsep (µs)	P1P2sep (µs)	NP2sep (µs)	P1area (V × µs)	Narea (V × µs)	P2area (V × µs)
Females													
Minimum	7.1	-2.4	0.21	319.6	119.2	35.4	148.7	27.5	59	31.5	35.2	56.9	20.6
Maximum	10.5	-3.18	0.48	652.8	179.2	55.9	419.5	42.5	91.3	55	48.5	99.2	55.7
Mean	8.58	-2.74	0.363	419.27	142.65	46.75	229.88	34.69	79.67	44.98	43	75.2	31.02
± S. E.	0.3	0.08	0.026	25.57	5.37	1.7	21.37	1.36	3	2.08	1.14	3.71	2.96
N	12	12	12	12	12	12	12	12	12	12	12	12	12
Males													
Minimum	7.1	-2.29	0.32	290.6	117.5	39	134.2	31.9	70.5	38	38.9	63.9	27.6
Maximum	8.8	-3.02	0.55	568.7	171.3	61.3	336.2	45.2	106.3	61.1	52.1	104.2	49.1
Mean	7.91	-2.69	0.472*	395.3	140.9	49.8	204.69	37.33	84.01	46.69	45.02	80.46	38.38
± S. E.	0.15	0.07	0.018	19.09	4.13	1.85	13.12	1.087	2.85	1.85	1.09	3.71	1.92
N	13	13	13	13	13	13	13	13	13	13	13	13	13
Juveniles													
Minimum	2.83	-2.6	0.19	352.7	133.9	39.8	178.9	30.5	65.9	35.3	40.8	61.9	26.6
Maximum	5.45	-3.5	0.55	759.8	269.8	61.6	428.4	44.8	103.7	61.5	58.4	113.1	48.8
Mean	4.66	-2.85	0.426	486.21*	177.81**	51.52	256.88	39.22	86.89	47.67	51.05**	85.07	36.66
± S. E.	0.18	0.07	0.023	29.19	8.28	1.45	19.48	0.96	2.36	1.57	1.31	3.55	1.56
N	15	15	15	15	15	15	15	15	15	15	15	15	15

SL, standard length; Namp, amplitude of the N peak; P2amp, of the P2 peak, EODdur, total EOD duration; P1dur, duration of the P1 phase; Ndur, of the N phase; P2dur, of the P2 phase; P1Nsep, interval or separation between P1 and N peak; P1P2sep, between P1 and P2 peak; NP2sep; between N and P2 peak; P1area, area under P1 phase; Narea, area under N phase; P2 area, area under P2 phase.
*, **, Difference from one (*) or both (**) other groups of fish significant (*P* < 0.05) according to a one-way ANOVA (*F* > 3.96, *D.F.* =37, Tukey's post tests).
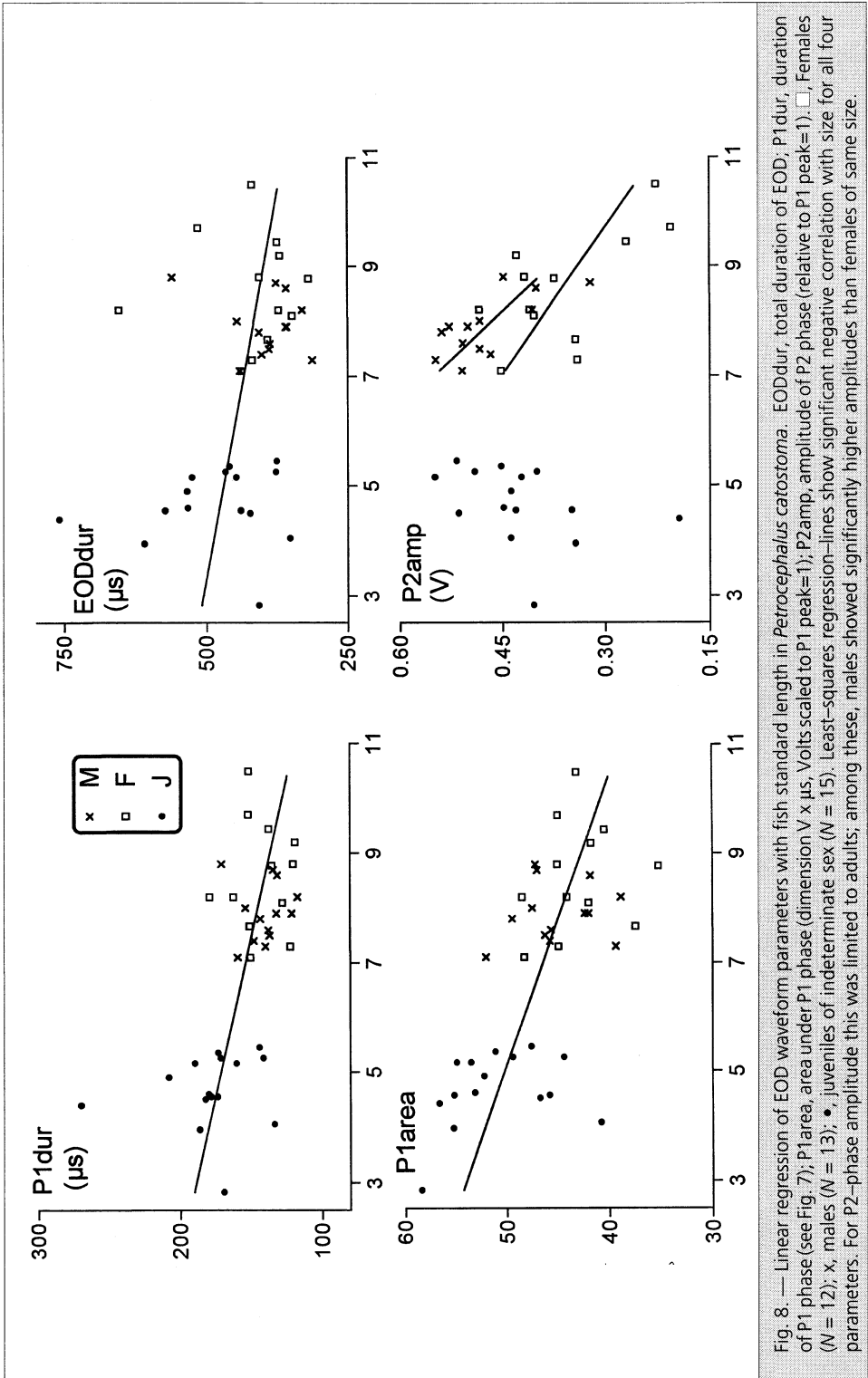
Fig. 8. — Linear regression of EOD waveform parameters with fish standard length in *Petrocephalus catostoma*. EODdur, total duration of EOD; P1dur, duration of P1 phase (see Fig. 7); P1area, area under P1 phase (dimension V x μs, Volts scaled to P1 peak=1); P2amp, amplitude of P2 phase (relative to P1 peak=1). □, Females (N = 12); x, males (N = 13); •, juveniles of indeterminate sex (N = 15). Least-squares regression—lines show significant negative correlation with size for all four parameters. For P2-phase amplitude this was limited to adults; among these, males showed significantly higher amplitudes than females of same size.

Table 4. — Linear regression of an EOD waveform parameter, P2 amplitude (scaled to P1 amplitude =1) in *Petrocephalus catostoma*.

	r*	F	P†	±S.E.M. (slope)	slope	P‡	Y-intercept	±S.E.M. (Y-intercept)	P§	P&
Females (N =12)	-0.6384	6.88	0.0255	0.0212	-0.0556	0.4125	0.84	0.183	0.0168	0.7331
Males (N =13)	-0.727	12.33	0.0049	0.0245	-0.0859		1.151	0.194		0.4242
Juveniles (N =15)	0.381	2.21	0.1609	0.0321	0.2038	—	0.204	0.151	—	0.972

* Correlation coefficient.
† For the hypothesis that the slope of a regression line equals zero.
‡ For the hypothesis that the slopes of the regression lines are equal.
§ For the hypothesis that the elevations, or Y-intercepts, of the regression lines are equal.
& For the hypothesis that the data deviate from a straight line (linear model).

Therefore, it is concluded that over most (or all) of the life of a *P. catostoma* of either sex, P1–phase area and duration decrease continuously, hence, also total EOD duration. Probably beginning with gonadal recrudescence, a second trend can be recognized: females and males both develop a relatively weaker P2–phase amplitude with increasing size so that the triphasic EOD waveform approaches a biphasic one (although this was not quite reached in the present fish). At equal size, male P2–phase amplitudes were stronger than those of females although there was clearly overlap between the sexes.

Compared to *M. macrolepidotus*, the spectral frequency content of *P. catostoma* EODs was higher and more wide–band. Four adult individuals of almost the same size showed great differences in peak amplitude frequencies (of 5781 and 6708 Hz for the two males; 7137 and 8873 Hz for the two females), and –20–dB points which were 21 392 and 23 160 Hz in the two males; 25 820 and 32 500 Hz in the two females (Fig. 9). Fish of all sex or age groups had little or no D.C. component to their EODs as shown by the fact that the sum of the areas for the three EOD phases (P1, N, P2) was close to zero (Table 3).

Gonadal maturity

Mormyrids possess a single gonad only that is usually located on the left body side. Whereas shape and size of eggs are not different from those of better–known fish, sperm cells are unusual in having no flagella (Mattei *et al.*, 1972); this was also true in the two species studied here.

Marcusenius macrolepidotus

The gonads of the fish used for the present study spanned the whole range from immaturity to sexual maturity (Fig. 10). Small females tended to possess small, immature ovaries with stage III
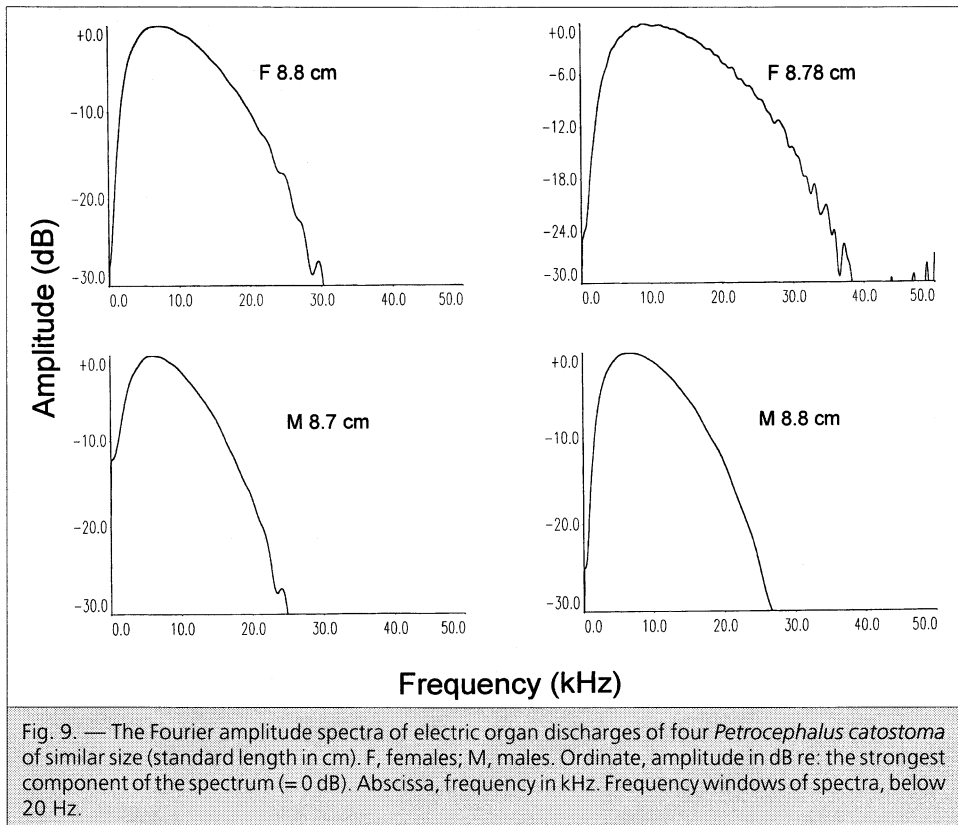
Fig. 9. — The Fourier amplitude spectra of electric organ discharges of four *Petrocephalus catostoma* of similar size (standard length in cm). F, females; M, males. Ordinate, amplitude in dB re: the strongest component of the spectrum (= 0 dB). Abscissa, frequency in kHz. Frequency windows of spectra, below 20 Hz.

oocytes (see, for example, Takashima & Hibiya, 1995) as the most advanced stage (Fig. 10A); that is, these females were unable to reproduce at the time of capture. Most females, however, had considerably more advanced oocytes, and a large proportion of fish were fully capable of reproducing (stage VI oocytes or eggs; Fig. 10B). For the population, body size and oocyte diameter were related by a sigmoid function (Fig. 10C; sigmoid not shown). At 10.6–12.5 cm body size, maturation of stage III oocytes occurred, as apparent especially from their marked increase in size. This corresponds well to field data for several species of mormyrids (Blake, 1977; Kolding *et al.*, 1992) where sexual maturity occurred when fish had reached about 40% of the maximum size for that species; this would be 12 cm for *M. macrolepidotus* that attains a maximum size of 30 cm (Skelton, 1993; Bell-Cross & Minshull, 1988).

According to these authors the time of reproduction is in the rainy season (October–April; summer in Caprivi), and the present data agree with this (fish were collected in March). In mid–March the breeding period was clearly not yet finished in the study area because the ovaries were huge in the larger females at least, often displacing the bowels to an unbelievable extent; some females losing eggs during anaesthesia in 2–phenoxyethanol. Further evidence in support of a breeding season as given above are two "babies" of 3.5 and 4.55 cm also caught in March, a small juvenile of 7.3 cm caught in September (in none of these could the gonads be found during careful dissection), and a female of 19.5 cm

standard length also caught in September. This fish had a completely spent ovary (an empty–looking brown bag of considerable size) containing stage III oocytes (Fig. 10C, ■), like some immature females about half its size. Stage III oocytes seem to be characteristic for the reproductively inactive state both in adults during the non–spawning season and immatures.

For the male sex a similar picture emerged. Among the smallest individuals were six sexually immature ones (11–11.8 cm; Fig. 10D), four males ranging from 11.3–12.1 cm that were intermediate (Fig. 10E), while all others had sexually mature testes (Fig. 10F). In immature testes such as the one shown in Fig. 10D very rarely a cyst of spermatids or of earlier stages (for example, secondary spermatocytes) could be found; there was virtually no lumen to the canals which appeared inactive. Testes of this stage (designated stage 0) were exceedingly small and difficult to find in the body cavity; histology was necessary for certain identification as gonad tissue. In the intermediate stage (designated stage 1) sperm was present but also a high proportion of cysts with earlier stages (Fig. 10E, four fish from 11.3–12.1 cm). Sexually mature testes of big size, with plenty of sperm and wide testicular canals were found in the large majority of males, from 11.6 cm onwards (stage 2; Fig. 10F).

Fig. 12 shows that, although some sexually mature males lagged behind their group, on the whole both P–phase and N–phase duration of the EOD increased with the stage of testicular maturity, as defined above.

Petrocephalus catostoma

All fish considered "adults" in the present study had at least 7.1 cm standard length; hence, were well beyond the 40%–maturity criterion established in other mormyrids that was also found to be true for the *M. macrolepidotus* of the present study. A few of the biggest juveniles (up to 5.45 cm) of Fig. 8 would, therefore, qualify for small adults because 40% of *P. catostoma*'s maximum size of 13 cm is 5.2 cm; not, however, according to Bell–Cross (1974) who gives 15 cm as the maximum known size.

All fish except two had been collected in winter, and the gonads of the fish designated "juveniles" were so small they could not be found during careful dissection. The gonads of all "adults" (except those of the two collected in summer) were all regressed, and not fit for reproduction. Sperm or spermatids were not present in male gonads, and the lumen of canals was reduced to zero or almost zero (stage 0, Fig. 11A). Only one male (of 7.9 cm standard length) had traces of sperm that were hard to find, and very few canals with a lumen (up to 15 μm wide).

Females showed a similarly regressed picture; their most advanced oocytes were of stage III (Fig. 11B). Maximum oocyte diameter ranged from 130–198 μm only. In some ovaries big atretic oocytes were also present; these stained only lightly and had convoluted membranes and other structures in their interior that were absent in viable oocytes. The only fish that appeared fit for reproduction were the two females of 9.7 and 10.5 cm collected in March that had enormous ovaries carrying a large number of ripe eggs of around 860 μm diameter (Fig. 11C).

DISCUSSION

Marcusenius macrolepidotus

The present paper establishes a sexual dimorphism in EOD waveform in a mormyrid fish, *Marcusenius macrolepidotus*. Juveniles and females both displayed EODs of short duration,
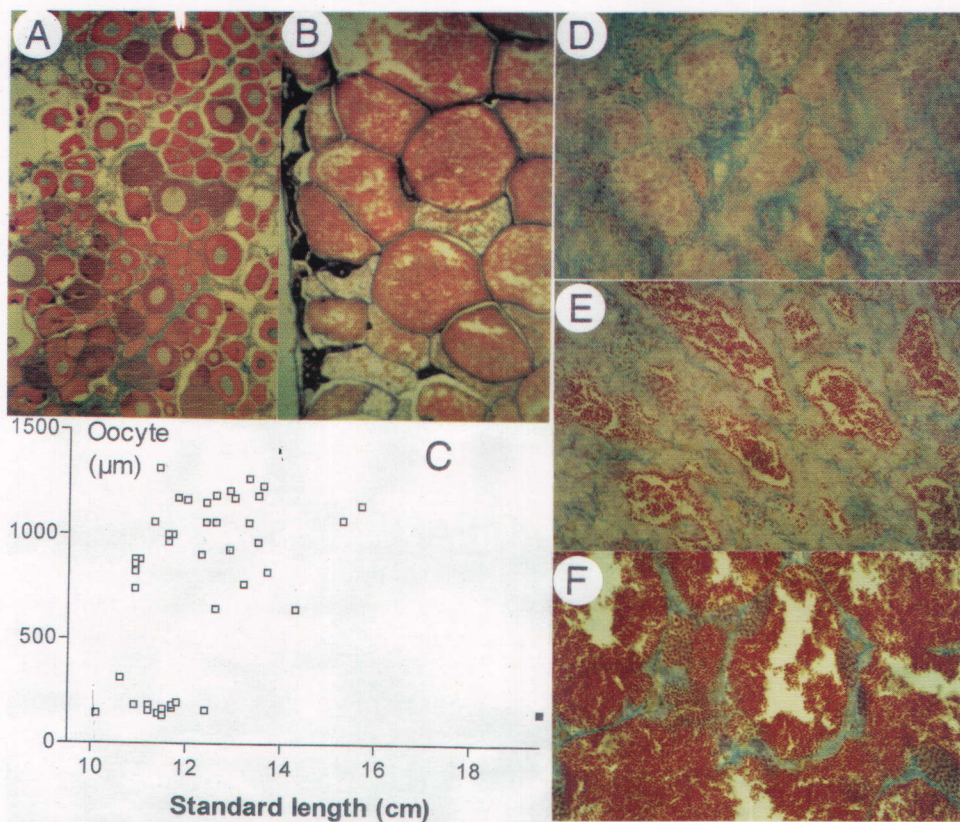
Fig. 10. — Gonadal recrudescence in *Marcusenius macrolepidotus* collected in summer. A,B, ovaries; D–F, testes (x 400). (A) immature ovary with oocytes up to stage III (x 100); (B) mature oocytes present (x 25). (C) maximum oocyte diameter as a function of standard length for all females (■, the single female collected in winter). (D) immature testis of stage 0, as defined in text. (E) intermediate stage; (F) mature stage.
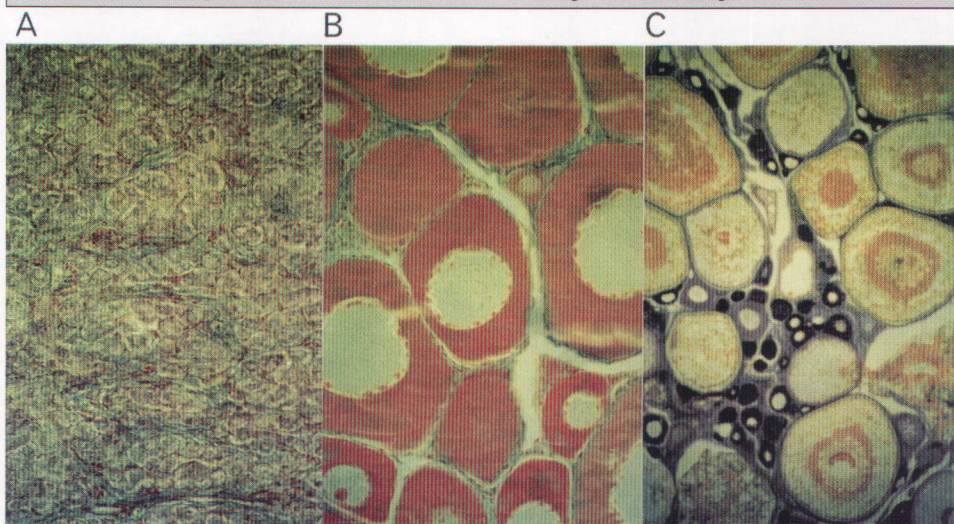

Fig. 11. — Histology of gonads in adult *Petrocephalus catostoma*. (A) winter testis (x 400); (B) winter ovary (x 400); (C) ovary from a fish collected in summer, showing mature oocytes (x 50).
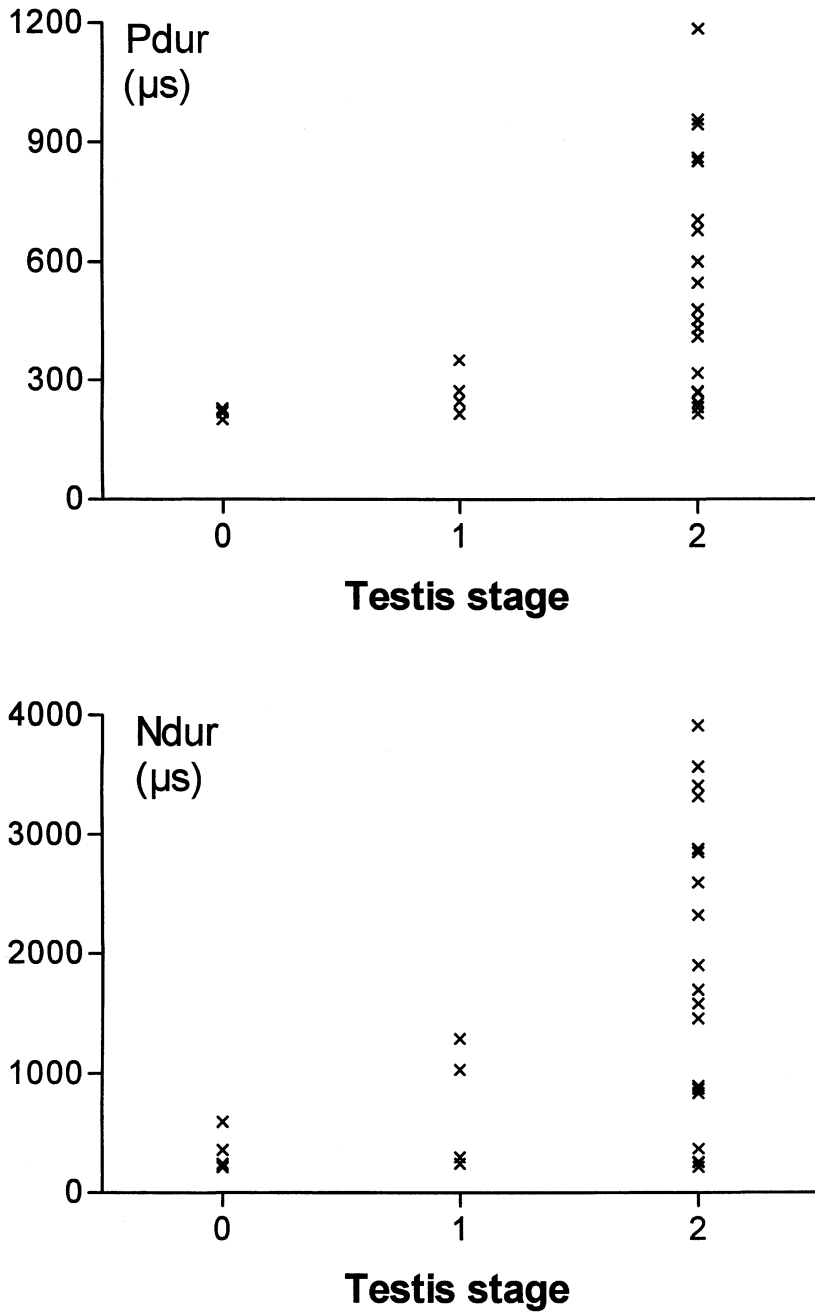
Fig. 12. — In EODs of male *Marcusenius macrolepidotus*, the duration of the P– (upper panel) and N–phase (lower panel) was related with testis development. Stage 0, no sperm; stage 1, sperm present but also a high proportion of cysts with earlier stages; stage 3, massive sperm.

whereas the EODs of sexually mature males were of long duration. For a population of considerable size, with known time and place of origin, the transition from a juvenile short EOD to the long EOD of a sexually mature male was shown, and this change was correlated with body size and maturity stage. EODs were recorded with minimal distortion in the field; by scrutinizing more than a dozen anatomical characters, the species identity of all specimens was established; the sex and the maturity stage were determined by histology.

The EOD dimorphism seen in the M. macrolepidotus must have been selected for sexually, (1) because of the great difference between male and female EODs resulting in two distinct forms: male EODs were of up to 11.5 times longer duration than juvenile ones of average duration that are also typical for most females (up to 2–3 times in the cases described by Hopkins [1988] and Landsman [1995]), and (2) only in M. macrolepidotus males an abrupt change of EOD duration occurred correlated with the onset of sexual maturity, whereas in females no size– or maturity–related EOD changes were observed at all. There are wide, male–specific regions of no overlap with the females in the diagrams for the analysed EOD characters.

That the transition from a short– to a long–duration EOD in male M. macrole-pidotus occurs correlated with sexual maturity gives clues as to the possible function of the dimorphism (sexual advertising), its evolution (sexual selec-tion), as well as the mechanism by which it is brought about in ontogeny (hormones of the gonad–pituitary axis; review, Nelson, 1995). These hypotheses repre-sent a research program for many years.

Besides a low–frequency amplitude spectrum (Fig. 6), M. macrolepidotus males with EODs of the longest durations tended to show a strong D.C. component (Fig. 5). This is especially intriguing because there might be two selective advantages associated with such an EOD for a male: (1) by not only stimulating the females' tuberous, high–frequency sensitive electroreceptors but also their ampullary, "low–frequency" receptors (review, Zakon, 1988), a male might be able to signal its state of maturity and attract more females (conversely, the females had a criterion by which to judge the males). (2) Because ampullary receptors are the most sensitive electroreceptors, the EOD of a male would gain a greater efficiency for advertising over a greater range.

However, there seems to be a cost associated with displaying a "low–frequency" EOD with a strong D.C. component: the two or three biggest males (up to 18.5 cm standard length) were not among those with the most male–like EODs; these were around 14 cm or even below. Merron (1993) has observed that certain predatory catfish (Clarias species) have specialized on pack–hunting (during their spectacular "catfish runs" upstream when the water level is dropping between September and November), with M. macrolepidotus (64%) and P. catostoma (26%) being the main prey. Like all catfish these predators, of which the sharptooth catfish Clarias gariepinus is the principal one, possess ampullary electroreceptors that are well–known for their high sensitivity in the very low–frequency range (Lissmann & Machin, 1963; Peters & Bretschneider, 1981; Peters & van Ieperen, 1989; Teunis et al., 1990; Bretschneider & Peters, 1992). The median standard length of 456 M. macrolepidotus collected from 363 catfish stomachs was 12.5 cm (Merron, 1993), that is, exactly the size when males develop an EOD of long duration and strong D.C. component (Figs 4,5); it would be interesting to know whether the fish eaten by catfish were predominantly male.

Electrosensory thresholds of trained, food–rewarded *C. gariepinus* to play-backs (method: Kramer & Weymann, 1987) of field–recorded *M. macrolepidotus* EODs are low (103 μV_{p-p}/cm) for a male discharge of long (4.7 ms) duration, and much higher (757 μV_{p-p}/cm) for a shorter (2.4 ms) male EOD, whereas the catfish are insensitive to female (0.49 ms) EODs played back at an amplitude as generated by an adult fish (Hanika & Kramer, 1996). Therefore, the presumed sexual selection for EODs of even longer duration seems to be counterbalanced by predator pressure, and males with EODs of the longest duration might have a short (but sweet) life. The absence of a D.C. component to *P. catostoma*'s EOD (as apparent from Table 3) may account in part for its greatly reduced catch rate compared to that of *M. macrolepidotus*.

Petrocephalus catostoma

In contrast to the sexual dimorphism of EOD waveform observed in *M. macrolepidotus*, a "sex difference" (as defined in the Introduction) rather than a sexual dimorphism was found for the EOD waveform of *Petrocephalus catostoma* where both sexes showed similar, size–correlated EOD waveform changes: the regression lines were parallel (same slopes) although the elevation of the lines differed by a small, but significant amount, leading to wide overlap between the sexes (Fig. 8). *P. catostoma* male EODs have, on average, a higher P2–phase amplitude (relative to the P1 phase) than the EODs of females of the same size, although small females may show a higher P2 amplitude than sufficiently big males. Whereas in *M. macrolepidotus* beyond a certain size all males displayed a long EOD, in *P. catostoma* there was wide overlap in P2–phase amplitudes between males and females of similar, including big, size. Therefore, it is proposed that in *P. catostoma* the EOD–related sex difference is not the result of sexual

selection, but due to an (anabolic) side effect of androgenic hormones, as proposed for *Pollimyrus isidori* (Bratton & Kramer, 1988): an androgenic hormone leads to a stronger head–positive potential P (neurally evoked by spinal electromotor nerves that are acetylcholinergic; review, Bass, 1986); the electrically triggered N phase of opposite polarity and short duration is, therefore, evoked earlier, dividing the longer–lasting P potential into two sections or phases (P1 and P2) such that the P2–peak amplitude relative to that of the P1 peak is higher in males than in females.

A similar correlation with size probably is the underlying reason for the great intraspecific variability of the P1/P2–ratio (and disparate views on the topic; see Introduction) in the EOD of *Pollimyrus isidori* (apparently, *Pollimyrus adspersus* rather than true *Pollimyrus isidori* that are very similar have been studied in all or most papers from the "electric fish community", including the present author's lab; J. Crawford, personal communication, based on Bigorne, 1990).

For juveniles and females of a few species (especially of the systematically unclear *"Brienomyrus brachyistius"* complex; see Introduction) injections with androgenic hormones (but also estradiol) have shown that the duration of the EOD pulse lengthened in certain specimens but not in others (review by Hopkins, 1988; for additional species or putative species, see Landsman, 1995). However, because results in pharmacological experiments depend on so many variables in largely unknown territory (e.g., concerning the dose, the right kind of molecule, and pharmaco–kinetics; Landsman, 1995; Kramer, 1973), this cannot be considered strong evidence for sexual dimorphisms in EOD waveform under natural conditions. For determining EOD waveform differences between the sexes, the study of wild

populations of fish where the necessary hormones and other factors are provided endogenously, complemented by gonad histology or some other technique for assessing the maturity stage (Zakon *et al.*, 1991), seems the better way.

Although this has not been convincingly demonstrated yet in mormyrids (see Introduction), EOD waveforms could vary with season; a seasonal reproduction in both species of the present study was confirmed (Skelton, 1993; Bell-Cross & Minshull, 1988; histology data of the present study). In *P. catostoma* females a seasonally varying EOD waveform can be excluded because of the two sexually mature females that were collected in "summer"; their EODs agreed well with those of the other females. For males, however, there is no such information available yet, but the hypothesis seems far–fetched in this species: the differences between size and sex groups were small and of a statistical nature; there was no increased scatter in the male sex that would indicate any potential for the selection of accentuated characters in evolution (Burkhardt & de la Motte, 1987), and nonlinearities were not present in any of the correlations.

Although not studied yet, there appears to be a fundamental difference between *P. catostoma* and *M. macrolepidotus* in how they signal in order to find mates. Considering that there are about 200 species of mormyrids this is not too surprising, and the phylogenetic distance between the two species studied here is relatively large, with *P. catostoma* being the more derived species (Van der Bank & Kramer, 1996). In *M. macrolepidotus* direct recognition of mates by the difference in EOD duration (or D.C. component and spectral frequency content; Figs 5,6) is most likely; in *P. catostoma* this does not seem to be the case, and mate recognition might be facilitated by inter–discharge interval pattern and behavioural/ecological context (Bratton & Kramer, 1989; Crawford, 1991), and perhaps sound signals (Crawford *et al.*, 1986), as in *Pollimyrus adspersus (isidori)*.

ACKNOWLEDGMENT

REFERENCES

Bass, A. H. 1986. Electric organs revisited: evolution of a vertebrate communication and orientation organ. *In* : Bullock, T. H. & Heiligenberg W. (eds.), *Electroreception*, John Wiley, New York, pp. 13-70.

Bastian, J. 1990. Electroreception. *In* : Stebbins W. C. & Berkeley M. H. (eds.), *Comparative perception, vol. II: Complex signals*, John Wiley, New York, pp. 35-89.

————. 1994. Electrosensory organisms. *Physics Today,* February 1994: 30-37.

Batschelet, E. 1975. *Introduction to mathematics for life scientists.* Springer-Verlag, Berlin.

Bell-Cross, G. 1974. A fisheries survey of the Upper Zambezi River System. *Occasional Papers of the National Museums and Monuments of Rhodesia Series B (Natural Sciences)* 5: 279-338.

Bell-Cross, G. & Minshull, J. L. 1988. *The fishes of Zimbabwe.* National Museums and Monuments of Zimbabwe, Harare.

Bigorne, R. 1990. Révision systématique du genre *Pollimyrus* (Teleostei, Mormyridae) en Afrique de l'Ouest. *Rev. Hydrobiol. trop.* 23: 313-327.

Blake, B. F. 1977. Aspects of the reproductive biology of *Hippopotamyrus pictus* from lake Kainji, with notes on four other mormyrid species. *J. Fish Biol.* 11: 437-445.

Bratton, B. O. & Kramer, B. 1988. Intraspecific variability of the pulse-type discharges of the African electric fishes, *Pollimyrus isidori* and *Petrocephalus bovei* (Mormyridae, Teleostei), and their dependence on water conductivity. *Exp. Biol.* 47: 227-238.

————. 1989. Patterns of the electric organ discharge during courtship and spawning in the mormyrid *Pollimyrus isidori*. *Behav. Ecol. Sociobiol.* 24: 349-368.

Bretschneider, F. & Peters, R. C. 1992. Transduction and transmission in ampullary electroreceptors of catfish. *Comp. Biochem. Physiol.* 103A: 245-252.

Burkhardt, D. & de la Motte, I. 1987. Physiological, behavioural, and morphometric data elucidate the evolutive significance of stalked eyes in Diopsidae (Diptera). *Entomol. Gener.* 12: 221-233.

Crawford, J. D. 1991. Sex recognition by electric cues in a sound-producing mormyrid fish, *Pollimyrus isidori*. *Brain Behav. Evol.* 38: 20-38.

————. 1992. Individual and sex specificity in the electric organ discharges of breeding mormyrid fish (*Pollimyrus isidori*). *J. exp. Biol.* 164: 79-102.

Crawford, J. D., Hagedorn, M. & Hopkins, C. D. 1986. Acoustic communication in an electric fish, *Pollimyrus isidori* (Mormyridae). *J. Comp. Physiol. A* 159: 297-310.

Crawford, J. D. & Hopkins, C. D. 1989. Detection of a previously unrecognized mormyrid fish (*Mormyrus subundulatus*) by electric discharge characters. *Cybium (Paris),* 13: 319-326.

Graff, C. 1989. Firing activity of the weakly-electric fish *Marcusenius macrolepidotus* (Mormyridae, Teleostei): logarithmic repartition of inter-pulse intervals, and sequential inequality testing. *Behav.* 109: 258-284.

Graff, C. & Kramer, B. 1992. Trained weakly-electric fishes *Pollimyrus isidori* and *Gnathonemus petersii* (Mormyridae, Teleostei) discriminate between waveforms of electric pulse discharges. *Ethology,* 90: 279-292.

Hanika, S. & Kramer, B. 1996. Elektrosensorische Beutedetektion beim afrikanischen Kiemensackwels *Clarias gariepinus* Burchell, 1822 (Clariidae, Siluriformes) (Electrosensory prey detection in the African sharptooth catfish, *Clarias gariepinus*). *Verh. Dtsch. Zool. Ges.* 89.1: 275

Hopkins, C. D. 1980. Evolution of electric communication channels of mormyrids. *Behav. Ecol. Sociobiol.* 7: 1-13.

————. 1988. Neuroethology of electric communication. *Annu. Rev. Neurosci.* 11: 497-535.

Hopkins, C. D. & Bass, A. H. 1981. Temporal coding of species recognition signals in an electric fish. *Science* 212: 85-87.

Kolding, J., Tirasin, E. M. & Karenge, L. 1992. Growth, mortality, maturity and length-weight parameters of fishes in Lake Kariba, Africa. *NAGA, The ICLARM Quarterly* 15: 39-41.

Kramer, B. 1973. Chemische Wirkstoffe im Nestbau-, Sexual- und Kampfverhalten des Sonnenbarsches *Lepomis gibbosus* (L.) (Centrarchidae, Teleostei). *Z. Tierpsychol.* 32: 353-373.

————. 1979. Electric and motor responses of the weakly electric fish, *Gnathonemus petersii* (Mormyridae), to play-back of social signals. *Behav. Ecol. Sociobiol.* 6: 67-79.

————. 1990. *Electrocommunication in teleost fishes: Behavior and experiments.* Springer-Verlag, Berlin.

————. 1994. Communication behavior and sensory mechanisms in weakly electric fishes. *In* : Slater P. J .B., Rosenblatt J. S., Snowdon C. T. & Milinski M. (eds.), *Advances in the Study of Behavior*, Academic Press, San Diego, CA, pp. 233-270.

————. 1996. *Electroreception and communication in fishes* (Progress in Zoology, vol. 42). Gustav Fischer Verlag, Stuttgart.

————. 1997. Electric organ discharges and their relation to sex in mormyrid fishes. *Naturwissenschaften,* 84: 119-121.

Kramer, B. & Kuhn, B. 1993. Electric signalling and impedance matching in a variable environment: the electric organ of a mormyrid fish actively adapts to changes in water conductivity. *Naturwissenschaften,* 80: 43-46.

————. 1994. Species recognition by the sequence of discharge intervals in weakly electric fishes of the genus *Campylomormyrus* (Mormyridae, Teleostei). *Anim. Behav.* 48: 435-445.

Kramer, B. & Westby, G. W. M. 1985. No sex difference in the waveform of the pulse type electric fish, *Gnathonemus petersii* (Mormyridae). *Experientia,* 41: 1530-1531.

Kramer, B. & Weymann, D. 1987. A microprocessor system for the digital synthesis of pulsed or continuous discharges of electric fish (or animal vocalizations). *Behav. Brain Res.* 23: 167-174.

Landsman, R. E. 1991. Captivity affects behavioral physiology: plasticity in signaling sexual identity. *Experientia,* 47: 31-38.

————. 1993. Sex differences in external morphology and electric organ discharges in imported *Gnathonemus petersii* (Mormyriformes). *Anim. Behav.* 46: 417-429.

————. 1995. Sources of plasticity in behavior and its physiology: sex, hormones, environment and the captivity model. *In* : Moller, P. (ed.), *Electric fishes: history and behavior,* Chapman & Hall, London, pp. 303-343.

Landsman, R. E., Jou, S. H. & Moller, P. 1987. Stress obscures signalling of sexual identity in *Gnathonemus petersii* (Mormyriformes). *In* : Idler D.R., Crim L.W. & Walsh J.M. (eds.) *Reproductive physiology of fish,* Memorial University of Newfoundland, St. John's, Newfoundland, pp. 307.

Landsman, R.E. & Moller, P. 1993. Captivity and signal plasticity in mormyrid fish communication. *J. Comp. Physiol. A* 173: 732-733.

Lissmann, H. W. & Machin, K. E. 1963. Electric receptors in a non-electric fish (*Clarias*). *Nature,* 199: 88-89.

Lücker, H. & Kramer, B. 1981. Development of a sex difference in the preferred latency response in the weakly electric fish, *Pollimyrus isidori* (Cuvier et Valenciennes) (Mormyridae, Teleostei). *Behav. Ecol. Sociobiol.* 9: 103-109.

Mattei, X., Mattei, C., Reizer, C. & Chevalier, J. 1972. Ultrastructure des spermatozoïdes aflagellés des mormyres (Poissons Téléostéens). *J. Microscopie (Paris),* 15: 67-78 + 3 plates.

Maynard Smith, J. 1991. Theories of sexual selection. *Trends Ecol. Evol.* 6: 146-151.

Merron, G. S. 1993. Pack-hunting in two species of catfish, *Clarias gariepinus* and *C. ngamensis* in the Okavango delta, Botswana. *J. Fish Biol.* 43: 575-584.

Moller, P. 1995. *Electric fishes: History and behavior.* Chapman & Hall, London.

Moller, P. & Brown, B. 1990. Meristic characters and electric organ discharge of *Mormyrops curviceps* Roman (Teleostei: Mormyridae) from the Moa river, Sierra Leone, West Africa. *Copeia* 1990: 1031-1040.

Nelson, R. J. 1995. An *introduction to behavioral endocrinology.* Sinauer, Sunderland, MA.

Peters, R. C. & Bretschneider, F. 1981. Electroreceptive microampullae in the African mudfish *Clarias lazera* (Cuv. and Val., 1840). *In* : Szabo T. & Czéh G. (eds.) *Sensory physiology of aquatic lower vertebrates,* Pergamon Press/Akadémiai Kiadó, Budapest, pp. 13–27

Peters, R. C. & van Ieperen, S. 1989. Resting discharge and sensitivity of ampullary electroreceptors in *Clarias gariepinus* related to convergence ratio during ontogeny. *Brain, Behav. Evol.* 34: 43-47.

Postner, M. & Kramer, B. 1995. Electrosensory thresholds in larvae of the weakly electric fish *Pollimyrus isidori* (Mormyridae, Teleostei) during ontogeny. *J. Exp. Biol.* 198: 783-791.

Rankin, J. C. & Jensen, F. B. (eds.) 1993. *Fish ecophysiology.* Chapman and Hall, London.

Romeis, B. 1989. *Mikroskopische Technik,* 17th edn. (Böck, P., ed.). Urban & Schwarzenberg, München.

Scheffel, A. & Kramer, B. 1997. Electrocommunication and social behaviour in *Marcusenius senegalensis* (Mormyridae, Teleostei). *Ethology,* 103: 404-420.

Skelton, P. H. 1993. *A complete guide to the freshwater fishes of southern Africa.* Southern Book Publishers, Halfway House (South Africa).

Teunis, P. F. M., Bretschneider, F. & Peters, R. C. 1990. Convergence ratio and transduction in catfish electroreceptive organs. *Comp. Biochem. Physiol.* 97A: 405-410.

Takashima, F., Hibiya, T. (eds.) 1995. *An atlas of fish histology. Normal and pathological features.* Gustav Fischer Verlag, Stuttgart.

Van der Bank, F. H. & Kramer, B. 1996. Phylogenetic relationships between eight African species of mormyriform fish (Teleostei, Osteichthyes): resolution of a cryptic species, and reinstatement of *Cyphomyrus* Myers, 1960. *Biochem. Syst. Ecol.* 24: 275-291.

Van der Bank, F. H. & van der Bank, M. 1995. An estimate of the amount of genetic

variation in the snoutfish *Marcusenius macrolepidotus* (Peters, 1852). *Water SA* 21: 265-268.

von der Emde, G. & Zelick, R. 1995. Behavioral detection of electric signal waveform distortion in the weakly electric fish, *Gnathonemus petersii. J. Comp. Physiol. A* 177: 493-501.

von Holst, D. 1987. Physiologie sozialer Interaktionen - Sozialkontakte und ihre Auswirkungen auf Verhalten sowie Fertilität und Vitalität von Tupajas. *Physiologie aktuell,* 3: 189-208.

Westby, G. W. M. & Kirschbaum, F. 1982. Sex differences in the waveform of the pulse-type electric fish, *Pollimyrus isidori* (Mormyridae). *J. Comp. Physiol. A* 145: 399-403.

Zakon, H. H. 1988. The electroreceptors: diversity in structure and function. *In* : Atema J., Fay R. R., Popper A. N. & Tavolga W. N. (eds.), *Sensory biology of aquatic animals,* Springer-Verlag, Berlin Heidelberg New York Tokyo, pp. 813-850.

Zakon, H. H., Thomas, P. & Yan, H.-Y. 1991. Electric organ discharge frequency and plasma steroid levels during gonadal recrudescence in a natural population of the weakly electric fish *Sternopygus macrurus. J. Comp. Physiol. A* 169: 493-499.