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Permanent and seasonal expressions of sexual dimorphisms in a weakly electric fish, *Mormyrus rume proboscirostris* Boulenger 1898 (Mormyridae, Teleostei)

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Synopsis

Several sexually dimorphic characters of the anal-fin complex in the mormyrid fish, *Mormyrus rume proboscirostris*, assist during courtship when the male envelops the female's anal fin with its own to form a common spawning pouch (anal-fin reflex). We found that developmental growth and seasonally cycling gonadal activity selectively affect their expression. The structures defining the anal fin undergo a permanent sexually dimorphic transformation at a time when ripe spermatozoa first appear in the testis of young males. However, the expression of a dorsally directed indentation of the posterior ventral body wall, affecting the dorsal margin of the anal fin, appeared to be more plastic as it correlated with the gonadosomatic index, that is, testis size. We surmised that this indentation is influenced by cyclic anabolic action on muscle involved with the execution of the anal-fin reflex.

Introduction

African freshwater mormyrid fishes generate and perceive electric organ discharges (EODs) that comprise their principal means of spatial orientation and social communication (reviews by Hopkins 1981, 1986, Kramer 1990, Moller 1995, von der Emde 1998). The environmental factors that control their cyclic reproduction are related to high water conditions, the most important cue being the associated decrease in water conductivity affecting gonadal maturation (Kirschbaum 1987, 2000, Kirschbaum & Schugardt 2003). Several secondary behavioral (EOD-related) and structural sexual dimorphisms facilitate the fish's reproductive behavior. During courtship the male displays the anal-fin reflex, enveloping the female's anal fin with its own to form a temporary spawning pouch (Iles 1960, Kirschbaum 1987, Kirschbaum & Schugardt 1995). The courtship scenario for *Mormyrus rume proboscirostris*, the species of choice in this study, unfolds as follows (Schugardt 1997): at nightfall, for a period of time, a male will follow a female that will eventually determine the spawning site by turning around her long axis over the chosen site while the male circles around her in the opposite direction. When the female abruptly stops turning, the male positions himself alongside the female such that their bodies are aligned along their long axes forming a short-lived trough-like formation. With its large 'feathery' anal fin the male envelops the female's anal opening, both spawn, and the fertilized eggs sink to the bottom. The forming of a spawning pouch seems to reflect an adaptive reproductive strategy considering the fact that mormyrid spermatozoa lack motility due to the absence of a flagellum (Mattei et al. 1972).

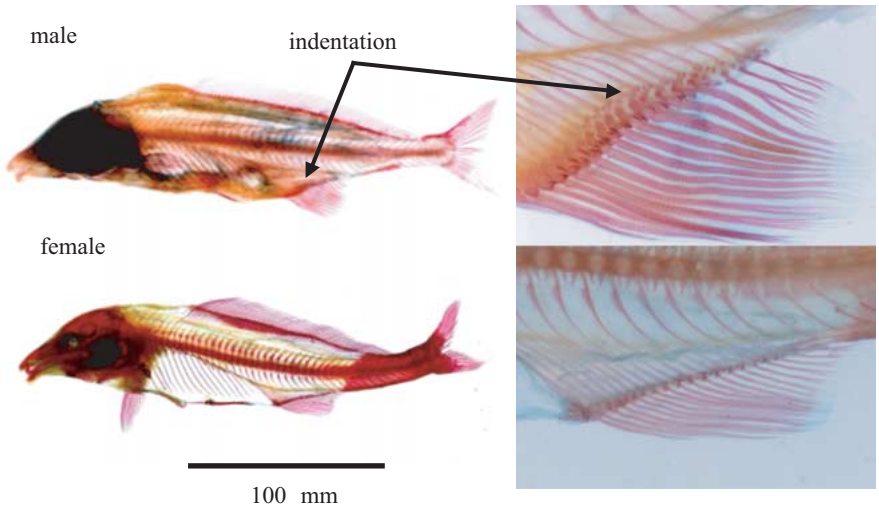

Figure 1. Cleared and stained specimens illustrate sexual dimorphisms in the mormyrid fish, *M. r. proboscirostris*. Males exhibit a dorsally directed indentation of their ventral body wall involving the dorsal margin of their anal fin (arrow). Females, in contrast, show a more straight dorsal margin. Insets: enlargement of the anal-fin complex demonstrates the expanded bases ('spurs') of several rays in males which are absent in females.

The anal-fin reflex requires both osteological and muscular support, and the expression of both is thought to result in a dorsally directed indentation of the posterior ventral body wall in males (Brown et al. 1996). We assume that the massive expansion affecting the bases of a select number of anal fin rays in the adult male provides the substrate for muscle attachment that would facilitate the anal-fin reflex (Brown et al. 1996, Pezzanite & Moller 1998, Voustianiouk 2003, A. Herfeld pers. commun.). Androgens appear to drive the normal development of this expansion as suggested by androgen-treated juveniles and adult females that resulted in male-typical transformations in two mormyrids (*Brienomyrus niger* Günther 1866: Herfeld & Moller 1998, *Gnathonemus petersii* Günther 1862: Voustianiouk 2003, Greisman & Moller unpubl. observ.). A comparable expansion is essentially absent in adult females (Figure 1).

This study was designed to explore select structural sexual dimorphisms that are associated with the performance of the anal-fin reflex in *M. r. proboscirostris*. Based on a survey of preserved specimens of known developmental and maturational stages we have investigated the role of developmental growth and adult gonadal status as they affect permanent or plastic transformations in the anal-fin complex (anal-fin length, anal-fin area, basal anal-fin ray expansion, and body wall indentation). We hypothesized that the male-typical osteological characters are transformed permanently during development whereas the dorsally directed ventral body wall indentation, which is presumably due to an increase in musculature, follows the seasonal changes in gonadal status.

Material and methods

Subjects

Mormyrus rume proboscirostris (*M. r. proboscirostris*) is endemic to the upper runs of the River Congo (Gosse 1984). Fish used in this study were bred in the laboratory at the Leibniz-Institute of Freshwater Ecology and Inland Fisheries in Berlin, Germany, following the regimen introduced by Kirschbaum (1987, 1992, 1995). By simulating rainy season conditions one can induce gonadal maturation and, conversely, by simulating dry season conditions, gonadal regression. (For further details and selection of specimens, see Results.)

Histology/radiography

Fish were sacrificed with an overdose (500 mg l^{-1}) of MS 222 (tricaine methanesulfonate, Sigma), and the gonad was immediately removed. Mormyrids possess only one developed gonad, on their left side. The gonad

was weighed (GW), measured and the gonadosomatic index determined (GSI = [GW/(BW-GW) × 100]). The material was fixated in Bouin (24 h) and transferred into 70% ethanol. Small portions of the gonad were embedded in paraffin using an automatic embedding device (BAVIMED™), sectioned (5 µm), and stained following Domagk (in Romeis 1989: no. 1535).

Fish were radiographed (Hewlett-Packard, model Faxitron 43807 N) under low-intensity radiation (30–40 KVP) for 120 s. Representative specimens were cleared and stained (Taylor & Van Dyke 1985). All radiographs were scanned into computer (Epson, Perfection 1200) for morphometric and meristic analyses of the anal-fin complex using commercial imaging software (SigmaScan™ Pro).

The following measures were taken (Figure 2): (1) the length of the anal fin (AFL), (2) the total fin area (TFA, Figure 2b) as defined by the boundary of the distal points of all 21 fin rays and the most dorsal points of all anal-fin ray bases, (3) the basal area of each of the first 18 individual rays (IBRA, Figure 2b), yielding a total basal ray area (Σ18 IBRAs = TBRA) (*M. r. proboscirostris* have 20–21 anal-fin rays, but only the first 18 rays were evaluated as the measuring error increased with a decrease in size of the last two or three fin ray bases), (4) the number of rays with expanded bases 'spurs' (SPR), (5) the location of the most dorsally directed indentation (Figure 2a) as defined by ray site (RMAX) (shown for males in Figure 2a: P1), and (6) the indentation angle associated with this site as defined by the tip of the most dorsally directed ray (RMAX = P1), the most dorsal point of the first anal-fin ray basis (P2), and the most dorsal point of the last anal-fin ray basis (P3). The measurement of the indentation angle in females was based on RMAX at ray sites 3–8. The angular measurement was always taken from the ray site with the maximum dorsal body wall indentation, but the basal area of this ray was not always maximally expanded.

To assess the possible influence of other factors than regular growth on the area measures (TFA and TBRA), we standardized these measures by adjusting for inter-individual size differences and defining two size independent indices: TFA-I as defined by $TFA \times AFL^{-2}$, and TBRA-I as defined by $(TBRA \times AFL^{-2})100$. These indices represent a 'unit area measure' and we expected any effects of regular growth to result in a constant value, whereas other factors should affect a change. We chose the AFL as reference because of its structural contiguity to our measures TFA and TBRA. Bone expansion occurs in three dimensions. As the total basal anal-fin ray area and volume increase proportionally, we considered the area measure representative.

Data were subjected to ANOVAs with Newman–Keuls *post-hoc* comparisons ($\alpha = 0.05$), multiple regression analysis, and *t*-tests for independent

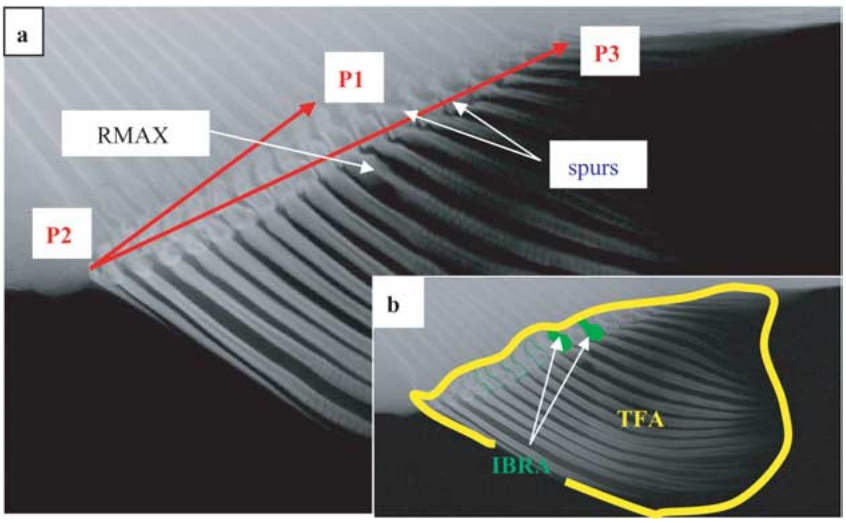

Figure 2. Radiographs of the anal-fin complex of a male *M. r. proboscirostris* illustrating the morphometric and meristic measures used in this study: (a) (AFL = P2–P3), number of rays with expanded bases 'spurs' (SPR), location of the most dorsally directed indentation (RMAX = P1), and indentation angle defined by P1, P2, and P3; (b) TFA and basal area of individual rays (IBRA).

Table 1. The effect of size (SL) and gonadal status (GSI) on the sexual differentiation of four characters of the anal-fin complex in the mormyrid fish, *M. r. proboscirostris*.

Character	Standard length (SL)	Gonadosomatic index (GSI)
TBRA		
Males	0.89 (0.769)	0.68 (0.203)
Females	0.88 (0.904)	0.68 (−0.03)
Number of SPR		
Males	0.56 (0.313)	0.59 (0.401)
Females	0.48 (0.211)	0.51 (0.355)
Location of RMAX		
Males	0.47 (0.471)	0.292 (0.001)
Females	0.33 (0.154)	0.34 (0.219)
Indentation angle		
Males (ray sites # 9–12)	0.38 (0.013)	0.59 (0.587)
Females (ray site # 3)	0.52 (0.344)	0.51 (0.246)

Multiple regression analysis: correlation coefficients and β-values (in brackets). Significant correlations are underlined.

Table 2. Results of statistical analyses.

				df	p
ANOVA 1	Size × sex	F_{size}	20.0	2, 57	<0.0001
		$F_{interaction}$	5.0	2, 57	<0.0001
ANOVA 2	Size × sex	F_{size}	74.2	2, 68	<0.001
		F_{sex}	10.29	1, 68	<0.002
ANOVA 3	Size × sex	F_{size}	69.3	2, 58	<0.0001
		F_{sex}	49.1	1, 58	<0.0001
		$F_{interaction}$	27.6	2, 58	<0.0001
ANOVA 4	IBRA	F	18.48	17, 468	<0.001
ANOVA 5	Size × sex	F_{size}	110.06	2, 58	<0.0001
		F_{sex}	155.18	1, 58	<0.0001

Size refers to standard length of fish; IBRA – individual basal fin-ray area.

samples using a commercially available statistics package (STATISTICA™). We have noted the applicable tests in the text and reported the results in Tables 1 and 2.

IACUC approval

All procedures involving live animals conducted at the Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Berlin, were in compliance with local, state and federal regulations and approved by the Institutional Animal Care and Use Committee. Data obtained and analyzed in New York at the American Museum of Natural History (radiography) were exclusively from preserved specimens following completion of the Berlin portion of this project.

Results

Breeding procedures and selection of specimens

Breeding pairs ranged in size from 215 to 272 mm (males) and from 168 to 241 mm (females) and were about 2 years old (Schugardt 1997). Gonadal recrudescence and regression were induced by respectively simulating dry and rainy seasons. First, over a period of 83 days, water conductivity was gradually decreased from high levels (800–1,200 μS cm^{-1}; high levels are encountered during the dry season) to low levels (200 μS cm^{-1}; lower levels occur during the rainy season). Then, over a period of 63 days, water conductivity was raised again to its dry season value. Modifying Kirschbaum's (1987) original procedure, Schugardt (1997) was able to induce spawning without varying the water level and interspersing periods of simulated 'rainfall' by just manipulating water conductivity.

Under the laboratory-imposed breeding regimen, following 2 months of dry season conditions, the testis in adult males appeared as a small band between the swim bladder and the intestinal tract with some sperm left from the previous cycle and spermatogonia (Figures 3a and 4a). Following 3 weeks of simulated rainy season, the testis expanded caudally with numerous sperm, and 6 weeks later, expanded further appearing still more voluminous with numerous sperm and a few spermatogonia (Figures 3b, 4b, and c). With the onset of the new simulated dry season, the gonad regressed in size and volume and, after 6 weeks, was indistinguishable from the original condition prior to onset of the artificial rainy season (noting a decreased number of sperm and first-order spermatocytes). In females, following 3 months of dry season conditions, the slightly transparent, fully regressed ovary containing barely developed oocytes (primary growth stage) was located on the left side ventral to the swim bladder (Figures 3c and 4d). Three weeks later, under the simulated rainy season, the ovary expanded in a ventral-caudal direction and increased in volume with numerous oocytes in different developmental stages. At the end of the 6-week rainy season, the ovary containing oocytes at maturity stage III (vitellogenesis) expanded still further occupying a large space in the body cavity with the intestinal tract being pushed ventrally (Figures 3d, 4e and f). Three weeks into the dry season, the ovary had considerably decreased in volume with only oocytes in the primary growth stage present.

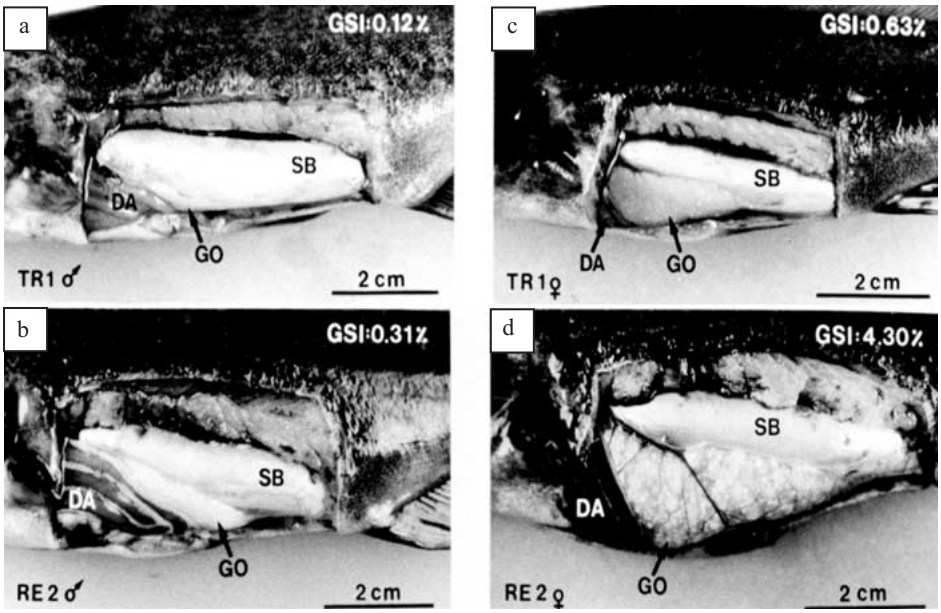

Figure 3. Effects of simulated dry (TR1) and rainy seasons (RE2) on gonadal size (GO) and GSI in males (a, b) and females (c, d). SB – swim bladder; DA – gut. Simulated rainy season triggers gonadal recrudescence.

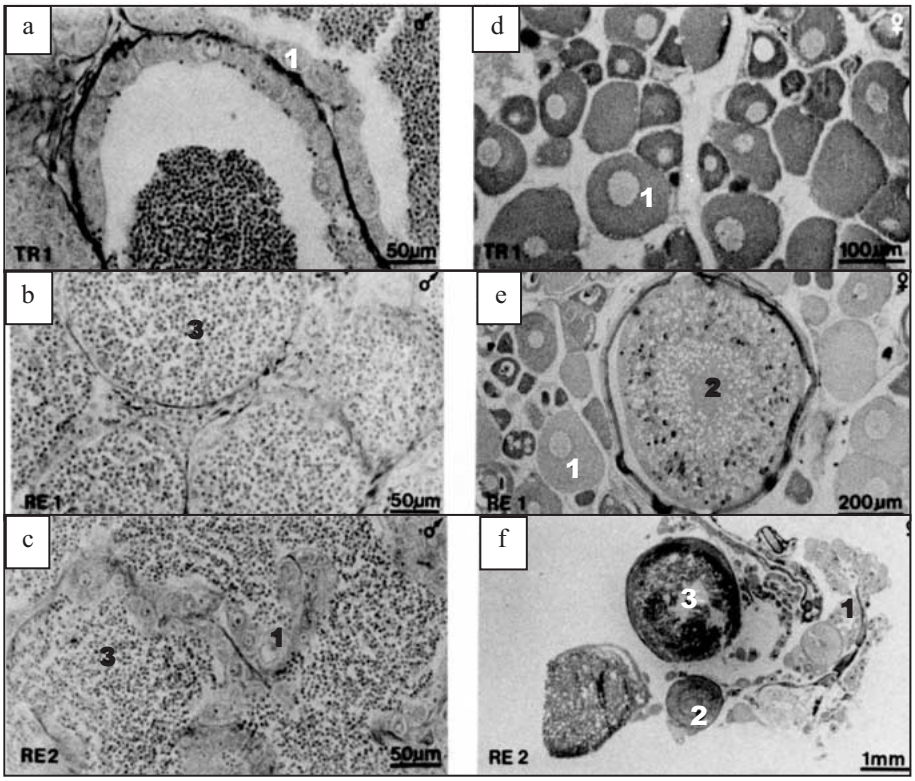

Figure 4. Effects of simulated dry (TR1) and rainy seasons (RE1, RE2) on spermiation (a–c) (1 – spermatogonia, 3 – spermatozoa), and oocytic maturation (d–f) (1 – stage I oocytes, 2 – stage II oocytes, 3 – stage III oocytes (vitellogenesis)).

Fish did not grow during reproductive periods. From their offspring we surveyed 42 males (range: SL 76–282 mm) and 33 females (range: 75–215 mm) (deposited with the American Museum of Natural History: AMNH, lot 232025). Fish were removed from stock tanks at various stages of their development and simulated rainy–dry season conditions. Based on size, we distinguished between juveniles, young (intermediate), and adult specimens. Following Schugardt (1997), fish were also assigned to 'dry' and 'rainy season' based on their GSI measures. Stages of gonadal maturation follow the terminology of Wallace & Selman (1981) for oogenesis and Grier (1981) for spermatogenesis.

Juveniles ranged from 75 to 110 mm with gonads containing exclusively spermatogonia and oocytes stage 1, respectively. On average, males measured 90.3 [mean] ± 8.9 [SD] mm (n = 9), and females 92.5 ± 15.1 mm (n = 10).

Young intermediates ranged from 125 to 147 mm with the testis in some males already containing sperm, but the ovary in all females was still undeveloped. On average, males measured 133.2 ± 4.6 mm (n = 6; GSI data were available from 6 fish with 5 dry and 1 rainy season specimens), and females 138.7 ± 7.4 mm (n = 3; GSI data from 3 fish with 3 dry and no rainy season specimens).

Adults with either fully developed or regressed gonads ranged from 152 to 282 mm. On average, males measured 189.2 ± 35.4 mm (n = 27; GSI data from 20 fish with 10 dry and 10 rainy season specimens), and females 175.9 ± 20.7 mm (n = 20; GSI data from 18 fish with 10 dry and 8 rainy season specimens).

General effects of growth (SL) and gonadal conditions (GSI)

To evaluate the nature of the shared effects of developmental growth and gonadal status on the selected anal-fin characters in *M. r. proboscirostris*, we performed a multiple regression analysis (Table 1). Both TFA and the TBRA were significantly correlated with growth in both sexes, whereas the gonadal condition of the fish had no significant influence on these two measures. In either sex the expression of expanded ray bases (SPR) and the site of the most dorsally indented ray (RMAX) were not correlated with SL and GSI. The indentation angle in females, too, was not significantly correlated with size or gonadal status. The indentation in males, however, was significantly affected by GSI (i.e. testis size) but not by the size of the fish (growth). In the following we will address the specific effects of fish size (growth) and gonadal status on the selected anal-fin characters as they are expressed in males and females.

Anal-fin characters related to fish size (growth): TFA, TBRA, SPR, RMAX

The anal fin in juvenile males and females is indistinguishable in shape and size. The growth curves were best fitted as power functions (males: $TFA = 0.0003\ SL^{2.5}$, $R^2 = 0.85$, $p < 0.001$ and females: $TFA = 0.003\ SL^{1.9}$, $R^2 = 0.86$, $p < 0.001$). At about 130–140 mm SL, we noticed first externally visible signs of a sexual dimorphism when the male's anal fin exhibited a clear rounding of its distal portion and ripe sperm was observed for the first time in some of these fish. Adult *M. r. proboscirostris* males were clearly distinguishable from females by size and shape of their anal fin (see Figure 1). The TFA in adult males significantly exceeded that of juvenile and young intermediate males (Figure 5a) as well as all females (ANOVA 1,

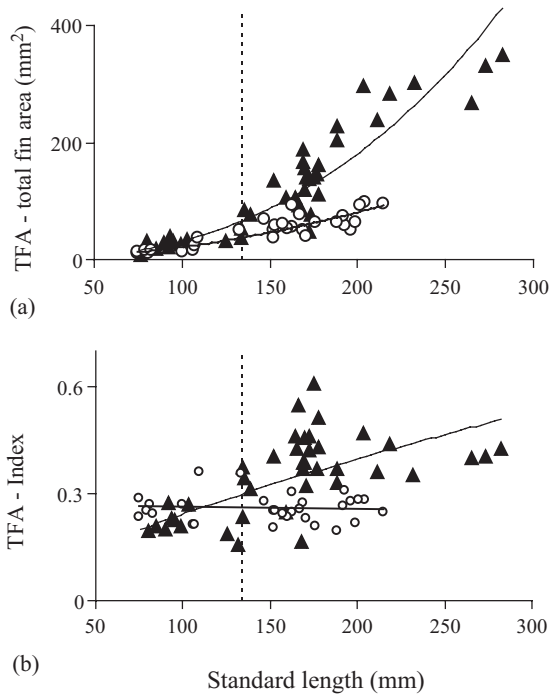

Figure 5. Relationship between size and TFA in male (▲) and female (○) *M. r. proboscirostris.* (a) TFA in adult males exceeded that of juvenile and young intermediate males as well as all females. (b) When the area measure was adjusted for size (TFA-Index), the index remained constant in females, but increased significantly in males. Hatched vertical line denotes the mean size of intermediate males.

Table 2), size × sex, showed significant main and interaction effects. When the area measure was adjusted for size (Figure 5b), the index (TFA-I) remained, as predicted, constant in females (TFA-I = 0.28), but increased significantly in males(TFA-I = $0.009\,SL^{0.71}$, $R^2 = 0.43$, $p < 0.001$).

The AFL influences the size of the TFA. Thus, we found AFL to be significantly affected by size but also by sex (ANOVA 2, Table 2). A sexual dimorphism affecting the anal fin length appeared to be already present in juveniles although this small difference was only significant in adult fish. The relationship between SL and AFL was nearly linear, but best fitted to power functions: AFL (males) = $0.193\,SL^{0.88}$ ($R^2 = 0.91$) and AFL (females) = $0.102\,SL^{0.98}$ ($R^2 = 0.88$).

The TBRA was affected by growth and sex (Figure 6a). The growth curves were best fitted by linear functions (males: TBRA = 0.16 SL – 13.95, $R^2 = 0.89$, $p < 0.001$, and females: TBRA = 0.03 SL – 1.43, $R^2 = 0.75$, $p < 0.001$). Concurring with the expression of a male-typical anal fin, the TBRA became sexually dimorphic when ripe sperm was first observed in young intermediate males. The TBRA in adult males differed significantly from TBRA in juvenile and young intermediate males, as well as from all females. TBRA in intermediate males differed already significantly from juvenile females (ANOVA 3, Table 2).

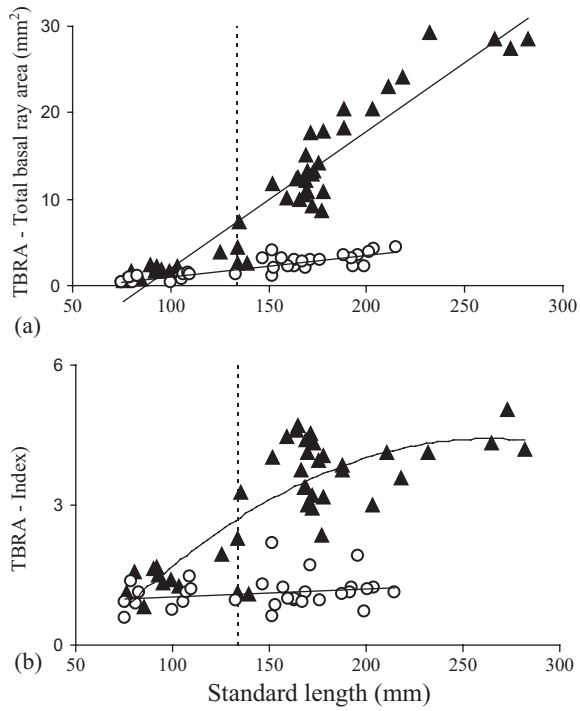

Figure 6. Relationship between size and TBRA in male (▲) and female (○) *M. r. proboscirostris.* (a) TBRA was affected by growth and sex. Concurring with the expression of a male-typical anal fin (see Figure 5), TBRA became sexually dimorphic when ripe sperm was first observed in young intermediate males (hatched vertical line). (b) When TBRA was adjusted for size (TBRA-Index), the index remained constant in females, but increased in males.

When the area measures were adjusted for size (Figure 6b), the area index (TBRA-I) remained, again as predicted, constant in females (TBRA-I = 0.86, slope b = 0.002, $R^2 = 0.04$, $p > 0.05$), but increased in males from 0.82 in juveniles to a maximum of 5.1 in adults. The best fit between SL and TBRA-I within the size range surveyed was represented by a binomial function: TBRA-I = $0.0001\,SL^2 + 0.05\,SL - 2.68$ ($R^2 = 0.69$, $p < 0.001$).

Figure 7 illustrates a ray-by-ray evaluation of the IBRA in males and females. In males we noted a growth-related, caudally directed extension of the number of spur-bearing rays (SPRs) ranging over up to 16 ray sites beginning at ray site 3 (Figure 7a). On average, we counted 9.8 ± 3.7 SPRs in young intermediates and 14.2 ± 1.4 SPRs in adults. In adult males, the basal area of 12 expanded rays (sites 3–14) remained unchanged (mean ± SD per ray: 1.15 ± 0.1 mm^2, but differed from that of the first two and the last four rays (0.44 ± 0.21 mm^2) in both adult dry and rainy season males (ANOVA 4, Table 2). The maximum dorsally directed body wall indentation, on average, was associated with ray site 9.2 ± 0.8 in intermediate, and 10.9 ± 0.9 in adult males (RMAX, range: 9–12).

Unlike other mormyrids (e.g. *Gnathonemus petersii*: Pezzanite & Moller 1998), female *M. r. proboscirostris* occasionally also possess a few slightly expanded rays. In contrast to males, however, there was no caudally directed extension of SPRs related to size (growth). The expanded rays ranging in number from 0 to 5 remained associated with ray sites 3–8 in intermediate and adult females (Figure 7b). In adult fish, the basal area of 7 expanded rays (sites 2–8) remained unchanged (0.25 ± 0.04 mm^2). The TBRA in adult males exceeded that of females by a factor of 5.7 (ANOVA 5, Table 2).

Anal-fin characters related to gonadal conditions: indentation angle

We have measured the maximum dorsally directed body wall indentation in both males (rays sites 9–12) and females (ray site 3). As reported (see Table 1), the associated indentation angles increased with size in

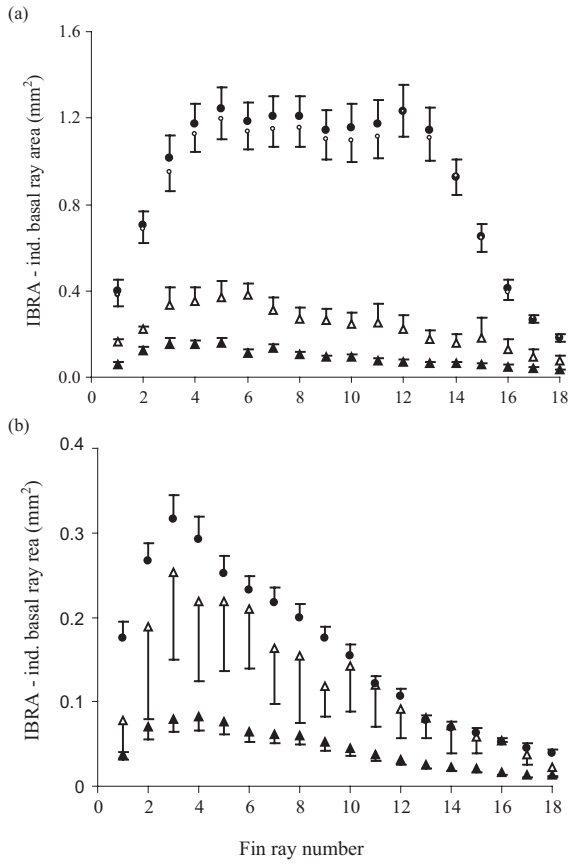

Figure 7. Growth-directed, sexually dimorphic transformation of individual anal-fin ray bases (IBRA, rays 1–18) in *M. r. proboscirostris* (a, males; b, females). Symbols refer to ▲ – juveniles (75–110 mm), young intermediates (125–147 mm), and ●, ○ – adults (152–282 mm). In adult males, the number of expanded rays extends caudally involving up to 12 rays beginning at ray site 3, whereas in females, the most expanded rays remain associated with ray site 3. There was no difference between dry (○) and rainy season adult males (●). Lines represent moving averages over two consecutive measures. Note the four-fold larger maximum expansion in males.

both sexes, but only in adult males was this indentation significantly affected by the fish's gonadal status. There was a significant difference between the indentation angles in dry season (8.8°) and rainy season males (12.8°) ($t_{18} = 3.64$, $p = 0.0019$).

Discussion

We have investigated a set of sexually dimorphic characters of the anal-fin complex in the mormyrid fish, *M. r. proboscirostris*, and suggest that developmental growth and seasonally cycling gonadal activity selectively affect their expression. We have identified both permanent, GSI-independent expressions of sexual dimorphisms as well as GSI-dependent plastic transformations affecting the outward appearance of the fish's posterior ventral body wall.

The correlation of the anal-fin characters with developmental stage (size), GSI, and sex strongly suggested that structures such as fin rays (fin area) and select anal-fin ray bases (area, expanded ray bases) in males undergo a permanent sexually dimorphic transformation at a time when ripe spermatozoa first appear in the testis of young males. In adult males, the most dramatic differentiation became apparent with a caudally directed extension of the number of rays with basal fin-ray expansion (spurs) involving up to 16 rays. These changes were independent of the fish's gonadal status.

In contrast to females of other surveyed mormyrids, adult female *M. proboscirostris* sometimes possess slightly expanded anal-fin rays. The associated indentation in females was exclusively growth-dependent and there were never more than five expanded rays as compared to 15–16 in males. It seems likely that these arise as a 'correlated trait' to that in males; there is to date no known functional significance in females.

The ventral body wall indentation affecting the dorsal margin of the anal fin, on the other hand, appeared to be more plastic in its expression as it clearly correlated with the GSI, that is, relatively larger testes affecting larger indentations and relatively smaller testes affecting smaller indentations. In many teleosts, seasonally fluctuating hormone titers affect morphological changes in the size of the testes in tandem with spermiation and/or spawning as indicated by GSI, that is, high androgen levels correlate with large GSI values (Gazola & Boirella 1997, Holland et al. 2000).

Permanent and cyclic structural sexual dimorphisms are a common phenomenon in fish. Adult males of all *Polypterus* species possess a much larger anal fin, stronger developed anal-fin musculature, and often a higher number of anal-fin rays than females (Kamataga et al. 1993, Bartsch & Britz 1996). The indentation of the body wall in *Polypterus* males resembles that observed in male mormyrids, as initially illustrated by Budgett (1907) for *Polypterus* and Boulenger (1909) for mormyrids. It remains to be demonstrated whether this dimorphism also plays a role in the reproductive behavior of these fish. Males of many live bearing Poeciliidae (guppies, mosquitofish, and swordtails) permanently transform select anal-fin rays into a functional gonopodium (e.g. Rodriguez-Sierra & Rosa-Molinar 1990, Rosa-Molinar et al. 1996). During

the breeding season, males of the bottlenose catfish, *Ageneiosus* sp., modulate the spinulation, length, and diameter of the dorsal-fin spine (Ferraris 1988).

The seasonal cyclicity of gonadal steroids appears to impact on the expression of the body wall indentation in *M. r. proboscirostris*. We propose that the observed difference in the angular measure (as a quantifier of this indentation) is likely due to anabolic action of the fish's circulating androgens, possibly 11-ketotestosterone, on muscle tissue. We infer that seasonally dependent androgen titers associated with the measured changes in GSI cause changes in muscle volume, which in turn, during recrudescence, become indirectly manifest in an increase in the angular measure.

In teleost fishes, androgens can have permanent organizational effects on peripheral structures, that is, secondary sexual characters such as bone and muscle (e.g. Brantley et al. 1993a, Herfeld & Moller 1998, Rosa-Molinar et al. 1996, Zakon 2000). In the absence of an endocrine profile on *M. r. proboscirostris*, we can only infer that the timing of these permanent and seasonal transformations might be related to differences in sensitivity thresholds of the target tissue or differential androgen action (involving selectively only one of the gonadal steroids, that is, testosterone, 11-keto testosterone, or testosterone-aromatized estradiol).

Such plausible anabolic effects on the anal-fin musculature in mormyrids mirror the effect of seasonally fluctuating androgen levels on these fish's electric organ (which is of myogenic origin) and the EOD it generates (Bass 1986a, b, Bass & Hopkins 1983, 1985, Landsman 1993a, 1995). Electrocytes in males are significantly larger with many more membrane infoldings than those in females which taken together results in longer lasting EODs (caused by higher membrane capacitance and delayed timing of the depolarization of the anterior membrane) (Bass 1986a, Bass et al. 1986, Freedman et al. 1989).

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