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Oxygen consumption in weakly electric Neotropical fishes

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Abstract Weakly electric gymnotiform fishes with wave-type electric organ discharge (EOD) are less hypoxia-tolerant and are less likely to be found in hypoxic habitats than weakly electric gymnotiforms with pulse-type EOD, suggesting that differences in metabolism resulting from EOD type affects habitat choice. Although gymnotiform fishes are common in most Neotropical freshwaters and represent the dominant vertebrates in some habitats, the metabolic rates of these unique fishes have never been determined. In this study, O_2 consumption rates during EOD generation are reported for 34 gymnotiforms representing 23 species, all five families and 17 (59%) of the 28 genera. Over the size range sampled (0.4 g to 125 g), O_2 consumption of gymnotiform fishes was dependent on body mass, as expected, fitting a power function with a scaling exponent of 0.74, but the O_2 consumption rate was generally about 50% of that expected by extrapolation of temperate teleost metabolic rates to a similar ambient temperature (26°C). O_2 consumption rate was not dependent on EOD type, but maintenance of scan swimming (continuous forwards and backwards swimming), which is characteristic only of gymnotiforms with wave-type EODs, increased O_2 consumption 2.83±0.49-fold (mean±SD). This suggests that the increased metabolic cost of scan swimming could restrict gymnotiforms with wave-type EODs from hypoxic habitats.

Keywords Gymnotiforms · Electric fish · Electric organ discharge · Metabolism · Amazon · Scan swimming

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Introduction

The ability to generate electric fields for electrolocation and electrocommunication evolved independently in two groups of freshwater teleost fishes: the Neotropical gymnotiforms and African mormyriforms. The order Gymnotiformes comprises some 148 nominal species ascribed to 28 genera and five families, and is distributed from Mexico to Argentina (Albert 2001). Gymnotiforms occur in almost every lowland aquatic habitat and often represent a dominant component of the fish fauna, especially in floodplains (Crampton 1996, 1998a) and deep river channels (Lopez-Rojas et al. 1984; Lundberg et al. 1987). Specialized electric organs in these fishes produce an electric organ discharge (EOD) that creates an electric field in the surrounding water, and this field is subsequently detected by arrays of electroreceptors on the body surface (reviewed by von der Emde 1997). Because the magnitude of the EOD never exceeds a few hundred millivolts, gymnotiform fishes are known as weakly electric (the only exception is *Electrophorus electricus*, commonly known as the electric eel, which can generate electric fields 1,000 times stronger).

The EODs of gymnotiforms can be categorized as:

1. Pulse-type EODs, which consist of discrete, periodic discharges separated by intervals of electrical silence, ranging in repetition rate from 1 to about 120 cycles per second (Hz) depending on the species
2. Wave-type EODs, which consist of continuous discharges that range in repetition rate from ca. 35 to more than 1800 Hz (Bennett 1971; Crampton 1998a; pers. obs.). The EODs of some gymnotiforms are the fastest and most stable biological oscillations known (Moortgat et al. 1998). Within the gymnotiforms, pulse-type EODs are generated by fish in the families Gymnotidae, Hypopomidae, and Rhamphichthyidae, whereas wave-type EODs are generated by fish in the families Apteronotidae and Sternopygidae. All mormyriform species except one, *Gymnarchus niloticus*, generate pulse-type EODs.

Interestingly, EOD type is correlated with habitat type. Crampton (1998b) reported that gymnotiforms with pulse-type EODs are tolerant of experimental hypoxia and are able to survive in habitats characterized by persistent and protracted periods of hypoxia, whereas gymnotiforms with wave-type EODs are intolerant of experimental hypoxia, are ecologically restricted to well-oxygenated waters of rivers and streams, and only rarely inhabit the seasonally hypoxic floodplain habitats. Crampton (1998b) noted three specific differences between pulse-type gymnotiforms and wave-type gymnotiforms that could contribute to their differences in hypoxia tolerance and habitat selection. First, some hypoxia-tolerant gymnotiforms with pulse-type EODs are capable of aerial respiration (Carter and Beadle 1931; Crampton 1996), potentially allowing maintenance of aerobic metabolism even in anoxic water. Second, while some species with pulse-type EODs can modulate the EOD repetition frequency and can cease discharging for periods of up to several seconds when alarmed or during courtship (Black-Cleworth 1970; Westby 1975; Hagedorn and Heiligenberg 1985; Crampton 1998b), species with wave-type discharges rarely switch off the EOD or alter EOD frequency, except during social communication or jamming-avoidance response (Hopkins 1974; Hagedorn and Heiligenberg 1985; Heiligenberg 1991). Third, species with pulse-type EODs alternate between swimming and rest during periods of EOD activity and usually rest with their body in or on the substrate during the daytime, whereas species with wave-type EODs swim continuously and maintain scan swimming as a normal part of their foraging behavior (Lannoo and Lannoo 1993; Nanjappa et al. 2000). In scan swimming, which is specific to fishes with wave-type EODs, the fish constantly moves forwards and backwards near the substrate, thereby creating amplitude-modulated changes in the voltage detected by the electroreceptors, which is probably important for processing the electrosensory information at the higher sensory level (MacIver et al. 2001). If scan swimming during foraging is energetically expensive, this could contribute to the inability of fishes with wave-type EODs to tolerate prolonged periods of hypoxia and their scarcity in hypoxic habitats.

As an alternative, or complementary, explanation for differences in hypoxia tolerance and habitat distribution among gymnotiform fishes, Crampton (1998b) suggested that the generation of wave-type EODs might require the expenditure of more energy than the generation of pulse-type EODs, thereby reducing the hypoxia tolerance of fish with wave-type EODs. Although the mechanisms by which the electric field is generated and detected in both gymnotiforms and mormyriforms have been well studied (e.g., Heiligenberg and Bastian 1984; Bass 1986; Bastian 1986; Bullock and Heiligenberg 1986; Heiligenberg 1987; Hopkins 1988, 1999; Bell et al. 1993; Kramer 1995; Caputi et al. 1998; Assad et al. 1999; Stoddard et al. 1999), the metabolic cost of EOD generation has never been measured and is difficult to estimate. Furthermore, the metabolic costs that are specific to active electrolocation, whether for pulse-type or wave-type EODs, must also include the costs of processing the information at higher sensory levels. That this cost may be considerable is suggested by the large brain size of gymnotiform and mormyrid fishes relative to that of other fish taxa (Albert et al. 1999; Chapman and Hulen 2001) and the mormyrid brains high O_2 consumption rate relative to the rest of the body (up to 60% of total O_2 consumption in *Gnathonemus petersii*; Nillson 1996). Consequently, it is not clear if weakly electric fishes have metabolic rates that are substantially higher than those of other freshwater fishes, and it is not known if the metabolic costs associated with the EOD mode (i.e., pulse-type vs. wave-type), whether due to EOD generation, sensory processing, or scan swimming, are substantially different from each other and might therefore constrain habitat choice.

In the present study we test three hypotheses:

1. Weakly electric gymnotiform fishes have comparatively high O_2 consumption rates
2. Gymnotiform fishes with wave-type EODs have higher O_2 consumption rates than those with pulse-type EODs
3. Scan swimming by gymnotiform fishes with wave-type EODs significantly increases their O_2 consumption and might therefore constrain habitat choice.

Materials and methods

Fish collection and maintenance

Gymnotiform fishes were collected from the Amazon and Nanay rivers near Iquitos, Peru in March and April 2001. The authors collected most of the fishes, with the remainder being obtained from local fishermen or tropical fish wholesalers (who had in turn obtained the fishes from local fishermen). None of the specimens were in breeding condition. Most measurements of O_2 consumption were carried out at one of four locations in or near Iquitos, Peru: the Allpahuayo-Mishana reserve, the Parque Quistococha preserve, the Red Tail Cat Aquarium in Iquitos, and in an Iquitos hotel. With the exception of the two *Brachyhypopomus brevirostris* from the Parque Quistococha preserve and the *Magosternarchus raptor*, which were studied immediately after collection, all fishes were maintained unfed in aerated water for at least 16 h prior to measurement of O_2 consumption. For each fish, the water source was chosen to match as closely as possible the conductivity of the water from which the fish was collected (i.e., from blackwater or whitewater sites, or aquarium water in the case of fish obtained from wholesalers). Water from the same source was used in the respirometer. In all cases, O_2 consumption was measured no more than 48 h after collection.

Respirometry

Measurements of O_2 consumption were performed during daylight hours, when the fish were expected to be least active (Crampton 1998a). O_2 consumption rates were determined in an intermittent, recirculating respirometer, shown schematically in Fig. 1. This respirometer provided a constant water current (0.4–1 cm sec^{-1} average velocity) throughout the experiment. The respirometer chamber ranged in volume from 25 ml to 3.6 l and consisted of a clear PVC pipe (1.25–7.6 cm inner diameter) that was constructed to match the size of the fish. An electrode at each end of this chamber was connected to an amplifier with a loudspeaker, providing confirmation that all fish were generating EODs during the

recording periods. At the beginning of an experiment, an individual fish was placed into the respirometer chamber and allowed at least 30 min of acclimation. During this period, the respirometer was operated in its open mode, in which the water circulated through a large aerated reservoir. To measure the O_2 consumption rate, the respirometer was changed to its closed mode, in which the circulating water bypassed the reservoir and was therefore not aerated. As a result, the animals metabolism caused the water P_{O_2} to decline, and this decline was monitored as the change in dynamic fluorescence quenching of an O_2-sensitive fluorophore on the tip of a fiber optic probe (FOXY-R probe, USB-LS-450 pulsed LED excitation source and USB2000 fluorometer, all from Ocean Optics Inc., Dunedin, Fla.). The fluorescence was digitized and continuously recorded on a laptop computer. The P_{O_2} was typically allowed to decrease by less than 10% and was never allowed to drop below 85% of air-saturation, at which point the respirometer was placed back in the open mode. Successive measurements of O_2 consumption were performed with each fish until the rates of O_2 decline in two consecutive measurements differed from each other by less than 10%, indicating that a relatively stable rate of O_2 consumption had been achieved. All O_2 consumption data presented in this paper represent the average of at least two such consecutive recordings from each fish.

All specimens were initially placed in the respirometer such that they were oriented headfirst into the water current (i.e., facing upstream). Most fishes remained in this orientation, but some either turned around within the chamber to face downstream or periodically reversed their orientation throughout the recording periods. To determine whether variation in activity level (i.e., swimming or inactivity) significantly biased the measurements of O_2 consumption, the activity of each fish was ranked from 1 to 3 to represent which activity predominated during the recording periods, with 1 representing inactivity, 3 representing swimming (including scan swimming), and 2 representing alternation between inactivity and swimming.

After its O_2 consumption rate had been determined, each fish was weighed wet, anesthetized, and preserved in fixative for deposition and cataloguing at the Florida Museum of Natural History. The calibration slope and offset of the O_2 probe were set at least daily using air-saturated water and water deoxygenated with sodium sulfite as standards, assuming an O_2 solubility of 1.91 mmol l^{-1} $Torr^{-1}$, corrected to dry air and assuming 760 Torr atmospheric pressure. To correct for linear drift of the O_2 probe output (due to photobleaching of the O_2-sensitive fluorophore), the calibration offset was corrected between each experimental trial by standardizing with air-saturated water. Control trials (without a fish in the respirometer chamber) were performed to determine the O_2 consumption rate due to other biological activity, and this rate was subtracted from the total O_2 consumption rates obtained for each fish. The entire respirometer system (except the computer and O_2 probe electronics) was housed in a large, insulated cooler. Water temperature was maintained at the expected habitat temperature (25–27°C) by adding ice to the cooler as necessary. The temperature variation within each trial was typically less than 1°C. For measurements at field sites, a 12-volt automobile battery powered the respirometer pump, O_2 probe system, and computer.

In the above experiments, each fishs activity level during the recording periods was observed, but recordings of O_2 consumption were made irrespective of behavior. In a second set of experiments, performed at the University of Florida, the effect of scan swimming on O_2 consumption was specifically investigated. These studies used the gymnotiform *Apteronotus albifrons*, which generates wave-type EODs. These fish were obtained from a local aquarium fish retailer. Each experiment was begun in the afternoon, at which time one fish was placed in the respirometer. This fish was allowed to acclimate overnight while the respirometer was operated in open mode. The following morning, when the fish was typically swimming gently to maintain its position in the chamber but was not scan swimming (although still generating continuous EODs), its O_2 consumption rate was measured for several successive trials. A small metal object, such as a paper clip or a small spring, was then added to the respirometer chamber. This usually elicited scan swimming movements by the fish as it investigated the object, during which the rate of O_2 consumption was measured in several successive trials. The object was then withdrawn and, once the fish had ceased scan swimming movements, the rate of O_2 consumption was again recorded.

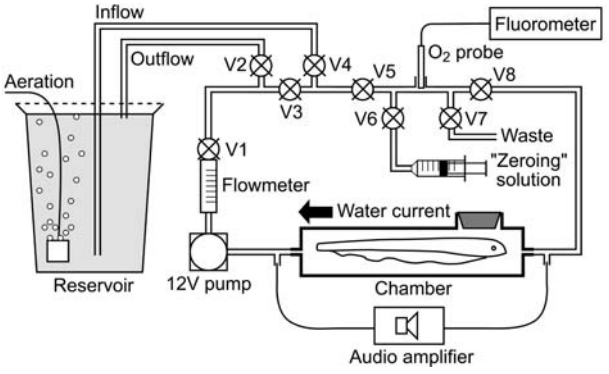

Fig. 1 Schematic diagram of respirometer used to measure O_2 consumption in gymnotiform fish. The fish was placed in a respirometer chamber constructed of PVC pipe. Several such chambers were constructed, ranging in volume from 25 ml to over 1 l (pipe inner diameter from 1.25 cm to 7.6 cm) to accommodate a variety of fish sizes. A 12-volt magnetic water pump circulated water through polyethylene tubing (6.3 mm inner diameter) from the chamber and into a reservoir, and then from the reservoir back into the chamber. All tubing connections were made with watertight compression fittings. A fluorometric O_2 probe, inserted in-line with the water flow, was used to monitor water P_{O_2}. Water flow was controlled by adjusting seven valves (*V1–V7* in the diagram). V1 was a needle valve that regulated the water flow rate from 60 ml min^{-1} to 3.5 l min^{-1}, to maintain a constant average current velocity of 0.4–1 cm sec^{-1} in the chamber. Flow rate was monitored with a flow meter attached to the pump. During acclimation of the fish and between measurements of O_2 consumption, the respirometer was operated in open mode, in which water circulated through a reservoir that contained aerated water. For this mode, V3, V6, and V7 were closed, and V2, V4, V5, and V8 were open. During measurement of O_2 consumption, the respirometer was operated in closed mode, in which the water circulated in a closed loop that bypassed the reservoir. For this mode, V2, V4, V6, and V7 were closed, and V3, V5, V6, and V8 were open. The system volume (exclusive of the chamber) during closed mode was 82 ml. For calibration of the O_2 probe, all valves except V6 and V7 were closed, and a zeroing solution of sodium sulfite in water was injected from a syringe, past the O_2 probe and into a waste container. At all times when a fish was in the respirometer, EOD output was monitored with an audio amplifier attached to electrodes at either end of the chamber. For measurement of O_2 consumption rate of the largest fish (*Orthosternarchus tamandua*), a separate respirometer was constructed as shown above, except that all tubing was 1.25 cm inner diameter PVC pipe and the total respirometer volume was 3.6 l

Statistics

Curve fits for O_2 consumption rate as a function of body mass were calculated by least squares, non-linear regression using the power function $y=am^b$. To test for differences in O_2 consumption rate as a function of EOD type or activity level, the differences were analyzed using analysis of covariance (ANCOVA), with $\log_{10}$-transformed O_2 consumption rate as the dependent variable, activity level and $\log_{10}$-transformed wet body mass as covariates, and EOD type as a cofactor. To determine whether scan swimming significantly increased metabolism, O_2 consumption rates for fish at rest and during scan swimming were compared using a paired *t*-test. Statistical analyses were performed using SYSTAT v.10.2 (SYSTAT

Table 1 Characteristics of gymnotiform species for which O_2 consumption rates were measured. The table includes the species and family names, the EOD type (*P* pulse, *W* wave), the maximum size (in cm total length), the typical habitat(s) of each species, the locality from which each specimen was obtained, the length of each specimen, and the specimens identification number (ID), as used in Fig. 3. For four species, specimens were obtained from more than one locality, as denoted by a letter after the ID number. N/A indicates that information was not available. Maximum size data are from Albert (2003a, 2003b), Albert and Crampton (2003), Campos-da-Paz (2003), and Ferraris (2003)

Species information					Specimen information		
Species	Family	EOD	Max length (cm)	Typical habitat	Locality	Length (cm)	ID
Adontosternarchus balaenops	Apteronotidae	W	25 cm	Whitewater river channels	N/A, via Red Tail Cat Aquarium	17	1
Apteronotus albifrons	Apteronotidae	W	50 cm	Whitewater and blackwater river channels	Rio Amazonas	19–22	2
Apteronotus bonaparti	Apteronotidae	W	27 cm	Whitewater and blackwater river channels	N/A, via Red Tail Cat Aquarium	16	3
Brachyhypopomus beebei	Hypopomidae	P	20 cm	Floodplain lakes, swamps, and streams	Stream at km 22 Iquitos-Nauta	4.3–8.9	4
Brachyhypopomus brevirostris	Hypopomidae	P	35 cm	Floodplain lakes, swamps, and streams	Rio Nanay: Mixana	6.7	5a
					Stream at km 22 Iquitos-Nauta	25	5b
					Parque Quistococha	25	5c
Eigenmannia cf. *virescens*	Sternopygidae	W	35 cm	Floodplain lakes, swamps, and streams	Stream at km 22 Iquitos-Nauta	4.1–6.2	6
Gymnorhamphichthys cf.*rondoni*	Rhamphichthyidae	P	26 cm	Streams	Rio Nanay: Mixana	18	7
Gymnotus carapo n. ssp.	Gymnotidae	P	39 cm	Floodplain lakes, swamps, and streams	Rio Nanay: Mixana	37	8
Gymnotus sp nov.	Gymnotidae	P	19 cm	Unknown	N/A, via Ucayali Aquarium	11	9
Hypopygus lepturus	Hypopomidae	P	10 cm	Streams	Rio Nanay: Mixana	7.5	10a
					Stream at km 22 Iquitos-Nauta	10	10b
Magosternarchus duccis	Apteronotidae	W	27 cm	Whitewater river channels	Rio Amazonas, via Belen fisherman	21	11
Magosternarchus raptor	Apteronotidae	W	20 cm	Whitewater river channels	N/A, via Red Tail Cat Aquarium	22	12
Orthosternarchus tamandua	Apteronotidae	W	44 cm	Whitewater river channels	N/A, via Red Tail Cat Aquarium	13–44	13
Parapteronotus hasemani	Apteronotidae	W	38 cm	Whitewater and blackwater river channels	N/A, via Red Tail Cat Aquarium	10–25	14
Platyurosternarchus macrostomus	Apteronotidae	W	40 cm	Whitewater river channels	Rio Amazonas, via fisherman	38	15
Rhamphichthys sp. A	Rhamphichthyidae	P	113 cm	Whitewater and blackwater river channels	Rio Nanay: Mixana	18	16a
					N/A, via Red Tail Cat Aquarium	33	16b
Steatogenys elegans	Hypopomidae	P	30 cm	Whitewater and blackwater river channels	N/A, via Red Tail Cat Aquarium	13	17a
					Rio Nanay, via Aquarium	15	17b
Sternarchella schotti	Apteronotidae	W	40 cm	Whitewater river channels	N/A, via Red Tail Cat Aquarium	25	18
Sternarchogiton nattereri	Apteronotidae	W	25 cm	Whitewater river channels	N/A, via Red Tail Cat Aquarium	18	19
Sternarchorhynchus sp. A	Apteronotidae	W	26 cm	Whitewater river channels	Rio Amazonas, via fisherman	25	20
Sternarchorhynchus curvirostris	Apteronotidae	W	41 cm	Blackwater river channels	Rio Nanay, via Perufish Aquarium	11	21
Sternarchorhynchus mormyrus	Apteronotidae	W	54 cm	Whitewater river channels	N/A, via Red Tail Cat Aquarium	24	22
Sternopygus macrurus	Sternopygidae	W	141 cm	Rivers, Floodplain lakes, streams	Rio Nanay: Mixana	48	23

Software, Inc.), with probabilities less than 0.05 being considered significant.

Results

A total of 33 gymnotiform specimens, representing 23 species, were collected for the measurements of O_2 consumption in Peru. The species, family, EOD type (pulse or wave), maximum reported length for that species, typical habitat preference, collection site (in the cases where this information was available), and specimen length of each fish are listed in Table 1. The body mass of fishes obtained for the study ranged in size from 0.4 g for the smallest, *Brachyhypopomus brevirostris*, to 125 g for *Orthosternarchus tamandua*, with a mean of 22.1 g.

When the respirometer was switched to its closed mode, the water P_{O_2} gradually declined due to consumption of O_2 by the fish (Fig. 2). Although O_2 consumption was measured during the day, when most gymnotiforms are least active (Crampton 1998a), the fish exhibited a variety of activity levels in the respirometer, ranging from continual scan swimming movements to almost complete inactivity. Among the inactive behaviors, some fish rested nearly motionless on their side at the bottom of the chamber, while others allowed their tail to rest against the downstream end of the chamber, apparently minimizing the need to swim against the current. These behaviors, which were ranked as activity level 1, are both observed in natural populations (Crampton, pers. obs.). Most fish, however, swam gently in the water current throughout the recording periods, maintaining their position in the chamber. This was ranked as activity level 2 (intermittent swimming) or 3 (majority of time spent swimming). Of the 33 fish for which O_2 consumption was measured, the activity of 26 could be reliably ranked (8, 7, and 11 fish at activity levels 1, 2, and 3, respectively), and ANCOVA demonstrated that there was no significant effect of activity on the O_2 consumption rate ($F_{2,21}$=0.34, P=0.72). Because most of the fishes were at least occasionally active, the O_2 consumption rates reported in the present study are more likely to be representative of routine O_2 consumption rates than of resting (or standard) O_2 consumption rates (McNab 2002).

As expected, the rate of O_2 consumption was strongly dependent on body mass (Fig. 3), with the data closely fitting the power function $y=0.0076x^{0.733}$ (solid regression line in Fig. 3; r^2=0.86, $F_{1,31}$=180, P<0.001). This relationship remained valid when the data were segregated by EOD type (Fig. 3; pulse-type EODs: $y=0.0071x^{0.71}$, r^2=0.86, $F_{1,12}$=73, P<0.001; wave-type EODs: $y=0.0092x^{0.69}$, r^2=0.77, $F_{1,17}$=56, P<0.001). The rate of O_2 consumption did not differ as a function of EOD type, whether analyzed by comparison of linear regressions through log-transformed data ($F_{2,29}$=0.62, P for coefficient=0.28, P for scaling exponent=0.95) or by ANCOVA ($F_{1,30}$=1.2, P=0.28). The respirometer temperature was successfully maintained between 25°C and 27°C for measurements of O_2 uptake in 29 of the 33 fishes, but high air temperatures in the field caused the water to reach between 29°C and 31°C for measurements in four fish: *B. brevirostris* (ID 5c; two specimens), *Hypopygus lepturus* (ID 10a), and *Rhamphichthys* sp. A (ID 16a). Removing the data from these four fish from the analyses described above had no effect on the relationship between O_2 consumption and body mass ($0.0076x^{0.735}$, r^2=0.85; comparison with the regression through the complete data set: $F_{2,58}$=0.02, P=0.99) and the rate of O_2 consumption remained independent of EOD type ($F_{2,25}$=0.40, P=0.24).

For nine species, O_2 consumption was measured for more than one individual per species. To determine

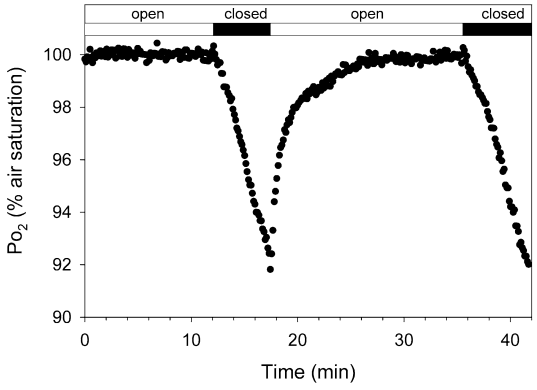

Fig. 2 Change in respirometer P_{O_2} (as percentage of air-saturation) during measurement of O_2 consumption over time (min). These representative data demonstrate the O_2 probe output while the respirometer was operated in open mode (indicated by an *open bar* above the data), during which the water was circulated through an aerated reservoir, and during closed mode (indicated by a *filled bar* above the data), during which the water bypassed the reservoir. The rate of decrease in P_{O_2} during each of the closed periods (i.e., the slope of a linear regression through each data set) was used to calculate the rate of O_2 consumption

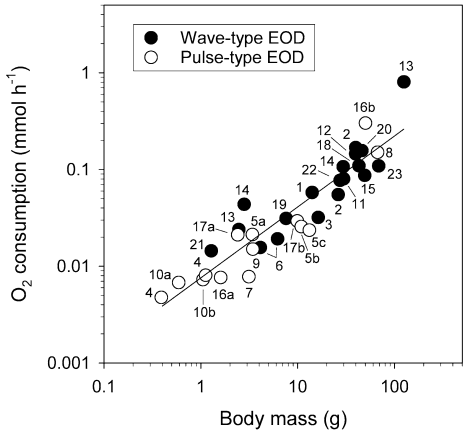

Fig. 3 O_2 consumption rate (mmol O_2 h^{-1}) as a function of body mass (g) for 23 species of weakly electric gymnotiform fish. *Solid circles* represent fish with wave-type EODs, while *open circles* represent fish with pulse-type EODs. Note that both axes are log-scaled. The text next to each symbol represents that fishs ID number from Table 1, which provides the species name and locality from which each fish was collected. The regression line represents a best-fit power curve through the entire data set

whether the most conservative statistical analysis yielded similar results, the following treatments were performed. First, data were averaged for the four species in which two or more individuals of each species were similar in mass: the two *A. albifrons* (ID 2), the three larger specimens of *B. brevirostris* (ID 5b and 5c), the two specimens of *Eigenmannia* cf. *virescens* (ID 6), and the two specimens of *H. lepturus* (ID 10a and 10b). Second, analyses of covariance were performed as above (with O_2 consumption as the dependent variable, mass as the covariate and EOD type as a cofactor), but with each of the following species represented by only one specimen per analysis: *B. brevirostris* (ID 5a and average of 5b and 5c), *Orthosternarchus tamandua* (ID 13), *Parapteronotus hasemani* (ID 14), *Rhamphichthys* sp. A (ID 16a and 16b) and *Steatogenys elegans* (ID 17a and 17b). In 31 of the 32 possible combinations, no significant difference was detected, with the one exception ($F_{1,23}$=6.0, P=0.023) being a data set without values for the larger *Rhamphichthys* sp. A (ID 16b) and the larger *O. tamandua* (ID 13). In summary, it appears likely that O_2 consumption of gymnotiforms is not dependent upon EOD type.

To determine whether scan swimming significantly increased the rate of O_2 consumption, we determined O_2 consumption in *A. albifrons* both during scan swimming movements and in the absence of scan swimming. For the four fish studied, which ranged in mass from 5 g to 25 g, the O_2 consumption rate during scan swimming was 2.83 ±0.49-fold higher (mean±SD) than during non-scan swimming (Fig. 4, t_3=−7.5, P=0.005).

Discussion

Gymnotiform fishes are well suited to comparative studies of behavior and physiological ecology. Details of natural history, alpha-level diversity, and phylogeny are now sufficiently understood in species representing each of the major gymnotiform lineages to generate and test biologically compelling evolutionary and ecological hypotheses (Albert et al. 1998; Stoddard 1999). The 23 species examined for this study ranged in EOD repetition rate from 15 to 1800 Hz (Crampton 1998a, 1998b) and included representatives from all the major lowland Amazon habitats, from all five families of gymnotiforms (Fig. 5), and from 16 (59%) of the 27 genera recognized by Albert (2001).

As has been shown for vertebrates in general (reviewed by McNab 2002), the allometric relationship of O_2 consumption rate with body mass in weakly electric gymnotiform fish follows the standard power model of $y=am^b$, where y is the metabolic rate, a is a coefficient, m is the body mass, and b is the scaling exponent. The scaling exponent determined for gymnotiforms in this study (0.73) is quite close to the scaling exponent of 0.79 determined for other teleosts by Clarke and Johnston (1999), which contains a meta-analysis of 138 studies of resting metabolic rate in 69 teleost species. Therefore, the data presented here demonstrate that scaling of metabolism with body size for weakly electric gymnotiform fishes is not substantially different from that of other teleosts. The fishes with pulse-type EODs obtained for this study tended to be smaller than those with wave-type EODs. To determine whether this was due to sampling error, we

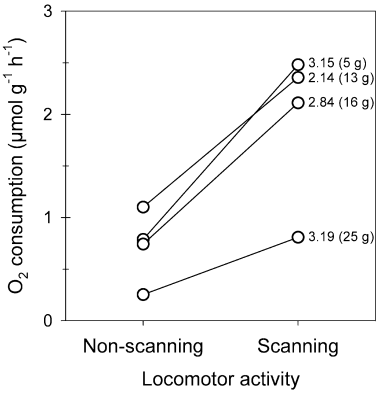

Fig. 4 Change in mass-specific O_2 consumption rate (µmol O_2 g^{-1} h^{-1}) with scan swimming in *Apteronotus albifrons*. Four fish are represented, with the O_2 consumption rate during non-scan swimming and scan swimming for each fish connected by a line. The number next to each symbol represents the ratio change in O_2 consumption between non-scan swimming and scan swimming, with the mass of that fish (g) in parentheses

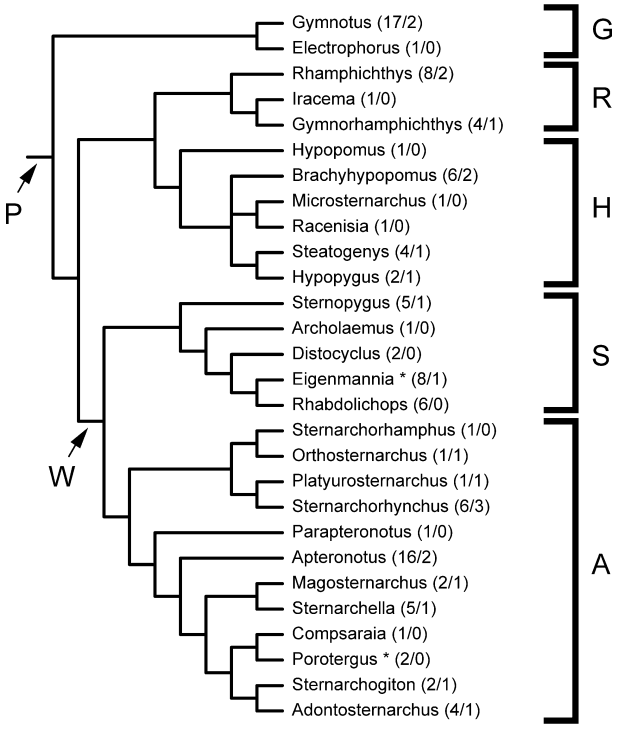

Fig. 5 Phylogenetic distribution of the 23 gymnotiform species examined. Numbers in parentheses are number of valid species/number of species for which metabolic data are reported. Tree topology, diversity estimates, and character-state optimizations are from Albert (2001). * generic monophyly uncertain, *A* Apteronotidae, *G* Gymnotidae, *H* Hypopomidae, *P* pulse-type EOD, *R* Rhamphichthyidae, *S* Sternopygidae, *W* wave-type EOD. Note that metabolic data are reported for 16 (59%) of the 27 genera, and all five families

compiled the maximum lengths, as reported in Albert (2001), for all 148 known species of weakly electric Gymnotiformes (Fig. 6; note that the strongly electric *E. electricus* was excluded from our analysis). Species with pulse-type EOD (64 species), in comparison to species with wave-type EOD (85 species), possess a similar mean body length (31.2 cm vs. 30.9 cm, respectively), but a smaller modal (18.0 cm vs. 25.0 cm) and median (22.3 vs. 29.0 cm) body length and a larger range of body lengths (7.8–113 cm vs. 12–60 cm), consistent with the size distribution of fishes in our study.

We hypothesized that high energetic costs of EOD generation and processing would cause weakly electric fishes to have higher metabolic rates than other teleosts. However, the O_2 consumption rates of weakly electric gymnotiform fishes in this study were, on average, much lower than that expected for other teleosts at a similar temperature (Fig. 7). Specifically, the estimated relationship of O_2 consumption rate with body mass was about 50% of the expected value for teleost fishes of a similar size range extrapolated to 26°C (*solid line* in Fig. 7; Clarke and Johnston 1999; see the Fig. 7 legend for calculation methods). Interestingly, the metabolic rate of gymnotiform fishes in this study was similar to that of three weakly electric mormyrid fishes (Fig. 7, *filled symbols*; Nillson 1996; Chapman and Chapman 1998; Chapman et al. 2002). Comparable studies on the metabolic rates of other tropical freshwater fishes are few, but it is notable that several also report low routine O_2 consumption rates. For example, Chapman and colleagues compared the O_2 consumption rates of the hypoxia-adapted haplochromine cichlids *Pseudocrenilabrus multicolor*, *Prognathochromis venator*, and *Astatotilapia velifer* (Rosenberger 1997), and the Nile perch (*Lates niloticus*, Schofield and Chapman 2000), with Winbergs standard curve for freshwater fishes (Winberg 1961), all of which were studied at ca. 19–21°C, and found that all were 30% to 61% of the metabolic rate expected for other teleosts. Consequently, it is not clear whether a low metabolic rate is a characteristic that evolved independently in both weakly electric gymnotids and mormyrids, or whether tropical fish species, perhaps especially those from hypoxic habitats, have lower metabolic rates in general than the better studied temperate fish species. It is important to recognize, however, that these comparisons with temperate species are achieved by mathematically adjusting the measured metabolic rates with empirically derived Q_{10} values (e.g., Winberg 1961; Clarke and Johnston 1999), which may ultimately be invalid for tropical fish species.

There is large taxonomic variation in O_2 consumption among other teleosts (Winberg 1961; Clarke and Johnston 1999), but the present study of gymnotiforms in non-breeding condition nonetheless suggests that the energetic costs of EOD generation and processing do not increase their total metabolic rate above that expected by extrapolation from other teleosts. This would indicate that either these costs are low relative to the remaining metabolism, or that the remaining metabolism is low relative to the total metabolism of other teleosts. Although Nillson (1996) reported that 60% of O_2 consumption in the African electric fish *Gnathonemus petersii* is due to brain metabolism, the measured O_2 consumption rate of brain tissue in that study was multiplied by a correction factor of two to compensate for an assumed depression caused by experimental techniques. Therefore, the derived value for mormyrid brain metabolic rate may be an overestimate. In any case, while gymnotiforms, like mormyriforms,

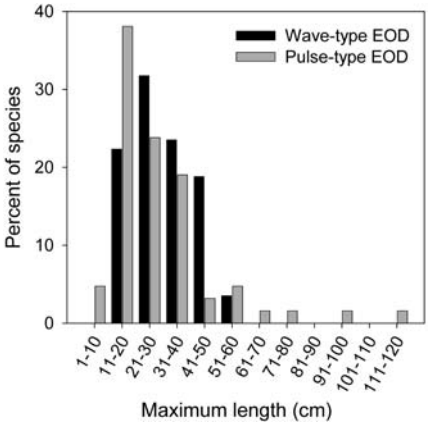

Fig. 6 Maximum known total length (cm) for 148 known species of weakly electric Gymnotiformes (the strongly electric eel *Electrophorus electricus* is excluded from this data set). Species are divided by EOD type (85 species with wave-type EOD and 64 species with pulse-type EOD). Data are from Albert (2001). Frequencies are reported as the percentage of total known species for that EOD type

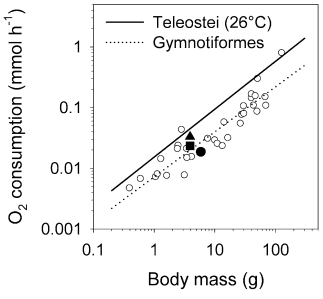

Fig. 7 Comparison of O_2 consumption rates (mmol h^{-1}) for gymnotiform fishes at 25–27°C (*open circles* and *dotted regression line*), published O_2 consumption rates of three African mormyrid fishes (*filled symbols*), and the theoretical resting O_2 consumption rates of other teleosts at 26°C (*solid line*). Data for gymnotiform fishes are from Fig. 3. The three mormyrid fishes are *Gnathonemus petersii* (*filled circle*), measured at 26°C (Nillson 1996), and *G. victoriae* (*filled triangle*) and *Petrocephalus catostoma* (*filled square*), for both of which the published O_2 consumption rate was for 20°C (Chapman and Chapman 1998; Chapman et al. 2002). In this figure, the metabolic rates for the latter two mormyrids were adjusted to 26°C by assuming a Q_{10} of 1.83 (Clarke and Johnston 1999). The line representing Teleostei at 26°C was calculated using values in Clarke and Johnston (1999), in which it was proposed that the O_2 consumption rate of a standard 50 g fish would follow the Arrhenius model of $\ln R = 15.7 - 5.02(1000T)^{-1}$, where R is the resting metabolic rate (mmol h^{-1}) and T is absolute temperature. For the figure, the equation $R = am^b$ was solved for the coefficient a by inserting the calculated value of 0.336 mmol h^{-1} at 26°C for R, body mass of 50 g for m, and scaling exponent of 0.79 for b, as proposed by Clarke and Johnston (1999) for teleosts over a temperature range of 40°C. This yielded the relationship $R = 0.0152m^{0.79}$ (*solid line*)

possess relatively large brains in comparison to other teleosts (Albert et al. 2000), the data in the present study indicate that any resulting increased brain metabolism in gymnotiforms is not sufficient to raise the routine metabolic rate above that of other teleosts.

An important consideration is whether the fishes in this study exhibited normal metabolic rates while in the respirometer. In fact, we recognize two factors that may have elevated the O_2 consumption rates in this study. First, although almost all fish were unfed for at least 16 h prior to measurement of O_2 consumption, it is not certain that the fish were completely post-absorptive, and therefore some O_2 consumption may have been due to metabolism associated with digestion. Second, some fish may not have become fully acclimated to the respirometer prior to recording of O_2 consumption, thereby causing an increased metabolic rate due to factors such as handling stress. This is supported by the observation that O_2 consumption rates of *A. albifrons* specimens studied in the laboratory during non-scan swimming and following 12 h acclimation (Fig. 4) were lower than that of comparably sized fish that were only allowed shorter acclimation periods (Fig. 3; these shorter periods were necessitated by the time and resource constraints of the recordings conducted at field sites in Peru). In contrast, the metabolic cost of EOD production may have been reduced by electrical insulation produced by the plastic animal chamber and tubing of the respirometer, which may have increased the resistance to current flow, thereby resulting in a decreased current flow and decreased EOD power costs. However, the net effect, if any, on the whole-animal O_2 consumption rate would be small if the metabolic cost of EOD generation is low relative to the metabolic rate.

In at least two families of gymnotiform fishes, stress and social interactions with a conspecific can alter EOD amplitude, and therefore presumably also alter O_2 consumption due to EOD generation. In *Sternopygus*, which generates wave-type EODs, EOD amplitude has been reported to decrease after social isolation (Triefenback, pers. comm. in McAnelly et al. 2003), and at least one species of *Sternopygus* can vary its EOD amplitude by up to ten-fold within less than a second when maintained in isolation in a laboratory aquarium (Crampton et al. 2003). In *Brachyhypopomus* spp., which generate pulse-type EODs, EOD amplitude varies in a diel pattern in males, especially during the breeding season, and can be reduced by stress and increased by interactions with a conspecific (Franchina and Stoddard 1998; Franchina et al. 2001; P. Stoddard, pers. comm.). However, brachyhypopomids are unique in that the males electric organ grows dramatically during the breeding season (Hopkins et al. 1990). Additionally, the fishes used in the present study were not in breeding condition and were maintained individually in containers prior to measurement of O_2 consumption, and there is no evidence for substantial amplitude changes in response to diel rhythm or stress in the gymnotiform taxa Gymnotidae, Apteronotidae, and *Eigenmannia* (Crampton, pers. obs.). Conclusive determination of the metabolic cost associated with EOD generation relative to the whole-animal metabolic rate will probably require measurement of O_2 consumption both with and without EOD generation (while leaving other metabolic activities unaltered). This may ultimately be possible using a respirometer with high time resolution, since complete cessation of the EOD occurs behaviorally (without surgical or chemical intervention) for a few seconds or minutes in some gymnotiforms with pulse-type EODs (Crampton 1998a, 1998b).

Crampton (1998b) found that gymnotiform species with wave-type EODs are very rarely present in habitats characterized by low dissolved O_2 and are generally intolerant of experimental hypoxia. This suggested the presence of a metabolic constraint to the utilization of wave-type EODs in hypoxic water, such as an increased metabolic cost of EOD generation or processing. However, we found that the O_2 consumption rates for gymnotiforms with pulse-type EODs were not significantly different from those with wave-type EODs, suggesting that the metabolic costs associated with these two different EOD types are not substantially different, at least in proportion to the whole-animal metabolic rate. One reason for this small difference may be that wave-type EODs, although typically generated at higher repetition rates than pulse-type EODs, are usually weaker in peak-to-peak amplitude (Hopkins 1976; Assad et al. 1998; Rasnow and Bower 1996; Stoddard 2002), which would tend to minimize the added metabolic cost associated with generating a higher frequency EOD. An additional reason is that although there is a correlation between the size of the medullary pacemaker nucleus and EOD repetition frequency (ca. 400–1700 Hz in adult apteronotids vs. ca. 0.1–900 Hz in other gymnotiforms; Crampton 1998a), this nucleus constitutes less than 1% of total neural volume, so differences in the size of this structure would be unlikely to contribute substantially to the whole-animal metabolic rate. Furthermore, although weakly electric fishes have proportionally larger brains than other teleosts, EOD type and repetition frequency are not correlated with total brain volume or with the volume of the primary electrosensory brain structures (i.e., electrosensory lateral line lobe, corpus cerebelli) in gymnotiform fishes (Albert et al. 1998, 2000, unpubl. obs.). Therefore, our experiments provide no evidence that differences in the metabolic costs of EOD generation and processing contribute to the restriction of gymnotiforms with wave-type EODs from hypoxic habitats.

An alternative factor affecting habitat distribution is that some weakly electric gymnotiforms with pulse-type EODs have the capacity for aerial respiration, which is not true of gymnotiforms with wave-type EODs (Crampton 1998b). However, the absence of aerial respiration in species with wave-type EODs is probably more readily viewed as a consequence—rather than a cause—of their absence from hypoxic waters. Specifically, the phylogenetic distribution of aerial respiration among extant gymnotiforms suggests it evolved many times among closely related species with pulse-type EODs (Sullivan 1997). Therefore, the evolution of aerial respiration may be regarded as much more plastic

than the transition between pulse- and wave-type EODs, which occurred only once, very early in the evolution of Gymnotiformes. The observation that aerial respiration is restricted to gymnotiform fishes with pulse-type EODs is consistent with the hypothesis that inhabiting hypoxic waters promotes the evolution of aerial respiration. In this regard, gymnotiforms are similar to many groups of Amazonian fishes that have evolved numerous independent adaptations to periodic short-term episodes of hypoxia and anoxia (Val et al. 1998).

One factor that we suggest restricts weakly electric gymnotiforms with wave-type EODs from hypoxic habitats is their requirement for scan swimming. Unlike other fishes, gymnotiforms keep the body and tail rigid and use undulations of their highly elongate anal fin for locomotion. Because movement of the body and tail is minimized, this maintains the electroreceptors at constant relative positions, presumably minimizing the alterations of the perceived electric field that would otherwise be created by the fishs own swimming movements (Nanjappa et al. 2000). It is not known whether the cost of transport (power per unit distance) for gymnotiforms is different from that of other fishes. Evolution of anal-fin locomotion occurred in association with the origin of active electrolocation and the pulse-type EOD, and prior to the origin of wave-type EODs and scan swimming (Albert 2001), so anal-fin locomotion presumably evolved to enhance electric field detection, rather than decrease the costs of locomotion. Consequently, anal-fin swimming may represent a trade-off that benefits electroreception at the cost of locomotion efficiency. This trade-off may be especially important during scan swimming, which consists of continuous acceleration and deceleration followed by reversal of motion, and which must therefore require substantial energy simply to overcome inertia. We found that the rate of O_2 consumption increased almost threefold during scan swimming compared with non-scan swimming in the gymnotiform *A. albifrons*. While the ratio of maximal aerobic metabolic rate to standard metabolic rate can exceed 10 in fast-swimming, streamlined fish (Brett and Groves 1979), it varies considerably taxonomically and is unknown for gymnotiforms. For that reason, it is not clear whether a ratio of three approaches the aerobic threshold for weakly electric fish. Nonetheless, since scan swimming is maintained almost continually during foraging activity in species with wave-type EODs (Crampton and Albert, pers. obs.), we propose that these gymnotiforms have higher O_2 requirements than gymnotiforms with pulse-type EODs, and consequently may be less able to tolerate hypoxic environments.

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