



## SYMPOSIUM

### Energetics of Sensing and Communication in Electric Fish: A Blessing and a Curse in the Anthropocene?

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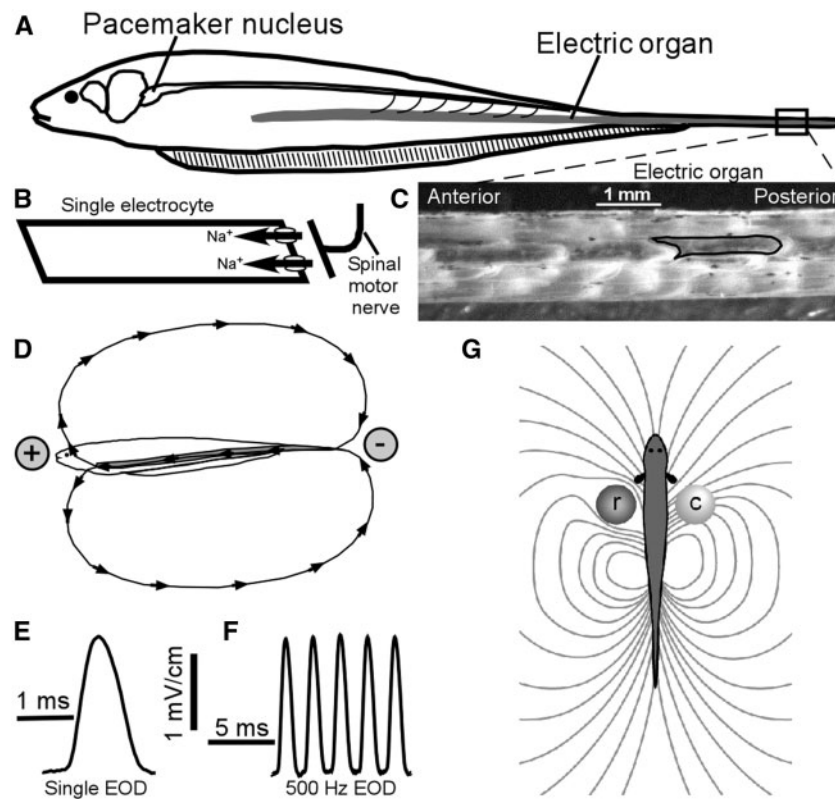
**Synopsis** Weakly electric freshwater fish use self-generated electric fields to image their worlds and communicate in the darkness of night and turbid waters. This active sensory/communication modality evolved independently in the freshwaters of South America and Africa, where hundreds of electric fish species are broadly and abundantly distributed. The adaptive advantages of the sensory capacity to forage and communicate in visually-unfavorable environments and outside the detection of visually-guided predators likely contributed to the broad success of these clades across a variety of Afrotropical and neotropical habitats. Here we consider the potentially high and limiting metabolic costs of the active sensory and communication signals that define the gymnotiform weakly electric fish of South America. Recent evidence from two well-studied species suggests that the metabolic costs of electrogenesis can be quite high, sometimes exceeding one-fourth of these fishes’ daily energy budget. Supporting such an energetically expensive system has shaped a number of cellular, endocrine, and behavioral adaptations to restrain the metabolic costs of electrogenesis in general or in response to metabolic stress. Despite a suite of adaptations supporting electrogenesis, these weakly electric fish are vulnerable to metabolic stresses such as hypoxia and food restriction. In these conditions, fish reduce signal amplitude presumably as a function of absolute energy shortfall or as a proactive means to conserve energy. In either case, reducing signal amplitude compromises both sensory and communication performance. Such outcomes suggest that the higher metabolic cost of active sensing and communication in weakly electric fish compared with the sensory and communication systems in other neotropical fish might mean that weakly electric fish are disproportionately susceptible to harm from anthropogenic disturbances of neotropical aquatic habitats. Fully evaluating this possibility, however, will require broad comparative studies of metabolic energetics across the diverse clades of gymnotiform electric fish and in comparison to other nonelectric neotropical fishes.

#### The Superpowers of Electric Fish

As children, many of us wished for the kinds of superhuman powers possessed by comic-book superheroes: the ability to fly, to leap tall buildings, or to see through walls in complete darkness with X-ray vision. While humans can only wish for such powers, these capabilities are common and often unremarkable in the animal kingdom. We take flight for granted in more than 10,000 species of birds (Hoyo et al. 1992; Gill and Wright 2006). Dozens of different vertebrate and invertebrate animals can jump over 10 times their own body height, the rough equivalent of a human

jumping over a five-story building (Vogel 2003; Sillar et al. 2016). And some animals, the weakly electric gymnotiform and mormyridiform fishes of South America and Africa, even possess a type of X-ray vision that lets them “see” in darkness and, to some degree, through objects and barriers.

Nocturnal weakly electric fish image their worlds and communicate using self-generated electric fields in the water surrounding their bodies (Caputi et al. 1998; von der Emde 1999, 2006; Caputi and Budelli 2006; Marsat et al. 2012). These electric fields are produced by electric organ discharges (EODs),



**Fig. 1** Electric signal production and electrolocation in gymnotiform fish. (A) The electric signal is produced by an electric organ discharge (EOD), resulting from the synchronized action potentials (APs) of the electrocytes in the electric organ (EO). A brainstem pacemaker nucleus elicits the electrocyte APs via spinal electromotor neurons that innervate the electrocytes. (B) Simplified schematic of an electrocyte. These are large multinucleated cells, typically greater than 1 mm in length, with an innervated cholinergic synapse on the cell's posterior region. Activation of the cholinergic synapse initiates the AP by  $\text{Na}^+$  influx through voltage-gated  $\text{Na}^+$  channels. The electrocyte's morphology and ion channel distributions direct the ionic current flow along the rostral–caudal body axis. (C) A section of the tail, with skin removed to expose the electric organ and electrocytes, which are densely packed within the EO. A single electrocyte is outlined in black. (D) The simultaneous APs of all electrocytes in the EO generate current that moves forward toward the head, following a return path through the water toward the tail. By convention, headward current is measured as positive (upward). (E) A single EOD waveform corresponds to one cycle of coordinated APs in the EO. (F) The EOD waveform from a wave-type fish (*E. virescens*) with EOD frequency of  $\approx 500$  Hz. (G) The EOD creates an approximate dipole field around the body which produces electrical potential differences across the skin that are detected by electroreceptors in the skin. Objects more resistive (R) or conductive (C) than the surrounding water produce distortions in the fields that are detected by the electroreceptor array. Neural analysis of inputs from the electroreceptors derives information about the shape, location, and composition of nearby objects. Panels A–F adapted from Ban et al. (2015).

which in turn are produced by the simultaneous action potentials of a thousand or more electric organ cells known as electrocytes (Bennett 1971; Markham 2013). Some species, known as pulse-type fish, generate EODs at  $\sim 10$ – $120$  Hz with long, irregular intervals between EODs. A second group, known as wave-type fish, produce high-frequency EODs ( $\sim 100$ – $2000$  Hz) at regular uniform intervals, thereby creating sinusoidal signals. When the EOD is transduced to sound with an audio amplifier, pulse fish sound like a stuttering gas lawnmower, while wave fish sound like pure tones from the middle octaves of a piano.

Weakly electric fish image their surroundings at surprisingly high resolution by detecting distortions

of the electric fields caused by nearby objects (Fig. 1). This unique active sensory modality gives electric fish the aquatic analog of X-ray vision. Ambient light is not needed and electricity penetrates conductive materials in the water, enabling these fish to image their surroundings in complete darkness, gain information about the composition of these objects, and even detect objects behind visually opaque but electrically conductive barriers (von der Emde 2006; Catania 2014, 2015). Weakly electric fish also broadcast their electric signals to nearby conspecifics as their primary communication modality.

At the mention of electric fish, one might assume that these are rare and unusual creatures restricted to a small number of highly specialized habitats. This



**Fig. 2** Distribution and abundance of Gymnotiformes (adapted from Crampton 2011). Inset: global map with outlined area expanded in full figure. Darker red shading of a region indicates a greater proportion of total gymnotiform species inhabiting the region. Region abbreviations: AM, Amazon (63.7% of known species); GU, Guianas (14.0%); MA, Middle America (3.3%); NE, Northeast (3.3%); NW, Northwest (7.0%); OR, Orinoco (29.8%); PA, Paraná-Paraguay-Uruguay (10.2%); PS, Pacific Slope (5.1%); SE, Southeast (4.7%). Gray shading indicates regions uninhabited by gymnotiform fishes.

assumption could not be further from the truth. Weakly electric fish are arguably among the more successful clades of freshwater fish in South America (Albert and Crampton 2005; Crampton 2011) and Africa (Lavoue et al. 2000; Sullivan et al. 2000) with more than 200 distinct species abundantly and broadly distributed on each continent. Sensing and communicating with electricity likely confers significant adaptive advantages for weakly electric fish. The ability to image the aquatic world with electricity allows these fish to forage at night and in high-turbidity waters, thus gaining access to visually concealed prey items while at the same time avoiding predation by visually-guided predators (reviewed by von der Emde 2006). Communication with electricity also avoids detection of their signals by predators that target the visual or auditory communication signals of their intended meals. While electric fish are vulnerable to electroreceptive piscivores such as siluriform catfish, even in these cases weakly electric fish reduce this risk by employing biophysical tricks to cloak their electric signals from such predators (Stoddard 1999; Stoddard and Markham 2008). Here we consider potential costs that accompany the many advantages of electrosensory systems. We will focus our discussion on the

South American gymnotiform fishes because there is substantially more data available for this group on the energetics, physiology, and regulation of electric signal generation.

Although a few clades of neotropical fishes are more diverse and abundant than the Gymnotiformes, such as the siluriform catfishes and the Characiformes (e.g., piranhas and tetras), weakly electric gymnotiform fish are one of the most speciose and abundant fish clades in the neotropical waters of South America (Crampton 2011). Gymnotiform fish are widely distributed throughout most of Central and South America, ranging from southern Mexico to northern Argentina (Albert and Crampton 2005; Fig. 2). The Amazon River basin is the center of diversity for Gymnotiformes, with the combined Amazon, Orinoco, and Guiana regions hosting roughly 75% of the nearly 220 species of the order as well as representatives of all but one of its 33 genera.

Outside of the Amazon, gymnotiform assemblages are observed in most lowland neotropical aquatic habitats, including major river channels, floodplains, lowland terra firme streams, and upland streams, with every populated region containing a polyphyletic species assemblage (Albert and Crampton 2005; Crampton 2011). In these habitats, Gymnotiformes can compose a significant portion of the local biomass, particularly in benthic river habitats (Crampton 2007). Trawling samples from both the whitewater and blackwater deep channel streams of the Tefé region of Northwestern Brazil found that gymnotiforms comprised more than 75% of the biomass (Lundberg et al. 1987, 1996; Marrero 1987; Goulding et al. 1988; Marrero and Winemiller 1993). While these samples likely failed to catch large bottom-dwelling pimelodid catfishes, which are expected to form significant portions of the local biomass, these fish prey primarily upon gymnotiformes, and it is unlikely that they outweigh their prey (Reid 1983; Lundberg et al. 1996; Albert and Crampton 2005). Gymnotiforms also comprise significant portions of the biomass in several floodplain environments in or near the upper Amazon basin, accounting for 11–64% of the biomass in floating meadow sites (Crampton 1996). Within coastal stream habitats in French Guiana, gymnotiforms formed approximately 25% of the local biomass (Westby 1988).

Throughout the neotropics, then, weakly electric fish are neither rare nor unusual. These fish have extensively colonized a broad range of aquatic habitats likely by exploiting their electric sensory and communication systems—but at what price? The chief costs of any animal signal, whether a

communication signal or an active sensory signal, are predation risk and the metabolic cost of signal generation. Because electric fish depend on their electric signals for sensory performance, these signals must be emitted around the clock at species-specific rates ranging from 10 Hz to above 2000 Hz. As a result, both the predation risks and metabolic costs of signal generation are ever present. Predation pressures, however, are common to all neotropical fishes whereas the metabolic costs of electrogenesis are specific to the weakly electric gymnotiforms. We therefore focus here on surveying recent findings concerning the metabolic costs, energetic constraints, and energy-conserving adaptations related to EOD production. We also extend this survey by considering whether the metabolic demands of EOD production might cause weakly electric fish to be disproportionately affected by anthropogenic disturbances on neotropical aquatic ecosystems.

### Metabolic Costs of Electric Signaling

At an intuitive level, one would expect that the physiological processes required for fish to generate electric fields outside the body would be metabolically expensive. Because the EOD is a direct function of the synchronized action potentials of electrocytes within the electric organ, the cost of EOD production should arise primarily from the same factors that incur high metabolic costs of neural activity in other systems: the maintenance of membrane potentials, synaptic transmission, and especially the costs of action potential generation (Attwell and Laughlin 2001; Niven and Laughlin 2008; Howarth et al. 2012). In electrocytes, as in all excitable cells, action potentials are transient changes in membrane voltage that are initiated by inward  $\text{Na}^+$  current ( $I_{\text{Na}}$ ) and terminated by outward  $\text{K}^+$  current ( $I_{\text{K}}$ ). These currents are driven by ionic concentration gradients across the cell membrane and  $\text{Na}^+/\text{K}^+$  Adenosine triphosphatases (ATPases; sodium–potassium pumps) must restore the ionic gradients after each action potential (Bean 2007) by hydrolyzing one ATP for every three  $\text{Na}^+$  ions that are returned to the extracellular space. The ionic currents generated by single electrocytes are orders of magnitude larger than those of central neurons—in some cases exceeding 10 microAmps (McAnelly and Zakon 2000; Sierra et al. 2005; Markham et al. 2013)—strongly suggesting a correspondingly high metabolic demand.

Surprisingly, some early theoretical analyses suggested that EOD production consumes a small fraction of the animal's energy budget (Hopkins 1999) while others measured only moderate costs of EOD

production but without reference to the animal's total energy budget (Aubert and Keynes 1968; Keynes 1968; Bell et al. 1976). A survey of metabolic rates across several species of weakly electric gymnotiforms found that overall metabolic rate did not scale with species-specific EOD rates and that the overall metabolic rates for electric fish were no higher than what would be predicted for nonelectric teleost fish at neotropical temperatures (Julian et al. 2003)—a finding that could be interpreted to mean that electrogenesis adds little to overall metabolic rates or that electric fish have a lower metabolism overall.

In contrast, more recent experimental and theoretical analyses that partitioned EOD production costs from other metabolic expenses suggest that the metabolic cost of electrical signaling can be quite high. In the first such study, Salazar and Stoddard (2008) pharmacologically isolated the cost of EOD production in the pulse fish *Brachyhypopomus pinnicaudatus* (now *B. gauderio*; Giora and Malabarba 2009) and found that while females invested very little energy in the EOD, the costs were as high as 22% of the daily energy budget in males.

A comprehensive theoretical analysis of EOD production costs for the wave fish *Eigenmannia virescens* (Salazar et al. 2013) incorporated the costs of electrogenesis in the electric organ as well as the metabolic costs of the brainstem pacemaker that synchronizes electrocyte action potentials and the afferent sensory neurons that process the electrical image. Their estimated electric organ cost was  $7 \times 10^{13}$  ATP per EOD cycle, and the combined metabolic demand of electric organ, pacemaker, and afferent processing amounted to 28% of the routine metabolic rate for a fish with EOD rate of 400 Hz (Salazar et al. 2013), well within the species range of 200–600 Hz (Hopkins 1974). In a separate study, our computational model of *E. virescens* electrocytes constrained by electrophysiological data for the electrocyte's voltage-gated ionic conductances predicted a metabolic cost of  $1\text{--}3 \times 10^{10}$  ATP per action potential for each electrocyte (Markham et al. 2013). Assuming a population of 1000 electrocytes in the electric organ leads to an estimated total cost of  $1\text{--}3 \times 10^{13}$  ATP per EOD cycle, in very close accordance with the estimates of Salazar et al. (2013). At an EOD rate of 400 Hz, the resulting demand would be on the order of  $10^{16}$  ATP  $\text{s}^{-1}$  for EOD production alone.

We later confirmed these rather extreme theoretical predictions through electrophysiological measurements of  $\text{Na}^+$  influx during the electrocyte action potential (Lewis et al. 2014). The metabolic cost of

**Table 1** Experimentally-measured metabolic costs of electrically-excitable tissue types

Tissue	Organism	Condition	ATP g <sup>-1</sup> s <sup>-1</sup>	Source
Electric organ	<i>E. virescens</i>	400 Hz rate	3.47 × 10 <sup>16</sup>	Lewis et al. (2014)
Skeletal muscle	Human	Resting	1.10 × 10 <sup>16</sup>	Gibala et al. (1997)
Skeletal muscle	Human	Exercising	6.02 × 10 <sup>17</sup>	Gibala et al. (1997)
Brain	Human	Alert	7.40 × 10 <sup>16</sup>	Sokoloff (1969)
Brain	Human	Sleeping	4.48 × 10 <sup>16</sup>	Sokoloff (1969)
Heart	Rat	60 beats min <sup>-1</sup>	1.26 × 10 <sup>16</sup>	Haworth et al. (1983)
Retina	Rabbit	Darkness	9.89 × 10 <sup>16</sup>	Ames et al. (1992)
Retina	Rabbit	Light	6.92 × 10 <sup>16</sup>	Ames et al. (1992)

Note: Values are given for each gram of wet tissue mass.

action potentials arise primarily from the Na<sup>+</sup>/K<sup>+</sup>ATPase which hydrolyzes one ATP for every three Na<sup>+</sup> ions it returns to the extracellular space (Laughlin et al. 1998; Attwell and Laughlin 2001). We found that ATP required for each electrocyte action potential was 2.2 × 10<sup>10</sup> ATP per electrocyte action potential (2.2 × 10<sup>13</sup> ATP per EOD assuming 1000 electrocytes in the electric organ), squarely within the range of earlier computational predictions. These cellular-level findings were corroborated by organismal-level respirometry which found costs of ~10<sup>14</sup>–10<sup>15</sup> ATP per EOD, ultimately amounting to greater than 30% of routine metabolic rate (Lewis et al. 2014). Taken together, these analyses provide additional evidence that electric signaling demands a significant fraction of the daily energy budget in both slow-discharging pulse fish and in high-frequency wave fish.

Given the broad diversity of gymnotiform species across dimensions such as physiology, ecology, and life history, it is important to be cautious in extrapolating from experimental work on only two species to the full clade of Gymnotiformes. It is possible that the metabolic costs of EOD production are highly variable when considered across the entire clade. Additional comparative studies that quantify the metabolic cost of EOD production across a much larger range of gymnotiform species will allow a better understanding of how consistent or variable these costs are across species. In the case of wave-type fish, experimental measurement of EOD energetics can be accomplished by relatively simple respirometry methods such as those used by Lewis et al. (2014), making such experiments possible in field settings with access to large numbers of gymnotiform species. Partitioning the costs of EOD production in pulse-type fish is more challenging, but refinements of the methods applied by Salazar and Stoddard (2008) could also potentially be applied in field settings.

## Comparative Energetics of Signaling

Expressing the metabolic costs of EOD production in ATP s<sup>-1</sup>, as we have done here, is a convenient way to quantify the absolute metabolic cost from existing physiological data, but provides little information about how metabolically expensive EOD production is compared to other electrically active tissue types, or compared to other animal communication signals. Abundant data are available in both cases, with metabolic demand typically measured instead as the rate of O<sub>2</sub> consumption per unit mass. To facilitate comparisons across studies we have converted all reported metabolic rates to consumption of ATP g<sup>-1</sup> s<sup>-1</sup> based on the common simplifying assumption that each O<sub>2</sub> molecule ultimately provides 5 ATP molecules (Howarth et al. 2012; Salazar et al. 2013; Lewis et al. 2014).

We first compared metabolic costs for electric organ of *E. virescens* to published experimentally-measured metabolic costs for skeletal muscle, cardiac muscle, brain, and retina—tissues among the most metabolically costly for any vertebrate (Table 1). Electric organ is approximately equal on a first-order comparison to all of these metabolically-demanding tissues except for skeletal muscle during exercise, which consumes ATP at a rate one order of magnitude higher than all other tissues and conditions. With the exception of skeletal muscle, the other comparison tissues (heart, brain, and retina) comprise a small fraction of total body weight, with the human brain being the highest weight relative to body size (~2%; Sokoloff 1989; Niven and Laughlin 2008). In contrast, electric organ comprises a much larger fraction of total body weight, in the range of ~10% of body weight (Salazar et al. 2013), which would further magnify the cost of EOD production compared with other tissues such as brain or retina that represent only a small proportion of body weight. In order to fully contextualize the metabolic costs of electric organ in gymnotiform fish, however,

the most appropriate comparisons would be to the metabolic costs of tissues such as brain, heart, and muscle in gymnotiforms and other nonelectric neotropical fish, allowing a more complete picture of the energetic budgets of these groups. Such comparative studies are an important avenue for future research.

The costs of EOD production also can be meaningfully compared to the metabolic costs of other animal communication signals. In one of the most comprehensive reviews to date, Stoddard and Salazar (2011) compared the published metabolic costs of animal communication signals across a broad sampling of insects and vertebrates. Their analysis revealed that, on an instantaneous second-to-second basis, the absolute metabolic costs of signaling by electric fish are far outstripped by the communication signals of several birds, amphibians, insects, and arachnids. An important consideration, however, is the total duration of signaling in a 24-h period. In electric fish, communication signals are coupled to an active sensory system and are therefore emitted 24 h per day, unlike other expensive acoustic or mechanical signals that are emitted only for brief periods. We therefore compare the cost of EOD signaling to the most expensive communication signals identified by Salazar and Stoddard (both in absolute energetic costs and those with the highest costs relative to whole-body metabolism), such as drumming by Wolf Spiders, the calls of Carolina Wrens, or the trilling of katydids (Table 2). This comparison shows that the absolute costs of electric signaling are quite a bit lower on a second-to-second basis for electric fish. However, if we assume that the non-electric animals spend a total of 2-h signaling per day, compared with 24 h for electric fish, then the costs of electric signaling begin to rival and even exceed the costs of the other signals (Table 2) both in absolute terms and when compared to whole-body metabolism. While metabolic demands of electric signaling are on the low end of the range for the pulse fish *B. gauderio*, the costs of signal generation for the wave fish *E. virescens* are at the top of this range, and increase exponentially with EOD frequency as reported by Lewis et al. (2014). The particularly high costs for wave type fish almost certainly stem from constant EOD rates of several hundred Hz compared with highly variable EOD rates of just ~10–100 Hz in pulse fish.

### Energy-Saving Adaptations

Many weakly electric fish display a range of adaptations at the molecular, cellular, and behavioral levels that likely serve to tune the physiology of EOD production to improve its energy efficiency. At the level of

individual electrocytes, the kinetics of the voltage-gated  $\text{Na}^+$  and  $\text{K}^+$  currents that produce the electrocyte action potential are tightly co-regulated (McAnelly and Zakon 2000) according to the EOD pulse width within and across individuals (Ferrari et al. 1995; Dunlap et al. 1997; McAnelly and Zakon 2007). One outcome of this coregulation is the reduction of energetically wasteful overlap between depolarizing  $\text{Na}^+$  currents and repolarizing  $\text{K}^+$  currents (Alle et al. 2009; Carter and Bean 2009). We recently found that electrocytes of *E. virescens* repolarize the action potential with  $\text{Na}^+$ -activated  $\text{K}^+$  ( $\text{K}_{\text{Na}}$ ) channels (Markham et al. 2013), rather than voltage-gated  $\text{K}^+$  channels as has been found for all other species where data on electrocyte ionic currents is available (Shenkel and Sigworth 1991; Ferrari and Zakon 1993; Sierra et al. 2007; Markham and Zakon 2014). Repolarizing the electrocyte action potential with  $\text{K}_{\text{Na}}$  channels might serve to further minimize the wasteful overlap of  $\text{Na}^+$  and  $\text{K}^+$  currents (Markham et al. 2013) thereby improving the energy efficiency of EOD production for high-frequency wave type fish. Subsequent findings, however, open up the possibility that  $\text{K}_{\text{Na}}$  channels serve a different purpose in *E. virescens* because of the large spatial separation of  $\text{K}_{\text{Na}}$  channels and voltage-gated  $\text{Na}^+$  channels in electrocytes (Ban et al. 2015).

Behavioral strategies also serve to reduce the energetic demands of EOD production. Pulse-type fish reduce EOD rate during resting hours to decrease EOD costs (Silva et al. 2007; Stoddard et al. 2007), but such a strategy is not available for wave-type fish. Several species of pulse- and wave-type electric fish modulate their EOD waveforms on a circadian rhythm, reducing amplitude (and therefore energy expenditure) during daytime hours when the fish are inactive, then increasing EOD amplitude at night when fish are foraging and socially active (Hagedorn 1995; Franchina and Stoddard 1998; Franchina et al. 2001; Markham et al. 2009; Sinnett and Markham 2015). These modulations in EOD waveform are hormonally-mediated by melanocortin peptide hormones that rapidly alter the action potential characteristics of the electrocytes (Markham and Stoddard 2005, 2013; Markham et al. 2009, 2013). This process is best understood in the wave species *E. virescens* and *Sternopygus macrurus*, where circulating melanocortins cause the rapid insertion of up to 50% more voltage-gated  $\text{Na}^+$  channels into the electrocyte membrane within a matter of minutes (Markham et al. 2009). This produces a corresponding increase in  $\text{Na}^+$  current in the electrocyte, EOD amplitude at the organismal level, and energetic expenditure on the EOD. The ability to so rapidly alter the signal amplitude and its corresponding costs allows these

**Table 2** Experimentally-measured metabolic costs of animal communication signals in comparison to resting metabolic rates

Organism	Source	Signal ATP g <sup>-1</sup> s <sup>-1</sup>	Duration (hours day <sup>-1</sup> )	Signal ATP g <sup>-1</sup> d <sup>-1</sup>	Resting ATP g <sup>-1</sup> d <sup>-1</sup>	Instantaneous ATP <sub>Signal</sub> / ATP <sub>Rest</sub>	24-h ATP <sub>Signal</sub> / ATP <sub>Rest</sub>
Arachnids							
Wolf Spider <i>Hygrolycosa rubrofasciata</i>	Kotiaho et al. (1998)	1.71 × 10 <sup>17</sup>	2	1.23 × 10 <sup>21</sup>	7.10 × 10 <sup>20</sup>	20.82	1.73
Insects							
Trilling cricket <i>Anurogryllus arboreus</i>	Prestwich and Walker (1981)	1.36 × 10 <sup>17</sup>	2	9.61 × 10 <sup>20</sup>	1.02 × 10 <sup>21</sup>	11.35	0.95
Short-tailed cricket <i>A. muticus</i>	Lee and Loher (1993)	3.38 × 10 <sup>17</sup>	2	2.44 × 10 <sup>21</sup>	5.48 × 10 <sup>21</sup>	5.33	0.44
Trilling Katydid <i>Euconocephalus nasutus</i>	Stevens and Josephson (1977)	5.89 × 10 <sup>17</sup>	2	4.24 × 10 <sup>21</sup>	8.41 × 10 <sup>21</sup>	6.05	0.50
Trilling cricket <i>Gryllotalpa australis</i>	Kavanagh (1987)	1.82 × 10 <sup>17</sup>	2	1.31 × 10 <sup>21</sup>	1.35 × 10 <sup>21</sup>	11.63	0.97
Amphibians							
Squirrel treefrog <i>Hyla squirella</i>	Prestwich et al. (1989)	7.88 × 10 <sup>16</sup>	2	5.67 × 10 <sup>20</sup>	4.52 × 10 <sup>20</sup>	15.07	1.26
Birds							
Carolina Wren <i>Thryothorus ludovicianus</i>	Eberhardt (1994)	3.37 × 10 <sup>17</sup>	2	2.43 × 10 <sup>21</sup>	1.15 × 10 <sup>22</sup>	2.54	0.21
Gymnotiform weakly electric fish							
Feathertail knife fish (female) <i>B. gauderio</i>	Salazar and Stoddard (2008)	5.97 × 10 <sup>14</sup>	24	5.16 × 10 <sup>19</sup>	1.39 × 10 <sup>21</sup>	0.04	0.04
Feathertail knife fish (male) <i>B. gauderio</i>	Salazar and Stoddard (2008)	4.74 × 10 <sup>15</sup>	24	4.10 × 10 <sup>20</sup>	3.21 × 10 <sup>21</sup>	0.13	0.13
Glass knife fish (200 Hz) <i>E. virescens</i>	Lewis et al. (2014)	4.82 × 10 <sup>14</sup>	24	3.69 × 10 <sup>19</sup>	2.86 × 10 <sup>19</sup>	1.29	1.29
Glass knife fish (300 Hz) <i>E. virescens</i>	Lewis et al. (2014)	1.30 × 10 <sup>15</sup>	24	1.12 × 10 <sup>20</sup>	4.90 × 10 <sup>19</sup>	2.29	2.29
Glass knife fish (500 Hz) <i>E. virescens</i>	Lewis et al. (2014)	3.47 × 10 <sup>15</sup>	24	3.01 × 10 <sup>20</sup>	9.60 × 10 <sup>19</sup>	3.13	3.13

Notes: Values are given for each gram of body mass. Table format and species selection based on Stoddard and Salazar (2011).

fish to enhance EOD amplitude only during periods of activity or social interaction, while reducing signal amplitude and metabolic costs at all other times.

### Constraints Imposed by the Costs of Signaling

Given the apparently high metabolic costs of EOD signaling, it is likely that these costs would impose constraints on the ecology and behavior of weakly electric fish. Consistent with this prediction, high-frequency wave-type fish are restricted to well-oxygenated habitats (Crampton 1998) possibly because of higher metabolic demands and the inability to reduce demand by reductions in EOD frequency (Reardon et al. 2011; see also Table 2). Only pulse-type fish were found in hypoxic habitats, likely

facilitated by lower EOD rates and the ability to breathe air (Crampton 1998).

Consistent with Crampton's (1998) observations, the wave-type fish *E. virescens* and *Apteronotus leptorhynchus* reduce EOD amplitude but not frequency within minutes of exposure to hypoxic conditions (Reardon et al. 2011). This response to metabolic stress would reduce metabolic costs of EOD production, but also would produce a corresponding degradation of electrosensory performance. It is not yet known whether hypoxia-induced reductions of EOD amplitude reflect an absolute energy shortfall in the electric organ, or a physiologically proactive mechanism for conserving energy in hypoxic conditions.

Under metabolic stress caused by food deprivation, *E. virescens* reduces EOD amplitude but not frequency as it does under hypoxia. However, EOD

amplitude changes occur over the course of hours to days. Reduced EOD amplitude in this case does not reflect an absolute energetic limitation in the electric organ, but is instead a proactive response mediated by the peptide hormone leptin (Sinnott and Markham 2015). While the mechanism(s) by which leptin regulates EOD amplitude are not yet known, preliminary evidence suggests that leptin acts directly on the electric organ to regulate EOD amplitude (McCauley, unpublished observations).

In both cases, reductions of EOD amplitude in response to metabolic stress stand to compromise both sensory performance and the communication function of the EOD. The resulting reduction of sensory capability could potentially magnify the effects of metabolic stress to the extent that the ability to locate prey and other food items is degraded. Interestingly, the pulse-type gymnotiform *B. gauderio* does not reduce EOD amplitude to conserve energy during food deprivation, and males actually increase their signaling effort in social contexts, likely as a terminal investment in reproduction (Gavassa and Stoddard 2012). The differences in response to food deprivation between *E. virescens* and *B. gauderio* could reflect differences in EOD costs between these species and/or their different reproductive life-histories as *B. gauderio* are semelparous breeders that rarely survive to a second reproductive season, while *E. virescens* are iteroparous breeders that live for many years.

### The Threat of the Anthropocene

As is the case in aquatic systems throughout the world, the aquatic habitats of neotropical fish are coming under acute pressure from anthropogenic changes. These include immediate and near-term ecological impacts such as those associated with dams, agriculture, deforestation, industry, and mining (Reis 2013), as well as a broad range of potential long-term disturbances associated with anthropogenic climate change (Castello and Macedo 2016). Disruptive anthropogenic developments already are having widespread and significant impacts on neotropical aquatic habitats, with little hope for abatement in the near future (Reis 2013; Castello and Macedo 2016). Looking forward, the impending long-term consequences of climate-change for neotropical aquatic systems are diverse, harder to predict, and seemingly inevitable (Pachauri et al. 2014; Castello and Macedo 2016).

Could anthropogenic disturbances with metabolic consequences disproportionately harm weakly electric fish that rely on metabolically expensive sensory

and communication systems? Many of the ongoing anthropogenic disturbances to aquatic habitats reduce water oxygenation and severely disrupt regimes of primary and secondary productivity (Neill et al. 2001; Barletta et al. 2010; Freitas et al. 2012; Bleich et al. 2015; Castello and Macedo 2016), potentially creating “dual threat” conditions of hypoxic water and low dietary energy availability. All fish, of course, would have to compromise some aspect(s) of ongoing physiology under metabolic stress from hypoxia and/or food restriction. Only in electric fish, however, would this metabolic stress directly degrade the animal’s primary sensory modality. Recent studies demonstrate that both hypoxic conditions (Reardon et al. 2011) and reduced food availability (Sinnott and Markham 2015) can cause severe reductions in EOD amplitude. The resulting decrease in sensory performance (Rasnow 1996) would likely hinder navigation, foraging, and prey detection in the very conditions where these fish most need their electrosensory systems to relocate and search out dietary energy sources.

A less obvious cause of metabolic stress for electric fish is extreme fluctuations in water conductivity. Altered ionic concentrations of course will induce physiological stress in any fish given the physiological adaptations required to maintain gill respiration. For electric fish, however, increased water conductivity further worsens this already challenging situation because the spatial extent of the electric field shrinks as water conductivity increases. At least some electric fish overcome this challenge by increasing their EOD amplitude (Kramer and Kuhn 1993). However, re-expanding the signal space requires an exponential increase in electric organ output (Hopkins 1999) and the only known physiological mechanisms for increasing EOD amplitude (Markham et al. 2009) would require significant additional metabolic investment imposing additional metabolic stress.

Extreme fluctuations of water conductivity are indeed occurring more frequently in the neotropics. Across the Amazon basin water conditions normally vary on an annual flood pulse cycle (Junk et al. 1989). High water levels during flood stage increase nutrient availability, increase oxygen saturation, and reduce, while low water levels during the drought stage increase water conductivity, decrease oxygen saturation, and reduce primary productivity (Junk et al. 1989; Henderson and Crampton 1997; Melack and Forsberg 2001; Tomasella et al. 2011; Ropke et al. 2015). Anthropogenic forces already are amplifying both the frequency and severity of the flood pulse cycle (Marengo et al. 2011;



Tomasella et al. 2011; Gloor et al. 2013). The Amazon basin historically averages one extreme hydrological event per decade, but there have been four extreme events (two droughts and two floods) in the past 10 years (Cox et al. 2008; Marengo et al. 2011; Satyamurty et al. 2013). Unfortunately, current models indicate that these extreme variations are likely to continue and worsen (Cox et al. 2008; Marengo et al. 2011; Lobon-Cervia et al. 2015), potentially to the detriment of electric fish that not only must adapt their respiratory physiology, but also must invest more energy in their active sensory outputs to accommodate water conductivity changes.

### The Curse of a Superpower

A near-universal theme in the genre of comic-book superheroes is that their extraordinary superpowers are both a blessing and a curse (Gavaler 2015). Could the same be true for weakly electric fish? The “X-ray vision” of electrosensory systems in electric fish is a kind of neuroecological superpower. The ability to generate and detect electric fields in the water has allowed these fish to broadly inhabit two continents with great success. We have reviewed here recent experimental evidence that electrogenesis can come with a heavy metabolic price, and evidence that electrosensory systems can be compromised under conditions of metabolic stress, whether by hypoxia, shortfalls of dietary energy availability, or rapidly changing water chemistry. If disruptive conditions such as these increase in frequency and/or severity as a result of anthropogenic disturbances, the very sensory adaptations that contribute to the broad success of weakly electric fish could potentially be neutralized or even become a liability.

Fully exploring the potential threats that anthropogenic disruptions might pose to gymnotiform fish will require a much better understanding of the metabolic physiology of EOD production and its responses to metabolic stress. While the currently available data indicate that the costs of EOD production are high in both pulse- and wave-type gymnotiform fish, it is possible that the metabolic costs of EOD production are not significant or limiting for all gymnotiform clades. Data on the energetics of EOD production are therefore needed for a much broader sampling of gymnotiform species than the two species where data are currently available. Also important will be detailed comparative analyses of the energetic budgets of weakly electric fish compared with other neotropical fishes to conclusively determine whether the costs of electrogenesis amplify the detrimental effects of metabolic stress in electric

fish compared with nonelectric fish. Finally, coupling this work with increasingly accurate models for predicting and quantifying the effects of anthropogenic disruptions on neotropical aquatic ecosystems should enable better predictions of the coming impacts of the Anthropocene on gymnotiform fishes.

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