HORMONAL CONTROL IN THE REPRODUCTION AND ELECTRIC ORGAN DISCHARGE MODULATIONS IN GYMNOTIFORMES: A REVIEW

Carolina Escamilla-Pinilla. Doutoranda em Biologia de Água Doce e Pesca Interior no Instituto Nacional de Pesquisas da Amazônia (INPA). carolina.escamilla@inpa.gov.br
Samuel Carvalho De Benedicto. Professor do Programa de Pós-Graduação em Sustentabilidade da Pontifícia Universidade Católica de Campinas (PUC-Campinas). samuel.benedicto@puc-campinas.edu.br

ABSTRACT

The electrogenic and electroreceptive fish from the Order Gymnotiformes are part of the great diversity of freshwater fish in the Amazon region where they achieve their highest diversity. These fish possess electric organs to emit electric currents and electroreceptors to detect variations in their own generated electric field. They can recognize and discriminate themselves based on frequency and temporal components of their Electric Organ Discharges (EOD). They can modulate their EODs to avoid detection by eavesdropping predators and communicate social status and sexual state. Most of these fish can exhibit EOD waveforms notably different, and they can even produce sexually dimorphic EODs as a suggestion for recognition during courtship. These EOD properties can change in different temporal scales and respond according to the physical and social environment mediated by hormones. Therefore, in this article we reviewed the latest research regarding hormonal control in the reproduction process and EODs´ modulations in electric fish through a thorough systematic bibliographic search in the SCOPUS data base using the following key terms “Hormones AND Electrocommunication” and “Reproduction AND Gymnotiformes.” We found that in these fish, the reproductive cycle depends on environmental conditions such as pH, conductivity, water level and rainfall. Also, the reproductive strategies they commonly present are “K-strategy” or “equilibrium strategy,” and fractional spawning was the life history strategy more characteristic. On the other hand, we found that steroid sex hormones play an important role in in the modulation of the temporal and spectral EOD parameters in a long-time basis possibly aiding in sex recognition during courtship behavior at maturity. In this way, due to the ecological and biological importance of these electric fish for the sustainability of the Amazon region it is imperative that more studies turn their focus on reproduction and EOD communication properties to better understand their adaptive response to environmental variation within this region and the reproductive strategies they engage on.

Keywords: Weakly electric fish, Hormones, Reproduction, Modulations, Electric Organ Discharges, Neotropics.

1. INTRODUÇÃO

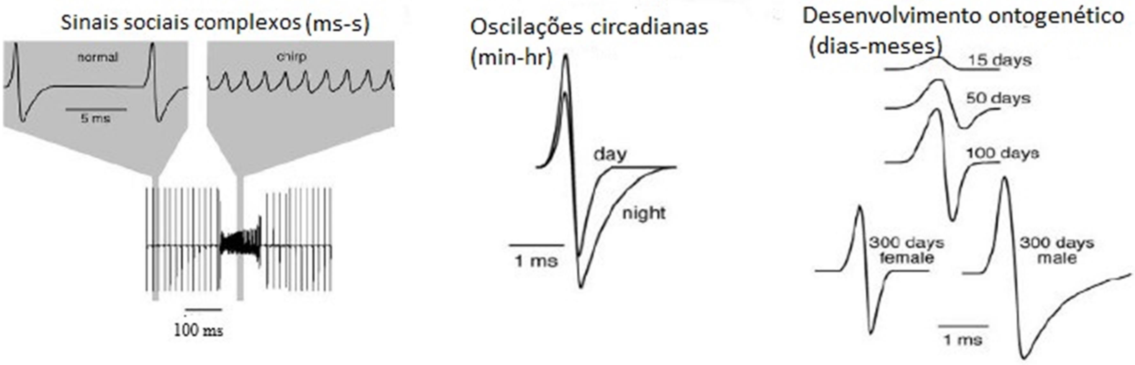
The Neotropical region possess a great diversity of freshwater fish with more than 8,000 species described, with 2,716 valid species in the Amazonian region (Reis et al., 2016; Dagosta & Pinna, 2019). Recent studies from the Amazon region suggest that variations in geology, clime, soil, topography, habitat type and vegetation structure could influence species composition and distribution patterns of freshwater species (Thessler et al., 2005; Tuomisto et al., 2014; Ritter et al., 2018). Additionally, the high gamma diversity and species turnover of freshwater fish found in the Amazon region have generated an increased interest in studying these aquatic environments (Albert et al., 2011; Reis et al., 2016). As part of these great diversity there are now 164 species of electrogenic and electroreceptive fish from the Order Gymnotiformes (Reis et al., 2016; Dagosta & Pinna, 2019). Gymnotiforms achieve their highest diversity in the Amazon region inhabiting diverse aquatic systems such as, major rivers, flood plains and small terra firme streams popularly known as "igarapés"; and varied water type chemistry such as, black, white, and clear water systems that have been described for this region (Albert & Crampton, 2005). These fish possess electric organs to emit electric currents and electroreceptors to detect variations in their own generated electric field (Hopkins, 1972; von der Emde, 2006). The Electric Organ discharges (EODs) are used for these fish to communicate sex, social status, motivational state, and are useful for taxonomy and species identification in the field (Albert & Crampton, 2006; Dunlap et al., 2017). Thus, understanding the electromotor system and its influence over the behavior of these fish is important for the sustainability of the Amazon region due to their high diversity and wide distribution range.

The EODs have mainly two communicative functions: 1) identify other species since they are specie specific, and 2) share internal physiological states through the modulation in EOD shape and temporal pattern of the inter pulse intervals (IPI) (Macadar & Silva, 2007). During social interactions electric fish can communicate species, sex, size, and reproductive state using one or more EOD properties, such as: frequency, shape and duration of every pulse, and spectrum frequency and amplitude (Albert & Crampton, 2005; Dunlap et al., 2017). The shape and duration of every pulse are a function of size and geometry of the electrocytes (electric generating cells), number and localization of the electric excitable faces of each electrocyte (rostral or caudal), innervation patterns, and concentration and types of ionic channels in the electrocyte´s membrane (Albert & Crampton, 2005). The modulations in frequency can vary between a few milliseconds up to a fraction of minutes, and together with the amplitude variations of each pulse, they can communicate information about sexual identity, maturity stage and position within a dominant hierarchy (Zakon, 2002). In addition, these EOD properties can change in different temporal scales and respond according to the physical and social environment (Black-Cleworth, 1970; Schwassmann, 1976; Squire & Moller, 1982; Kramer, 1990; Hopkins, 1999; Stoddard, 2006; Fugère et al., 2010).

Some of these complex social signals are known as "chirps" or modulations in the repetition rate, waveform, or EOD duration in a short-time basis over a few seconds of which have been reported during agonistic or courtship behavior (Stoddard et al*.*, 2006) (Figure 1.). Other type of EOD modulations can occur within a few minutes to hours also known as circadian oscillations over which individuals significantly increase the communicative power of the EOD at night when they are more active increasing the repetition rate and EOD waveform while maintaining a lower repetition rate when resting during the day (Franchina & Stoddard,

1998) (Figure 1.). Finally, modulations and waveform variation in a long-time scale of weeks up to months can occur during the sexual differentiation in response to specific environmental stimuli or steroid sex hormones at the time of sexual maturation (Stoddard et al., 2006) (Figure 1).

Figure 1: Modified scheme presenting the EOD modulations in repetition rate and waveform



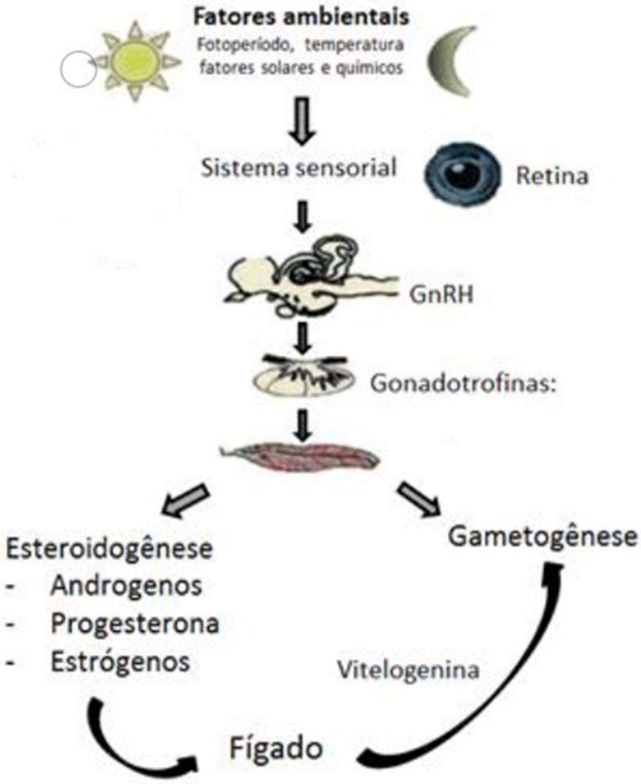
Source: Modified from Stoddard et al. (2006).

In Figure 1, we see from left to right, the fast variations or complex social signal; intermediate variations or circadian oscillations; and finally, the long-time variations that occur during sexual differentiation and ontogenetic development

Fish possess different life history strategies also known as the set of characteristics that a specie can express to be reproductively successful, and at the same time be able to guarantee population equilibrium (Vazzoler, 1996). These reproductive events depend on multiple triggers such as endogenous factors (self-originated) like physiologic; or proximal factors (external environmental conditions) such as pH, water conductivity, water level, rainfall stimulation and food availability (Kah et al., 1993, Kirschbaum, 1995). In other words, life histories are shaped by the interaction between these factors, where the extrinsic factors are ecological impacts on survival and reproduction, and the intrinsic factors are the tradeoffs among life history traits and lineage-specific constraints on the expression of genetic variation (Stearns, 2000).

The integration of all these stimuli is accomplished by the hypothalamus-hypophysis-gonad axis, which in turn oversees producing all the appropriate hormones in response to the environmental stimulus received and finally it helps in the development of the gonads and the formation of gametes during the reproductive cycle (Kah et al., 1993). In other words, when an external stimulus is received and it is perceived by the sensory organs, such as temperature or photoperiod, that signal is transported by neurons in the central nervous system where that information will be processed initiating a secretion of the Gonadotrophin Releasing Hormone (GnRH), that at the same time regulated the secretion of two gonadotrophic hormones, Follicle Stimulating and Luteinizing Hormones (FSH and LH) in the hypophysis. These hormones are released into the bloodstream and through specific receptors they are collected in the gonads to stimulate the production of gonadal steroid hormones (steroidogenesis) and induce gametogenesis (Kah et al., 1993; Souto et al., 2017) (Figure 2.).

Figure 2. Scheme of the neuroendocrine regulatory process of the hypothalamus-hypophysis-gonad axis in teleost fishes



Source: Modified from Souto et al. (2017).

Thus, understanding how endogenous and proximal factors affect the reproductive process and life history strategies through hormonal control specifically over behavioral responses such as the EODs at the time of maturity can certainly bring more insight on what fish communicate during their reproductive encounters. In a similar way, to understand the reproductive events is of great importance to a species sustainability since it is the process by which species can maintain itself transferring all the variations that can occur to its genome to all its descendants. In this article we proposed to review the latest research regarding hormonal control in the reproduction process and EODs´ modulations in electric fish. We will discuss the main papers that characterized and analyzed the reproduction cycle, reproduction strategies and life history strategies in Gymnotiformes. Also, we will describe which hormones are involved in the short time response of EOD modulations and pulse waveform variation and how they influence the communication process. Finally, we will discuss which hormones are involved in the long-time response of EOD modulations and pulse waveform variation and how these changes might affect the behavioral properties of the electric discharge.

2. MATERIALS AND METHODS

We performed a systematic bibliographic searched in the SCOPUS data base through the Universidad Javeriana Colombia research platform using the following key terms "Hormones AND Electrocommunication" and "Reproduction AND Gymnotiformes" for which we obtained 315 and 29 documents, respectively. Of these results we focus on the most relevant papers that analyzed and characterized the reproduction biology, life history strategies, and hormone-mediated variation in the electric discharge especially during courtship or maturity stages. We tried no to focus on papers that analyzed the hormonal influence over social encounters, antagonistic behavior, or circadian rhythms. We examined several papers of which we will discuss separately in two main topics: reproduction biology characteristics and hormonal influence over the variations in the electric discharges from a time-scale perspective.

3. RESULTS AND DISCUSSION

3.1 Reproduction Biology

From the searched we performed we obtained 29 papers that analyzed aspects of the reproductive biology in electric fish, mainly focusing on the following Genus: *Apteronotus, Brachyhypopomus, Sternopygus, Gymnotus*. The main topics discussed were life history parameters and their implications in reproductive effort, the types of reproductive strategies, characterization of the reproductive cycle in a temporal scale, and the effects of proximal factors over the reproductive cycle and strategies in natural populations. We will focus on discussing the reproductive period and the main environmental conditions that trigger it, some of the reproductive strategies these fish engage on, and what the life history parameters say about the reproductive biology of electric fish.

Reproductive period

Reproduction cycles occur at the time of the year when survival of the offspring will be highest, and they will depend on environmental factors that vary seasonally known as "zeitgebers" (Kirschbaum, 1979). In tropical freshwater fish such as, Gymnotiformes, the reproductive cycles depend on environmental conditions such as pH, conductivity, water level and rainfall (Kirschbaum, 1979; Kirschbaum & Schugardt, 2002). In experiments done in laboratory with *Eigenmannia* it was observed that decreasing water conductivity and pH, increasing water level and imitating rainfall led to gonad maturation; on the contrary, increasing water conductivity led to gonad regression (Kirschbaum, 1979). Studies conducted in the wild by Waddell et al. (2019) revealed that the reproductive period of some species of *Brachyhypopomus* that inhabit dry land streams from the Amazon basin in Peru was synchronized with the end of the dry season and beginning of the raining season probably due to an increase in food resources and a decrease in predation. Overall, in the order Gymnotiformes, these environmental conditions seem to influence reproductive period determination in a bigger way than the degree of relationship between the taxa, being an adaptative condition instead of an inherited character (Giora et al., 2014).

Reproduction strategies and life history patterns

As it has been mentioned throughout this paper, tropical species present distinctive reproductive patterns as adaptations to temporal and spatial variation in the environmental conditions, predation pressure, and food resources (Winemiller, 1989). For example, Winemiller (1989) analyzed the reproductive strategies and population variations of 71 freshwater fishes during one year of sampling in a terra firme stream in Venezuela and defined these species as seasonal strategists: *Adontosternarchus devenanzii* (Apteronotidae), *Hypopomus sp*. (Hypopomidae), *Eigenmannia virescens* (Sternopygidae); and as equilibrium strategist: *Gymnotus carapo* (Gymnotidae).

Other studies done in a stream in Rio Grande do Sul, Brazil, found that *Brachyhypopomus gauderio* present long reproductive periods, low values of relative fecundity, high first gonadal maturation sizes which are superior to 40% of the maximum length of the species fitting the concept of late maturation, and almost all have parental care behavior described or observed (Giora et al. 2014). Similar life history strategies have also been reported for other gymnotiform species such as *Gymnotus aff. Carapo, Brachyhypopomus draco, Eigenmannia trilineata, Brachyhypopomus bombilla* (Cognato & Fialho, 2006; Schaan et al., 2009; Giora & Fialho, 2009; Giora et al., 2012). These life history characters that have been previously reported among these species fit the description originally proposed by Pianka (1970) as "K-strategy" and the one proposed by Winemiller (1987) as "equilibrium strategy, both hypotheses are associated with higher juvenile survivorship because of greater parental investment in individual progeny. Other life history strategies, such as, fractional spawning has also been registered for *B. gauderio* and all the gymnotiform species studied up until now from high (Quintana et al. 2004; Cognato & Fialho, 2006; Schaan et al., 2009; Giora and Fialho, 2009; Giora et al., 2012; Barbieri & Barbieri, 1982), and low latitudes (Kirschbaum, 2000; Kirschbaum & Schugardt, 2002; Assuncao & Schwassmann, 1995; Crampton & Hopkins, 2005); thus, being consider as a general characteristic of the order Gymnotiformes.

3.2 Hormonal Influence over the EODs

Now regarding the role of electrocommunication in social behavior and how its regulated by hormones we found 315 papers in our researched that discussed different EOD parameters and their cellular substrates, the type of hormones involved and their physiological pathways, studies performed in the field that analyzed levels of endogenous hormones, and in the lab applying doses of exogenous hormones, and finally the actions of hormones over the electric signal parameters from a temporal scale. We will discuss this last topic within the next paragraphs focusing mainly on the EOD parameter and how it changes in response to the concentration of the hormones and the effect it has on the electrocommunication among these fish during social interactions specially at maturity.

Among the teleost fishes, the integration of all these stimuli is mediated by the hypothalamus-hypophysis-gonad axis, which oversees the production of hormones according with the environmental stimulus received, and finally, it aids in the development of gonads and the formation of gametes during the reproduction cycle (Kah et al., 1993). In this way, when an external stimulus is perceived by the sensorial organs, such as temperature or photoperiod, that signal will be transported through the neurons to the central nervous system where it will be processed, and a secretion of Gonadotrophins Releasing Hormones (GnRH) will be initiated which in turn regulates the secretion of gonadotrophic hormones Follicle Stimulating (FSH) and Luteinizing Hormone (LH) at the hypophysis. These hormones are liberated within the bloodstream and through specific receptors they are captured by the gonads, where they stimulate the production of steroid gonad hormones (steroidogenesis) and induce gametogenesis (Kah et al., 1993; Souto et al., 2017).

Short-time Response

The EOD modulations in the repetition rate, waveform or duration of the EOD pulse can occur in a short-time period around few seconds, such as the so called complex social signal or “chirps,” which have been reported during antagonistic or courtship behavior (Stoddard et al*.,* 2006). These EOD variations can also occur within minutes or hours, such as circadian oscillations where the EOD rate increases substantially at night allowing individuals to significantly increase the communicative power of their EODs while during the day, they save energy by having a lower EOD rate when they are at rest (Franchina & Stoddard, 1998). The hormones that regulate these modulations are known to be peptides of serotonin or melanocortin, alpha melanocyte stimulating hormone (a-MSH) and/or adrenocorticotropic hormone (ACTH)) that act via melanocortin receptors on electrocytes (electric organ cells) (Dunlap et al., 2017). These hormones act directly on the central and peripheral nervous system where they increase or decrease the amplitude or duration of the EOD pulse by altering the concentration of ionic channels in the electrocytes´ membrane (Markham & Stoddard, 2005, Markham et al., 2009).

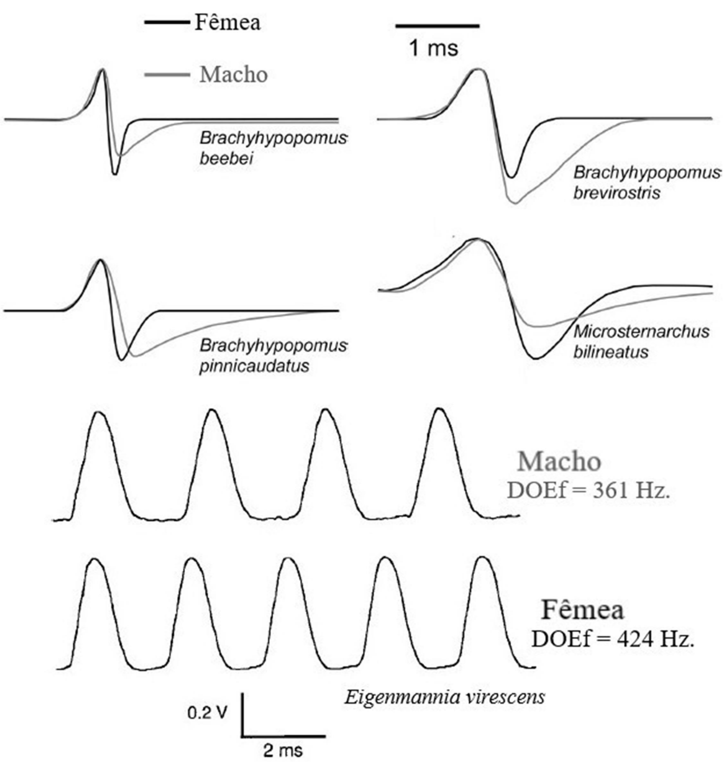
Long-time Response

There are EOD modulations that can last from weeks up to months and they occur during sexual differentiation. These modulations are mediated by important environmental stimuli, such as, food availability, decrease in water conductivity, or presence of a possible sexual partner or competitor, which in turn activate a series of physiological responses regulated by sex steroid hormones at the beginning of sexual maturation (Stoddard et al*.,* 2006). These androgens regulate the expression of sexual aspects involved in sexual recognition by masculinizing the EOD waveform increasing its amplitude, repetition rate or pulse duration (Bass & Hopkins, 1984; Moore et al*.,* 2005; Ball et al., 2008; Bass, 2008; Allee et al., 2009; Godwin, 2010; Goldina et al., 2011).

It has been reported that high levels of plasma 11-Ketotestosterone (11-KT) during the reproductive period correlates positively with testicular size and with EOD amplitude and duration of the second phase in *Brachyhypopomus gauderio* males (Gavassa et al., 2011). On the contrary, high levels of plasma 17β estradiol (E2) feminize or reduce the EOD repetition rate in mature *Apteronotus leptorhynchus* females (Schaefer & Zakon, 1996). Additionally, high levels of plasma testosterone in these females can decrease the EOD repetition rate and increase EOD “chirps,” which function as indicators of oviposition readiness (Dulka & Maler, 1994).

The mechanisms of sexual selection promote the emerging and fixation of dimorphic characters through the choice of males by females and the competition between males or vice-versa (Rapp Py-Daniel & Cox-Fernandes, 2005). Among species of gymnotiforms there are reports of sexual dimorphism in the EOD waveform, duration and/or repetition rate during the reproductive period allowing individuals a greater reproductive success since this secondary sexual character is preferred by the opposite sex because it reinforces the honesty of the EOD as a viable condition of mates (Gavassa et al., 2012; Smith, 2013). In species such as *Brachyhypopomus pinnicaudatus,* males present a greater EOD amplitude and duration in one of the pulse phases which can become even more exaggerated during the night when they are more active and during courtship or egg-laying behavior (Hopkins et al*.,* 1990; Franchina & Stoddard, 1998; Silva et al., 1999) (Figure 3.). In other species of the family Apteronotidae, both females and males can present differences in the EOD repetition rate, waveform, and pulse duration (Smith, 2013). Surprisingly, in *Eigenmannia* and *Sternopygus* species occurs a "reverse" sexual dimorphism, where males present a decrease in the EOD repetition rate compared with females (Hopkins, 1972; Dunlap & Zakon, 1998) (Figure 3.).

Figure 3: Examples of sexual dimorphic EODs from some gymnotiform species



Source: Modified from Dunlap and Zakon (1998) and Stoddard (2009).

In Figure 3, at the top 4 species from the Hypopomidae family (pulse type fishes), where males present a greater second phase duration of the EOD. However, at the bottom, in the female specie from the family Sternopygidae (wave type fish) presents a greater EOD frequency and EOD pulse duration

4. CONCLUSSION

In this article we proposed to review the latest research regarding hormonal control in the reproduction process and EODs´ modulations in electric fish. We found that in Gymnotiformes, the reproductive cycle depends on environmental conditions such as pH, conductivity, water level and rainfall probably due to an increase in food resources and a decrease in predation. Overall, it seems these environmental conditions influence reproductive period determination more strongly than the degree of relationship between the taxa, being an adaptative condition instead of an inherited character. We also found a sort of consensus among authors that described the reproductive strategies of these fishes as "K-strategy" or "equilibrium strategy" due to the higher juvenile survivorship possibly because of greater parental investment in individual progeny. Also, from all the life history strategies reported in these papers, fractional spawning was the common, thus being consider as a general characteristic of the order Gymnotiformes. However, considering the lack of data on life history of gymnotiforms from the northern portion of their distribution – e.g., relative fecundity, first gonad maturation size, and duration of the reproductive period – the definition of reproductive patterns and strategies for all order representatives occurring in that region still needs further investigation. On the other hand, we found that in these electric fish steroid sex hormones play an important role in the induction of gametogenesis, but also, in the modulation of the temporal and spectral EOD parameters in a long-time basis possibly aiding in sex recognition during and courtship behavior at maturity. Finally, due to the ecological and biological importance of these electric fish for the sustainability of the Amazon region it is imperative that more studies turn their focus on reproduction and EOD communication properties to better understand their adaptive response to environmental variation within this region and the reproductive strategies they engage on.

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