Tracking activity patterns of a multispecies community of gymnotiform weakly electric fish in their neotropical habitat

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Abstract

Being able to track animal movement and interactions in their natural habitat is fundamental to understanding their ecology and evolution. And yet, tracking the behavior of freely roaming and untagged animals in natural environments is notoriously challenging. Weakly electric fish with their continuously active, individual-specific electric organ discharge (EOD) are ideal subjects for monitoring undisturbed individual behavior. We here present automated, EOD-based tracking methods that allow for discerning presence and movement of multiple fish simultaneously. Applying our technology for monitoring a multispecies community of wave-type weakly-electric fish in their natural habitat in Darién, Panamá (*Apteronotus rostratus*, *Eigenmannia humboldtii*, and *Sternopygus dariensis*), we found consistent upstream movements in all three species after sunset followed by downstream movements in the second half of the night. Extrapolating these movements and using estimates of fish density obtained from additional transect data, we hypothesize that some fish might cover at least several hundreds of meters of the stream per night. Most fish, including *Eigenmannia*, were traversing the electrode array solitarily. From *in-situ* measurements of the decay of the EOD amplitude with distance of individual animals we estimated that fish can detect conspecifics at a distance of up to approximately 1.7 m for *Apteronotus* and 2.5 m for the two other species. Our recordings also emphasize interactions of the electric fields between the three species resulting in complex electrosensory scenes. EOD-based tracking provides an unprecedented window into the so-far hidden life history of weakly electric fish and makes it possible to study their behaviors at an unmatched level of detail.

Summary statement

Electrode arrays combined with automated data analysis allow to continuously track movement patterns and to deduce the complexity of electrosensory scenes of weakly electric fish in their natural neotropical habitats without tagging.

Introduction

Recent advances in high-precision technologies for tracking behaving animals allow for a new level of high-throughput studies in the neurosciences (Anderson and Perona, 2014; Egnor and Branson, 2016; Gomez-Marin et al., 2014; Mathis et al., 2018) as well in the fields of ecology and animal behavior (Dell et al., 2014; Hughey et al., 2018). Tracking animals in natural environments, however, still is notoriously difficult: the size and complexity of natural, cluttered environments are challenging for video-based techniques (Dell et al., 2014). Many studies have applied animal-mounted antennae, senders or loggers, such as GPS loggers, that have been used, for example, on baboons, storks, and even insects (Strandburg-Peshkin et al., 2015; Flack et al., 2018; Menzel et al., 2005), or acoustic emitters for large fish that are then tracked via hydrophones (Baktoft et al., 2015). In addition to tracking identity and movements, communication signals or physiological parameters are of interest and usually require additional sensors to be mounted on the animal (Cvikel et al., 2014), or to be distributed in the field (Rodriguez-Munoz et al., 2010).

Weakly electric fish provide a unique possibility for monitoring identity, movements, and communication signals without disturbing the fish by recording their electric organ discharges (EODs; Fig. 1 A, Kirschbaum, 1983; Meyer et al., 1987) by means of an electrode array in their natural habitats in neotropical streams (Fig. 1 B–E, Henninger et al., 2018). The EOD is an integral part of an active electrosensory system that the fish use for detecting prey (Nelson and MacIver, 1999), navigation (Fotowat et al., 2013), and communication (Smith, 2013). Little is known about behaviors of these fish in their natural habitats. A few exceptions are non-quantitative observations on activity patterns (Lissmann and Schwassmann, 1965; Steinbach, 1970; Friedman and Hopkins, 1996) and group hunting (Arnegard and Carlson, 2005).

As early as 1985, Hagedorn and Heiligenberg suggested to use electrode arrays for monitoring the cryptic behavior of weakly electric fish. Only recently has the great potential of tracking identity, movements, and communication signals by recording EODs been acknowledged and tested in the lab (Jun et al., 2013; Matias et al., 2015) and in the field (Madhav et al., 2018; Henninger et al., 2018). The frequency of electric organ discharges (EODf) in wave-type fish is species- and individual-specific and, in constant environments, remains remarkably stable over many hours and days (Bullock, 1970; Moortgat et al., 1998), providing individual frequency tags ideally suited for tracking individual fish. Data recorded with an electrode array in the field revealed unexpected insights into the courtship behavior and its electrosensory implications of the brown ghost knifefish, *Apteronotus rostratus* (Henninger et al., 2018).

Here, we first quantified the performance of our automated approach for EOD-based tracking of electric fish in the field (Henninger et al., 2018). Sensitive electrodes distributed in the habitat picked up frequency and amplitude of the EODs of close-by weakly electric fish (Fig. 1 B, E). From the recorded signals (Fig. 1 F), we were able to infer identity and movement of multiple individuals without having to tag or disturb them. The performance of three algorithms for position estimation were compared using data obtained in the lab and with simulations. We then applied this technology to continuously monitor a multi-species community of weakly electric fish in a small stream in Darién, Panamá over more than 24 hours, and to quantify individual EOD characteristics, activity and movement patterns.

Results

Identification of individual electric fish by EOD frequency

Individual wave-type fish differ in the frequency of their EODs. Extracting the EOD frequency (EODf) from the raw data thus allows identification of individual fish. This conceptionally simple task is complicated by the fact that in general more than a single fish is picked up by an electrode (Fig. 1 F). Furthermore, because EOD waveforms of wave-type fish are distorted sine waves, the resulting frequency spectra of individual fish contain harmonics, i.e., peaks at multiples of the fundamental EODf. Together this results in complex frequency spectra where peaks originating from individual fish are intermingled (Fig. 2 A, B).

We solved this problem by analyzing the frequency spectra for periodically occuring peaks (i.e., harmonics,

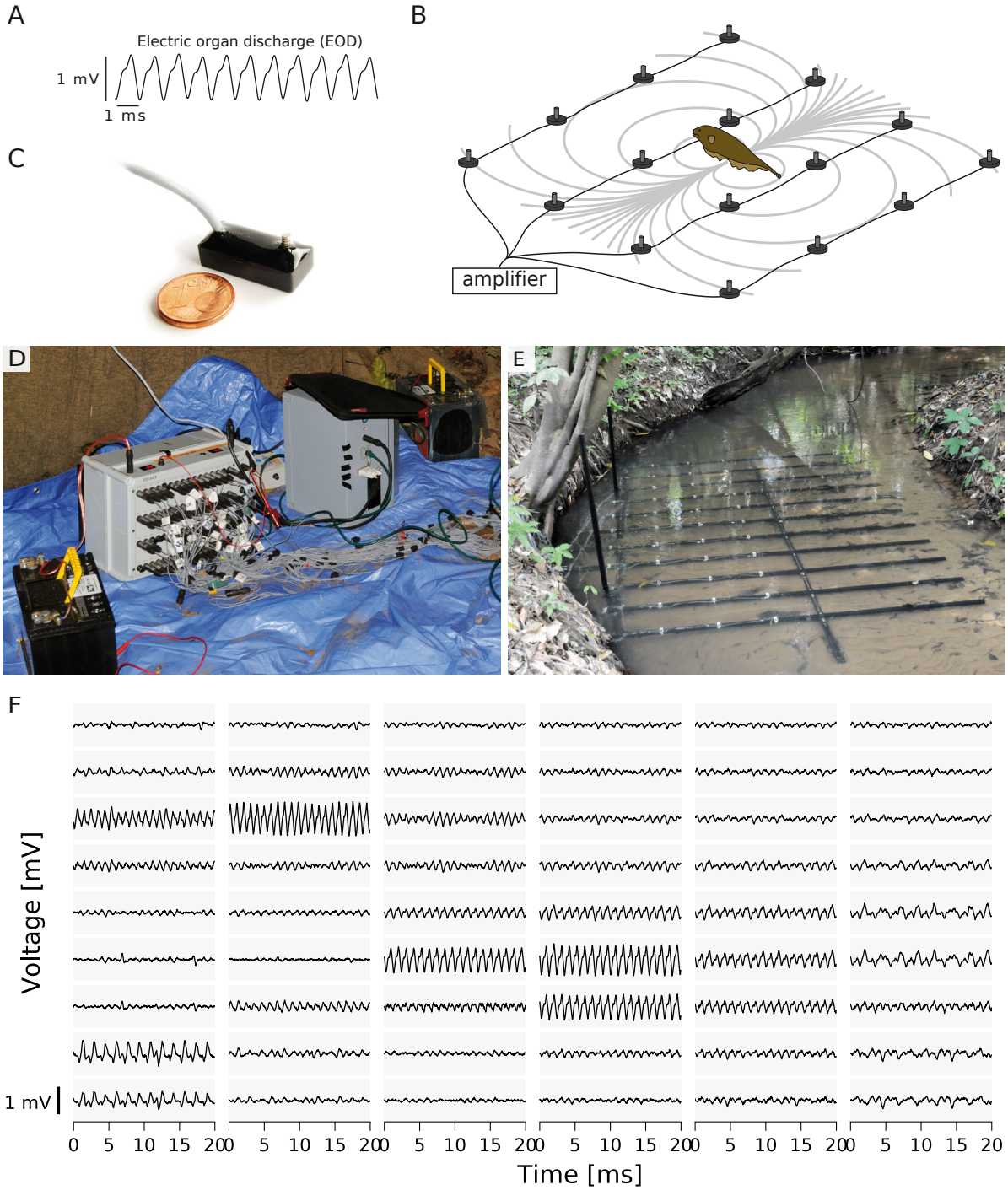

Figure 1: Recording electric fish in their natural habitat. A) Quasi-sinusoidal EOD waveform of *A. rostratus* ($\sim 580 - 1100$ Hz). B) The EOD generates a dipolar electric field (gray isopotential lines) that we recorded with an electrode array. C) Electrode headstage. The actual electrode is the stainless-steel screw. D) 64-channel amplifier (gray box to the left) and recording computer (right box) powered by two car batteries (black with yellow handle). E) The electrode array at our recording site in a small stream in Darién, Panamá. White plastic holders keep the headstages (C) in place. Electrodes were positioned partly beneath the undercut banks, allowing to record electric fish hiding and interacting deep in the root masses. F) Raw electrode data. Each of the 54 gray boxes shows the recorded voltage of one of the electrodes as they are arranged in the grid. Three *A. rostratus* are concurrently present, a low-frequency female (lower left) and two high-frequency males (upper left and center). The EOD of each fish is captured simultaneously by multiple electrodes.

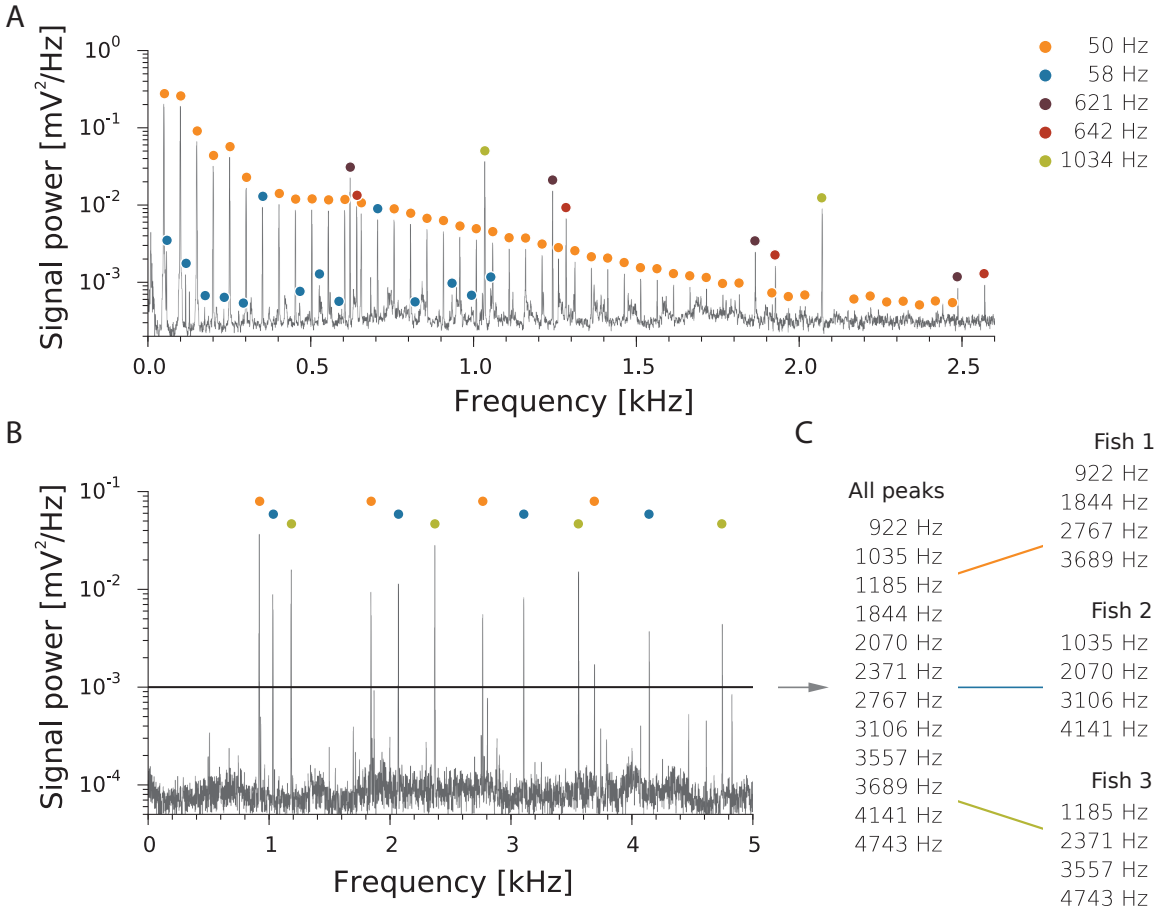

Figure 2: Extraction of fundamental EOD frequencies from power spectra. A) Example power spectrum of the signal from one electrode of the array recorded in Darién, Panamá. The EODs of five concurrently present electric fish of two species clutter the power spectrum with many intermingled peaks. Two low-frequency *Sternopygus dariensis* marked with orange and blue dots (< 200 Hz) and three high-frequency *Apteronotus rostratus* (> 580 Hz, purple, red, and green dots) can be extracted from the power spectrum. Detected EODs are displayed on the right. Colored markers indicate the EODs' harmonic structures. B) Power spectrum of the EODs of three concurrently present *Apteronotus*. C) Peak detection generates a list of prominent frequencies (left), which are sorted into groups of fundamental frequencies with their harmonics (right). The power spectra of A and B are based on different recording sequences.

Fig. 2 A, B) and assigning them to individual fish (Fig. 2 B, C, see methods). In a next step, individuals detected on single electrodes were matched with those of similar fundamental frequencies found on other electrodes, and finally matched over sequential time steps to generate temporal consistency. This algorithm allowed us to robustly and automatically analyze large datasets containing the EODs of many electric fish from different species.

Dipole-like far-field of EODs

Crucial for studying electric fish behavior and their interactions is knowledge about each individual's position and movement over time. For determining effective layouts of the electrode array and for choosing a suitable localization approach, we extended previous studies (Heiligenberg, 1973; Knudsen, 1975; Rasnow et al., 1993; Rasnow and Bower, 1996) and measured the electric field's amplitude distribution of an *Apteronotus albifrons* over longer distances in a large rectangular outdoor tank. As expected, the measurements resembled the field created by an electric dipole (Fig. 3). The EOD amplitude was attenuated with distance from the electric fish and was modulated as a function of the angle relative to the body axis of the fish. A modified dipole, Eq. 3, fitted to the data resulted in a good description of the measured EOD amplitudes (Fig. 3 B) with exponent $q = 1.63$ and amplitude

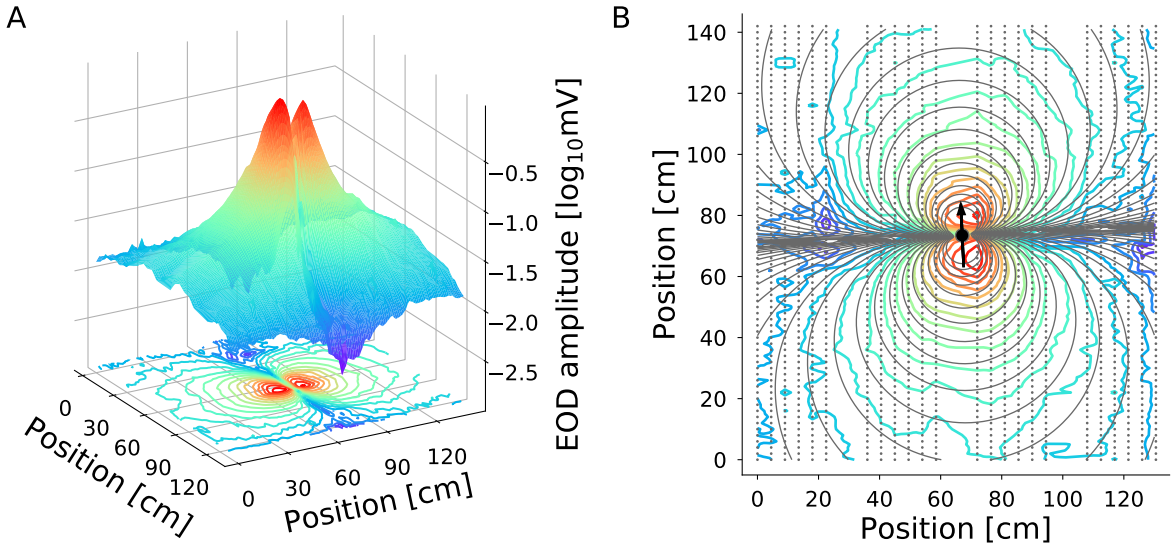

Figure 3: Spatial amplitude distribution of the EOD's electric field potential of an *A. albifrons* measured in a large tank in the horizontal plane. The data was assembled from 108 sequential measurements. A) Absolute values of the measured EOD amplitude. B) Dipole model (gray lines) fitted to the data shown in A. The fish is located at the center and is oriented upwards (arrow).

factor $P = 29\,\mathrm{mV\,cm}^q$.

EOD-based localization of electric fish

Next, we evaluated the performance of three algorithms for estimating fish position. A simple estimate of 2D fish location and orientation was based on a spatial average of electrode positions weighted by the EOD amplitudes measured at the electrodes. In one version we used all available electrodes to compute the fish location, and in another version only the four electrodes with the largest EOD amplitudes. The third method fitted a dipole model Eq. (3) to the measured EOD amplitudes.

When applied to the measurements from Fig. 3 where the fish is positioned in the center and at the vertical level of the electrode grid (inter-electrode distance: 30 cm), all three estimators performed reasonably well with median position errors of about 5 cm (Fig. 4 A). Increasing the distance between electrodes to 108 cm resulted in a minor increase of the median estimation error to about 10 cm.

In reality, however, fish swam not only at the center of the electrode array. We therefore tested the performance of the three position estimators in simulations in which we varied the static position, orientation, and level above the electrode array as well as the electrode spacing (Fig. 4 B). Fitting the dipole model required narrow electrode spacing and performance deteriorated dramatically for fish swimming outside the plane of the electrode array. Using data from all electrodes of the array for the weighted spatial-average estimate resulted in errors of the same size as the electrode spacing. Only when using the four electrodes with the largest EOD amplitudes was the position estimate of the weighted spatial average largely independent of the level above the electrode array and the error was much smaller than the electrode spacing — although this estimate does not relate to the underlying physics of the electric field. We therefore used this measure for all further analysis.

Position and orientation estimates of moving fish

We also studied how position estimation performs with moving fish. A fish moving with a speed of 10 cm/s (Nelson and MacIver, 1999) along a circular trajectory was simulated. Again, the median of the position errors was clearly below 10 cm (Fig. 5 A), which corresponds to the length of a small-sized, mature *Apteronotus rostratus* (Meyer et al., 1987). Likewise, the medians of the orientation errors were small and well below 15°. The weighted spatial

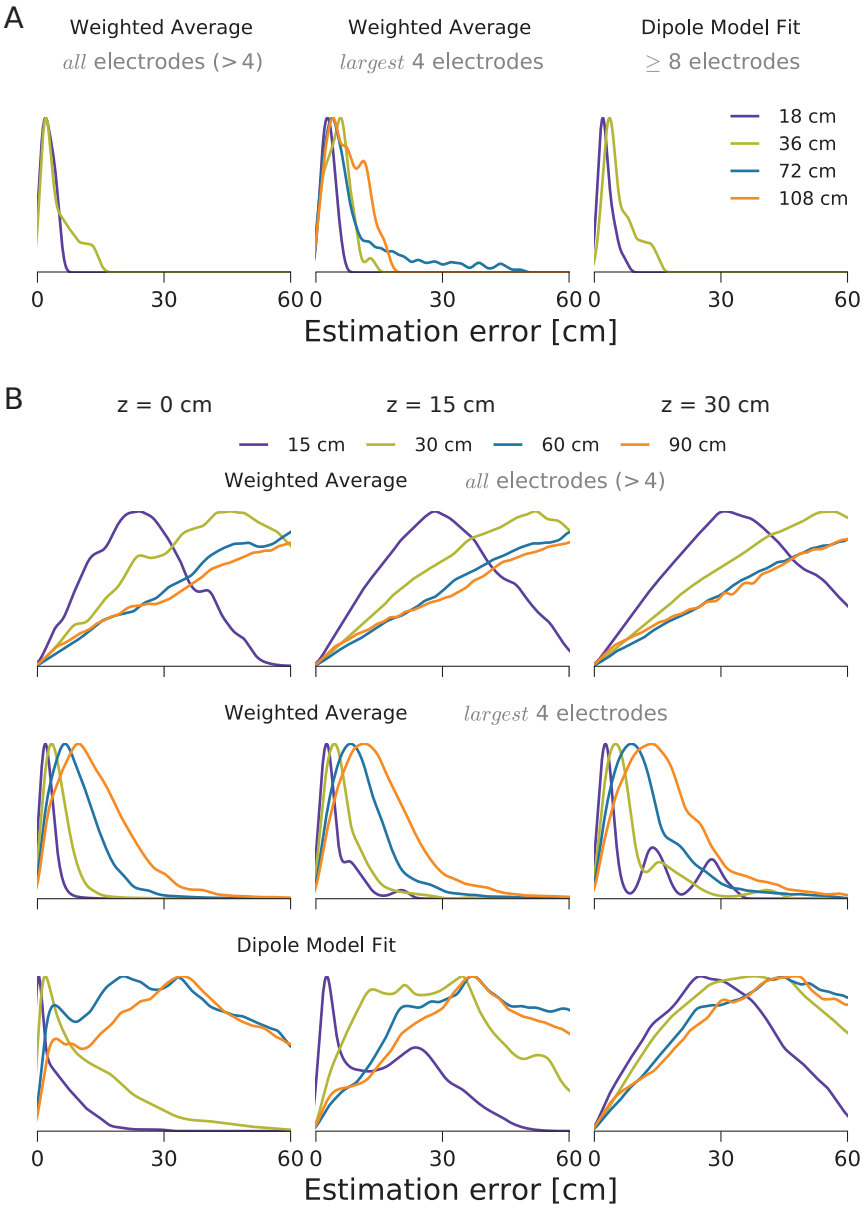

Figure 4: Evaluation of the performance of three algorithms for position estimation. A) The distribution of localization errors for different electrode spacings and algorithms applied to the *A. albifrons* data measured in a big tank (Fig. 3). B) Distribution of localization errors computed from simulations for three different levels of the true fish location above the plane of the electrode array (columns). Only the weighted average taken over the four electrodes with the largest power consistently resulted in the smallest localization errors that stayed well below the electrode spacing.

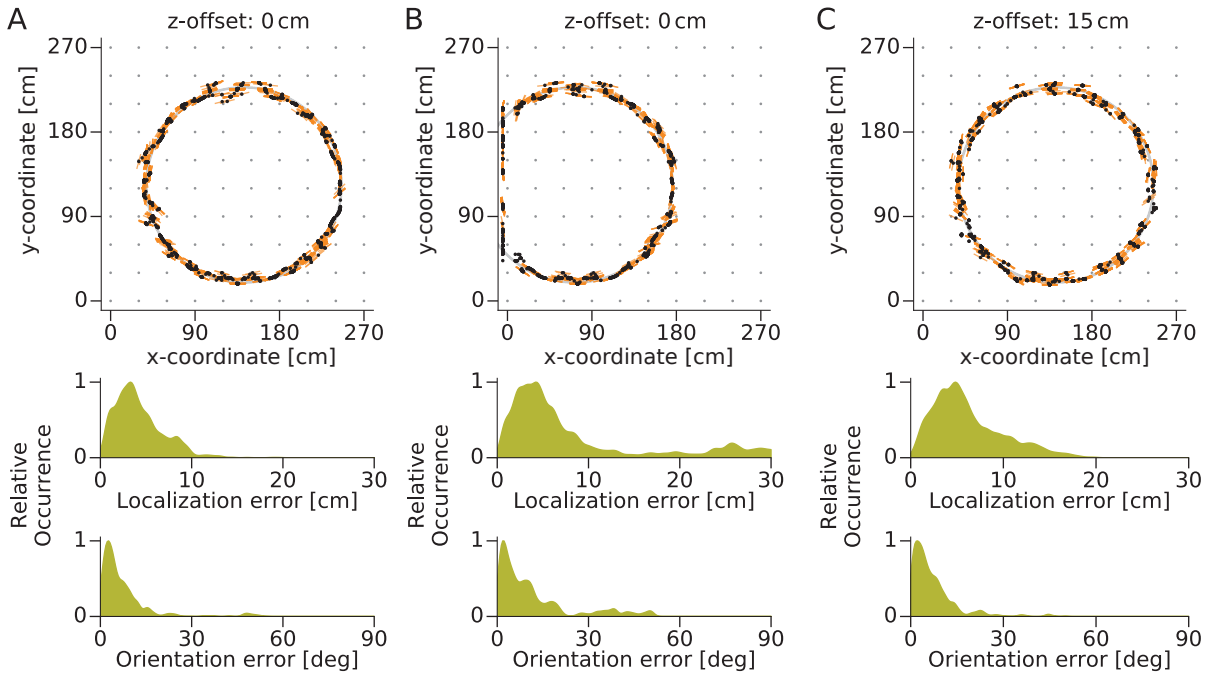

Figure 5: Performance of position and orientation estimates of simulated moving fish. Top: The estimated, non-smoothed 2D-locations (black dots) and orientations (orange lines) were compared to the simulated fish locations (gray line) and orientations. Center and bottom: Distributions of errors in the estimation of localization and orientation. A) Simulated movement on level with the electrode array. B) Movement on level with the electrode array, but partially outside of the array. Errors include the difference to the known fish location and orientation for the time period the fish moves outside the array. C) Simulated movement 15 cm above the electrode array.

average was unable to follow fish positions outside the boundaries of the electrode array. Therefore the error of the position estimate increased as soon as the fish trajectory extended beyond the electrode array (Fig. 5 B). For fish trajectories vertically offset from the grid plane, the median and spread of the localization error slightly increased, while the orientation error remained almost unchanged (Fig. 5 C). In summary, the simulations demonstrated that the algorithm computing a spatial average of the four electrodes with the largest signal was suited for tracking electric fish moving within the electrode array's limits with uncertainty below an adult fish's body length.

With the hardware and the analysis techniques in place, let us now turn to the results obtained from the data recorded in a stream in Darién, Panamá.

Diurnal activity patterns

The spectrogram obtained from 25 hours of almost continuous recording demonstrates the richness and complexity of frequencies present in a natural habitat of gymnotiform weakly electric fish (Fig. 6 A). Extracting the fundamental frequencies allowed for assessing the presence of species and of individual fish over the course of the recording (Fig. 6 B). In this example we registered 461 EOD detections, i.e. fundamental frequencies that were tracked in a row with possible interruptions of less than 10 s. The number of detections was likely higher than the total number of individuals, because the same fish may have left and reentered the recording area over the course of the recording.

A histogram of the frequencies of the EOD detections revealed three distinct frequency ranges corresponding to three wave-type species (Fig. 6 C): *Apteronotus rostratus* occupied the highest frequencies from ~ 580 to 1100 Hz. Right below were *Eigenmannia humboldtii* between ~ 200 and 580 Hz. *Sternopygus dariensis* covered the lowest frequencies ($\sim 40 - 220$ Hz) and shared its frequency range with the pulse-type fish *Brachyhypopomus occidentalis*. We confirmed this classification by inspection of the EOD waveforms.

The number of EOD detections per 15 minute time bin was on average significantly larger during the night than during the day ($p = 1.1 \times 10^{-22}$, Welch's t-test; Fig. 6 D), directly demonstrating the nocturnal activity of weakly

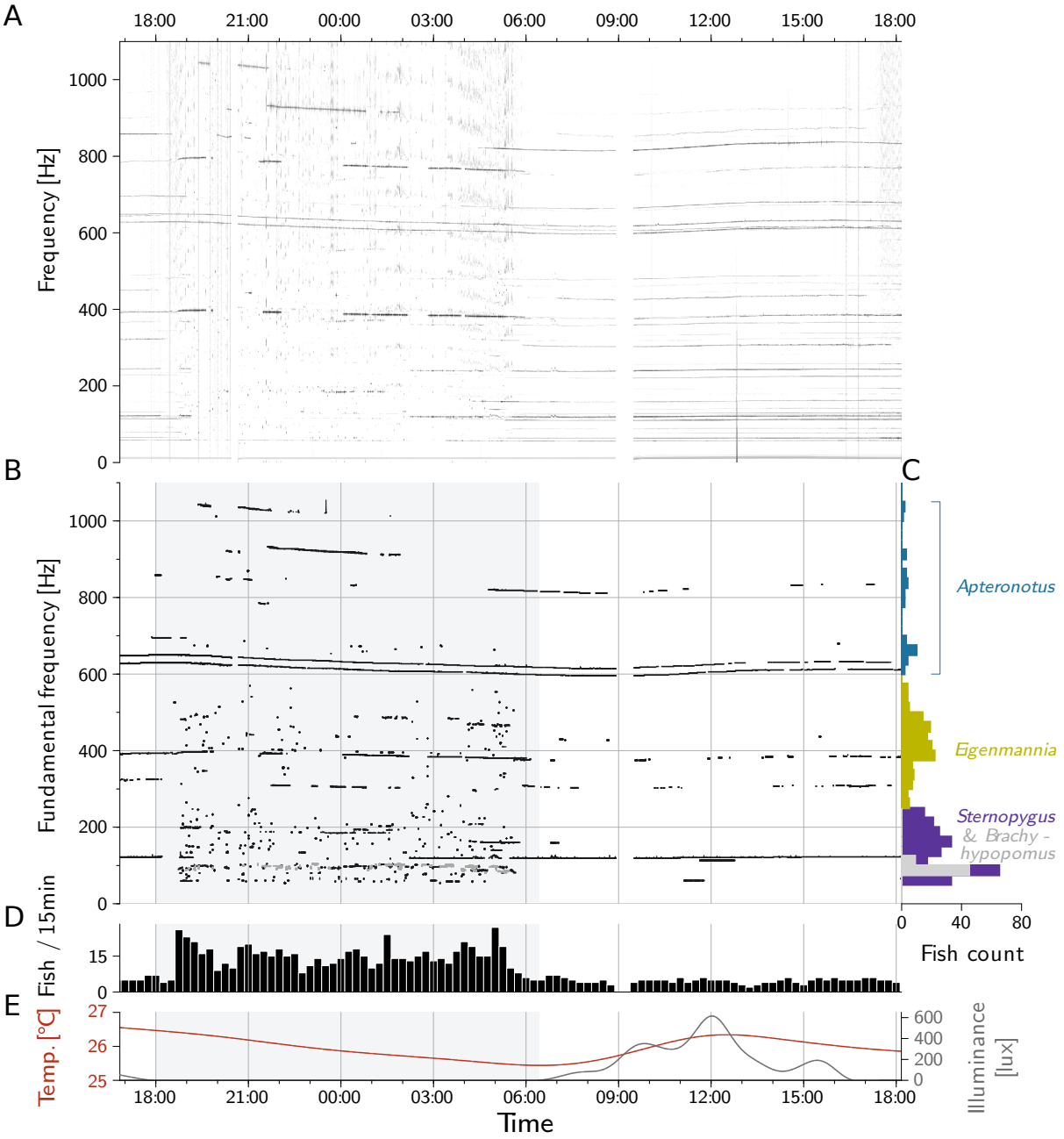

Figure 6: Electric fish tracked continuously over 25 hours (2012-05-10 to 2012-05-11). A) Spectogram of the 25 hours of EOD recording. Spectrograms of all 54 channels were merged. B) Fundamental frequency traces extracted from the recording. Each dot and horizontal line indicates the fundamental frequency trace of an individual detected electric fish. C) Histograms of the EODfs shown in B separated into species. D) Temporal histogram of fish detections. Bin size is 15 minutes. D) Water temperature (red) and light levels (gray) during the recording period. Gray rectangles indicate nighttime. The interruption of the recording at 9 am was due to a switch of car batteries needed to power the setup.

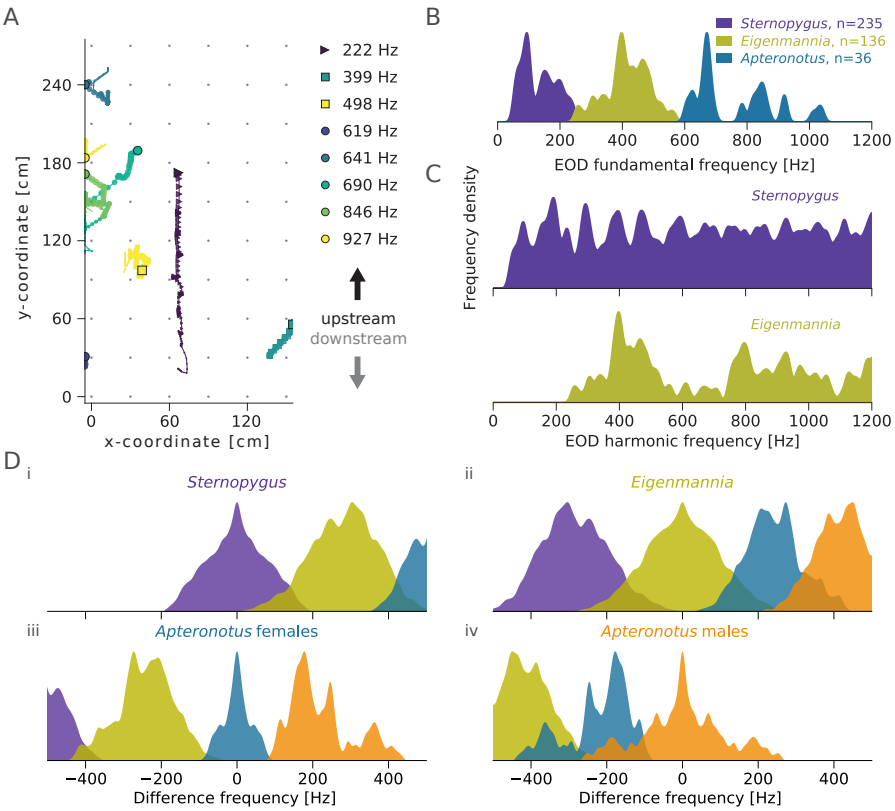

Figure 7: EOD interactions arising in a multispecies community of gymnotiformes. A) Example of concurrently present individuals of three sympatric species of electric fish recorded in the field. Legend indicates species and EOD fundamental frequency (triangle: *Sternopygus dariensis*, squares: *Eigenmannia humboltii*, circles: *Apteronotus rostratus*), tails indicate positions of the last 5 seconds. B) Histograms of fundamental EOD frequencies. Same as in Fig. 6 C, but histograms of each species are normalized to their respective maximum value. C) Histogram of presence of fundamental EOD frequencies and their harmonics demonstrate that harmonics of lower frequency species like *Sternopygus* and *Eigenmannia* extend well into the frequency ranges of higher frequency fish. D) Histograms of difference frequencies computed as the difference between all fundamental EOD frequencies of one species (colored histograms) and the fundamental EOD frequencies of another species (indicated by the title of the panels). Because of the considerable overlap between the histograms, it seems unlikely that the fish can differentiate between species based solely on EOD frequency differences.

electric fishes (see illumination levels in Fig. 6 E). EOD frequency is known to be sensitive to water temperature (e.g., Dunlap et al., 2000). Therefore, diurnal changes in EOD frequency were expected given the temporal variation in water temperature (e.g., the two fish right above 600 Hz in Fig. 6 E).

Multispecies EOD interactions

When looking at the reconstructed movements of individual fish, we found many scenes in which fish of different species were simultaneously present and in close proximity of each other (Fig. 6 B,Fig. 7 A). The simultaneous presence of three wave-type species gave rise to complex interactions of their EOD waveforms.

First, harmonics of EODs with significant power easily extended into the frequency bands of species with higher fundamental frequencies. For example, the harmonics of an *Sternopygus* were, at times, of similar power as the fundamental frequencies of *Apteronotus* (Fig. 2 A). Whereas the fundamental frequencies of the three wave-type electric fish species were separated (Fig. 7 B), the harmonics of the lower-frequency fish *Sternopygus* and *Eigenmannia* clearly extended into the frequency range of the respective higher-frequency fish, i.e. *Eigenmannia* and *Apteronotus* (Fig. 7 C), where they could superimpose with the fundamental frequencies.

Second, the superposition of the EODs of two fish results in a beat, a periodic amplitude modulation, which is encoded by the electrosensory system (Bastian, 1981). The frequency of the beat is given by the the difference be-

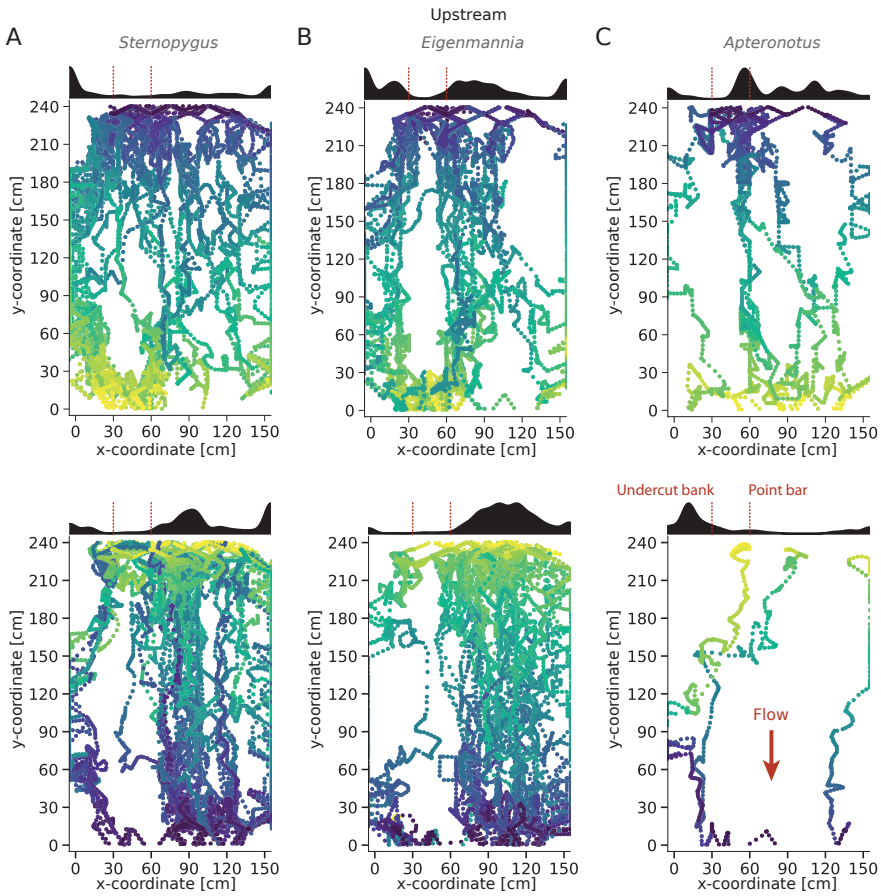

Figure 8: Trajectories of directed movements in the field. Top panels: upstream movements, bottom panels: downstream movements. A) *Sternopygus dariensis*, B) *Eigenmannia humboldtii*, C) *Apteronotus rostratus*. Color encodes relative time between entering (purple) and leaving (yellow) the recording area. Shown are trajectories of all 173 directed movements extracted from the 25 hour recording shown in Fig. 6. Movement traces have been smoothed with a running average (width=200 ms). Water flows from top to bottom (arrow in C). Histograms on top of the panels show distribution of the x-coordinate of the traces for the central 60 cm $< y <$ 120 cm. Red vertical lines separate regions: undercut bank, main channel, point bar.

tween the fundamental EOD frequencies of the two fish. In contrast to the absolute fundamental EOD frequencies, these frequency differences are ambiguous, i.e. they cannot be used by an individual fish to unequivocally determine the species of another fish. For example, a positive frequency difference perceived by a *Sternopygus* could have been induced by another *Sternopygus* or by a low-frequency *Eigenmannia* (Fig. 7 Di). Negative frequency differences perceived by an *Apteronotus* male could have been induced by either a rivaling male, a conspecific female, or even an *Eigenmannia* (Fig. 7 Div).

Movement patterns

The ability to track individual movements enabled us to study species-specific movement patterns. Many of the detected fish stayed only for a short time within the electrode array (Fig. 6 B). In fact, they often simply swam straight through the array. From the 461 electric fish detections over 25 hours, a subgroup of 173 detections showed directed movement, i.e. a fish entered the electrode array on one end and left it at the opposite end in less than one minute (23 ± 10 s; range: 10 to 58 s), either with or against the direction of water flow (Fig. 8).

Movement activity set on sharply after nightfall. Individuals of all species had a strong tendency to move upstream in the first half of the night and downstream in the second half, a pattern most pronounced in the larger populations of *Sternopygus* and *Eigenmannia* (Fig. 9 A). Most fish were swimming solitarily through the grid. Only 8 % of 98 *Sternopygus* detections, 6 % of 65 *Eigenmannia* and none of 10 *Apteronotus* were swimming

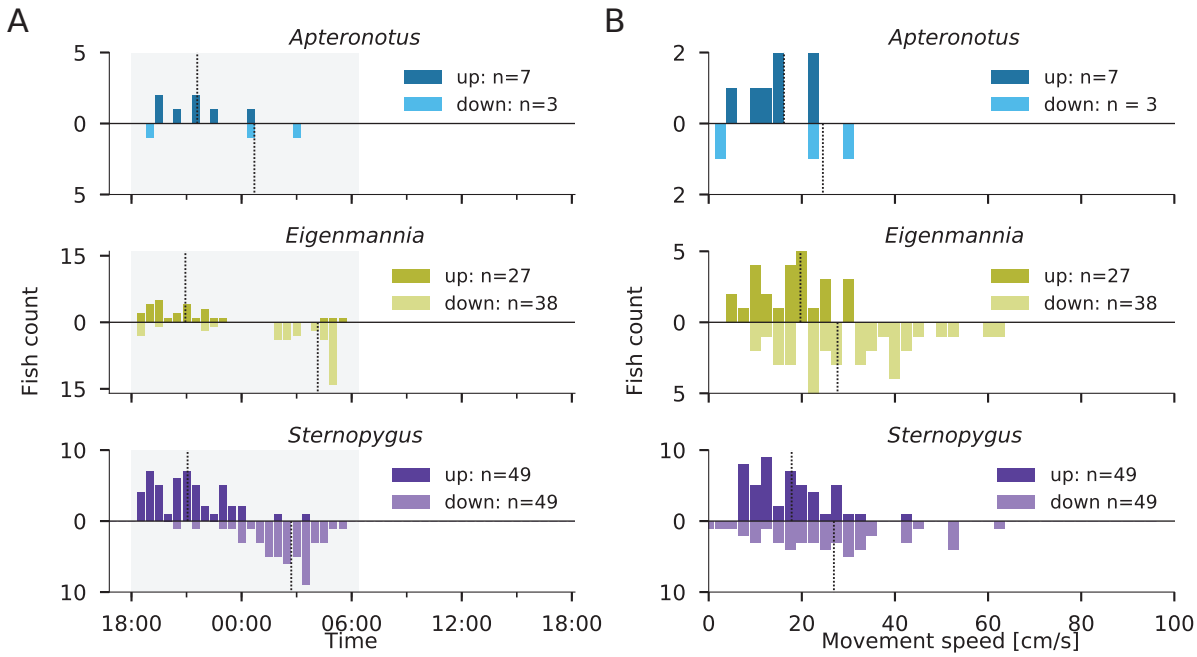

Figure 9: Statistics of directed movements of wave-type fish species. A) Time of occurrence of directed upstream and downstream movements of *Apteronotus*, *Eigenmannia*, and *Sternopygus*. The fish tended to swim upstream during the first half of the night and downstream in the second half. Nighttime is indicated by the gray background. B) Corresponding average movement speeds along the y-coordinate of the electrode array. Dashed lines indicate median times and speeds. Histograms are based on the trajectories shown in Fig. 8.

simultaneously with a conspecific into the same direction through the electrode array.

Upstream swimming *Sternopygus* and *Eigenmannia* showed a preference to swim along the root masses (on the left side of each panel of Fig. 8): 39 % of 49 *Sternopygus* (Poisson test: $p < 0.01$) and 26 % of 27 *Eigenmannia* ($p = 0.18$) moving upstream stayed within 30 cm of the undercut bank. In contrast, 92 % of 49 *Sternopygus* ($p \ll 0.001$) and 95 % of *Eigenmannia* 38 ($p \ll 0.001$) moving downstream stayed farther than 60 cm away from the undercut bank, preferring the point bar inside the meander bend. Neither up- nor downstream swimming fish where swimming in the main channel between 30 to 60 cm from the undercut bank ($p < 0.01$ for *Sternopygus* and *Eigenmannia*).

We quantified the average movement speeds along the stream (y-coordinate of the electrode array) of the tracked individuals (Fig. 9). *Sternopygus*, *Eigenmannia*, and *Apteronotus* were moving upstream with a median speed of $v_{up} = 17.8$, 19.7, 16.2 cm/s, respectively. Later in the night they were swimming downstream with $v_{down} = 26.9$, 27.7, 24.5 cm/s, respectively. Neither in the first nor the second half of the night did we find significant differences between the median times or the median swim speeds of the three species (Mann-Whitney U-tests with Holm-Bonferroni correction, $p > 0.05$). Upstream movements were slower than downstream movements for all species (Mann-Whitney U-tests: *Sternopygus*: $u = 686$, $p < 0.001$, *Eigenmannia*: $u = 222$, $p \ll 0.001$, *Apteronotus*: $u = 9$, $p = 0.41$), suggesting a distinct influence of the stream's water flow on swim speed. From the median upstream and downstream swim speeds the water velocity Eq. (4) could be estimated to be about $v_{stream} = 4.2$ cm/s, which is at the low end of water velocities of lowland streams (Crampton, 1998). The average swim speeds Eq. (5) of the three species relative to the water can also be deduced: *Sternopygus*: $v_{fish} = 22$ cm/s, *Eigenmannia*: $v_{fish} = 24$ cm/s, *Apteronotus*: $v_{fish} = 20$ cm/s.

Based on the median speeds and times and assuming that the fish were continuously swimming upstream and then back downstream with constant speed and no interruptions by foraging, mating, etc., the maximum distances the fish could have traveled upstream within one night were 2.2 km, 3.0 km, and 1.1 km for *Sternopygus*, *Eigenmannia*, and *Apteronotus*, respectively. On the other hand, we found approximately 15 fish of each species hiding in root masses during the day per 100 m of stream, as measured along a 160 m long transect directly upstream of the

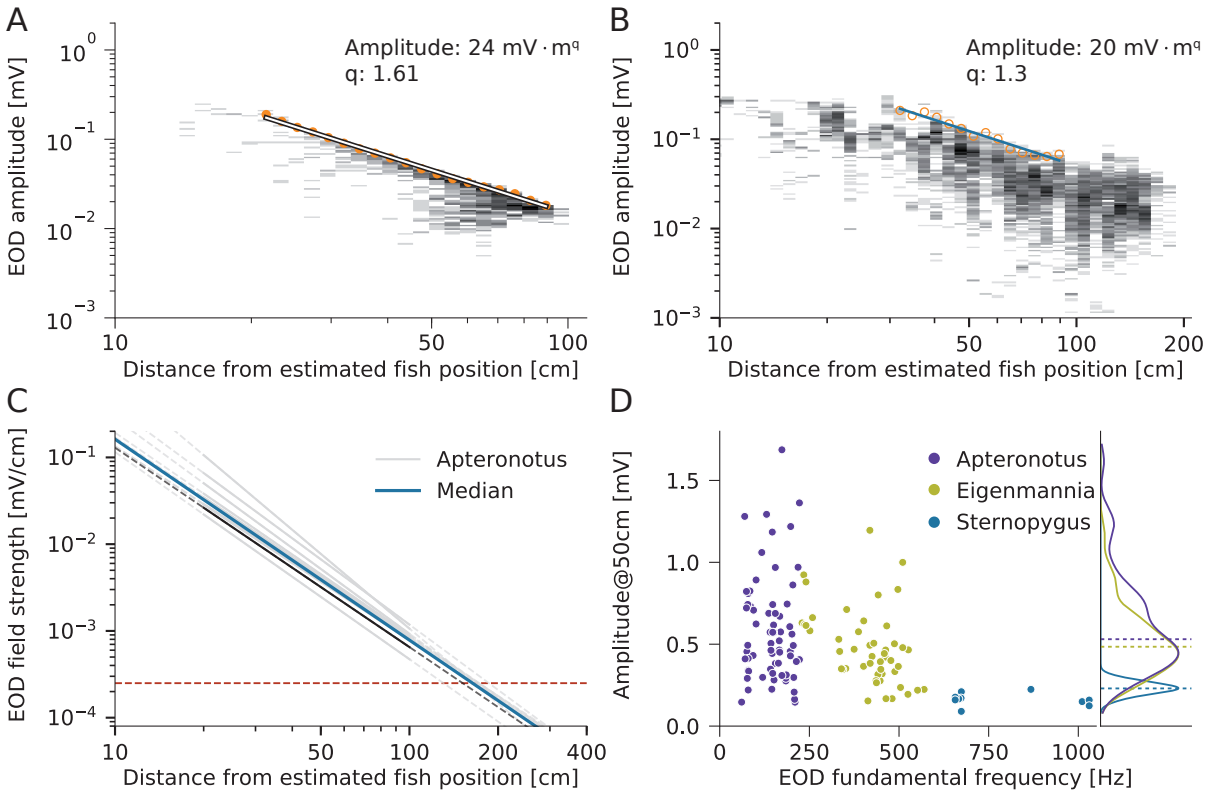

Figure 10: Estimation of EOD amplitude and its decay over distance. A) 2D-histogram of measures of EOD amplitudes obtained from all electrodes at various distances from the *A. albifrons* measured under controlled conditions in a tank (Fig. 3). Orange markers represent the mean of the largest 20% of EOD amplitudes per distance bin and were fitted with a power law function, Eq. (3) (line). B) 2D-histogram of EOD amplitudes for an example *A. rostratus* male (EOD$f = 1030$ Hz) tracked in the field. The largest 5% of EOD amplitudes per bin were used for the estimate (blue). C) EOD field strength, the gradient of the EOD amplitude, for the twelve *A. rostratus* from Fig. 9 (short lines; black: estimate from B, median in blue) with behavioral detection threshold (red horizontal dashed line). D) EOD amplitude estimates versus corresponding EOD frequencies for all three species. Histograms to the right show corresponding distributions of the EOD amplitudes, dashed lines indicate medians. *Sternopygus*: $n = 69$, *Eigenmannia*: $n = 49$, *Apternonotus*: $n = 10$.

electrode array. Thus, the number of fish we observed traversing the electrode array upstream in one night (Fig. 9) likely came from at least 330 m (*Sternopygus*), 180 m (*Eigenmannia*), and 50 m (*Apteronotus*) of stream adjoining our electrode array. However, as some fish appeared to be quite stationary within or close to our electrode array even at night (Fig. 6 B), traversing fish were likely recruited from longer stretches of the stream. Thus, the true distances covered by the moving fish in one night likely lie between several hundred meters and a few kilometers.

EOD field characteristics

An important aspect of electric fish interactions are the effective signal intensities occuring during these interactions, which are determined by the individual EOD amplitudes and their spatial distribution. The distribution of EOD potentials over the electrode array (Fig. 10 A, B) allowed us to infer the EOD amplitude and the exponent of the power-law decay *in situ*.

For the example of *A. albifrons* recorded in a large outdoor tank, the estimated exponent $q = 1.61$ is similar to the one obtained by fitting the dipole potential based on Eq. (2) to the data ($q = 1.63$, Fig. 3 B). For the fish traversing the electrode array (Fig. 8 and Fig. 9), the exponents of the power-law decay of EOD amplitude with distance were on average $q = 1.34 \pm 0.24$ and did not differ significantly between the three species (Mann-Whitney U-tests, $p > 0.25$).

The quantity that is measured by electroreceptor organs is the electric field, Eq. (7), i.e. the spatial derivative

of the electric field potential (Fig. 10 C). Considering the known sensitivities of the electrosensory system for the closely related *A. albifrons* based on behavioral studies (0.5 μV/cm peak-to-peak ampltitude at 100 μS/cm, Knudsen, 1975), we estimated the effective detection range of *A. rostratus* from the field data according to Eq. (8) to 166 ± 14 cm ($n = 10$) under the encountered natural conditions (Fig. 10 C). Similarly, we estimated the detection ranges for *Sternopygus* and *Eigenmannia* under the same conditions and using the same sensitivity (Fleishman et al., 1992; Knudsen, 1974, 1975) to be 255 ± 76 cm ($n = 97$) and 253 ± 54 cm ($n = 64$), respectively.

Our approach allows to compare EOD amplitudes within and across species. Usually, EOD amplitude is measured between a pair of electrodes positioned at the head and the tail of the fish. Since we did not know how large the fish were, we used the EOD amplitude at a distance of 50 cm computed from Eq. (2) as a robust measure for each fish's EOD amplitude. The calculated EOD amplitudes were broadly distributed within each of the three species of wave-type weakly electric fish (*Sternopygus*: 0.47 ± 0.30 mV; *Eigenmannia*: 0.46 ± 0.23 mV; *Apteronotus*: 0.16 ± 0.04 mV, Fig. 10 D). Whereas *Sternopygus* and *Eigenmannia* had similar EOD amplitude distributions (Mann-Whitney U-test $p > 0.31$), *Apteronotus* EOD amplitudes were clearly smaller than the former (Mann-Whitney U-test $p \ll 0.001$). Only *Eigenmannia* showed a negative correlation between EOD amplitude and EODf (Pearson's $r = -0.28$ and $p = 0.03$, *Sternopygus*: $r = 0.14$, $p = 0.17$; *Apteronotus*: $r = -0.13$, $p = 0.72$).

Discussion

We developed a new technology for tracking undisturbed and untagged individual wave-type electric fish based on their own, continuously active EOD. This technology was applied to track the movements of three species of gymnotiform electric fish in their natural habitat during breeding season and to characterize individual electric field properties. We quantified the population's nocturnal activities and revealed distinct movement patterns in the three monitored species.

EOD-based individual tracking

Video tracking of behaving animals is well established for laboratory setups and allows for high throughput screening (Anderson and Perona, 2014; Mathis et al., 2018). Yet, video-based methods commonly rely on high contrast images and unobstructed line-of-sight, which make them challenging to use in natural habitats (Dell et al., 2014). Recent advances in miniaturization make loggers and transmitters attached to the animals an interesting opportunity for studying behavior in the wild (Cvikel et al., 2014; Krause et al., 2013; Strandburg-Peshkin et al., 2015; Flack et al., 2018). However, this approach requires to catch and recatch the animals in order to attach the logger and to retrieve the data. Importantly, it has been shown that tagging can have a negative impact on the animal's fitness (Saraux et al., 2011).

In contrast, EOD-based tracking exclusively relies on the fish's own, continuously emitted signals and therefore does not disturb the animals. This tracking approach allows for following individuals over time (Madhav et al., 2018), provides direct access to the fish's communication signals (Henninger et al., 2018), and excels in terms of sub-second temporal resolution and a decent spatial resolution of about 10 cm. However, physical interactions like mouth wrestling or tail nipping, which could easily be detected visually in the lab (Triefenbach and Zakon, 2008), are inaccessible and can only be inferred indirectly, if at all, from EOD signals, context, and movement dynamics.

Previously, observing activity of wave- and pulse-type electric fishes in natural habitats was based on transects recorded with single electrodes (e.g., Steinbach, 1970; Friedman and Hopkins, 1996). Small electrode arrays have so far been only used in controlled conditions in the lab (Jun et al., 2013; Matias et al., 2015) and for brief recordings in the field (Madhav et al., 2018). In our present study and in Henninger et al. (2018), we scaled this approach up to obtain data on natural behaviors of freely moving weakly electric fish in the field over extended periods of time.

Species-specific EOD frequencies

At our field site in Darién, Panamá, we found three sympatric wave-type species with quite well separated EODf ranges: two Sternopygidae, *Sternopygus dariensis* with EOD frequencies below 220 Hz and *Eigenmannia hum-*

boldtii at 200 – 580 Hz, and one member of the Apteronotidae, *Apteronotus rostratus*, with EODfs ranging from 580 Hz to 1100 Hz. A similar separation between *Sternopygus* and *Eigenmannia* was previously found in Guyana (Hopkins, 1974b), coastal Surinam (Hopkins and Heiligenberg, 1978), Rio Negro (Bullock, 1969; Steinbach, 1970), and Napo River in eastern Ecuador (Stamper et al., 2010). EOD frequencies above 600 Hz are usually occupied by several sympatric species of gymnotiform fish. In Guyana *Apteronotus albifrons* overlapped with *Sternarchorhamphus macrostomus* (Hopkins, 1974a), in Rio Negro, five species shared frequencies above 800 Hz (Bullock, 1969; Steinbach, 1970), and in a whitewater river close to Manaus Kramer et al. (1981) found 28 species with EOD frequencies ranging from 300 to 1800 Hz.

Species identification based on EOD frequency was possible for our data, because only three species of wave-type fish are known for Panamá (Alda et al., 2013). The high densities of sympatric species sharing the same frequency band reported from the Amazon basin (e.g., Steinbach, 1970; Kramer et al., 1981) would pose a major challenge for future studies with an electrode array in these habitats. One would need to take into account additional characteristics of the EODs, such as the relative power of higher harmonics (Kramer et al., 1981).

Recognizing species that overlap in fundamental EOD frequency is not only a technical problem. Whether and how gymnotiform fish solve this problem themselves is not understood yet. *Eigenmannia* are able to discriminate female and male EOD waveforms even if they do not differ in EODf (Kramer, 1999), and *Apteronotus leptorhynchus* were shown to chirp more to the signal of a real fish than to a sinewave mimic (Hopkins, 1974a; Dunlap and Larkins-Ford, 2003). However, in another playback experiment, signals based on the EOD waveforms of different species failed to elicit differences in chirp responses in male *A. leptorhynchus* (Fugère and Krahe, 2010).

Weakly electric fish do not need to rely on their baseline EOD alone. Species-specific modulations of the EOD frequency and amplitude could also be used to infer species identity (Kramer et al., 1981). Whereas rises seem to be highly conserved between species, chirps and EOD waveforms appear to be evolutionarily labile (Turner et al., 2007), and thus are potential additional cues for species identification. The different types of chirps and EOD waveforms result in various degrees of conspicuousness of the resulting signals (Petzold et al., 2016) that may translate into discriminability by the electrosensory system. Chirps have also been suggested to aid disambiguation of the sign of high-frequency beats (Walz et al., 2014).

Note also, that the above mentioned field studies do not allow to resolve whether species are syntopic or cluster in separate microhabitats or in time (Kramer et al., 1981). Recordings of electric activity in the field (Stamper et al., 2010, and our data) clearly demonstrate that all three wave-type electric fish are both spatially and temporally coexisting in specific microhabitats.

EOD interactions across species

Electroreceptor neurons are tuned to EOD frequencies and are most sensitive approximately at the EOD frequency of the individual fish (Hopkins, 1976). Behavioral thresholds in a detection task were similarly tuned (Knudsen, 1974). In playback experiments *Eigenmannia* responded to stimulus frequencies mimicking conspecifics (Hopkins, 1974a) and in *Sternopygus* with sexually dimorphic EOD frequencies males only responded to stimulus frequencies mimicking females (Hopkins, 1972, 1974b). During interactions of two electric fish, the difference between the two EOD frequencies is the relevant frequency for the tuning of P-type electroreceptor afferents (Bastian, 1981; Walz et al., 2014). P-type afferents thus encode relative and not absolute EOD frequency in their firing rate (but see Sinz et al., 2017). The question arises whether allospecific EOD frequencies are encoded by P-type afferents or whether electric fish have species-specific frequency channels?

Weakly electric fish are clearly able to sense the EODs of their conspecifics (Henninger et al., 2018). Since the frequency range covered by wave-type gymnotiform fish is rather broad (about half an octave, Hopkins, 1974b, Fig. 6 C), the frequency differences resulting from interacting conspecifics can be relatively large (Fig. 7 D). An impressive example is the courting behavior of a 1035 Hz male *Apteronotus rostratus* towards a 620 Hz female, resulting in an 415 Hz frequency difference (Henninger et al., 2018). However, although conspecifics may share a unique range of EOD frequencies, frequency differences do not allow to unambiguously distinguish species (Fig. 7 D). This ambiguity of frequency differences could be resolved if individual fish "knew" about their relative

EOD frequency within their species' EOD frequency range. Interestingly, electroreceptors of both *Eigenmannia* and *Sternopygus* are indeed more sharply tuned the higher their best frequency (Viancour, 1979; Zakon and Meyer, 1983). Whether this sharper tuning at the upper end of a species' frequency range is enough to sufficiently suppress EODs of other species with higher EOD frequencies still needs to be shown. The related problem at the lower end of a species' frequency range remains.

In addition, the harmonics of species with lower fundamental EOD frequencies fall into the sensitive range of the receptor tuning of a species with higher fundamental frequencies (Fig. 7 C). Although smaller in power, these harmonics might then create a beat that can be encoded by the receptor neurons. This should be a problem in *Apteronotus* species, in particular. Fish of this genus have much lower EOD amplitudes than *Sternopygus* and *Eigenmannia* (Fig. 10 D). Consequently, the harmonics of even a *Sternopygus* can be of similar power to that of the fundamental frequency of *Apteronotus* (Fig. 2 A). This suggests that high-frequency fish should be able to perceive and interact with species of lower EOD frequencies. Indeed, *A. leptorhynchus* has been shown to increase chirp rate in response to playbacks and interactions with *Sternopygus macrurus* and *Brachyhypopomus gauderio* in the lab (Dunlap et al., 2010). Heterospecific interactions have also been reported for mormyrid electric fish (Scheffel and Kramer, 2006).

Movement patterns

Our data from the electrode array allowed us to look beyond the mere presence of weakly electric fish species. Analyzing the movements of the recorded fish we found that about one third of the detections were fish that traversed the electrode array with or against the water flow (Fig. 8). At the beginning of their activity phase at the onset of the night fish of all three species were swimming upstream, whereas during the second half of the night the fish were preferentially swimming downstream (Fig. 9 A).

In contrast, a study on radio-tagged Australian graylings mainly found downstream movements over hundreds of meters and some upstream movements at the end of the night (Dawson and Koster, 2018). Based on transect data of general electric activity, Steinbach (1970) reported diurnal movements of gymnotiform fish over about one hundred meters from hiding places in deep waters during the day to shallow waters at night. Most available movement studies on fish in rivers, however, have not resolved diurnal movement patterns. Golden perch, carp, as well as the pulse-type weakly electric fish *Brachyhypopomus occidentalis*, for example, stayed within about one hundred meters for a few months, and only occasionally moved to a new home range farther away (Crook, 2004; Hagedorn, 1988).

We observed many upstream movements within and close to the root masses at the undercut bank, where water velocity was slowed down and where macroinvertebrates, potential prey, might hide and drift downstream. Downstream movements of the fish occurred more towards the shallower point bar at the inner side of the stream's bend with reduced water speeds. Based on the measured swimming speeds and on transect data we inferred a potential swimming range per night of at least a few hundreds meters and up to 3 km. This would be a rather large range for fish of about 20 cm length (Minns, 1995), but, as discussed above, most studies on fish migration behavior consider only movements from day to day, not within a single day. Depending on the taxon, movement distances can vary dramatically, but are positively correlated to fish length as well as stream size (Minns, 1995; Radinger and Wolter, 2014).

Solitary fish and the jamming avoidance response

Eigenmannia has been reported as a social fish species that is usually found in groups (Hopkins, 1974a). Tan et al. (2005) analyzed hundreds of snapshots of electric activity taken during the day and night in Ecuador. In most recordings multiple *Eigenmannias* were detected, but 10 to 20 % of the recordings contained only a single fish. In contrast, *Apteronotus* and *Sternopygus* have been mostly found solitary or in groups of two (Stamper et al., 2010). In the lab, groups of two are more frequent (Stamper et al., 2010), *Apteronotus* shows aggressive physical and electrocommunicative behavior (Triefenbach and Zakon, 2008), and only dominant males with the highest EOD frequency stay alone (Dunlap and Oliveri, 2002). In the field, however, aggressive electrocommunication seemed to be rare in *Apteronotus* (Henninger et al., 2018).

The analysis of our field data revealed that many fish were traversing the electrode array solitarily. This observation is in particular interesting for *Eigenmannia*. Of the 65 traversing *Eigenmannia humboldtii* observed in a single night, 61 were swimming solitarily, a large number considering typical shoal sizes of about five that have been reported for *Eigenmannia virescens* (Tan et al., 2005). This suggests that a substantial number of fish disperse from their group during the night either to forage on their own or to find mating partners.

This solitary aspect of their nighttime behavior might also put the discussion about jamming into a new context. *Eigenmannia*'s electrolocation performance is impaired by the presence of a conspecific with a similar EOD frequency (Heiligenberg, 1973), because the resulting low-frequency beat shadows signals evoked by objects (Behrend, 1977). By means of the jamming avoidance response *Eigenmannia* changes its EOD frequency such that the beat frequency is increased (Watanabe and Takeda, 1963; Bullock, 1969) and thus this jamming signal is moved outside the frequency band relevant for electrolocation (Nelson and MacIver, 1999; Fotowat et al., 2013). This behavior has been discussed as essential for shoaling *Eigenmannia* in order to maintain their ability to electrolocate despite the presence of conspecifics (Knudsen, 1974). With the possibility that *Eigenmannia* might forage solitarily, the selective pressure for an avoidance of jamming might be much smaller than assumed so far. Instead, the jamming avoidance response might have an additional social role of, for example, displaying or negotiating dominance.

This hypothesis is supported by the "jamming avoidance response" of *Apteronotus* that only increases EOD frequency (Heiligenberg et al., 1996), not necessarily resulting in an increase of beat frequency, but instead sometimes actively jamming a conspecific (Tallarovic and Zakon, 2005; Triefenbach and Zakon, 2008). *Apteronotus* has been argued to be less exposed and affected by jamming signals, because of its territoriality and the resulting spatial dispersion (Knudsen, 1974). Furthermore, *Sternopygus* does not show a jamming avoidance response (Bullock et al., 1975). This apparently matches the observation that this species is more solitary than other ones and thus appears not to be jammed by conspecifics. Nevertheless, it is able to closely interact with conspecifics during reproductive and occasional grouping behaviors (Hopkins, 1974b) and electrolocation of *Sternopygus* has been shown to be not impaired at all by jamming stimuli (Matsubara and Heiligenberg, 1978).

Far-field characteristics of EODs

The electric field geometry of electric organ discharges resembles a dipole field but its near field is asymmetrically distorted along the body axis because of the elongated electric organ (Heiligenberg, 1973; Assad et al., 1999; Chen et al., 2005). Only at distances larger than about two body lengths does the electric field approach the one of an ideal dipole (Knudsen, 1975). Although the shape of the measured far-field can be well described by an ideal dipole model (Fig. 3), the exponent describing the decay of the field amplitude with distance is with 1.6 clearly smaller than the exponent of 2 of the ideal dipole. The non-conducting bottom of the tank and the water surface induce boundary effects that compress the electric field and result in a reduced exponent (Fotowat et al., 2013). We observed an even stronger reduction of the exponent to 1.3 in the shallow water of our field site (Fig. 10). Reduced exponents enlarge detection distances for conspecifics and objects.

EOD-based localization of fish

We computed estimates of the position of the fish based on the power at a fish's EOD frequency measured on many electrodes of the array. Fitting a dipole model has been used successfully for estimating fish position (Jun et al., 2013; Madhav et al., 2018). However, these studies have not taken the reduced exponent in shallow water into account and assumed movements of the fish in the plane of the electrode array only. Our data and simulations show that the performance of the dipole fit deteriorates the farther the fish is above the plane of the electrode array and the closer it is at its borders (Fig. 4). A simple weighted average of the positions of the four electrodes with the largest signal amplitude turned out to be far more reliable, yielding localization errors below 10 cm, similar to the performance of the methods used in Madhav et al. (2018). In real-world scenarios, the dipole-like electric field can also be heavily distorted by objects like rocks, plants, and roots, where the fish like to hide. As long as such environments are not taken into account, model-based position estimates will be less precise and robust as well as computationally more demanding.

Detection ranges

The data of the electrode array allowed us to characterize the spatial properties of the electric fields for individual fish *in situ* (Fig. 10) without any special recording procedure (Knudsen, 1975; Stoddard et al., 2007). For the given situation in the habitat, characterized by a certain water conductivity, electric field compression by the water surface, and EOD strength, this allowed us to estimate the distance at which the electric field decayed down to the known behavioral sensitivities of several gymnotiform species to approximately 2 m. Within this range fish can detect and perceive each other, as we have shown in the field for attacks of a resident *A. rostratus* male towards an intruder (Henninger et al., 2018).

This detection range for conspecifics is much larger than typical distances of less than a body length for object detection (Knudsen, 1975). The minute changes induced by nearby objects (Nelson and MacIver, 1999; Chen et al., 2005; Fotowat et al., 2013) are much smaller than modulations induced by EODs of con- and allospecific electric fish. The situation weakly electric fish face resembles walking with a dim flashlight through a forest in the dark: only the immediate environment can be illuminated by the flashlight, but the flashlight of another person can be seen over a much larger distance.

EOD amplitudes

Our *in situ* characterization of electric fields also allowed to estimate the amplitude of the electric organ discharges (Fig. 10 D). EOD amplitude is known to be strongly correlated with fish size (length or weight) within *Eigenmannia* (Westby and Kirschbaum, 1981), *Sternopygus* (Hopkins, 1972), *Brachyhypopomus* (Hagedorn, 1988), and also across species, including *Apteronotus albifrons* (Knudsen, 1975). Thus, the more than tenfold variation of EOD amplitudes that we estimated for *Sternopygus* and *Eigenmannia* seems to reflect considerable variability in fish sizes. The EOD amplitudes of the relatively few *Apteronotus* that we detected were much more homogeneous than those of the two other species. Most of them were involved in courtship behaviors and thus may have been over some minimum size (Henninger et al., 2018).

EOD frequency has also been reported to correlate with fish size and to signal dominance, for *Apteronotus leptorhynchus* in the lab (Hagedorn and Heiligenberg, 1985; Dunlap, 2002) and for *Sternarchorhynchus* in the wild (Fugère et al., 2011). In contrast, our data do not show any correlation between EOD frequency and EOD amplitude for *Sternopygus* and *Apteronotus* (Fig. 10 D).

Natural sensory scenes

The data we extracted from our electrode-array recordings provide valuable information about natural sensory scenes of weakly electric fish that need to be processed by their electrosensory system. In Henninger et al. (2018), we found in courtship and aggression contexts of *Apteronotus* behaviorally relevant electrical signals of unexpected frequencies and amplitudes that have so far been largely neglected in neurophysiological studies.

The multispecies community we describe here (Fig. 6 and Fig. 7) hints at the complexity of signals gymnotiform fish are actually facing. Most of the behavioral and electrophysiological literature so far has focused on static interactions of two fish, but already relative movements induce higher order amplitude modulations of the resulting signals, so called "envelopes" (Yu et al., 2012). The interaction of more than two fish also results in envelopes and in specific behavioral responses (Partridge and Heiligenberg, 1980; Stamper et al., 2012). Courtship and agression behaviors of *Apteronotus* in our recordings demonstrate that the fish are able to selectively respond to specific fish in the presence of other nearby fish (Henninger et al., 2018). Here we introduced algorithms that allow to extract EOD frequencies and amplitudes of individual fish as well as distances between interacting fish, providing the basis for a detailed quantification of the complexity of social signals in natural scenes in the future.

The movements of the fish traversing the electrode array (Fig. 8) in combination with transect data along the stream hint at long-range navigation abilities of the fish in the range of several hundred meters up to potentially a few kilometers. In small-scale laboratory settings, gymnotiforms can be trained in spatial orientation tasks (Jun et al., 2016) and hippocampal-like circuitry has been described in their pallium (Elliott et al., 2017). How far the fish really travel along the stream, whether they return back to some preferred hiding place, and what cues they

rely on (electrical, lateral line, visual, or olfactory) are exciting questions for future studies with multiple smaller electrode arrays distributed along a stream.

Conclusion

By far most of our knowledge about the behavior of weakly electric fish is based on studies of captive fish in tanks. Quantitative observation of any fish species in their natural habitats has been next to impossible without tagging, even more so in species that exhibit a nocturnal and hidden life style. In contrast to non-electric fish, weakly electric fish can be detected based alone on their continuous electric organ discharges. This has been exploited in many of the outdoor studies, mostly by means of single electrodes used to locate the fish (e.g., Bullock, 1969; Steinbach, 1970; Hopkins, 1974a; Kramer et al., 1981; Hagedorn, 1988; Westby, 1988; Friedman and Hopkins, 1996; Tan et al., 2005; Stamper et al., 2010). Expanding this technique to arrays of tens of electrodes that monitor the activity of weakly electric fish over a whole day yields a plethora of valuable information on the secret lives of weakly electric fishes in tropical habitats as we have shown here and in Henninger et al. (2018). Many observations obtained from the electrode array revealed unexpected insights, like long-distance interactions between males and courtship behavior at extremely high beat frequencies (Henninger et al., 2018). The behaviors presented here emphasize the complexity of natural electrosensory stimuli, e.g., EOD interactions in multispecies communities and the moving behavior, that provide data on the statistics of natural electrosensory stimuli. These data can be used as valuable inspiration for future behavioral and neurophysiological studies in more specific laboratory experiments. Finally, our data demonstrate the large potential of EOD-based tracking for tackling exciting questions on the behavioral ecology of fish that have so far been out of reach.

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Materials and Methods

Field site

Data were recorded in Quebrada La Hoya, a narrow and slow-flowing creek, 2 km from the Emberá community of Peña Bijagual in the Tuira River basin, Province of Darién, Republic of Panamá (8°15′13.50″N, 77°42′49.40″W) in May 2012. At the recording site the water level ranged from 20 cm at the point bar to 70 cm at the undercut bank. The water temperature varied between 25 and 27 °C on a daily basis and water conductivity was stable at 150 – 160 µS/cm. See Henninger et al. (2018) for more details.

Field monitoring system

For the field recordings a custom-built, 64-channel electrode and amplifier system running on 12 V car batteries (npi electronics GmbH, Tamm, Germany) was used (Fig. 1 C–E). Signals from stainless-steel electrodes were directly fed into low-noise headstages encased in epoxy resin (1× gain, 10 × 5 × 5 mm, Fig. 1 C) that measured the potential of the electrodes against the one of a common ground that was buried about 10 m downstream into the bank of the

stream. After amplification and filtering by the main amplifier (100× gain, 1st order high-pass filter 100 Hz, low-pass 10 kHz) the signals were digitized with 20 kHz per channel at 16-bit using a custom-built low-power-consumption computer with two data-acquisition cards (PCI-6259, National Instruments, Austin, Texas, USA). Recordings were controlled with custom C++ software (https://github.com/bendalab/fishgrid) based on the comedi library for data acquisition on Linux (comedi.org). We used 54 to 64 electrodes, mounted on a rigid frame (thermoplast 4×4 cm profiles, 60 % polyamid, 40% fiberglass; Technoform Kunststoffprofile GmbH, Lohfelden, Germany), and arranged in a 9×6 array covering an area of 240×150 cm (30 cm spacing, about two to three times the body length of the fish). The electrode array was submerged into the stream and fixed about 30 cm below the water surface such that it covered the undercut bank side including the washed out root masses where the fish hide during the day.

Far-field measurement

The data shown in Figs. 3, 4, and 10 A were recorded in a large outdoor tank ($3.5 \times 7.5 \times 1.5$ m, $w \times l \times h$) at the Biocenter of the LMU, Martinsried, Germany. We used a 4×4 electrode array mounted on a PVC frame and spaced at 36 cm (108×108 cm, Georg Fischer GmbH, Albershausen, Germany). Water depth was adjusted to 60 cm, conductivity to 150 µS, and temperature to 23.5 °C. A weakly electric fish (*A. albifrons*, 18 cm) was placed within the center of the electrode array at the level of the electrodes, using a fish holder made of fine nylon mesh. During the measurement the fish did not change posture. In order to increase the spatial resolution we kept the position of the electrodes constant and instead adjusted the fish's location. In this way we sampled a grid with a total of 108 locations in 18×6 steps using a resolution of 2×4.5 cm.

Data analysis

Data were analyzed in Python 2.7 (www.python.org, https://www.scipy.org/, Hunter, 2007). Scripts and raw data (Panamá field data: 2.0 TB) are available on request. Data of the extracted EOD frequencies and position estimates are available at https://doi.org/10.12751/g-node.87584d. The core algorithms are accessible at Github under the GNU general public license (https://github.com/bendalab/thunderfish).

Individual identification

Individual fish were identified based on their EOD frequency and their EOD's harmonic structure. For each electrode we calculated power spectral densities (PSD, 8192 FFT data points, 5 overlapping sub-windows, overlap 50%, total width= 1.22 s) in subsequent analysis windows (85 % overlap). In the log-transformed PSDs we detected peaks using a relative threshold for the peak height (Todd and Andrews, 1999). The frequency resolution of the PSDs and peak positions was $\Delta f = 2.44$ Hz.

For finding conclusive harmonic structures we started with the frequency f_{max} of the peak with the highest amplitude and checked whether harmonics at integer multiples of this frequency were present. As the fundamental frequency, f_1, is not always the strongest frequency in an EOD's PSD, we checked for harmonic structures with fundamental frequencies at integer fractions of f_{max}, i.e. $f_1 = f_{max}/n$ for a small range of integers $n \leq 4$. Because of the discrete frequency resolution of the PSD, the fundamental frequency has an uncertainty of $f_{tol} = \pm\Delta f/2$. In practice we set f_{tol} slightly higher ($f_{tol} = \pm 0.7\Delta f$) because peaks are distorted when riding on the flank of larger peaks. When checking for harmonics at frequencies $f_i = i \cdot f_1$ with $i > 1$, the corresponding frequency tolerances $\pm i \cdot f_{tol}$ grow with the order i of the harmonics. Thus, the frequency tolerances get rather unspecific for higher harmonics, but at the same time subsequent harmonics of order i and j should also be separated by $(j-i)f_1$ within a tolerance of $2|j-i|f_{tol}$. Having identified a potential harmonic of the fundamental frequency we used its frequency f_i to improve the estimate of the fundamental frequency via $f_1 = f_i/i$. Thus, by means of the harmonics, fundamental frequencies can be estimated with higher accuracy than the frequency resolution of the PSD. This updating of f_1 was stopped as soon as a predicted harmonic was not present in the PSD.

The resulting group of harmonics was rejected if it contained less than three harmonics, if more than one of its frequencies was already contained in a harmonic group of another fundamental frequency, or if more than a quarter

of its harmonics were not detected in the PSD. Then, the group of harmonics was compared to the so far best group found for a given f_{max} and preferred if the sum of its peak amplitudes was larger and the number of missing harmonics was lower. This procedure was repeated until all peaks in the power spectrum of a certain amplitude that was higher than the detection threshold were considered. Finally, harmonic structures with fundamental frequencies below 40 Hz, above 1500 Hz, or at the mains hum at 60 Hz were discarded.

Temporal tracking of electric fish

In a second step, detected EOD frequencies were connected to previous data segments in order to track individual fish over time. If a fish with an EODf differing by less than 10 Hz was found in the previous detections, the new data was added, otherwise the fish was treated as a new candidate. If this candidate was detected robustly in the following analysis windows, typically over several seconds, it was marked as a confirmed fish detection. Otherwise, it was discarded as a false detection.

Estimation of location and orientation

For each detected fish the electrode's voltage traces were bandpass-filtered (Butterworth filter, 3rd order, 5× multi-pass, ±7 Hz width) at the fish's EODf. For each passband the signal amplitude was estimated each 40 ms using a root-mean-square filter over 10 EOD cycles multiplied by $\sqrt{2}$. These amplitudes were then used to estimate the location of each fish. In the following we describe the three algorithms tested for fish localization.

Weighted spatial averages A simple estimate of 2D fish location and orientation was based on a weighted spatial average. The fish position $\vec{x}$ was estimated from n electrodes i with the largest envelope amplitudes A_i at position $\vec{e}_i$ as a weighted spatial average, given by

$$\vec{x} = \frac{\sum_{i=1}^{n} \sqrt{A_i} \cdot \vec{e}_i}{\sum_{i=1}^{n=z} \sqrt{A_i}}. \tag{1}$$

For the variant that used only the four electrodes with the largest EOD amplitude, the position was computed only, if at least 2 electrodes with amplitudes greater than 15 µV were available. If at least 4 electrodes with amplitudes greater 1 µV were available, $n = 4$, otherwise $n = 2$. For the other variant that used all electrodes n was set to the number of electrodes of the electrode array.

The EOD of a fish can cause a very large amplitude on nearby electrodes because of the electric field's reciprocal dependence on distance. This effect results in a relatively large localization error, if a simple weighted spatial average is used, because the position estimate is pulled towards the strongest electrode. The localization error is reduced by using the square-root of the EOD amplitude, $\sqrt{A_i}$, as a weight, which reduces the impact of electrodes with large EOD amplitudes.

For approximating fish orientation, we first divided the electrodes into two subgroups of opposite polarity. Because the EOD amplitudes are extracted as absolute values, polarity information of the EOD on the respective electrodes is missing and has to be estimated in an additional analysis step. The polarity of the electrodes was determined by calculating the correlations of the electrodes' bandpass-filtered voltage traces (40 ms windows) relative to that of the electrode with the largest amplitude. Electrodes with correlations larger than $+0.9$ were assigned to one group and correlations smaller than -0.9 to the other. If both groups contained at least 4 electrodes, each group's center was estimated by calculating the weighted spatial average, Eq. 1. The direction of the vector connecting the centers of the two groups was an estimate of the orientation of the body axis of the fish.

Dipole model The potential generated by an ideal electric dipole at a distance r and an angle φ measured against the dipole moment is given by

$$\phi(r, \varphi, P) = P \frac{\cos \varphi}{r^q} \tag{2}$$

where the exponent $q = 2$ and P is an amplitude factor that absorbs the dipole moment and the permittivity of the medium. The electric organs of weakly electric fish can be approximated as constant current sources (Knudsen,

1975) and therefore P is proportional to the current produced by the electric organ and inversely proportional to the conductivity of the water (Madhav et al., 2018).

For estimating the position, orientation, and EOD amplitude of a fish we fitted the absolute value of the dipole model Eq. (2) to the EOD amplitudes recorded by the electrode array. This is a numerically difficult minimization problem, because of the large number of local minima between the singularities at the positions of the electrodes. We therefore introduced a regularizer α in the denominator, to remove these singularities and make the problem numerically more stable. We also treated the exponent of the power law as a free parameter q to phenomenologically account for the compression of the electric field by the non-conducting water surface (Knudsen, 1975). Together, these modifications yield the regularized dipole function, given by

$$\bar{\phi}(r,\varphi,P) = \left| P \frac{\cos\varphi}{r^q + \alpha} \right| \tag{3}$$

A weighted spatial average over all available electrodes was used to compute initial values for the optimization. The optimization was performed over two iterations using stepwise decreasing values for α (10^{-2} and 10^{-3}), and using the result of the first iteration as initial values for the last. The successful optimization directly yielded the dipole's location, orientation, its amplitude factor, and the potential distribution's effective power law. Since we were optimizing a function with 8 parameters, at least 8 data points, i.e. amplitude measurements from at least 8 electrodes, were necessary for a successful optimization.

Simulations To study the performance of the three proposed localization methods under ideal conditions, we simulated large electrode arrays (40×40) with spacings of $15-90$ cm and sampled many fish locations and orientations at the array's center quadrant (20×20 steps xy-resolution; 3 elevations; orientations between $0-180°$ with 4.5° resolution; 16400 samples/spacing, total). This configuration allowed for neglecting effects caused by the limits of the electrode array. Data were simulated with a dipole model using EOD field parameters extracted for *A. albifrons* and a power law with exponent -1.64 (Fig. 3).

In order to estimate the detection performance of our analysis chain for moving fish, we simulated the EODs of moving fish ($v = 10$ cm/s) generated with a horizontally oriented dipole model, Eq. (3) and electric field parameters extracted from our EOD field measurements. Electrodes were configured in a large array with 10×10 electrodes with a spacing of 30 cm, i.e. the same spacing as used at our field site. Data were generated using the same sample rate of 20 kHz as for the field data. For each sample we calculated the EOD's potential on each electrode and multiplied it with the current value of the EOD. The simulated fish moved a full circumference of a circular trajectory (103.3 cm radius), always with the circle positioned slightly off-center in relation to the electrode array's grid in order to sample many different fish-to-electrode configurations.

The noise floor in the field recordings was at about 1 µV. We therefore excluded electrodes with amplitudes below 1 µV from the position estimate to get comparable performances to the field situation.

Movement patterns

As a detection of a fish we defined data segments with a continuous detection of a specific EODf with gaps of no more than 20 seconds. As directed movements we classified detections that entered the electrode array in one third and left the array at the opposite third in the direction of the stream flow (the y-coordinate of the electrode array). We did not impose any time limit. Average upstream (v_{up}) and downstream (v_{down}) swim speeds were computed as the slope of a straight line fitted to each $y(t)$ trace in the central half of the electrode array ($y = 60$–180 cm). Using a larger or smaller part ($\pm 15\,cm$) of the electrode array did not change the results.

The measured upstream speed of a fish, $v_{up} = v_{fish} - v_{stream}$, is the swimming speed of the fish, v_{fish}, reduced by the water velocity of the stream, v_{stream}. Likewise, the measured downstream speed is $v_{down} = v_{fish} + v_{stream}$. By subtraction we get an estimate of the water velocity

$$v_{stream} = \frac{v_{down} - v_{up}}{2} \tag{4}$$

and by addition an estimate of the swimming speed of the fish

$$v_{fish} = \frac{v_{down} + v_{up}}{2} \ . \tag{5}$$

Since we did not know exactly which downstream swimming fish corresponded to which upstream swimming fish (the EOD frequency changes with temperature), we used the median speeds for the calculations.

Assuming the fish are constantly swimming with v_{fish} relative to the water body we would like to estimate how far a fish was able to swim upstream during one night if it returns after the time Δt_{total}. The fish can spend the time Δt_{up} for swimming upstream with v_{up} and the time Δt_{down} with v_{down} for swimming downstream. To be back in time, $\Delta t_{total} = \Delta t_{up} + \Delta t_{down}$ and the covered distances x need to match: $x = \Delta t_{up} v_{up} = \Delta t_{down} v_{down}$. From these two conditions follows for the distance covered by the fish

$$x = \Delta t_{total} \frac{v_{down} v_{up}}{v_{down} + v_{up}} \ . \tag{6}$$

For the time Δt_{total} we used the difference between the median times of upstream and downstream movements.

As the distance from the undercut bank we simply used the x-coordinates of the movement traces from the same segments as used for estimating swim speed.

Estimation of EOD field characteristics

The absolute potential of a dipole at a given distance varies because of its angular dependence via the cosine term in Eq. (2). Taking only the maximum measured values for each distance cancels out the angular dependence and we are left with a power law to be fitted to the data. This allowed for a robust estimate of the amplitude factor and the exponent of the power law decrease of electric field amplitude. To extract the maximum amplitudes, amplitudes obtained from bandpass-filtered data were binned logarithmically over distance and for each bin a fixed fraction of largest amplitudes (dependent on the amount of available data: 20% for the tank measurements, 5% for the field data) were extracted and averaged. A power law function, i.e. the dipole Eq. (2) with $\cos\varphi = 1$, was then fitted to the obtained amplitudes. Errors introduced by the inaccuracy of location estimation were particularly noticeable at small distances. At large distances the data hit the noise floor (Fig. 10 B). We therefore excluded distances below 20 cm and above 100 cm from the fit. Because the largest amplitudes were extracted as a substantial fraction of the data in each distance bin (5 or 20%), the method has an implicit bias to underestimate the amplitude factor. Note, however, that for fish moving vertically offset from the electrode's plane the proposed method profoundly underestimates both exponent and EOD amplitude. This effect can be compensated by fitting the amplitude distribution over larger distances only (Henninger, 2015).

For an estimation of the detection ranges we first computed the electric field strength $E(r)$ as the spatial derivative of Eq. (2) to

$$E(r) = \frac{\mathrm{d}}{\mathrm{d}r}\phi(r) = \frac{qP}{r^{q+1}} \tag{7}$$

where we have set $\cos\varphi = 1$. Given the sensitivity E we get for the maximum detection range

$$r = \sqrt[q+1]{\frac{qP}{E}} \tag{8}$$

Transects

We recorded positions of wave-type weakly electric fish along a 160 m long transect directly upstream of the electrode array on 2012-05-11 at around noon and on 2012-05-13 in the afternoon. We walked along the transect and located the fish by means of a fish-finder, a 30 cm long custom-made dipole electrode connected to an audio amplifier (Mini Amplifier-Speaker, RadioShack). For each fish we recorded the EOD for about 15 to 30 s (24 kHz, XL2 Audio and Acoustic Analyzer, NTi Audio GmbH, Essen) and its position. From the recordings we extracted

EOD frequencies using our thunderfish software (https://github.com/bendalab/thunderfish). Sometimes the same fish was present on several recordings, in that case we only counted the fish in the recording where it had the largest power and removed it from the other ones. We then counted the number of fish present in the transect for each species separately based on their EOD frequency. Division by the transect length results in the averaged fish density.

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