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Bioelectric Fields of Marine Organisms: Voltage and Frequency Contributions to Detectability by Electroreceptive Predators

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ABSTRACT

Behavioral responses of elasmobranch fishes to weak electric fields have been well studied. These studies typically employ a stimulator that produces a dipole electric field intended to simulate the natural electric field of prey items. However, the characteristics of bioelectric fields have not been well described. The magnitude and frequency of the electric field produced by 11 families of marine organisms were quantified in this study. Invertebrate electric potentials ranged from 14 to 28 μV and did not differ from those of elasmobranchs, which ranged from 18 to 30 μV. Invertebrates and elasmobranchs produced electric potentials smaller than those of teleost fishes, which ranged from 39 to 319 μV. All species produced electric fields within the frequency range that is detectable by elasmobranch predators (<16 Hz), with the highest frequencies produced by the penaeids (10.3 Hz) and the gerreids (4.6 Hz). Although voltage differed by family, there was no relationship between voltage and mass or length of prey. Differences in prey voltage may be related to osmoregulatory strategies; invertebrates and elasmobranchs are osmoconformers and have less ion exchange with the surrounding seawater than teleosts species, which are hyposmotic. As predicted, voltage production was greatest at the mucous membrane–lined mouth and gills, which are sites of direct ion exchange with the environment.

Introduction

Sensory stimuli are influenced by the medium in which they are produced and transmitted. For example, aquatic environments allow low-frequency sound waves to be broadcast over longer distances and more quickly than in air (Urick 1975). The aquatic environment has also facilitated the evolution of sensory systems unique to that environment, such as electrosensory and lateral line systems. Electroreception has independently evolved several times in the vertebrate lineage and persists in all elasmobranch, chondrostean, and sarcopterygian fishes; all monotreme mammals; and some teleost fishes and amphibians (Bullock et al. 1983). Electroreception was also recently described in the Guiana dolphin (Czech-Damal et al. 2012). Electroreception is most well studied in the elasmobranch fishes—the sharks, skates, and rays—and is used for prey detection (Kalmijn 1966; Kalmijn and Weinger 1981), conspecific recognition (Tricas et al. 1995), and predator detection (Sisneros et al. 1998; Kempster et al. 2012); it also has been hypothesized to play a role in navigation and orientation (Kalmijn 1982; Montgomery and Walker 2001).

All organisms produce minute yet dynamic electric fields that typically consist of direct current (DC) and alternating current (AC) components. Although the specific details regarding bioelectric fields are poorly understood, it is thought that standing DC fields surround an organism and result from ion leakage across mucous membranes, including the mouth, gills, cloaca, and siphons (Wilkens and Hofmann 2005). The standing DC field can also be modulated by the opening and closing of the mouth and pharynx during ventilation or from rhythmic limb movement, thus imparting a frequency component (Wilkens and Hofmann 2005). High-frequency AC fields (>20 Hz) arise from muscle contraction action potentials along the body of an animal (Kalmijn 1972, 1974; Wilkens and Hofmann 2005), but they are typically outside the detection range of electroreceptive marine organisms. Therefore, the standing and modulated DC electric fields are used by predators to detect and localize prey items in a highly conductive seawater environment (Kalmijn 1971, 1974; Eeuwes et al. 2008; Kimber et al. 2011).

The magnitude and frequency of bioelectric fields has been recorded for prey items of paddlefish (*Polydon spathula*; Wojtenek et al. 2001), teleosts (Patullo and MacMillan 2004; Eeuwes et al. 2008); elasmobranchs (Kalmijn 1972, 1974; Haine et al. 2001), and platypus (*Ornithorhynchus anatinus*; Taylor et al. 1992). However, there is limited information regarding variation in frequency, magnitude of the electric field along the body, and voltage decay with distance from the source. Kalmijn (1972, 1974) recorded voltage, or bioelectric potential, produced from a number of diverse elasmobranch prey items and reported that molluscs produce up to 10 μV, crustaceans and elasmobranchs produce up to 50 μV, and teleosts produce up to 500 μV. In a subsequent study, Haine et al. (2001) quantified the voltage and frequency produced by three species of teleosts and five species of invertebrates and reported that the voltage

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Table 1: Median sensitivity, maximum detection distance, and prey preferences of elasmobranch predators to prey-simulating electric stimuli

Species	Common name	Sensitivity (nV cm^{-1})	Detection distance (cm)	Preferred prey	Reference
Squalus acanthias	Piked dogfish	14	30	Teleosts, crustaceans[1]	Jordan et al. 2011
Mustelus canis	Dusky smoothound	29	26	Crustaceans[2]	Jordan et al. 2011
Urobatis halleri	Round stingray	29	40	Crustaceans[3]	Jordan et al. 2009
Myliobatis californica	California bat ray	48	40	Bivalves, crustaceans[4]	Jordan et al. 2009
Pteroplatytrygon violacia	Pelagic stingray	40	30	Squid, teleosts[5]	Jordan et al. 2009
Dasyatis sabina	Atlantic stingray	5	44	Crustaceans[6]	McGowan and Kajiura 2009
Sphyrna tiburo	Bonnethead shark	47	22	Crustaceans[7]	Kajiura 2003
Carcharhinus plumbeus	Sandbar shark	30	32	Crustaceans, teleosts[8]	Kajiura and Holland 2002
Sphyrna lewini	Scalloped hammerhead	25	31	Crustaceans, teleosts, elasmobranchs[9,10]	Kajiura and Holland 2002

Note. To facilitate comparison, all studies referenced here used the same bioelectric field generator and behavioral analysis. References for diet composition are as follows: 1 = Jones and Geen 1977, 2 = Gelsleichter et al. 1999, 3 = Valadez-Gonzalez et al. 2001, 4 = Gray et al. 1992, 5 = Wilson and Beckett 1970, 6 = Cook 1994, 7 = Cortes et al. 1996, 8 = McElroy et al. 2006, 9 = Clarke 1971, 10 = Bush 2003.

was greater at the mucous membranes, especially on the head, than the rest of the body. These studies provided some information regarding the magnitude and frequency of the electric field; however, specific details are lacking.

Although there is a paucity of information regarding the characteristics of bioelectric fields of elasmobranch prey, the behavioral sensitivity of elasmobranchs to prey-simulating electric fields has been described for several species (table 1). Bioelectric fields are complex and multipolar in nature (Kalmijn 2000). Since higher-order fields (quadrapole, octopole) decay extremely rapidly with distance from the source, bioelectric fields are best approximated as a dipole. A bioelectric field stimulus generator that creates a dipole electric field in seawater has been used in behavioral studies to quantify the sensitivity of elasmobranch fishes to weak electric fields (Kajiura and Holland 2002; Kajiura 2003; Jordan et al. 2009; McGowan and Kajiura 2009). The stimulus generator produces an electric field magnitude intended to replicate prey bioelectric fields based on measurements by Kalmijn (1972, 1974). Although these studies described a range of bioelectric field intensities for groups of marine organisms, a lack of detail makes it difficult to adequately simulate a target prey item's electric field.

The goals of this study were to (1) quantify the bioelectric potential from a variety of invertebrate and vertebrate elasmobranch prey items, (2) characterize the voltage at different locations along the body of fish and with increasing distance, (3) quantify the frequency at which the electric field is modulated as a result of ventilation, and (4) quantify the voltage produced by the bioelectric field stimulus generator previously employed to investigate behavioral responses of elasmobranchs to prey-simulating electric fields.

Material and Methods

Animal Collection

Four species of invertebrates and 11 species of vertebrates from 11 families and five classes were chosen as representative elasmobranch prey items for this study (table 2). All specimens were collected from South Florida waters and were acclimated to the laboratory conditions in a flow-through seawater system (35-ppt salinity and 25°–27°C) for a minimum of 24 hours before experiments began. Mass (g) and length (cm) data were collected from all individuals. Shell length (distance between lateral shell margins) was recorded for bivalves, total body length was recorded for arthropods, and total lengths were recorded for all fishes (table 2). Bivalve body mass was determined by subtracting the weight of the empty shell from the shelled animal. All experiments were conducted in accordance with Florida Atlantic University Institutional Animal Care and Use Committee protocol A09-20.

Experimental Apparatus

An electrophysiological technique was employed to quantify the voltage produced by selected elasmobranch prey items. Individual prey items were secured in an acrylic experimental tank (89 cm × 43 cm × 21 cm) equipped with flow-through seawater. A nonpolarizable Ag-AgCl electrode (E45P-M15NH; Warner Instruments, Hamden, CT) was fitted with a seawater/agar-filled glass capillary tube that terminated in a 100-μm tip. The tip of the recording electrode was positioned <1 mm from the source (mouth, gills, or body of prey item, as specified below), and a similar reference electrode was positioned in the far corner of the experimental tank. The output from the two electrodes was differentially amplified (DP-304; Warner Instru-

Table 2: Summary of species, total length (TL), mass, and sample size for elasmobranch prey measured in this study

Class	Order	Family	Species	*n*	TL range (cm)	Mass range (g)
Bivalvia	Veneroidea	Veneridae (hard clam)	*Mercenaria mercenaria*	6	8	57–76
Malacostraca	Decapoda	Penaeidae (shrimp)	*Penaeus setiferus*, *P. duorarum*	6	7–8	2–3
Merostomata	Xiphosurida	Limulidae (horseshoe crab)	*Limulus polyphemus*	6	13–16	33–49
Actinopterygii	Perciformes	Gerreidae (mojarra)	*Diapterus auratus*	5	11–14	21–42
		Haemulidae (grunt)	*Haemulon flavolineatum*	2	19–21	161–165
			Haemulon plumierii	1	14	52
			Haemulon purra	7	27–30	325–500
		Lutjanidae (snapper)	*Lutjanus griseus*	6	24–37	230–800
		Sphyraenidae (barracuda)	*Sphyraena barracuda*	4	18–43	27–500
	Siluriformes	Ariidae (catfish)	*Ariopsis felis*	3	35–37	397–410
	Tetradontiformes	Diodontidae (pufferfish)	*Chilomycterus schoepfi*	5	7–20	21–215
			Diodon holocanthus	4	18–19	172–298
Elasmobranchii	Carcharhiniformes	Sphyrnidae (bonnethead shark)	*Sphyrna tiburo*	5	21–34	42–157
	Myliobatiformes	Urolophidae (yellow stingray)	*Urobatis jamaicensis*	5	17–22	342–600

ments) at × 1,000–10,000, filtered (0.1 Hz to 0.1 kHz, 60-Hz notch; DP-304; Warner Instruments and Hum Bug, Quest Scientific, North Vancouver, British Columbia), digitized at 1 kHz using a Power Lab 16/30 model ML 880 (AD Instruments; Colorado Springs, CO), and recorded using Chart software (ver. 5; AD Instruments). All experiments were conducted at temperatures from 24°C to 27°C.

Electrophysiology Protocol

Voltage measurements were recorded from the most electrogenic (greatest electric signal) tissue in invertebrates: the incurrent siphon of the bivalves, the swimmerets of the penaeids, and the book gills of the horseshoe crabs. Recordings from fishes were made along the body to determine what body region is the most electrogenic. All frequency measurements were recorded from the gills except for the penaeids, in which the frequency at the swimmerets was reported. Voltage and frequency measurements were averaged from three recordings at each location on an individual prey item. The mean voltage and frequency were reported and used in statistical analyses. Power-spectrum analysis confirmed the fundamental frequencies of the background noise and bioelectric signals from the gills of each individual, which were averaged to determine the mean fundamental frequency for each family.

Bivalves. To measure the electric field from bivalves, an individual hard clam (*Mercenaria mercenaria*) was positioned with the siphons toward the water surface. The recording electrode was positioned at the opening of the incurrent siphon to record the DC field produced by ion exchange from the gill lamellae. The voltage difference between the siphon and baseline electrical activity in the tank was determined to quantify DC electric potential.

Arthropods. Shrimp (*Penaeus setiferus* and *Penaeus duorarum*) were secured to a 2-cm-long square acrylic block, approximately the length of the cephalothorax, with superglue applied to the dorsal surface of the carapace. The recording electrode was placed at the swimmerets on the abdomen of an individual shrimp for voltage and frequency recordings. Horseshoe crabs (*Limulus polyphemus*) were secured with Velcro straps to a plastic-mesh support on the dorsal carapace. The recording electrode was placed at the book gills of the horseshoe crab to record the magnitude and frequency of the bioelectric potential.

Teleost Fish. Fish were lightly anesthetized with MS-222 (1 : 12,000–1 : 20,000 wt : vol) to a level that allowed ventilation and slight movements of the fins but that eliminated whole-body movements. Individual fish were then restrained with Velcro straps on a submerged plastic-mesh frame positioned on the lateral side of the fish, opposite of the recording electrode. Voltage was recorded at four positions along the length of the fish: mouth, gills, midway between the gills and tail, and caudal peduncle. To quantify the decay of the electric field over distance, the recording electrode was placed at the mouth and

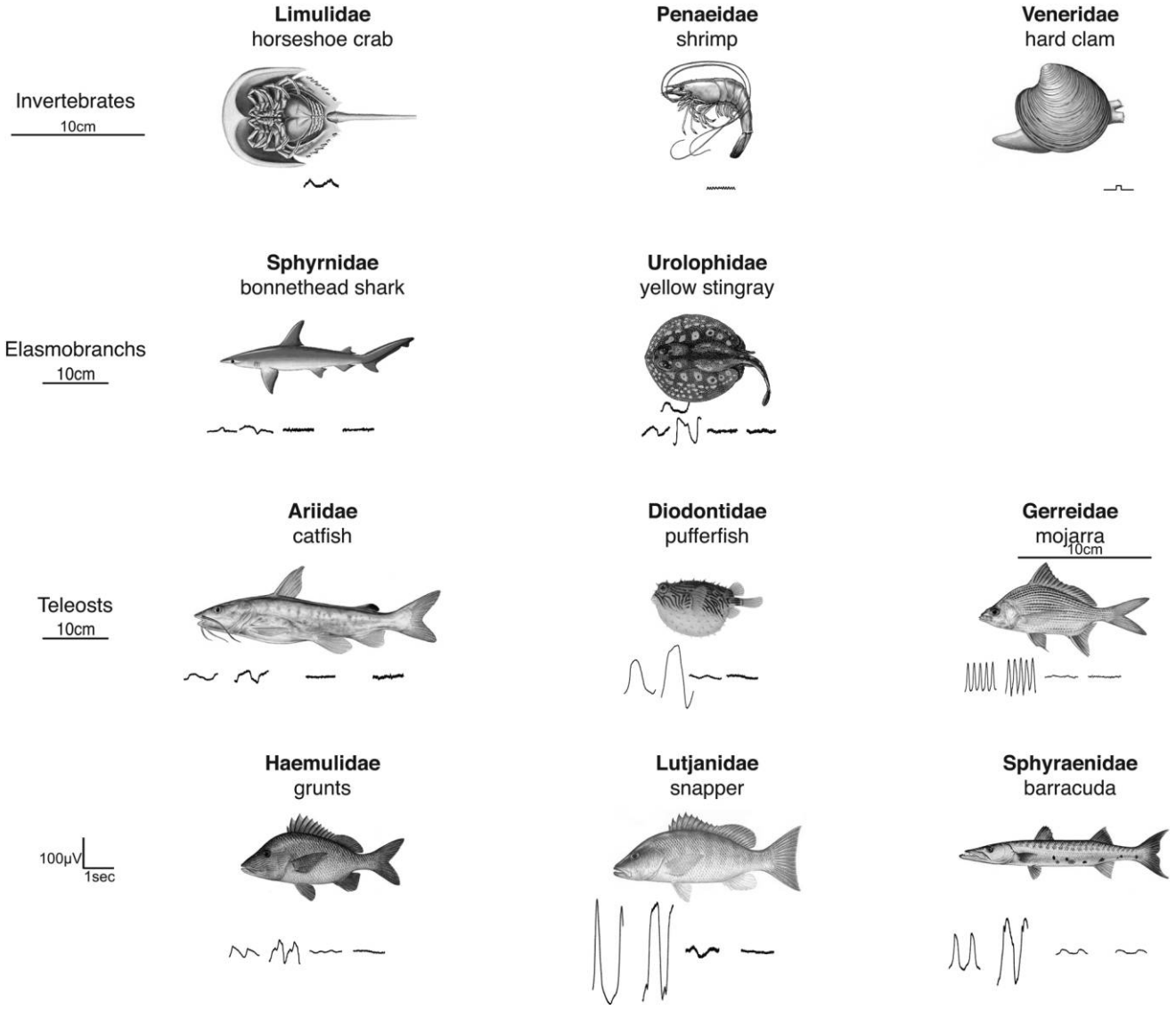

Figure 1. Waveform shape, amplitude, and frequency of electric potential measured from elasmobranch prey items. Electric field characteristics were recorded from 11 families of elasmobranch prey. Representative waveforms from an individual of each family are shown for each location measured. Prey are scaled to the mean total length (cm) for each family, and waveforms are scaled to the mean amplitude (μV) and frequency (Hz) for each family. All prey illustrations are reproduced with permission when necessary (Sphyrnidae, Ariidae, Gerreidae, Haemulidae, Lutjanidae, and Sphyraenidae are © Diane Rome Peebles; Urolophidae, © Gillian Harris; Penaeidae, permission by Florida Department of Agriculture and Consumer Services; Diodontidae, permission by Encyclopaedia Britannica). A color version of this figure is available in the online edition of *Physiological and Biochemical Zoology*.

the fish was moved away from the electrode in 1-cm increments using a computer-controlled linear translation track (eTrack-300 Linear Stage; Newmark Systems, Rancho Santa Margarita, CA). Fish were displaced until the signal was no longer greater than the background level of electrical noise in the tank. The mean of three voltage and frequency measurements was calculated for each individual from each location and distance increment.

To determine the distance at which an elasmobranch can electrically detect prey, the electric field (i.e., voltage gradient) was calculated as the first-order derivative of the recorded voltage. This equation was applied to literature values of elasmobranch electrosensitivity (Kajiura and Holland 2002; Kajiura 2003; Jordan et al. 2009; McGowan and Kajiura 2009) to predict the distance at which each teleost fish can be detected by elasmobranch predators.

Sharks. Juvenile bonnethead sharks (*Sphyrna tiburo*) were anesthetized and secured in the tank as described for teleost fishes. Sphyrnid sharks are obligate ram ventilators; therefore, the anesthetized sharks required supplemental ventilation with a submerged pump to move water over the gills between recordings.

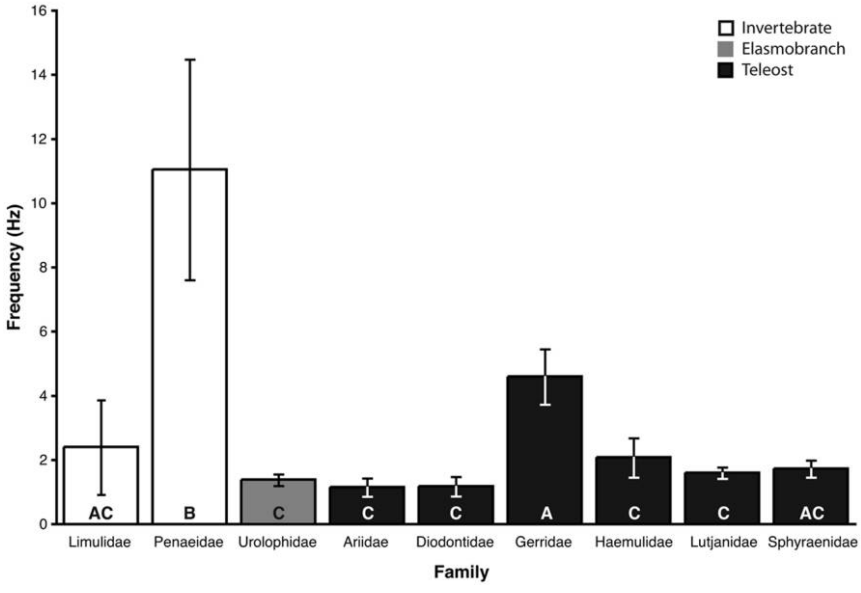

Figure 2. Mean frequency (±SD) produced by invertebrate and vertebrate prey items. Frequency was recorded from the swimmerets of the penaeids (shrimp) and from the gills of all other prey. All families produced frequencies within the range detectable by elasmobranchs (<16 Hz), and all families except Penaeidae and Gerreidae produced frequencies within the maximum range of sensitivity for elasmobranchs (≤2 Hz). Bars that share the same letter are not different.

Because these sharks do not rhythmically pump water over their gills, the temporal component (frequency) was not measured. The mean of three voltage measurements for each location was calculated for each individual.

Stingrays. Yellow stingrays (*Urobatis jamaicensis*) were anesthetized as described for teleosts and were secured with Velcro straps to a submerged, rigid mesh platform. Electric signals were recorded from the spiracle with rays in their natural orientation, and signals were recorded from the mouth, gills, middle of the ventral surface of the body, and base of the tail with rays oriented ventral side up. The mean of three voltage and frequency measurements was calculated for each individual.

Statistical Analyses. One-way ANOVAs with $\alpha = 0.05$ determined significant differences in mean voltage magnitude and frequency among families of elasmobranch prey and between locations on fish within a family. Data conformed to normality assumptions. Regression analyses tested for relationships between voltage magnitude and length or mass. All analyses were performed with JMP statistical software (ver. 9.0.2; SAS Institute, Cary, NC).

Bioelectric Field Generator Electric Potential

To verify the suitability of the bioelectric field stimulus generator (cf. Kajiura and Holland 2002) as a source of simulated bioelectric fields in behavioral assays, the voltage produced by the apparatus was measured at a range of current intensities at three temperatures (20°C, 25°C, and 30°C) and three salinities (0, 15, and 35 ppt). Because the resistive properties of water change with salinity and temperature, the range of applied currents in each combination was different. Current intensities were applied in 1-μA increments for freshwater (0 ppt) and 10-μA increments for brackish (15 ppt) and saltwater (35 ppt) treatments.

The stimulus generator was connected to an underwater cable that terminated in a pair of gold-plated stainless steel electrodes (Impulse Enterprise, San Diego, CA). Electrodes were connected to a pair of water-filled polyethylene tubes that were fitted to the underside of an acrylic plate that interfaced with the tank water through two 1-mm holes with a 1-cm separation distance that simulates a prey item. The plate was contained within an acrylic experimental tank (89 cm × 43 cm × 21 cm), and the water temperature was controlled with an aquarium chiller/heater unit (SeaChill TR5; Teco, Ravenna, Italy). The stimulus generator was powered by a 9-V battery with a multimeter connected in series to monitor applied current. A recording electrode was placed in the center of the 1-cm dipole, and the reference electrode was placed in the far corner of the experimental tank. Voltage produced from the stimulus generator was recorded in the same manner as reported for prey measurements. The voltage produced at each applied current was recorded twice and averaged. Resistance (Ω) at each temperature and salinity was calculated according to Ohm's law.

The decay of a 52-μV prey-simulating stimulus produced by the bioelectric field generator was quantified to determine whether the experimental tank constrained the measured voltage decay of prey items. A pair of seawater-filled polyethylene tubes connected to the electrode output of the stimulus gen-

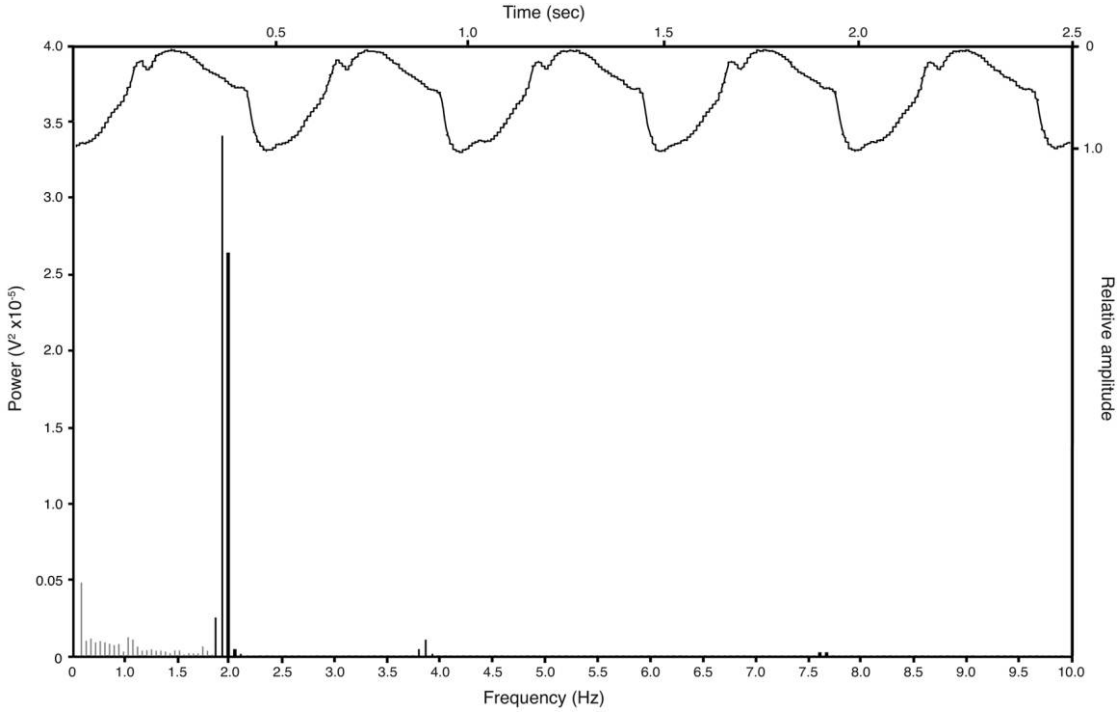

Figure 3. Sample power spectrum and waveform recorded from the gills of a barracuda (Sphyraenidae). The modulated prey signals (black) were dominated by a narrow-band fundamental frequency from 1.8 to 2.1 Hz, which correlated with periodicity of the waveform. Dominant noise frequencies (gray) were broadband and present from 0.06 to 1.7 Hz at ≤0.15% power of the prey signal. Power spectrum data are plotted on the primary axes, and waveform data are plotted on the secondary axes.

erator was positioned within the tank in a manner to mimic the position of fish during decay measurements. The tubing was secured to the mesh frame with a dipole separation distance of 1 cm, and the open ends were oriented toward the tip of the recording electrode in the same orientation as the fish mouths. The stimulus was moved away from the electrode in 1-cm increments until the stimulus was no longer larger than the ambient noise in the tank. The electric field was calculated as the derivative of voltage decay.

Results

Live Prey Electric Potential and Frequency

Bioelectric potentials (voltage) and frequencies differed dramatically among three families of invertebrates and eight families of fishes (fig. 1). The amplitude and shape of the recorded waveform varied among species and also at different locations along the body within a species. The ventilatory frequency ranged from 1.1 to 10.3 Hz (fig. 2). The frequency recorded from the swimmeret movement of the penaeids was 10.3 Hz and was significantly faster than the frequencies produced by ventilation by all other families (ANOVA; $F_{8,45} = 35.01$; $P < 0.0001$). The ventilatory frequency of the book gills in the horseshoe crab (Limulidae; 2.4 Hz) was not different from the ventilatory frequencies of the vertebrates. Gerreidae frequency (4.6 Hz) was faster than all other fishes but did not differ significantly from that of Sphyraenidae (2 Hz). A Fourier transform power-spectrum analysis revealed that the fundamental frequencies from all teleost and elasmobranch species were within 0.1 Hz of cyclic frequency measurements. Among the invertebrates, Penaeidae had a fundamental frequency of 9.5 Hz, compared with a cyclic frequency of 10.3 Hz, and Limulidae had a fundamental frequency of 1.9 Hz in the power spectrum, compared with a cyclic frequency of 2.4 Hz. The dominant frequency of the background electrical noise was 0.06 Hz and had very little power compared with the prey signal power (fig. 3).

Invertebrates and elasmobranchs produced significantly smaller electric potentials than most of the teleost fishes, except the catfish and mojarra (ANOVA; $F_{10,54} = 9.27$, $P < 0.0001$; fig. 4). Invertebrates produced a mean voltage of 17 μV, elasmobranchs produced a mean voltage of 25 μV, and teleosts produced a mean voltage of 164 μV, approximately eight times greater than that of the invertebrates and elasmobranchs.

Significant differences were also seen among the teleosts with the pufferfish (Diodontidae), snapper (Lutjanidae), and barracuda (Sphyraenidae) producing the greatest voltage. The catfish (Ariidae) produced the smallest mean voltage (39 μV), approximately one order of magnitude smaller than that of the snapper mean voltage (319 μV). There was no relationship between electric potential and total length or mass within or among families (table 3). Although there was a difference in mass between the two elasmobranch species, the voltage did

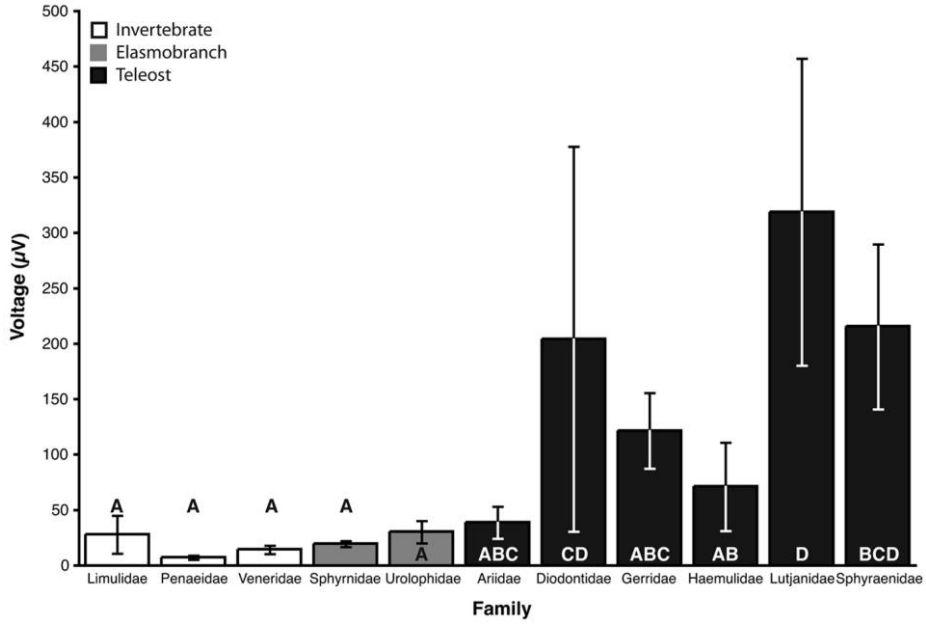

Figure 4. Mean electric potential (μV) for each family. The mean electric potential ($\pm$SD) differed among families. Invertebrates (16.8 $\pm$ 13.1 μV) and elasmobranchs (25.2 $\pm$ 9.0 μV) produced smaller potentials in general than teleosts fishes (163.8 $\pm$ 137.9 μV). Pufferfish (Diodontidae), snapper (Lutjanidae), and barracuda (Sphyraenidae) produced the greatest potential. Bars that share the same letter are not significantly different.

not differ (fig. 5). Additionally, within the teleosts the catfish and snapper were similar in mass but differed greatly in voltage.

The magnitude of the voltage was greater at the head (mouth and gills) of fishes than at the trunk and tail in all families, although they were not significantly different than those at the trunk and tail in some families (table 4). The largest signal was recorded from the lutjanids, which produced a mean potential of 319 μV at the gills.

Voltage produced from the invertebrates and elasmobranchs was too weak to be recorded away from the source; therefore, voltage decay was recorded for teleosts only. The electric potential was measured up to 15 cm away from the mouths of fish and decreased dramatically within the first few centimeters as an inverse power function (fig. 6). The electric field (i.e., voltage gradient) was derived from voltage-decay measurements to determine at what distance from the source an electric signal remained within detection range for elasmobranch predators (table 5). A mean sensitivity of 35 nV cm^{-1} for elasmobranchs was determined from literature values (Kajiura and Holland 2002; Kajiura 2003; Jordan et al. 2009, 2011; McGowan and Kajiura 2009); on the basis of this sensitivity, the detection distance for teleost fishes ranged from 32 to 75 cm (fig. 6; table 5).

Table 3: Summary of regression analyses of voltage against mass (g) and total length (cm)

	Mass			Total length		
Family	Regression equation	R^2	P	Regression equation	R^2	P
Sphyrnidae	$y = 17.141 + .031x$	.46	.21	$y = 11.729 + .302x$	.52	.17
Urolophidae	$y = 54.637 - .050x$	.24	.40	$y = 25.248 + .278x$	.00	.92
Ariidae[a]	...			...		
Diodontidae	$y = 76.896 + .745x$	.14	.33	$y = 23.885 + 11.022x$	.07	.49
Gerreidae	$y = 207.813 - 2.494x$	.36	.29	$y = 331.863 - 16.457x$	.24	.41
Haeumulidae	$y = 77.278 - .018x$	.00	.85	$y = 77.210 - .230x$	.00	.93
Lutjanidae	$y = 541.730 - .521x$	.61	.07	$y = 935.643 - 20.958x$	.52	.11
Sphyraenidae	$y = 172.099 + .187x$	.24	.51	$y = 181.834 + 1.050x$	.02	.85
Limulidae	$y = -25.778 + 1.320x$	.36	.21	$y = -90.079 + 8.070x$	.32	.24
Penaeidae	$y = 1.724 + 2.366x$	.13	.48	$y = -4.310 + 1.691x$	.09	.56
Veneridae	$y = 9.414 + .075x$	.02	.80	$y = 26.984 - 1.462x$	.01	.86
Among all families	$y = 39.948 + 3.461x$	.06	.07	$y = 72.126 + .152x$	.05	.07

[a]Mass and total length data were not available for all specimens, so regression could not be performed on Ariidae.

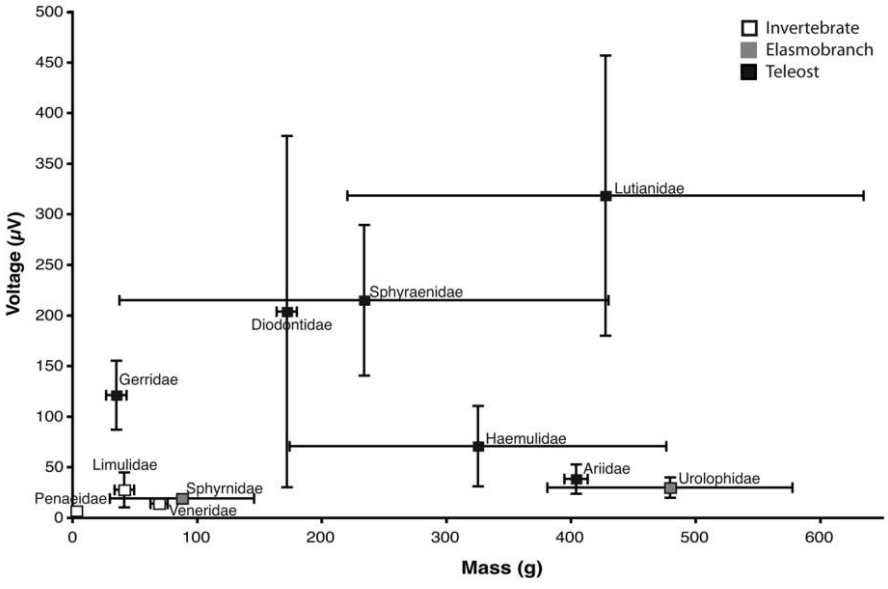

Figure 5. Voltage plotted against mass for all tested species (mean ± SD). There was no relationship between voltage and mass. The invertebrates had the smallest mass and the smallest potential. Although the bonnethead shark (Sphyrnidae) was smaller in mass than the yellow stingray (Urolophidae), they produced similar voltage. Teleosts showed the greatest variation in voltage and mass. The snapper (Lutjanidae) and catfish (Ariidae) were similar in mass, but the snapper produced nearly 300 μV more than the catfish.

Bioelectric Field Stimulus Generator Electric Potential

The bioelectric field stimulus generator sufficiently reproduced a wide range of biologically relevant electric stimuli that represented both invertebrate and vertebrate bioelectric fields (fig. 7). Resistance was inversely related to both salinity and temperature (table 6). The stimulus generator produced 665–1,615 μV at applied currents from 3 to 7 μA in freshwater, 111–1,317 μV at applied currents from 10 to 100 μA in brackish water, and 60–707 μV at applied currents from 10 to 100 μA in saltwater. Voltage produced by the stimulus generator was recorded up to 5 cm away from the source. The voltage decayed as an inverse square and the electric field decayed as an inverse cube with distance from the source (table 5).

Discussion

This study surveyed three families of invertebrate and eight families of fish prey that are consumed by elasmobranchs (table

Table 4: Voltage produced by teleost and elasmobranch fishes and invertebrate prey

Family	Mouth	Gills	Spiracle	Trunk	Tail	*F*, *P*
Sphyrnidae	18.2 ± 2.8^{A}	**18.5 ± 2.6**^{A}		10.6 ± 2.2^{B}	11.2 ± 2.6^{B}	21.7, <.0001
Urolophidae	26.5 ± 13.7^{A}	83.1 ± 32.4^{B}	**30.6 ± 10.1**^{A}	11.9 ± 6.7^{A}	8.6 ± 3.5^{A}	16.0, <.0001
Ariidae	23.1 ± 3.3^{AB}	**39.0 ± 14.4**^{A}		8.8 ± 4.0^{B}	14.1 ± 7.9^{B}	7.1, .01
Diodontidae	113.1 ± 91.9^{A}	**204.5 ± 173.7**^{A}		17.3 ± 9.6^{A}	11.5 ± 4.5^{A}	3.2, .04
Gerreidae	99.4 ± 55.3^{A}	**121.9 ± 34.2**^{A}		9.0 ± 1.7^{B}	7.2 ± 2.4^{B}	16.9, <.0001
Haemulidae	40.9 ± 19.7^{A}	**71.4 ± 39.8**^{B}		12.5 ± 7.3^{C}	11.0 ± 5.8^{C}	15.8, <.0001
Lutjanidae	299.0 ± 147.8^{A}	**319.1 ± 138.4**^{A}		37.8 ± 37.4^{B}	14.8 ± 4.7^{B}	15.2, <.0001
Sphyraenidae	114.6 ± 81.3^{AB}	**215.7 ± 74.4**^{A}		17.8 ± 19.2^{B}	16.0 ± 15.6^{B}	11.3, .0008

	Voltage
Invertebrates:	
Limulidae	**28.3 ± 17.3**
Penaeidae	**7.5 ± 1.8**
Veneridae	**14.6 ± 3.8**

Note. Voltage is reported as mean ± SD. Locations within a family that share the same letter were not different from each other. Locations (boldface) deemed the most biologically relevant for elasmobranch detection were used for comparisons among families. Only one location was recorded in invertebrates and was used in comparisons.

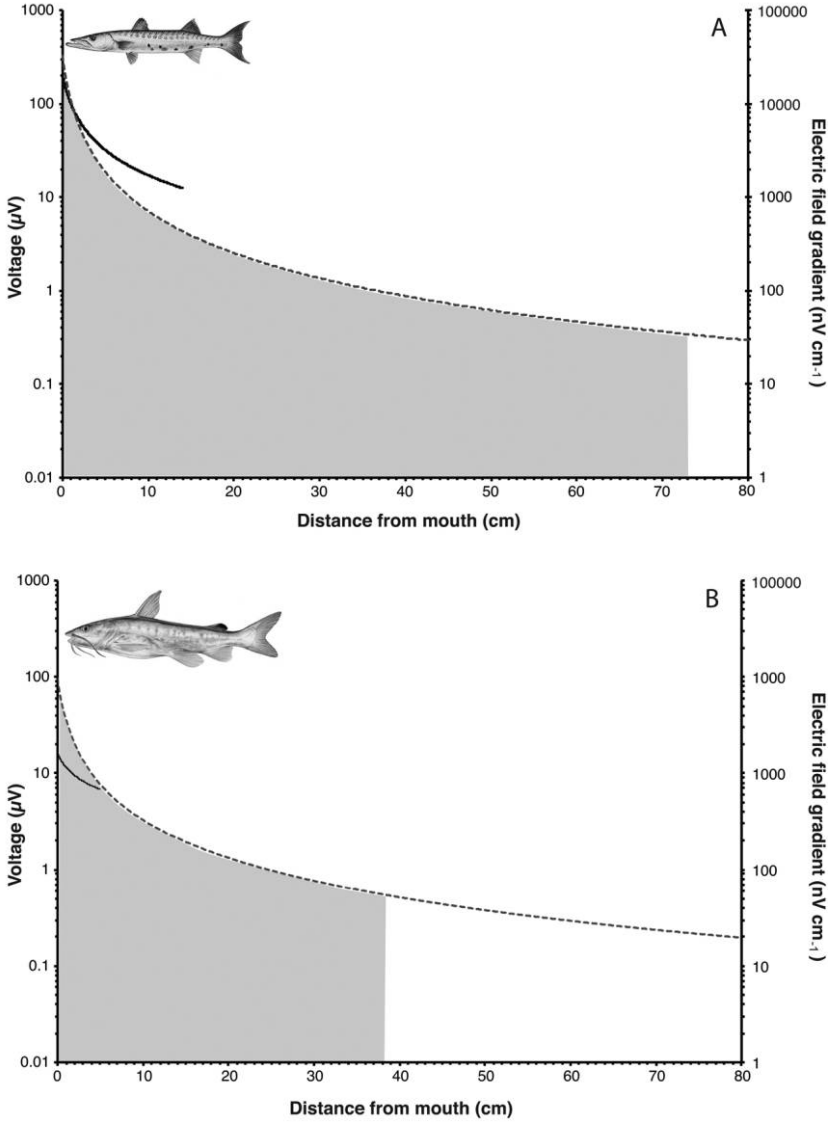

Figure 6. Sphyraenidae (*A*) and Ariidae (*B*) voltage and electric field decay. Voltage was recorded up to 15 cm away from the mouth of teleost fishes. For all teleosts, the magnitude of the voltage decreased as a power function (solid black line). The electric field (dashed line) was calculated as the derivative of the voltage. Elasmobranch median sensitivity of 35 nV cm^{-1} was used to determine the detection distance for elasmobranch predators. Shaded regions under the electric field line represent the range of distances in which each fish is detectable by elasmobranch predators. Fish illustrations are © Diane Rome Peebles. A color version of this figure is available in the online edition of *Physiological and Biochemical Zoology*.

1). The magnitude and frequency of bioelectric fields differed among families as well as among individuals. These results expand previous knowledge of the characteristics of bioelectric field production in elasmobranch prey.

Bioelectric fields in seawater are created by the release of charged ions from a biological source into a conductive medium (Kalmijn 1972; Wilkens and Hofmann 2005). The conductive properties of seawater enable propagation of these signals away from the source, and they can act as signals for predators to detect prey (Kalmijn 1966), for conspecifics to find mates (Tricas et al. 1995), and for prey to avoid predators (Sisneros et al. 1998). Marine animals release ions during their normal physiological processes of osmoregulation that take place at the gills, gastrointestinal tract, and renal glands (Foskett et al. 1983). Therefore, mucous membrane–lined openings associated with these organs are active sites of ion exchange with the external environment and were expected to produce higher-magnitude electric fields than the skin, which is relatively impermeable to ion and water loss (Foskett et al. 1983). Invertebrates and elasmobranchs maintain internal environments that are nearly isosmotic with their environment (Robertson 1953; Ballantyne 1997) and, therefore, were expected to produce smaller electric potentials than teleosts that are hyposmotic and lose more ions to the environment (Foskett et al. 1983).

Table 5: Point source voltage and electric field decay equations and theoretical elasmobranch detection distance from electric potential decay measurements, with a median sensitivity of 35 nV cm^{-1} for elasmobranchs

Family	Point source voltage	Electric field	Detection distance (cm)
Ariidae	$y = 15.98x^{-.48}$	$y = 7.62x^{-1.48}$	38
Diodontidae	$y = 76.55x^{-1.19}$	$y = 90.72x^{-2.19}$	36
Gerreidae	$y = 74.39x^{-1.27}$	$y = 94.77x^{-2.27}$	32
Haemulidae	$y = 32.65x^{-.67}$	$y = 21.78x^{-1.67}$	47
Lutjanidae	$y = 127.74x^{-.97}$	$y = 124.30x^{-1.97}$	63
Sphyraenidae	$y = 197.58x^{-1.02}$	$y = 201.33x^{-2.02}$	73
Prey simulating	$y = 118.59x^{-1.95}$	$y = 231.49x^{-2.95}$	20

Osmoregulatory strategies likely explained much of the difference in bioelectric potential between the large-potential hyposmotic teleosts and the small-potential isosmotic invertebrates and elasmobranchs.

Frequency Measurements

The oropharyngeal cavity of fish is the major site of ion exchange that results from osmoregulation. The rhythmic expansion and contraction of the buccal and pharyngeal cavities during respiration alternately exposes and encloses the mucous membranes of the oropharynx and results in a modulation of the standing DC electric field (Kalmijn 1974; Wilkens and Hofmann 2005). For most families, the ventilatory frequency was ≤2 Hz, which corresponds to the peak sensitivity frequency of elasmobranch electroreceptors. Only two families produced frequencies outside this range—both the Gerreidae (4.6 Hz) and the Penaeidae (10.3 Hz) had frequencies higher than those of the other families. The gerreids were the smallest of the fish studied, and their higher ventilatory frequency may reflect the metabolic demands of smaller organisms, which require greater oxygen consumption per unit mass than larger organisms (von Bertalanffy 1957). The frequency recorded from the penaeids reflects the collective movement of all pairs of the swimmerets rather than ventilatory movements. Ventilatory frequency has not been previously measured from crustaceans, in part because the gills are protected beneath the carapace (Bauer 1999), which inhibits propagation of electric fields away from the animal. Therefore, the electric field produced by the rhythmic movement of the swimmerets was considered to be the most biologically relevant source that is most likely to be detected by elasmobranchs. Higher-frequency stimuli that are outside the peak frequency range of elasmobranch electroreceptors, like the penaeids and gerreids, may possess sufficient power in their harmonics that are near the maximum sensitivity of the predator to stimulate electroreceptor cells. However, in the case of penaeids and gerreids, harmonics near the peak sensitivity (i.e., 1–2 Hz) were rare and were ≤1% of the power of the dominant frequency when present (fig. 3). Although the fundamental frequencies of the elasmobranchs and teleosts were within 0.1 Hz of the cyclic measurements, the fundamental frequencies of the invertebrates were 0.8 Hz (penaeids) and 0.5 Hz (limulids) lower than the cyclic measurements, which likely reflect the variation in frequency within an individual that was not seen in the vertebrates.

Frequency was not recorded from the venerids or sphyrnids because both had a constant water flow over the gills rather than the rhythmic water flow created by pumping water over the gills. Voltage oscillations for all other groups correlated to respiratory movements or to swimmeret movements in the penaeids. These data are similar to those reported by Haine et al. (2001) for three teleost species, *Pomacentrus amboinensis*, *Sillago sihama*, and *Gerres filamentosus*, which had electric field frequencies of approximately 1.5 Hz. Kalmijn (1972) reported low-frequency AC fluctuations (<20 Hz) in teleosts and that as frequency increased in an individual, electric potential increased accordingly. No such trend between voltage magnitude and frequency was seen in this study.

Voltage Amplitude

The signal location considered most likely to be detected by elasmobranch predators was used for interfamily comparisons. For teleost fishes and bonnethead sharks, the gills were used as the most biologically relevant signal, whereas the spiracle was used for stingrays. Only one location was measured from invertebrates and was used in comparisons of voltage magnitude among families. The mouth and gills of fish produced potentials that were 1.6–22.6 times greater than those of the trunk and tail (table 4). The greatest voltage of any family was 319 μV at the gills of Lutjanidae (table 4; figs. 4, 5). Similarly, Haine et al. (2001) recorded potentials from 40 to 100 μV at the head of teleost fish and from 1 to 2 μV at the caudal peduncle, although details that describe interspecific variation were not provided.

The electric potential was greater in teleosts than in invertebrates and elasmobranchs, as reported in previous studies (Kalmijn 1972, 1974; Haine et al. 2001), although there was some overlap in voltage production among the groups (figs. 4, 5). The invertebrates did not differ from the elasmobranchs and some teleost fishes, including the ariids, gerreids, and haemulids, even though the gerreids and haemulids produced voltage that was

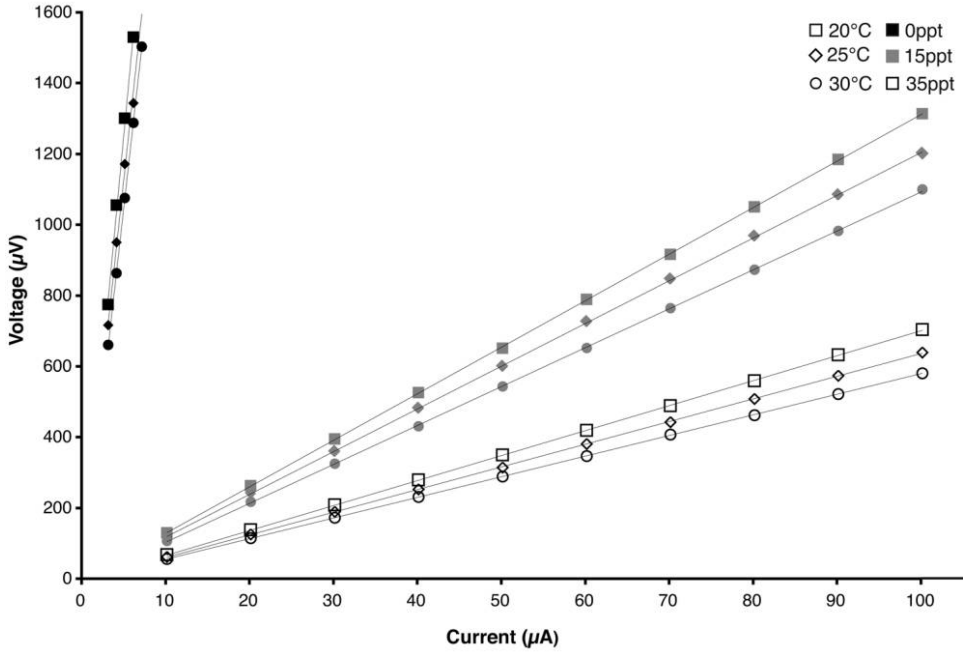

Figure 7. Voltage produced by the bioelectric field generator at a wide range of biological current intensities at three temperatures (20°C, 25°C, and 30°C) and salinity treatments (0, 15, and 35 ppt). Squares = 20°C, diamonds = 25°C, circles = 30°C, black = freshwater (0 ppt), gray = brackish (15 ppt), white = seawater (35 ppt). Equations and resistance values are provided in table 5.

nearly double that of the invertebrates and elasmobranchs (fig. 5). Although most potentials from elasmobranchs were similar to those reported by Kalmijn (1972; <50 μV), the gills of the urolophids produced an average potential of 82 μV. One individual produced 128 μV at the gills, which was equal to the average voltage for the gerreids and greater than that of the haemulids. Potentials greater than 2 mV were recorded from an individual pufferfish and an individual mullet, both of which were excluded from statistical analyses. Although these individuals were assumed to be outliers, they may be indicative of extremes of natural variation in electric fields in teleosts, and potentials of this magnitude have not been reported previously, even for wounded individuals.

The cause of the wide range of variation within the teleosts remains speculative. Although all bony fishes in this study are neopterygiians, the ariids belong to the basal teleost group, the ostariophysii, whereas all other fishes are among the most highly derived of the teleosts (Moyle and Cech 2004). Perhaps more important than the phylogenetic relationships among species is variation in gill surface area with greater gill surface facilitating a greater exchange of ions, leading to greater-magnitude electric potentials (Gonzalez and McDonald 1994; Nilsson 2007). Although gill surface area has not been strongly correlated to body size, it has been correlated to activity, with more active species possessing a greater area to accommodate higher oxygen demands (Gray 1954; Hughes 1966). In this study, the benthically associated ariids were considered the most inactive fish (according to criteria described by Gray 1954) and also had the smallest potential. Lutjanidae was considered the most active family in this study and produced the greatest potential. The diodonts, gerreids, haemulids, and sphyraenids are moderately active compared with the ariids and lutjanids, and they produced intermediate voltages. Future studies should investigate the relationship among fish activity, gill surface area, and voltage production to verify this hypothesis.

In addition to variation in electric potential among families of teleosts, there was also variation among individuals within a family. Some of the individual variation may be attributed to minor differences in electrode placement between individuals (Wilkens and Hofmann 2005) as well as to the stress of restraint and anesthesia throughout the experiments, which may have affected individuals differently. The individual variation in electric potential may also be attributed to unknown physiological states that differed among individuals. These differences likely reflect physiological responses that fish undergo as they encounter changes in oxygen, temperature, pH, and salinity in their environment.

This study failed to find a relationship between electric potential and mass or length within or among families (table 3). For example, the two elasmobranchs differed greatly in mass but produced similar bioelectric potentials (fig. 5). In contrast, the ariids and the lutjanids were similar in mass, but the lutjanids produced a voltage significantly greater than that of the ariids. Although the R^2 values obtained in regression analyses were too low to draw definitive conclusions, these results suggest that (1) the previously reported size-related differences in potential may have been due to small sample sizes that did not adequately account for the variation inherent in bioelectric field

Table 6: Current-voltage relationships and resistance (Ω) calculated from the bioelectric field generator

Temperature salinity (ppt)	20°C	25°C	30°C
0	$y = 251.05x + 39.03$	$y = 218.35x + 70.61$	$y = 211.03x + 26.64$
	$R = 260.1$	$R = 233.8$	$R = 216.9$
15	$y = 13.15x + 2.24$	$y = 12.07x + 2.84$	$y = 11.00x - 1.40$
	$R = 13.2$	$R = 12.2$	$R = 11.0$
35	$y = 7.05x + .43$	$y = 6.41x + .08$	$y = 5.82x + 1.70$
	$R = 7.1$	$R = 6.4$	$R = 5.9$

production or that (2) size-dependent electric fields may be limited to invertebrates (Haine et al. 2001; Patullo and Macmillan 2004; Kimber et al. 2011).

Voltage Decay and Elasmobranch Responses to Prey-Simulating Electric Fields

Electric signals were recorded up to 15 cm from the mouth of teleost species, with larger-magnitude signals being detected farther away from the source than small signals. This indicates that species with larger potentials, like the sphyraenids, can be detected from a greater distance than those with small signals, like the ariids (fig. 6). Voltage decayed over distance as an inverse power function (table 5). The first-order derivative of the power function yielded the electric field (μV cm^{-1}) and was calculated to determine the distance at which elasmobranchs would be able to detect teleost prey. An average sensitivity of 35 nV cm^{-1} obtained from literature values of elasmobranch electrosensitivity (table 1) was used to calculate the distance at which elasmobranch predators can detect their prey on the basis of electric signals (Kajiura and Holland 2002; Kajiura 2003; Jordan et al. 2009; McGowan and Kajiura 2009). Electric fields were reduced to 35 nV cm^{-1} between 32 cm (gerreids) and 75 cm (sphyraenidae; fig. 6). The 35nV cm^{-1} value was based on the median sensitivity from behavioral assays, and although most species responded to electric fields <1 nV cm^{-1} in these studies, the percentage of responses to electric fields of this magnitude is small (Kajiura and Holland 2002; Kajiura 2003; Jordan et al. 2009; McGowan and Kajiura 2009). Therefore, theoretical detection distances based on median sensitivity represent a conservative estimate. If the <1 nV cm^{-1} sensitivity is applied to the detection distance equation, the theoretical detection distance for the barracuda (Sphyraenidae) would be 4.4 m from the source, which is likely an overestimation due to difficulty in extrapolating data beyond the range recorded in the laboratory from electric fields that may have been artificially constrained by the limits of the tank. Additionally, limited electrical noise within the experimental tank compared with that present in natural environments complicate extrapolation to the natural environment at greater distances. Caution was taken to minimize these constraints by measuring electric fields in mid-water and by placing the plastic-mesh frame and acrylic block used to support study organisms on only one side of the organism, opposite of the recording electrode. The bioelectric field stimulus generator demonstrated voltage decay as an inverse square function and is indicative that the generator produced a near ideal dipole under the experimental conditions. Although we expected prey stimuli to decay at the same rate as the prey-simulating dipole, all fish voltages decayed at a rate slower than that of an ideal dipole. Bioelectric fields are more complex and not only are composed of a dipole electric field but also contain components that are quadrapole, octopole, and so on, which may account for the differences in signal decay between the prey-simulating stimulus and actual prey stimuli.

Behavior studies presented electric stimuli produced by the bioelectric field generator in the range of 39–64 μV to elasmobranchs to quantify sensitivity to weak electric fields. The magnitude of these stimuli is equivalent to the voltage produced by the mouth and gills of ariids and haemulids in this study. Elasmobranchs detect and orient to these simulated stimuli from 22 to 40 cm from the source (table 1), similar to predicted detection distances calculated in this study (table 5). The stimulus generator was designed to produce dipole electric fields that simulate those prey items measured by Kalmijn (1972). Voltage produced by the stimulus generator was recorded at temperatures and salinities (fig. 7) that reflect the physical properties of environments that are inhabited by elasmobranch fishes and that influence how electrosensory systems are used. We show that the stimulus generator does adequately simulate bioelectric fields of prey. Equations for the relationship among salinity, temperature, and voltage are provided (table 6) to facilitate selection of an appropriate prey-simulating stimulus for use in studies investigating electrosensitivity. Additionally, the stimulus generator produced a standing DC field only. With the frequency information described in this study, a new stimulus generator could be constructed to more accurately reproduce the modulation in this field that results from ventilatory activities of prey.

Bioelectric fields remain poorly understood. Future studies should further investigate sources of AC and DC potentials, behavioral responses of elasmobranch predators to different components of electric fields, sources of variation within and among groups, and size-related differences in potential by recording voltage from a wider range of sizes within species to better understand how electroreceptive fishes detect and localize prey using electric signals.

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