

SPECIAL ISSUE REVIEW PAPER

Electroreception in marine fishes: chondrichthyans

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Abstract

Electroreception in marine fishes occurs across a variety of taxa and is best understood in the chondrichthyans (sharks, skates, rays, and chimaeras). Here, we present an up-to-date review of what is known about the biology of passive electroreception and we consider how electroreceptive fishes might respond to electric and magnetic stimuli in a changing marine environment. We briefly describe the history and discovery of electroreception in marine Chondrichthyes, the current understanding of the passive mode, the morphological adaptations of receptors across phylogeny and habitat, the physiological function of the peripheral and central nervous system components, and the behaviours mediated by electroreception. Additionally, whole genome sequencing, genetic screening and molecular studies promise to yield new insights into the evolution, distribution, and function of electroreceptors across different environments. This review complements that of electroreception in freshwater fishes in this special issue, which provides a comprehensive state of knowledge regarding the evolution of electroreception. We conclude that despite our improved understanding of passive electroreception, several outstanding gaps remain which limits our full comprehension of this sensory modality. Of particular concern is how electroreceptive fishes will respond and adapt to a marine environment that is being increasingly altered by anthropogenic electric and magnetic fields.

KEYWORDS

Ampullae of Lorenzini, Chondrichthyes, Elasmobranchii, Holocephali, passive electroreception

1 | INTRODUCTION

Electroreception is a phylogenetically widespread sensory modality that has arisen several times throughout vertebrate evolutionary history but is most often seen in fishes, some amphibians and a few mammals. The electroreceptive system in many marine species includes ampullary organs that contain sensory cells and a network of canals that radiate from the ampullae to dermal pores. Ampullary electroreceptors are found in non-teleost fishes including the sharks, skates, rays and chimaeras (Chondrichthyes), bichirs and reedfishes (Polypteriformes), sturgeons and paddlefishes (Acipenseriformes), lungfishes (Dipnoi), coelacanths (Coelacanthiformes), caecilians and urodeles (Amphibia) and some teleosts (Siluriformes, Gymnotiformes and some Osteoglossiformes) that generally occupy freshwater

habitats. These electroreceptors develop from lateral line placodes, which makes them a derived form of sensory hair cells similar to those in the mechanosensory neuromast organs of the lateral line (Gilles *et al.*, 2012). This review provides historical and biological context of electroreception by focusing on how chondrichthyans use this sensory modality in their environment. We describe the current understanding of the passive mode of electroreception, the morphology, physiological function and behaviours mediated by the electrosensory system within an ecological context. These aspects are fundamental to understanding how electrosensitive species might respond to electrical changes in the marine environment. The review complements that of electroreception in freshwater fishes by Crampton (2019), which provides a comprehensive state of knowledge regarding the evolution of electroreception, particularly active electroreception and

electric signal generation in electric fishes. For further specific reviews on chondrichthyan electroreception, readers are referred to Collin and Whitehead (2004), Gardiner *et al.* (2012), Kajiura *et al.* (2010), Tricas and Sisneros (2004) and Wilkens and Hofmann (2005).

Electroreception in marine fishes is best known in chondrichthyans and this system was first described morphologically by Stenonis (1664) and Lorenzini (1678), for whom the sensory organs were named (*i.e.*, Ampullae of Lorenzini). Initially, the ampullae were proposed to function as mechanoreceptors (Dotterweich, 1932; Lowenstein, 1960; Murray, 1957, 1960a; Parker, 1909), temperature sensors (Hensel, 1955; Sand, 1937) and salinity sensors (Lowenstein & Ishiko, 1962), but the electroreceptive function was finally demonstrated by Murray (1960b) and Dijkgraaf and Kalmijn (1962).

The electroreceptors of obligate marine chondrichthyans detect very weak bioelectric potentials of *c.* 1 nV cm^{-1} (Jordan *et al.*, 2009, 2011; Kajiura, 2003; Kalmijn, 1972), but behavioural sensitivity declines by three orders of magnitude for euryhaline species in fresh water (McGowan & Kajiura, 2009) and by five orders of magnitude for obligate freshwater species (Harris *et al.*, 2015). The behaviours mediated by the electrosensory system include: orientation to prey-simulating electrical fields (Kalmijn, 1974, 1982; Pal *et al.*, 1982; Kimber *et al.*, 2011), foraging and prey capture (Bedore *et al.*, 2014, Blonder & Alevizon, 1988; Jordan *et al.*, 2009, 2011; Kajiura, 2003; Kajiura & Fitzgerald, 2009, Kalmijn, 1971, 1982; Tricas, 1982), conspecific detection (Tricas *et al.*, 1995), predator avoidance (Ball *et al.*, 2015; Kempster *et al.*, 2012a; Sisneros *et al.*, 1998), learning and habituation (Kimber *et al.*, 2014), and possibly for navigation using the geomagnetic field (Anderson *et al.*, 2017; Kalmijn, 1974, 1978, 1988, 2000; Newton, 2017; Newton & Kajiura, 2017; Paulin, 1995). Electroreception in chondrichthyans is specifically adapted for the passive detection of bioelectric fields, but a small number of chondrichthyan species emit biogenic electric organ discharges (EOD) that are used in prey capture (*e.g.*, electric rays Bray & Hixon, 1978; Lowe *et al.*, 1994) and possibly in conspecific communication (Bratton & Ayers, 1987; New, 1994).

As electroreception is an important sensory mode of Chondrichthyes (and has presumed functional importance in the less well known Coelacanthiformes and Acipenseriformes) a clear understanding of the biology of passive electroreception in the marine environment is essential in the context of interpreting its ecological significance. This is particularly important when considering how anthropogenic alterations to the natural electric and magnetic fields in the marine environment might affect the sensory biology of electroreceptive fishes and their ability to forage, avoid predators, find mates, orientate and migrate to suitable habitats.

2 | ANATOMY

The functional units of the chondrichthyan electrosensory system are a series of Ampullae of Lorenzini connected to a network of canals that radiate away from the ampullae and terminate at pores in the skin (Figure 1). Pores (< 1 mm diameter) are primarily located on the head of sharks and chimaeras with additional pores along the pectoral fins

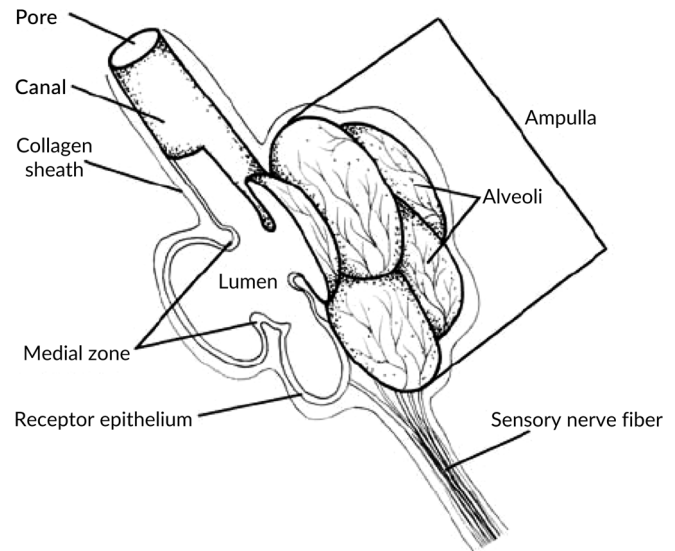


FIGURE 1 Schematic representation of a single ampulla of Lorenzini of a rhinobatid, *Aptychotrema rostrata*. The canal pore extends from a somatic pore, widening proximally to an ampullary bulb. The ampulla is formed by several alveoli arranged in a grape-like formation where the epithelium of adjacent alveoli and the canal is separated by the medial zone. A sensory nerve fibre extends from the proximal end of the ampulla. Reproduced with permission from Wueringer and Tibbetts, 2008

of batoids. Each pore is connected by a canal to a subdermal ampulla that is formed by several bulbous diverticula that are lined with hundreds to thousands of sensory hair cell receptors and support cells that comprise the sensory epithelium (Waltman, 1966). Tight junctions between the cells lining the walls of the canal and ampulla maintain an electrically resistant barrier between the internal lumen and external portions of the organs (Waltman, 1966). A glycoprotein gel with conductive properties similar to that of seawater (Waltman, 1966) fills the canal and ampullary lumen such that the surface pores are electrically connected to the apical portion of the sensory epithelium (Brown *et al.*, 2002, 2005). Bilateral clusters of three to five ampullae form in chimaeras and sharks and four to six clusters are found in batoids (Fields *et al.*, 1993; Rivera-Vicente *et al.*, 2011; Wueringer *et al.*, 2011; Wueringer & Tibbetts, 2008). Canals radiate away from the clusters in all directions and the spatial arrangement (Figure 2), combined with length of each canal, dictates the three-dimensional shape and sensitivity of the electroreceptive field (Rivera-Vicente *et al.*, 2011; Tricas, 2001).

Once an electrical signal is received and transduced by the receptor, it is transmitted from the apical to the basal portion of the sensory cell, across a ribbon synapse to an afferent neuron and ultimately enters the central nervous system (CNS) at the dorsal root of the anterior lateral line nerve. These primary afferents terminate in the ipsilateral portion of the dorsal octavolateral nucleus (DON) of the medulla oblongata of the hindbrain (Bodznick & Northcutt, 1980). The somatotopic arrangement is such that the anterior electroreceptor afferents project to the ventral portion of the DON, whereas those of the posterior receptors project to the dorsal DON (Bodznick & Boord,

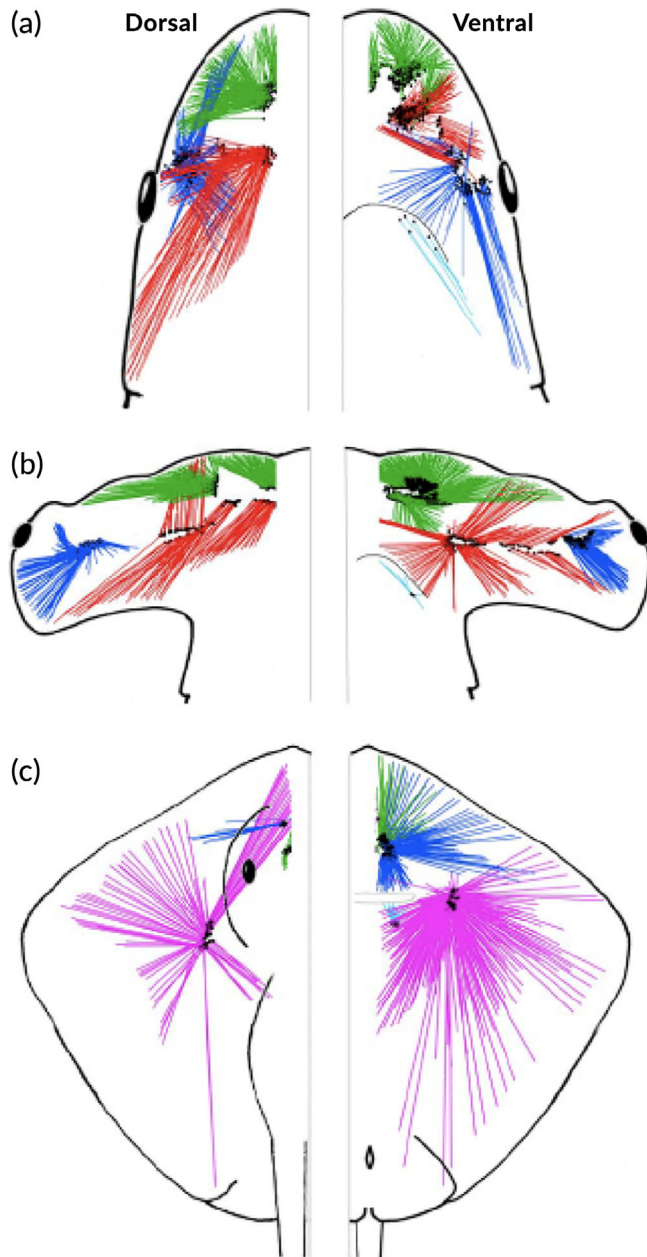


FIGURE 2 Horizontal view of the electrosensory arrays of (a) *Carcharhinus plumbeus*, (b) *Sphyrna lewini* and (c) *Dasyatis lata*. Canals with pores on the dorsal and ventral surface are shown on the left and right side of the figure, respectively. Canals from each ampullary group are: —, BUC; —, SOa; —, Sop; —, HYO. ●, Location of ampullae at the base of canals. Reproduced with permission from Rivera-Vicente *et al.* (2011)

1986). Ascending pathways continue from the DON to the contralateral portions of the optic tectum and the lateral mesencephalic nucleus of the mesencephalon (Bodznick & Boord, 1986; Schmidt & Bodznick, 1987), with continued projections to the telencephalon (Bodznick & Northcutt, 1984) and cerebellum (Tong & Bullock, 1982). Detailed work that integrates brain morphology, medulla development, electroreceptor pore distributions and environmental diversity into discerning patterns across chondrichthyan electrosensory ecology can be found in Kajiura *et al.* (2010).

2.1 | EcoMorphology

The number of electrosensory pores, their distribution along the body and the length and spatial orientation of ampullary canals will determine the size, shape and resolution of the electrosensory field. Pore number and location on the body is correlated with several potentially confounding factors including; phylogenetic relatedness, morphological similarity, species distribution within and across habitats and diet preferences (Kempster *et al.*, 2012b). To date, the ampullary pore numbers quantified range from the relatively low value of 148 in the Port Jackson shark *Heterodontus portusjacksoni* (Meyer 1793) (Raschii, 1984), to 3067 in the scalloped hammerhead shark, *Sphyrna lewini* (Griffith & Smith 1834) (Kajiura, 2001). Because individuals do not grow new pores or redistribute them during development, the electrosensory resolution decreases as the inter-pore distance increases throughout ontogeny (Kajiura, 2001). As the pores grow further away from the subdermal ampullae, the canals connecting them will lengthen and increase the sensitivity of the receptor cells (Sisneros *et al.*, 1998). Therefore, as chondrichthyans age they will experience a net loss of electroreceptive resolution, a gain in receptor sensitivity and a larger sensory field that samples a greater volume. A similar phenomenon is seen in species with morphological specialisations, such as the cephalofoil of *S. lewini* and the rostrum of the largetooth sawfish *Pristis pristis* (L. 1758), where cranial extensions allow the pores to spread further away from the ampullae and results in larger electrosensory fields and increased sampling areas (Kajiura, 2001; Wueringer, 2012; Wueringer *et al.*, 2011).

One example where phylogeny might dictate pore number instead of the increased surface area of morphological specialisations, is seen within the order Carcharhiniformes. The bull shark *Carcharhinus leucas* (Valenciennes 1839) lacks the cephalofoil of the sphyrnids but has up to 2913 pores (Whitehead *et al.*, 2015), which is similar to *S. lewini* (Kajiura, 2001). Conversely, the influence of phylogeny, morphology and habitat on pore number is difficult to discern in stingrays with similar morphologies and habitat distributions from the family Dasyatidae. The blue-spotted maskray *Neotrygon trigonoides* (Castelnau 1873) (or *Neotrygon kuhlii* (Müller & Henle 1841)), the estuary stingray *Hemistrygon fluviorum* (Ogilby 1908) and the brown whipray *Maculabatis toshi* (Whitley 1939) have similar pore counts of 1152, 1204 and 1074, respectively (Camilieri-Asch *et al.*, 2013; Gauthier *et al.*, 2018). These rays occur in nearshore bays with the exception of the euryhaline *H. fluviorum*. This species is distinct from its marine counterparts because it has smaller diameter pores with shorter canals (Camilieri-Asch *et al.*, 2013), which allow it to detect electrical stimuli in less saline mediums with lower electrical conductivity. In some cases, habitat might impose a strong selective pressure upon the number of pores in species with similar phylogenetic histories and morphological adaptations. Within the family Pristidae, the freshwater *P. microdon* occurs nearshore and often in fresh, turbid waters, whereas the narrow sawfish *Anoxypristis cuspidata* (Latham 1794) occupies clearer coastal and offshore waters. The twofold increase in pores seen in *P. microdon* compared with *A. cuspidata* would increase electroreceptive resolution in the freshwater

sawfishes and might allow them to forage more successfully in habitats with low electrical conductivity and reduced visual cues compared with the *A. cuspidata* (Wueringer *et al.*, 2011).

The location of pores along the body and the orientation of the subdermal ampullary canals determines the spatial representation and direction of the electrosensory field around the head (Riviera-Vicente *et al.*, 2011). The highest density of pores is found near the mouth (Figure 3) because the primary function of electroreception is to detect prey and correctly position the subterminal mouth during the final strike of foraging (Chu & Wen, 1979; Cornett, 2006; Kajiura *et al.*, 2010). Therefore, pore number and location correlate with the foraging strategy (Jordan, 2008; Raschi, 1986; Wueringer *et al.*, 2011). Yet they also reflect the habitat of a species with fewer pores spread across the body in those that inhabit clear offshore waters and dense aggregations of numerous pores in species that live among the benthos and in turbid waters (Jordan, 2008; Raschi, 1986; Wueringer

et al., 2011). Relatively few pores and low electrosensory resolution are seen in species that feed with an indiscriminate suction or ram-feeding method of prey capture. For example, the basking shark *Cetorhinus maximus* (Gunnerus 1765) and megamouth shark *Megachasma pelagios* (Taylor, Compagno & Struhsaker 1983) are pelagic planktivores (301 and 225 pores, respectively) that have most of their pores distributed dorsally (Figure 4) around the anterior margin of the mouth (Kempster & Collin, 2011a, 2011b). These fishes live in the clear water of the open ocean and approach large groups of their small prey directly from the side or below. Piscivorous chondrichthyans that live in the water column, such as the sandbar shark *Carcharhinus plumbeus* (Nardo 1827) or pelagic stingray *Pteroplatytrygon violacea* (Bonaparte 1832) can encounter prey in all three spatial dimensions and their pores are more evenly distributed dorsoventrally (Jordan, 2008; Kajiura, 2001). The Australian angel shark *Squatina australis* (Regan 1906) and wobbegong shark

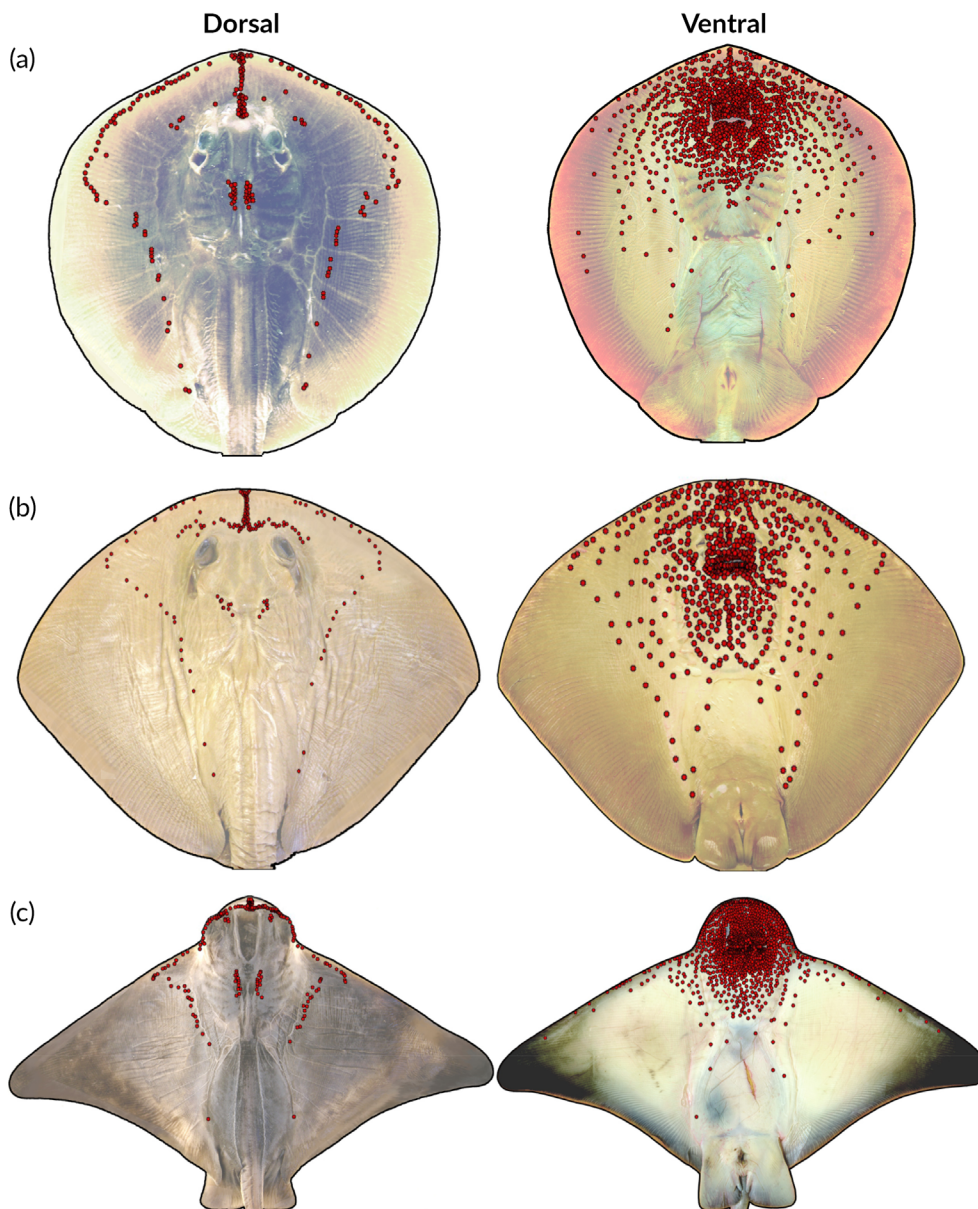
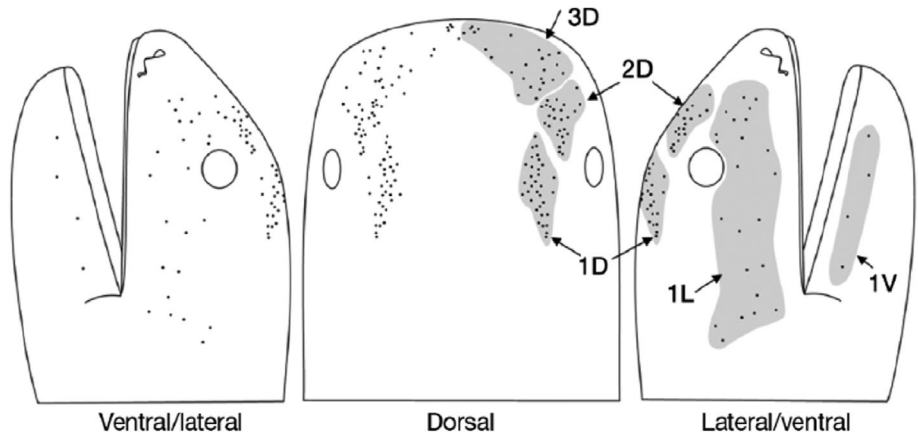


FIGURE 3 Electrosensory pore distribution maps of the dorsal and ventral surfaces of (a) *Urobatis halleri*, (b) *Pteroplatytrygon violacea* and (c) *Myliobatis californica*. Reproduced with permission from Jordan (2008)

FIGURE 4 Electrosensory pore distribution map of *Megachasma pelagios*. D, dorsal; L, lateral; V, ventral. Reproduced with permission from Kempster and Collin (2011b)



Orectolobus maculatus (Bonnaterre 1788) have the majority of their pores located dorsally (Figure 5) because they are benthic associated predators that ambush prey from below (Egeberg *et al.*, 2014). The yellow stingray *Urobatis jamaicensis* (Cuvier 1816) and *N. kuhlii*, are benthic species that forage on infaunal and epifaunal prey, which results in more pores along their ventral surfaces (Bedore *et al.*, 2014; Camilieri-Asch *et al.*, 2013). A high ventral: dorsal distribution is also seen in the shovelnose rays (Rhinobatidae) that forage on benthic prey but use their disc to pin and manipulate prey into their mouth (Wueringer, 2012; Wueringer *et al.*, 2009). On the other hand, the

pristids are related to rhinobatids but have the derived rostrum with a higher proportion of dorsal pores to facilitate feeding on free swimming prey (Wueringer, 2012; Wueringer *et al.*, 2012b).

Pore distribution and the percentage of coverage in the wing surface area of batoids correlates with swimming styles (Jordan, 2008) that range from undulating waves passing down the pectoral fins to the oscillation of the fins in a flapping motion. Genera that employ some form of undulatory swimming, such as *Raja* (L. 1758), *Urobatis* (Garman 1913) and *Himantura* (Müller & Henle 1837) (or *Dasyatis Rafinesque* 1810) (Rosenberger, 2001), use their fins for locomotion,

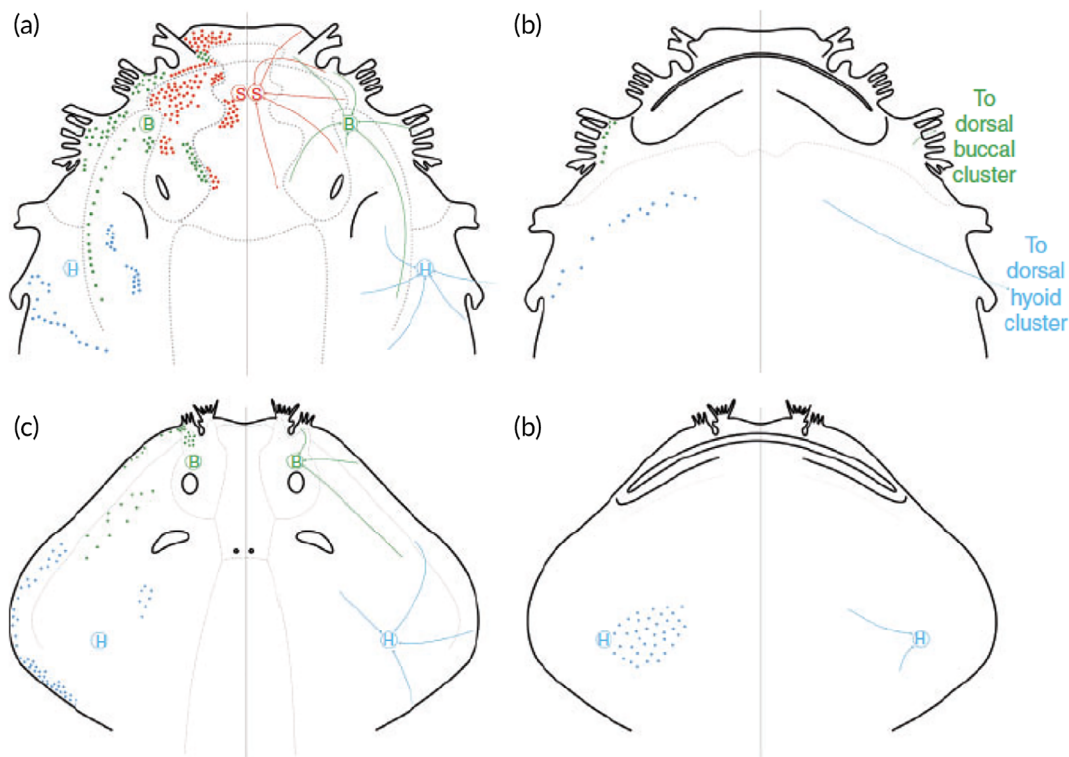


FIGURE 5 Distribution pattern of electrosensory pores on the (a) dorsal and (b) ventral surface of *Orectolobus maculatus* and (c) the dorsal and (d) ventral surface of *Squatina australis*. Approximate length and direction of canals associated with each pore cluster are highlighted (on the right side of the head) by arrows leading from the pore opening to the cluster of electroreceptors. —, The approximate position of the lateral line canals; S, superficial ophthalmic cluster; B, buccal cluster; H, hyoid cluster. Reproduced with permission from Egeberg *et al.*, (2014)

tactile prey detection and prey manipulation during capture. Consequently, they have more pores spread out to the anterior margins of the pectoral fins (Bedore *et al.*, 2014; Jordan, 2008). However, members of the genera *Aetobatus* (Blainville 1816), *Rhinoptera* (Cuvier 1829), *Myliobatis* (Cuvier 1816) and *Mobula* (Rafinesque 1810) are purely oscillatory swimmers (Rosenberger, 2001) that use their pectoral fins exclusively for locomotion. In these species, the pores are primarily restricted to the head and cephalic lobes (Bedore *et al.*, 2014; Jordan, 2008; Mulvany & Motta, 2014), which are the principal structures used for prey detection and capture. Limiting the pores to areas along the pectoral fins with minimal movement reduces the self-generated electrical noise created during locomotion and enhances the electrosensory signal-to-noise ratio.

The secondary function of electroreception is the detection of predators, which may be more important for embryonic and juvenile or early-life stage chondrichthyans that are less mobile, smaller and more vulnerable to predation than adults (Ball *et al.*, 2015). Benthic chondrichthyans resting on the substrate have limited routes of escape compared with pelagic species and are more likely to encounter predatory attacks from above or behind. Consequently, benthic species can distribute their anti-predatory countermeasures, such as cryptic coloration, tail barbs, fin spines and additional electrosensory pores, along the dorsal and posterior body surfaces. *Urobatis jamaicensis* and the round stingray *Urobatis halleri* (Cooper 1863) are small benthic batoids that have relatively more dorsal pores located near the posterior margin of its disc, whereas the benthopelagic cownose ray *Rhinoptera bonasus* (Mitchill 1815) and bat ray *Myliobatis californica* (Gill 1865) have the majority of their dorsal pores concentrated near the head (Bedore *et al.*, 2014; Jordan, 2008). The epaulette shark *Hemiscyllium ocellatum* (Bonnaterre 1788) is a small benthic species that has ampullary pores located near the pelvic fins (Winther-Janson *et al.*, 2012), a condition that has yet to be described in larger epibenthic or pelagic selachians. Large benthic batoids may rely more on their size and less on electroreception as a predatory deterrent. If so, this might explain why the shovelnose rays *Aptychotrema rostrata* (Shaw 1794) and *Glaucostegus typus* (Anonymous (Bennett) 1830) and the sawfishes, *P. microdon*, *Pristis clavata* (Garman 1906) and *A. cuspidata*, have dorsal pores located posterior to the eyes, spiracles and along the body toward the pectoral fins, but none along the pelvic fins (Wueringer & Tibbetts, 2008; Wueringer *et al.*, 2012a).

The shape of the sensory ampullae varies among species (Jørgenson, 2005; Gauthier *et al.*, 2018) and can be simple with a single enlarged diverticulum, as in the electric ray *Torpedo marmorata* (Risso 1810) or several simple ampullae can assemble into a group, as seen in six-gill sharks *Hexanchus* spp. In most elasmobranchs, the ampullae are more lobular with multiple diverticuli communicating with a single ampulla, whereas the ampullae of the chimaera, *Hydrolagus colliei* (Lay & Bennett 1839) have diverticuli that are more elongated. In some sharks the diverticuli form alveoli connected by ducts to the ampullary chamber. In contrast, the obligate freshwater stingrays *Potamotrygon motoro* (Müller & Henle 1841) have ampullae that are severely reduced to a single microampulla (Andres & von Düring, 1988). Similarly, the ampullae of *P. microdon* are smaller with

fewer alveoli than those of the marine *A. cuspidata* (Wueringer *et al.*, 2011). However, the euryhaline *H. fluviorum*, has larger macroampullae with more sensory epithelium than those of two sympatric marine species; *N. trigonoides* and *M. toshi* (Gauthier *et al.*, 2018). A unique adaptation within the family Dasyatidae is seen in the freshwater whipray, *Urogymnus dalyensis* (Last & Manjaji-Matsumoto 2008) that has clusters of macro and individual free ampullae that might be a unique adaptation to lower salinities (Marzullo *et al.*, 2011). The overall trend is that marine species have larger ampullae, whereas freshwater species have smaller ampullae.

A comparative study on the ampullary organ morphology of 40 species of skates found that deep water species have larger ampullae with more diverticuli and sensory epithelia compared with shallower species (Raschi, 1986; Raschi & Mackanos, 1987). Furthermore, skates in the aphotic zones generally have fewer electrosensory pores but with a larger proportion distributed along the dorsal surface compared with those that occupy photic waters (Raschi, 1986). If the number of pores in a species is limited by phylogenetic constraints, then increasing the overall amount of sensory epithelium, the pore diameter (Kajiura, 2001; Raschi, 1986), or the density of receptor to support cells within each diverticulum (Theiss *et al.*, 2011), could boost electroreceptive sensitivity. Diminished light levels at depth might result in deep water chondrichthyans using electroreception more than vision to find prey and could influence the morphology of the peripheral and CNS electrosensory structures (Kajiura *et al.*, 2010; Yopak *et al.*, 2007; Yopak & Montgomery, 2008).

Examples of sexual dimorphism in electrosensory morphology are seen in the lesser spotted catshark *Scyliorhinus canicula* (L. 1758) and blue-spotted fantail stingray *Taeniura lymma* (Forsskål 1775). Male *S. canicula* have larger ampullae, composed of bigger and more numerous alveoli, a greater sensory epithelial surface area and more sensory receptors than females and could result in males having a more sensitive electrosensory system than females (Crooks & Waring, 2013). Another dimorphism was shown in female *T. lymma* that have more anterior lateral line nerve (ALLN) nerve axons entering the DON than males, but both sexes have the same number of ampullary pores (Kempster *et al.*, 2013). These data suggest that female *T. lymma* might have a greater electroreceptive signal-to-noise ratio than males (Kempster *et al.*, 2013). Either of these dimorphisms could be a permanent or temporary morphological condition similar to the seasonal plasticity in electroreceptor physiology of the Atlantic stingray *Hyp- anus sabinus* (LeSueur 1824) (Sisneros & Tricas, 2000). These conditions could enhance the sensitivity of males to detect buried female conspecifics or the ability of females to discriminate between approaching males and predators. To our knowledge, the effects that ampullary morphology, pore diameter and afferent convergence have upon the threshold and dynamic range of electroreceptors, the size and shape of the electroreceptive field and behavioural sensitivity between species or sexes, are unknown.

These cases highlight that pore counts and distribution are informative data but that comparative studies on neuronal innervation, neuronal convergence, ampullary size, canal length and geometry could yield more insight about electroreceptive field volume,

sensitivity and function across species. One potential way to quickly acquire these data might be the use of diffusible-iodine contrast-enhanced micro computed tomography (DICE- μ CT), or a similar non-destructive technique, to image soft tissues in three dimensions at sub-micron resolution (Yopak *et al.*, 2019). If the soft tissue of the electrosensory system could be reconstructed in 3-D and the aforementioned variables quantified, then the receptor sensitivity, along with the size, shape and sampling area could be determined for a species. These data could be used in a comprehensive study across hundreds of species in order to tease apart the effects of phylogeny, morphology and ecology on chondrichthyan electroreception.

3 | PHYSIOLOGY

The sensory hair cells of the chondrichthyan ampullary organs function as passive electroreceptors that are stimulated by weak cathodal currents, or electrical stimuli that induce a negative charge at the pore, lumen and apical end of the receptor cell (Bodznick & Montgomery, 2005; Murray, 1962, 1965). The glycoprotein hydrogel inside the ampullary canals conducts protons (Josberger *et al.*, 2016) that allow charges that accumulate at the skin surface to be detected by the sensory receptors located several cm away within a subdermal ampulla. Electroreceptors, like other sensory hair cells, constantly release neurotransmitter and the associated afferent nerve fibres exhibit a resting discharge of action potentials (Bodznick & Montgomery, 2005). When the sensory cell detects a net positive charge, the discharge rate of the afferent nerve decreases, whereas a negative charge increases the discharge rate (Murray, 1962, 1965). The afferent firing rate linearly encodes stimulus intensity. Individual receptors respond best to stimuli with a vector parallel to that of the associated ampullary canal and the response rates decrease as the stimulus vector becomes more perpendicular.

Based on available evidence, elasmobranch electroreceptors can detect standing DC electric fields, but the receptor response diminishes rapidly after the initial onset of the DC stimulus. Consequently, electrophysiological studies show that the receptors are best tuned to sinusoidal, or AC, stimuli with low frequencies (0.1–15 Hz; Adrianov *et al.*, 1984; Peters & Evers, 1985; Montgomery, 1984; Tricas & New, 1998) and low voltages (20 nV cm⁻¹ - 25 μ V cm⁻¹; Montgomery, 1984; Murray, 1965; Tricas & New, 1998). The receptors of *H. colliei* respond to artificial square-wave electrical stimuli < 0.2 μ V cm⁻¹ (Fields *et al.*, 1993) but additional studies using sinusoidal waveforms and lower voltages are required to determine the extent of the physiological response of holocephalans to biologically relevant stimuli.

Depolarisation of the electroreceptor involves Ca²⁺ influx at the apical end of the cell through voltage-gated calcium channels. The wave of membrane depolarisation travels to the basolateral portion of the cell and Ca²⁺ influx causes the vesicular release of neurotransmitter from the ribbon synapse into the synaptic cleft (Bennett & Obara, 1986; Clusin & Bennett, 1979a; Clusin & Bennett, 1979b). Ca²⁺ influx leads to the efflux of K⁺ ions through Ca-gated K⁺ channels that deactivates the Ca²⁺ channels along the entire membrane and repolarises

the cell (Bennett & Obara, 1986; Clusin & Bennett, 1979a; Clusin & Bennett, 1979b). A complex interplay between L-type Ca²⁺ channels in the apical membrane and K and Ca-dependent Cl⁻ channels in the basolateral membrane maintains a balance between membrane conductance and current oscillation that results in signal amplification and high sensitivity across the electrosensory epithelium (Lu & Fishman, 1994, 1995). The sensory tuning of electroreceptors is dictated, in part, by the molecular structure of the ion channels embedded within the excitable membranes of the sensory cells. For example, the little skate *Leucoraja erinacea* (Mitchill 1825) has voltage gated calcium channels (Ca_v1.3) that maintain the low voltage threshold necessary for electroreceptor activation by weak bioelectric fields (Bellono *et al.*, 2017). The receptor cells of the skate also have calcium activated big-conductance (BK) potassium channels that regulate the gradual release of neurotransmitters across a relatively broad range of stimulus frequencies (Bellono *et al.*, 2017). Interestingly, the chain catshark *Scyliorhinus retifer* (Garman 1881) has the same low threshold voltage gated calcium channels (Ca_v1.3) as the *L. erinacea*, but the potassium channels are voltage gated (K_v1.3) and allow the receptor to respond best to relatively high voltages across a narrow frequency range (Bellono *et al.*, 2018). Consequently, *S. retifer* electroreceptors can release sub-maximal amounts of neurotransmitter in a nearly inexhaustible manner compared with those of *L. erinacea* (Bellono *et al.*, 2018). A few substitutions to the amino-acid sequence of the potassium-channel subunits results in a shift in the tuning of *S. retifer* receptors toward a narrow range of stimuli such as those produced by prey, whereas the receptors of *L. erinacea* are more broadly tuned to detect stimuli produced by prey and the electric organ discharges of conspecifics (Bellono *et al.*, 2018).

The receptor potentials of several receptor cells converge onto a single afferent nerve, which increases sensitivity and reduces the behavioural response threshold to stimuli below 1 nV cm⁻¹. The primary afferents exhibit spontaneous activity and have a resting discharge rate (8.6–52.1 spikes s⁻¹) that varies according to the species in question, the ontogenetic state of the individual and the ambient temperature of the experimental conditions (Montgomery, 1984; New, 1990; Sisneros & Tricas 2002; Tricas & New, 1998). For example, in the clearnose skate *Rostroraja eglanteria* (Bosc 1800) and *H. sabinus* the tuning of afferents from neonates to adults increases by c. 4 Hz and narrows by c. 10 Hz across the range of best frequency responses (Sisneros *et al.*, 1998; Sisneros & Tricas 2002). Primary afferent sensitivity increases as the ampullary canals grow longer (Sisneros & Tricas, 2000), which is shown in embryonic *R. eglanteria* that exhibit a fivefold increase in sensitivity as they grow into juveniles and an eightfold increase when they become adults (Sisneros *et al.*, 1998). Similar increases are seen in neonate *H. sabinus* that demonstrate a three and fourfold increase in sensitivity as they grow into juveniles and adults, respectively (Sisneros & Tricas, 2002).

As the electrochemical signal travels along the afferent nerves to the medulla of *L. erinacea* and thornback guitarfish *Platyrrhinoidis tri-seriata* (Jordan & Gilbert 1880) the ascending electrosensory neurons (AEN) of the DON exhibit lower average resting discharge rates (0–10 spikes s⁻¹) compared with the primary afferents that innervate the

ampullae (Bodznick & Schmidt, 1984; Montgomery, 1984; New, 1990). The AENs, like the primary afferents, are excited by low frequency (0.5–10 Hz) cathodal stimuli, inhibited by anodal stimuli (Adrianov *et al.*, 1984; New, 1990; Tricas & New, 1998) and exhibit a voltage sensitivity range from 2.2–34 spikes s^{-1} per $\mu V cm^{-1}$ (Conley & Bodznick, 1994; Montgomery, 1984). Ascending further up toward the midbrain, the neurons display no resting discharge but exhibit a wide range of voltage threshold (0.015–5 $\mu V cm^{-1}$) and frequency (0.2–30 Hz) responses (Bullock, 1979; Schweitzer, 1986). This is likely a function of signal convergence where multiple primary afferents synapse onto a single AEN in order to increase the sensitivity of second order AENs, filter out background noise and enhance the detection of weak bioelectric signals produced by prey, predators, or conspecifics. Electroreceptors are unlike the sensory hair cells of the octavolateralis systems in that they lack efferent innervation and modulation (Waltman, 1966). Consequently, the higher AEN pathways of the electrosensory system must filter out the self-generated noise created by ventilation and ion exchange via a process of common-mode suppression (Bodznick *et al.*, 1992; Bodznick & Montgomery, 1992; Montgomery & Bodznick, 1993, 1994; Nelson & Paulin, 1995). Current evidence suggests that a feed-forward mechanism is used where the electroreceptor afferents stimulate the highly sensitive primary AEN fibres and the less sensitive secondary fibres that run parallel to the primaries. These secondary fibres in turn use gamma-aminobutyric acid (GABA)-receptor mediated inhibition to eliminate the noise in the primary fibres caused by the respiratory induced signal common to the electroreceptors that have converged upon that particular AEN pathway (Rotem *et al.*, 2007, 2014).

3.1 | Physiological ecology

During ontogeny, the tuning of the electrosensory system shifts to accommodate changes in diet and sexual maturity. The high sensory resolution of juveniles is well suited to detect the subtle onset of small DC fields or low modulation AC fields, such as those produced by small, less mobile invertebrates (Bedore & Kajiura, 2013; Kalmijn, 1972, 1974). As chondrichthyans age, the spatial resolution of the sensory field decreases and receptor sensitivity increases. In growing *R. eglanteria* and *H. sabinus* the temporal resolution and low frequency response of the electroreceptors are enhanced due to increases in the resting discharge rate, bandpass filtering and frequency of best response (Sisneros & Tricas, 2002; Sisneros *et al.*, 1998). The trophic position and niche breadth of mature elasmobranchs is greater than juveniles because larger individuals forage on larger prey and additional species (Grubbs, 2010). Larger prey items have more gill, oral and cloaca epithelial surface area that leaks ions into the seawater, thereby creating DC electric fields with greater voltage potentials (Bedore & Kajiura, 2013; Kalmijn, 1972, 1974). The rhythmic ventilation of vertebrates and limb movement of invertebrates creates more discernible bioelectric signals as the baseline DC field is modulated into a sinusoidal AC field (Bedore & Kajiura, 2013; Kalmijn, 1972, 1974; Wilkens & Hofmann, 2005).

These factors combine to make larger prey more electrically conspicuous to electroreceptive predators. The increased sampling area and receptor sensitivity of older chondrichthyans should enable them to detect larger amplitude bioelectric fields from a greater distance. Early detection is crucial as larger prey are generally more mobile and might have a greater chance of escaping a predator than smaller individuals.

As chondrichthyans reach sexual maturity they must find mates during the reproductive season, which might be especially challenging for small batoids or selachians that employ diurnal visual crypsis. During the non-mating periods of the reproductive cycle, the physiological characteristics of the electroreceptor response in male and female *H. sabinus* are the same (Sisneros & Tricas, 2000). Likewise, it is reasonable to assume that the bioelectric fields generated by males and females are consistent throughout the year, barring some undescribed physiological changes in elasmobranch osmoregulation strategy or ventilation frequency associated with the reproductive season. However, at the onset of the mating season, male stingrays undergo spermatogenesis and have higher levels of circulating androgen steroid hormones (Tricas *et al.*, 2000). The hormones induce an increased resting discharge rate, elevated sensitivity to low frequency stimuli and downshift of the best frequency response and bandpass filtering of the electroreceptors in males (Sisneros & Tricas, 2000). These changes effectively adjust the physiological tuning of the male stingray electrosensory system from a generalised foraging and anti-predator function toward detecting the bioelectric fields produced by conspecific females. Males would probably incur substantial metabolic costs during the mating season as their electrosensory system is presumably less adept at finding prey items. Considering the research of Bellono *et al.* (2017, 2018), it is likely that these hormone-induced seasonal changes in electroreceptor sensitivity are due, in part, to altered gene expression patterns and molecular modifications to the ion channels within the receptor cells.

To date, most of the physiological studies on the chondrichthyan electrosensory system were conducted pre 2000 on a few small batoid species. For example, the activity of the electroreceptors and primary afferents to bioelectric stimuli has yet to be thoroughly examined in any selachian or holocephalan. More recently, Rotem *et al.* (2007, 2014) used a novel *in vitro* preparation in the bigeye houndshark *Iago omanensis* (Norman 1939) to investigate the response of the AENs to bioelectric stimuli and discern how stimuli are processed within the DON. This work highlights the importance of understanding how the chondrichthyan electrosensory system filters and integrates information without the efferent innervation that modulates the sensory hair cells in the related octavolateral modalities. Comparative physiological studies across phylogeny and ecotypes could address questions of how chondrichthyan electroreceptor function has evolved within the constraints of phylogeny and solved the selective pressures imposed by different feeding strategies and habitats. Finally, such physiological-based studies could give insight into how chondrichthyans perceive and interpret anthropogenic and natural electrical stimuli.

4 | BEHAVIOUR

4.1 | Prey detection

The electroreceptive function was first described by Kalmijn (1971) in a series of behavioural experiments on *S. canicula* and thornback rays *Raja clavata* (L. 1758) that were able to find European plaice *Pleuronectes platessa* (L. 1758) buried in the sand. Initially, the subjects were able to find prey hidden below the substrate when the visual, chemical and mechanical cues were eliminated. However, when the bioelectric cues were eliminated, the elasmobranchs were unable to detect the buried prey. Lastly, electroreceptive capability in the subjects was confirmed when the subjects detected buried electrodes that emitted prey-simulating electrical stimuli. Subsequent field

experiments have shown that nocturnally active swell sharks *Cephaloscyllium ventriosum* (Garman 1880) can locate prey in the dark using their electroreceptors (Tricas, 1982) and individual blue sharks *Prionace glauca* (L. 1758) and dusky smooth hound sharks *Mustelus canis* (Mitchill 1815) aroused by prey odorants will bite at electrodes emitting prey-simulating bioelectric stimuli (Kalmijn, 1982).

Laboratory-based behavioural choice assays later confirmed the preferential bite response to active electrodes emitting prey-simulating stimuli over control electrodes in the bonnethead shark, *Sphyrna tiburo* (L. 1758) (Kajiura, 2003), *S. lewini* (Kajiura & Fitzgerald, 2009), *C. plumbeus* (Kajiura & Holland, 2002), blacktip reef shark, *Carcharhinus melanopterus* (Quoy & Gaimard 1824) (Haine *et al.*, 2001), *H. portjacksonii* and shovelnose ray *Aptychotrema vincentiana* (Haacke

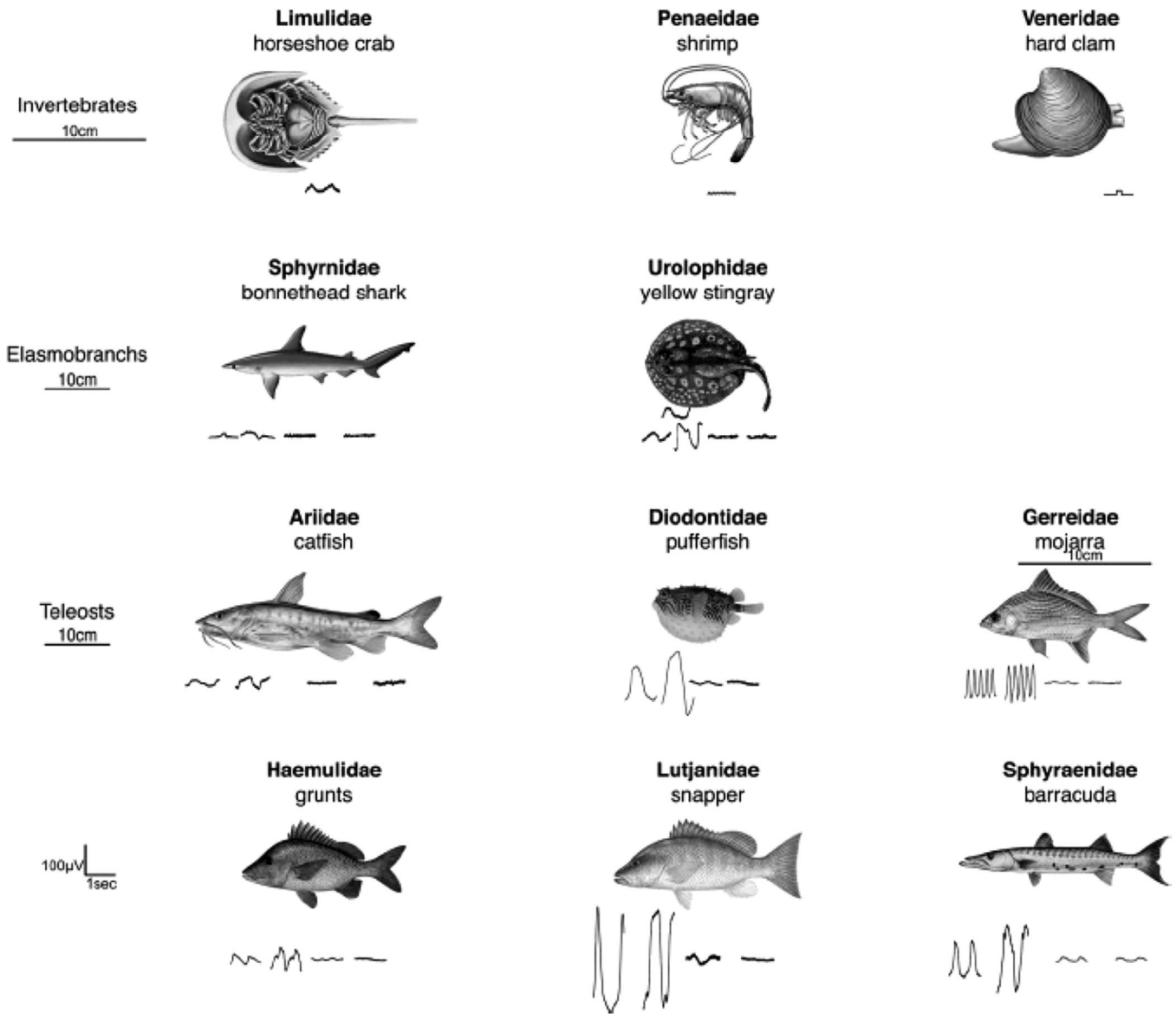


FIGURE 6 Representative waveform, shape, amplitude, and frequency of bioelectric field potentials measured from 11 families of elasmobranch prey items. The location of the waveform trace along the body indicates the recording location. Prey are scaled to the mean total length (cm) and waveforms are scaled to mean amplitude (μV) and frequency (Hz). Reproduced with permission from Bedore and Kajiura (2013)

1885) (Kempster *et al.*, 2016), *H. sabinus* (McGowan *et al.*, 2009), *M. californicus* (Gill 1865) *U. halleri* and *P. violacea*, (Jordan *et al.*, 2009), *U. jamaicensis* and *R. bonasus* (Bedore *et al.*, 2014), *P. motoro* (Harris *et al.*, 2015), *P. microdon* and *G. typus* and *A. rostrata* (Wueringer *et al.*, 2012a). The median behavioural sensitivity of elasmobranchs to prey simulating electrical stimuli ranges from 5–107 nV cm⁻¹ at distances of 22–44 cm (Jordan *et al.*, 2009, 2011; Kajiura, 2003; Kajiura & Holland, 2002; McGowan & Kajiura, 2009; Bedore *et al.*, 2014; Wueringer *et al.*, 2012a), which corresponds to the bioelectric potentials produced at the mouth, gills and cloaca (Figure 6) of common invertebrate (14–28 μV cm⁻¹), teleost (39–319 μV cm⁻¹) and small elasmobranch (18–30 μV cm⁻¹) prey species (Bedore & Kajiura, 2013).

The wide range of median responses could be correlated with the number of pores or their distribution across the body. Jordan *et al.* (2009) investigated the functional differences in pore number and distribution on behavioural sensitivity in three species of batoids and found that *U. halleri* had a significantly lower median voltage response than that of *M. californicus* and *P. violacea*. *Urobatis halleri* has a high ventral: dorsal pore ratio, significantly higher ventral pore density near the mouth and a greater percentage of its ventral surface covered by electrosensory pores (Jordan, 2008). A similar series of comparative studies on the freshwater sawfish, *P. micrdon*, *G. typus* and *A. rostrata*, showed that the freshwater pristids had the lowest median sensitivity, the highest number of pores and the largest spread of receptors across the body due to the rostrum (Wueringer *et al.*, 2012a, 2012b). It appears from these studies that species with lower median sensitivity thresholds have a high number of pores spread out along the surface of the body, which increases their sampling volume and sensitivity.

It should be noted that the aforementioned behavioural experiments on marine elasmobranchs were conducted using similar methods (Kajiura & Holland, 2002) on individuals from different age classes and families (Sphyrnidae, Carcharhinidae, Heterodontidae, Urotrygonidae, Dasyatidae, Myliobatidae, Pristidae and Rhinobatidae), with different body sizes and head morphologies. The authors reported similar minimum behavioural response thresholds to prey-simulating stimuli of c. 1 nV cm⁻¹. This similarity might indicate that ampullary electroreceptor sensitivity is limited by morphological constraints of canal length and the amount of sensory epithelium within an ampulla. Conversely, the limits of rapid bioelectric signal attenuation in seawater could impose a minimum behavioural threshold that the electrosensory system must overcome to effectively detect prey. If minimum behavioural sensitivity is dictated by ampullary morphology, then how might low voltage sensitivity be conserved across phylogeny? One possible factor is how the molecular components of the electrosensory cells shape the tuning curve and affect behavioural sensitivity. The conservation of minimum voltage sensitivity across chondrichthyan phylogeny, ontogeny and foraging habitats could be achieved by Ca_v1.3 channels within the electroreceptor cells (Bellono *et al.*, 2017, 2018). These low-voltage sensors could be expressed ubiquitously within ampullary electroreceptors. Furthermore, small species or juveniles with short canals or small ampullae, might express relatively more Ca_v1.3

channels within their receptor cells or have amino acid substitutions to the voltage sensor domain of the Ca_v1.3 subunits that increase channel sensitivity. Similarly, the variation in median behavioural sensitivity could be due to the expression of different K-channel subtypes (*e.g.*, BK, K_v, etc.) among individuals from different species and life stages to better adapt them to a particular foraging ecology (Bellono *et al.*, 2017, 2018).

The only known sexual differences in electrosensory mediated predatory behaviour were shown in *S. canicula* where males were less responsive than females to prey-simulating electric fields (Kimber *et al.*, 2009). It is possible that, similar to *H. sabinus*, the male *S. canicula* used in this study were experiencing seasonal changes in circulating androgens and their sensory tuning shifted toward a mating from a predation phenotype. To date, the potential morphological, physiological and molecular underpinnings of these sexual differences in prey detection responses and whether these behaviours are seen in other chondrichthyans remain unresolved. The influence of environment on behavioural electrosensitivity is best illustrated in the transition from marine to freshwater habitats. For example, the euryhaline *H. sabinus* in seawater (salinity 35) has a detection threshold of 0.6 nV cm⁻¹ but the threshold rises to 2 nV cm⁻¹ in brackish water (salinity 15) and up to 3 μV cm⁻¹ in fresh water (McGowan & Kajiura, 2009; freshwater value corrected by Harris *et al.*, 2015). The freshwater sensitivity is commensurate with that of the obligate freshwater *P. motoro*, which can detect voltages as weak as 5 μV cm⁻¹ (Harris *et al.*, 2015). This suggests that a reduced sensitivity and detection range of electrical stimuli in freshwater species (Crampton, 2019) occurs due to the lower conductivity and higher resistivity of fresh water compared with seawater and not the morphological adaptations of thicker skin and shorter ampullary canals seen in obligate freshwater elasmobranchs (Harris *et al.*, 2015).

4.2 | Conspecific detection

All elasmobranchs produce a standing DC bioelectric field due to the osmoregulatory exchange of salts at the gills (Kalmijn, 1971) and the rhythmic action of ventilation (*c.* 0.5–2 Hz) that modulates the strength of the bioelectric field into an AC field. This bioelectric signal can be used by individuals to detect cryptically concealed conspecifics during the mating season, as seen in the non-electrogenic *U. halleri* (Tricas *et al.*, 1995). Male stingrays use their electroreceptors to detect buried females that are receptive to mating and non-receptive females use their electric sense to locate other females and seek refuge from aggressive males (Tricas *et al.*, 1995). The physiological change underlying this behaviour involves a seasonal shift in electrosensory tuning of males due to the presence of androgen hormones (Sisneros & Tricas, 2000), as previously described. In skates, the axial musculature of the tail has evolved into a spindle-shaped electric organ that produces a weak EOD. Individuals produce the EOD more often in the presence of conspecifics than in isolation and the EOD is believed to serve as a mode of interspecific communication (Bratton & Ayers, 1987; New, 1994) instead of a defence

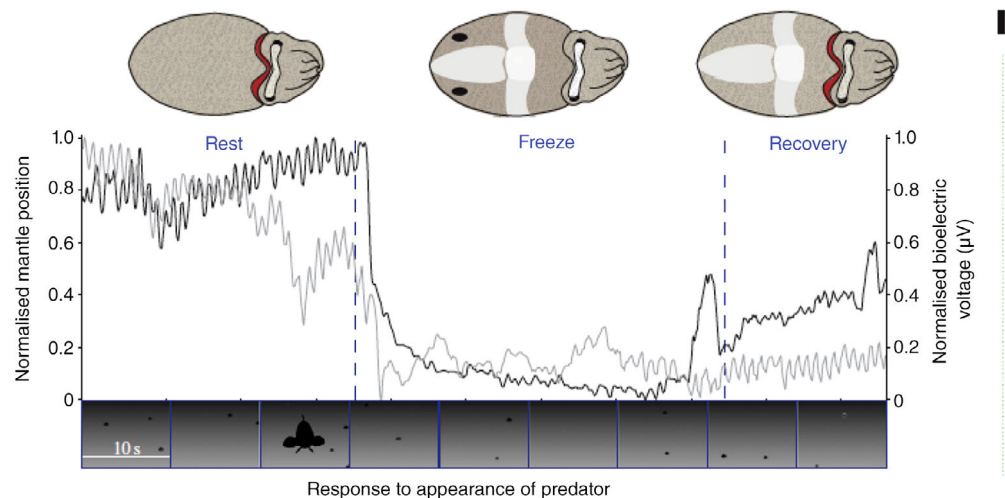
mechanism such as those of the electric torpedo rays (Torpediniformes). The pulse amplitude, duration, train length and pattern of the EODs in the little skate, *L. erinacea*, winter skate *Leucoraja ocellata* (Mitchill 1815) and clearnose skate, *R. eglanteria*, are species specific and coincide with the peak sensitivity of the skate electroreceptors (Bratton & Ayers, 1987; Mikhailenko, 1971; Mortenson & Whitaker, 1973; New, 1990, 1994; Sisneros *et al.*, 1998). Admittedly, little is known about the EOD and its potential role in communication behaviour among skates. However, these data support the idea that rajiform batoids may have a unique type of electrosensory tuning to the EOD within each species. If so, then species-specific tuning could be achieved, in part, by molecular adaptations to the ion channels within the membranes of the electroreceptor cells similar to those described in the *L. erinacea* by Bellono *et al.* (2017, 2018). The basal position of skates within Chondrichthyan phylogeny would enable researchers to study the evolution and molecular basis of electrosensory mediated communication and behaviour in vertebrates.

4.3 | Predator detection and bioelectric crypsis

Visually concealed elasmobranchs can use their electroreceptors to detect an approaching predator and alter their behaviour to eliminate their own conspicuous bioelectric, olfactory and hydrodynamic signals. Deploying secondary measures to reduce conspicuousness is useful for small benthic species, juveniles, and embryos that rely on crypsis to avoid predation. Oviparous chondrichthyans deposit egg cases into the environment where the embryo develops and hatches

once the yolk is consumed. During development, an embryo will move its tail rhythmically to flush fresh seawater through the egg case and facilitate the exchange of respiratory gases and metabolic wastes (Luer & Gilbert, 1985; Peters & Evers, 1985). Neonate chondrichthyans emerge with fully functional sensory systems, as shown by newly hatched *S. canicula* that will cease ventilation when exposed to weak, low frequency (0.1–1.0 Hz) electrical stimuli (Peters & Evers, 1985). Moreover, late term embryonic skates *R. eglanteria* and bamboo sharks *Chiloscyllium punctatum* (Müller & Henle 1838) within their egg cases will cease ventilation and rhythmic tail movements in response to similar predator-simulating electrical signals (0.5–2 Hz; $0.56 \mu\text{V cm}^{-1}$), which likely reduces any telltale bioelectric, hydrodynamic, or olfactory cues (Kempster *et al.*, 2012a; Sisneros *et al.*, 1998). Electroreceptor functionality and anti-predatory freeze behaviour are functional as early as the first one-third of embryonic development, as shown in *R. clavata* (Ball *et al.*, 2015). It is interesting to note that bioelectric crypsis works for the prey of elasmobranchs as well. The common cuttlefish *Sepia officinalis* will cease moving, ventilating and occlude their gill cavities when they are exposed to looming visual stimuli of teleosts and elasmobranchs but not decapod predators (Bedore *et al.*, 2015). When *C. limbatus* and *S. tiburo* were presented with a reduced bioelectric field that simulated the cuttlefish freeze behaviour (Figure 7), the sharks bit at the electrodes 50% fewer times than when cuttlefish resting stimuli were presented. These studies confirm that the freeze response reduces inadvertent bioelectric signals from reaching predators and diminishes the likelihood of an attack.

FIGURE 7 The frequency and amplitude of body movement and bioelectric cues of the cuttlefish *Sepia officinalis* are reduced in response to visual stimuli of looming predators. Each image of *S. officinalis* indicates the camouflage and state of mantle openings for each phase of the recording. Rest, quiescent, non-active, and gills are laterally exposed at the mantle cavity opening near the head; Freeze, motionless, body flattened, gills covered, which reduces amplitude and frequency of bioelectric cues; Recovery, transition from freeze to resting state. Camouflage, body movement and bioelectric cues return to within 1 SD of previous resting state. Primary y-axis + body movement, secondary y-axis = bioelectric voltage. Reproduced with permission from Bedore *et al.*, (2015)



4.4 | Conditioned behaviours mediated by electroreception

The electric sense of holocephalans has received little attention aside from an aversive conditioning study on *H. coliei* that was trained to avoid square-wave DC electrical stimuli $< 0.2 \mu\text{V cm}^{-1}$ (Fields *et al.*, 1993; Fields & Lange, 1980). Unfortunately, the dissimilarity between the methods used in this study and those on elasmobranchs prohibits direct comparison of electrosensory thresholds across the two subclasses of Chondrichthyes. Few researchers have used neutral electrical stimuli to investigate the learning or memory capabilities of elasmobranchs, but Kimber *et al.* (2011) showed that *S. canicula* can discriminate between the strength of two artificial DC fields and an AC and DC field of the same strength, but it is not able to distinguish between an artificial and natural DC field of the same strength. In a follow up study, *S. canicula* that were trained to associate an artificial DC electric field with a food reward could successfully perform the task after a 12 h memory window but failed to demonstrate memory retention after a 3 week interval (Kimber *et al.*, 2014). These results are congruent with previous work showing that ampullary electroreceptors rapidly attenuate to DC stimuli and respond best to changes in electric fields. As such, a change in field strength or modulations in frequency might be more obvious stimuli for *S. canicula* to detect and learn to associate with another stimulus. Appetitive conditioning was used to demonstrate that *U. jamaicensis* can distinguish between the positive and negative poles of an electric field (Siciliano *et al.*, 2013). Bioelectric field polarity discrimination could be used to derive the orientation of approaching predators, buried prey or conspecifics. As such, it is plausible that *U. jamaicensis* could then use this information to determine an optimal escape trajectory to avoid predation, the best placement of a predatory strike during foraging (Siciliano *et al.*, 2013), or the best approach toward a buried conspecific (Tricas *et al.*, 1995).

Lastly, it has been hypothesised that elasmobranchs might use their electroreceptors to detect the induction of an electrical current caused by an applied magnetic field to electrically conductive seawater (Kalmijn, 1978). If so, then an elasmobranch approaching a localised magnetic anomaly might experience the rapid onset of an induced electric field, which could stimulate the electroreceptors. This potential mechanism of indirect magnetic stimulus detection might explain how *U. jamaicensis* learned to associate randomly placed magnetic anomalies with food rewards and remember this association for 6 months (Newton & Kajiura, 2017).

4.5 | Aversive behavioural responses to stimuli mediated by electroreception

In an effort to deter elasmobranchs from interacting with fishing gear and reduce bycatch, several researchers have investigated the efficacy of electropositive lanthanide metals as shark repellents because rare-earth elements naturally shed electrons into seawater and create a potentially aversive electric field. To date, the results

have not shown a consistent trend of lanthanides deterring sharks from taking bait under similar conditions (McCutcheon & Kajiura, 2013, table 3). For example, some studies have demonstrated that rare-earth metals are aversive to sharks (Kaimmer & Stoner, 2008; Stoner & Kaimmer, 2008; Wang *et al.*, 2008), other studies have shown that lanthanides have no effect on foraging behaviour (Godin *et al.*, 2013; McCutcheon & Kajiura, 2013; Robbins *et al.*, 2011; Tallack & Mandelman, 2009) and still others have shown mixed results (Brill *et al.*, 2009; Hutchinson *et al.*, 2012; Jordan *et al.*, 2011). The lack of consistency in the species used, the study location (field or laboratory), testing sharks individually or in groups and the type of lanthanides used as aversive stimuli hampers comparison across experiments.

Similarly, strong permanent magnets have been used as sources of aversive stimuli to induce avoidance behaviours in elasmobranchs, including the southern stingray *Hypanus americanus* (Hildebrand & Schroeder 1928) (O'Connell *et al.*, 2010), Atlantic sharpnose, *Rhizoprionodon terraenovae* (Richardson 1837) and *M. canis* (O'Connell *et al.*, 2011a), great hammerhead shark *Sphyrna mokarran* (Rüppell 1837) (O'Connell *et al.*, 2015), white shark *Carcharodon carcharias* (L. 1758) (O'Connell *et al.*, 2014a), lemon shark *Negaprion brevirostris* (Poey 1868) (O'Connell *et al.*, 2011b, 2014b), *C. leucas* (O'Connell *et al.*, 2014c), *S. canicula* and *R. clavata*, (Smith & O'Connell, 2014), *C. plumbeus* (Siegenthaler *et al.*, 2016) and the blind shark *Brachaelurus waddi* (Bloch & Schneider 1801) (Richards *et al.*, 2018). However, it is unclear whether the repulsive effects reported were because the test subjects responded directly to magnetic stimuli or to induced electrical artefacts. The metallic components of permanent magnets could shed electrons into seawater and create a potentially aversive galvanic electric field. Likewise, a permanent magnet affixed to a movable object, such as an anti-shark net that can sway back and forth in an ocean current, will induce an AC electrical field into the surrounding seawater. Until further clarification is demonstrated, the most conservative interpretation of these studies is that the aversive responses of elasmobranchs to strong magnetic stimuli are mediated by the electrosensory system.

In some parts of the world, electrofishing beam-trawlers use aversive electrical pulses to disturb benthic fishes off the substrate making them vulnerable to capture by an oncoming trawl. Chondrichthyans that escape these trawlers might experience a temporary or permanent effect to the function of their electroreceptor system. However, pulsed DC electrical stimuli mimicking those used by commercial electrofishing trawlers was not shown to impair the electrosensory capabilities of *S. canicula* to prey-simulating electric fields (Desender *et al.*, 2017). Repeated exposures to potentially unpleasant stimuli over time may lead to a cumulative effect, such as a reduced physiological response of electroreceptors to bioelectric stimuli or behavioural changes in some species. The lack of knowledge on the effects of aversive stimuli highlight that additional studies on the effects of anthropogenic electric fields on the electrosensory abilities of benthic species are warranted.

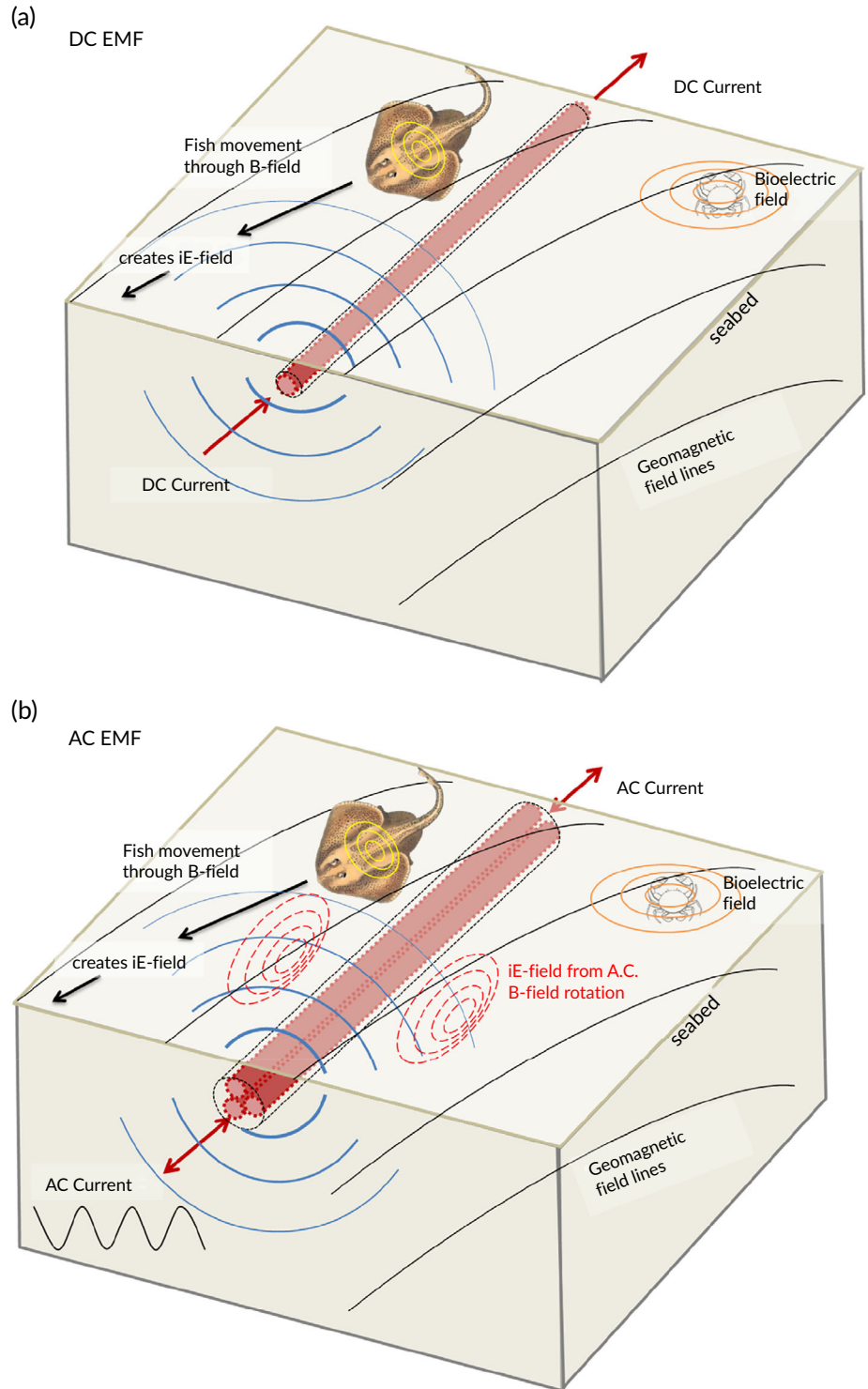
4.6 | Orientation, navigation and geomagnetic-stimulus detection

Magnetic field detection by chondrichthyans is discussed here briefly owing to the close link between electric and magnetic fields in the marine environment. The reader is also referred to the review of magnetoreception in fishes by Formicki *et al.* (2019).

Kalmijn (1982) and Pals *et al.* (1982) demonstrated that some species of elasmobranchs can be behaviourally conditioned to orient

toward electric dipoles during the onset of a DC field and can distinguish electrical gradients of $c. 5 \text{ nV cm}^{-1}$. This electrical sensitivity is well within the range of the induced electric fields produced by the physical movement of conductive seawater ($c. 500\text{--}8000 \text{ nV cm}^{-1}$) through the Earth's geomagnetic field (GMF, ---). Chondrichthyans could use this method to passively determine their orientation within oceanic and tidal currents (Paulin, 1995). Additionally, it has been hypothesised that the Ampullae of Lorenzini might detect location and

FIGURE 8 Depiction of natural and anthropogenic electric (E-field) and magnetic (B-field) fields encountered by an electroreceptive fish moving across the seabed. The separate E-field and B-field components of the electromagnetic fields (EMF) emitted by a buried subsea cable (Ⓢ) are shown as well as the ambient geomagnetic field (GMF, ---) and bioelectric fields from living organisms (Ⓢ). (a) The EMF associated with a DC subsea cable; (b) the EMF associated with a standard three core AC subsea cable with the current following a typical sine wave back and forth through each core. For both cables the direct E-field is shielded by cable material (black outer cable) but B-fields (---) are not able to be shielded, hence get emitted into the environment. An induced E field (iE-field) is created in the fish (---) as it moves through the B-field emitted by the cable. Localised iE-fields will also be induced by seawater moving through the B-field and the GMF. For the AC cable, the out-of-phase magnetic field emitted by each core of the cable causes a rotation in the magnetic emission which induces an iE-field in the surrounding conductive seawater (--- , emitting into the environment above the seabed). *n.b.* B-field is the common nomenclature for the magnetic field generated within a medium or environment as it is more easily measured and takes account of the permeability of the medium, it is measured in the SI unit of Tesla. Not to scale



directional cues from the GMF and possibly use them to actively orient and navigate during migrations (Kalmijn, 2000; Paulin, 1995). Electroreceptor-mediated magnetic field detection is proposed to occur indirectly *via* the mechanism of electromagnetic induction and would not require a true magnetoreceptor cell. For example, when a chondrichthyan swims through electrically conductive seawater and the GMF (Figure 8), it will generate a potentially detectable voltage drop across the electroreceptors. The magnitude of the induced electric field is a function of the swimming speed, the magnitude of the local GMF and the sine of angle between the swimming vector and that of the GMF (Kalmijn, 1978). Furthermore, the direction of the induced electric current is a function of the direction of the swimming and GMF vectors. In this manner, a swimming chondrichthyan could potentially derive a sense of its location and direction based on the differential stimulation of the electroreceptors distributed across its body (Kalmijn, 1981, 1984) coupled with the undulatory movements of its body as it swims (Paulin, 1995).

Behavioural and physiological studies have shown that elasmobranchs can detect artificially induced changes in the GMF. A general sensitivity to magnetic field stimuli has been demonstrated using behavioural conditioning in *S. lewini* and *C. plumbeus* (Anderson *et al.*, 2017; Meyer *et al.*, 2005) and short-tailed stingrays, *Bathytoshia brevicaudata* (Hutton 1875) (Walker *et al.*, 2003) and *U. jamaicensis* (Newton & Kajiuura, 2017). Kalmijn (1978) used behavioural conditioning to demonstrate that *U. halleri*, can discriminate direction of an applied GMF based on polarity. The ability to use GMF polarity to solve spatial tasks was confirmed in the *U. jamaicensis* (Newton, 2017), which can also detect changes in GMF strength and inclination angle (Newton, 2017), two magnetic cues that might be used to derive a sense of location. Electrophysiological studies on the common stingray *Dasyatis pastinaca* (L. 1758) and *R. clavata*, have shown that the Ampullae of Lorenzini afferents (Akoiev *et al.*, 1976; Brown & Ilyinsky, 1978) and the associated CNS neurons (Adrianov *et al.*, 1974) respond to changing, but not constant, magnetic fields. Furthermore, electroreceptor response rates were a function of magnetic stimulus intensity and the length of the associated ampullary canal, whereas the excitation or inhibition of a receptor depended upon the polarity of the applied magnetic fields relative to the orientation of the canal (Akoiev *et al.*, 1976; Brown & Ilyinsky, 1978). Intriguing experimental evidence indicates that the perception of magnetic fields by *C. plumbeus* might involve the electrosensory system and putative magnetoreceptive structures located in the shark's naso-olfactory capsules (Anderson *et al.*, 2017).

Despite recent advances in our knowledge of elasmobranch magnetic stimulus detection, several questions require further investigation. Two key aspects are: determining the mechanism of magnetic stimulus detection and demonstrating that migrating chondrichthyans actually use GMF cues to orient and navigate. Answering these questions can help uncover how anthropogenic EMFs might affect chondrichthyan electroreceptor function and the associated behaviours. To date, a putative magnetoreceptor that directly detects magnetic fields has yet to be found in any shark, skate, ray, or chimaera. However, if chondrichthyans use their electroreceptors to indirectly

detect magnetic fields, then it is unclear how they might distinguish between magnetic and electric cues. These avenues of study could give insight into how electroreceptors might encode bioelectric and GMF stimuli differently, or how central processing mechanisms might distinguish between magnetic and electric cues.

5 | THE POTENTIAL INFLUENCE OF ANTHROPOGENIC ELECTRIC AND MAGNETIC FIELDS

Anthropogenic sources of electric and magnetic fields are varied. They can be locally introduced to intentionally repel electroreceptive species as seen in studies that use magnets or high intensity electrical fields on anti-shark nets (O'Connell *et al.*, 2011a, 2014a). Electromagnetic fields (EMFs), can be emitted over large spatiotemporal scales by electric trawl fishing (Desender *et al.*, 2017), subsea high-voltage cable networks, transoceanic marine vessels, mineral prospecting and metallic infrastructure, such as railways and bridges (Gill *et al.*, 2014). The global increase in subsea electrical cable deployment from marine renewable energy installations and the expansion of communication cable networks has raised interest in whether electroreceptive marine fishes will be affected by the associated EMFs (Gill *et al.* 2012, 2014; Taormina *et al.*, 2018).

Subsea high-voltage cables emit weak magnetic and electrical artefacts with characteristics that depend upon the material used to construct the cable and whether the cable is conducting AC or DC electricity (Figure 8; Gill *et al.*, 2012b). The high-voltage current within subsea cables is contained inside the conductive cores that are insulated from seawater but magnetic field artefacts radiate orthogonally into the seawater with respect to the direction of electrical current flow. Cables that transmit DC electricity emit static magnetic fields but as a fish swims through the artefact, a low frequency electric field is induced around the fish. The three cores of AC cables create magnetic fields that are out of phase with each other and results in a rotating magnetic artefact that itself induces AC electric fields into the seawater. Elasmobranchs that swim through these magnetic anomalies are likely to detect the induced electric fields (Figure 8), which might disrupt electrosensory mediated prey detection or navigation through localised geographic areas (Gill *et al.*, 2014). Behavioural conditioning studies have shown that *S. canicula* cannot discriminate between artificial and natural DC electric fields (Kimber *et al.*, 2014). If this behavioural response is common among elasmobranchs, then it might explain why some sharks and rays are known to bite subsea cables. Comprehensive research that measures how individuals from multiple species, age classes and reproductive states, respond to various aforementioned EMF artefacts is necessary. If anthropogenic EMFs do affect electroreception, then further investigation into the molecular pathways of electroreceptor, afferent and CNS neuron function would be required to determine how electroreception is disrupted and uncover potential mitigation solutions.

6 | SUMMARY AND FUTURE RESEARCH

This review highlights that, while we understand some fundamental aspects of passive electroreception, a number of substantive questions remain. Classical studies on electrosensory anatomy, physiology and behaviour have provided foundational knowledge to better understand how the passive mode of electroreception functions within an ecological context. Studies on electroreception in marine fishes have focused on readily available and accessible elasmobranchs, which has resulted in an overrepresentation of relatively few taxa (e.g., Carcharhiniformes) and a severe lack of knowledge about other taxa (e.g., Echinorhiniformes; Pristiophoriformes). Nonetheless, comparative studies can be used to make reasonable assumptions about the general principles of the electroreceptive systems of underrepresented taxa within a particular habitat. Future studies should use a cross-disciplinary approach that combines laboratory and field-based studies across multiple levels of organisation to further our knowledge base and interpret how electroreceptive species perceive their world.

The functional outcome of the electroreceptive response depends on the stimulus and how it is interpreted. In the limited number of physiological studies conducted, there is a common best frequency response to low voltage and low frequency electric fields. However, these data have been established for < 0.1% of all chondrichthyans. It might be possible to use these data, along with the physical properties of the electrosensory system (e.g., canal length, orientation, gel conductivity) to model the electric field characteristics that would be detectable for other species. Unfortunately, these morphological data are lacking for most species, which hampers our ability to infer the physiological sensitivity and behavioural responses of species that are difficult to study in the laboratory. Anatomical methods, such as DICE μ CT, may provide opportunities to fill this knowledge gap by generating vast morphological datasets that could be used to predict which species are most sensitive and therefore, are likely to be most affected by encounters with anthropogenic EMFs.

Beyond simple detection of the stimulus, lies the complex question of how an organism interprets stimuli to derive an appropriate response. The electric field characteristics of potential prey items may vary widely, but all result in the items being recognised as prey. However, what is prey to one species, may be a predator to another, or even the same species at a different ontogenetic stage. Therefore, how electroreception functions through ontogeny, from being a predator detection system in the early life stages to a mate finding system in adults, highlights the importance of research on how electroreceptor plasticity facilitates adaptation to different sensory needs. Undoubtedly, this line of research would benefit from sequencing the genomes of key elasmobranch species and detailed studies on the molecular mechanisms that underlie chondrichthyan electroreception. Currently, the genomic sequences are known for a handful of the nearly 1300 chondrichthyans including: the whale shark *Rhincodon typus* (Smith 1828) (Read *et al.*, 2017), *C. punctatum*, cloudy catshark *Scyliorhinus torazame* (Tanaka 1908) (Hara *et al.*, 2018), white shark *C. carcharias* (Linnaeus 1758) (Marra *et al.*, 2019) and elephant shark *Callorhynchus*

milii (Bory de Saint-Vincent 1823) (Venkatesh *et al.*, 2014). *Leucoraja erinacea* is the nearest model elasmobranch species to date and the assembly of its genome is underway at www.skatebase.org (Wang *et al.*, 2012). These genetic studies have shown that some benthic associated species have very few odorant receptor genes expressed in the olfactory epithelium (Hara *et al.*, 2018; Venkatesh *et al.*, 2014) and it is likely that further genomic screens could lead to insights about chondrichthyan electrosensory phenotypes.

Comprehensive data on the behavioural response of electrosensitive fish to altered EMFs in the environment is lacking, therefore, it is not possible to fully assess whether anthropogenic electric or magnetic fields have any effect on chondrichthyans. The key factors that must be understood are how the characteristics of different EMF sources influence the neurological and cellular processes underlying electroreception. Dose-response studies will be important for understanding the relationship between EMF intensity, frequency, duration and the physiological and behavioural response of a species throughout ontogeny. Focusing future research on these themes will facilitate interpreting the reactions of electrosensitive fishes to, for example, power cables of different sizes or the effectiveness of electromagnetic repellents for fisheries and beach-net applications. Comparative studies that account for differences in phylogeny and habitat can uncover how adaptable different ecotypes, such as benthic species that rely heavily on electroreception to forage along the seafloor, might be in the face of a changing marine environment.

A firm foundation has been established for understanding electrosensory system function, but a better knowledge of the mechanism by which chondrichthyans detect electric and magnetic fields is required. Tying together new physiological, cellular and molecular research with robust behavioural studies will provide a fruitful avenue to disentangle how natural and artificial EMFs are perceived, how functional responses to stimuli are manifested and predict how anthropogenic activities will affect the electrosensory ecology of chondrichthyans. It is necessary to expand our understanding of electroreception by integrating biological disciplines with ocean physics and marine chemistry. Only then can we develop a robust understanding of how the different sources of electric and magnetic fields are detected by biological structures. Recent advances in molecular techniques, neurophysiological recording, 3-D imaging and computer modelling, will provide the tools for the next generation of scientists to provide greater clarity to this topic. The future of electroreception research hinges on an integrated approach that enables our understanding to go beyond our fundamental interests to applying the knowledge to better understand how species can cope with a modified environment.

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