

The distribution and abundance of electrosensory pores in two benthic sharks: a comparison of the wobbegong shark, *Orectolobus maculatus*, and the angel shark, *Squatina australis*

Channing A. Egeberg^A, Ryan M. Kempster^{A,C}, Susan M. Theiss^B,
Nathan S. Hart^A and Shaun P. Collin^A

^AThe UWA Oceans Institute and the School of Animal Biology, The University of Western Australia, 35 Stirling Highway, Crawley, WA 6009, Australia.

^BFisheries Queensland, Department of Agriculture, Fisheries and Forestry, GPO Box 46, Brisbane, Queensland 4001, Australia.

^CCorresponding author. Email: ryankempster@supportoursharks.com

Abstract. Electroreception is an ancient sense found in many aquatic animals, including sharks, which may be used in the detection of prey, predators and mates. Wobbegong sharks (Orectolobidae) and angel sharks (Squatinidae) represent two distantly related families that have independently evolved a similar dorso-ventrally compressed body form to complement their benthic ambush feeding strategy. Consequently, these groups represent useful models in which to investigate the specific morphological and physiological adaptations that are driven by the adoption of a benthic lifestyle. In this study, we compared the distribution and abundance of electrosensory pores in the spotted wobbegong shark (*Orectolobus maculatus*) with the Australian angel shark (*Squatina australis*) to determine whether both species display a similar pattern of clustering of sub-dermal electroreceptors and to further understand the functional importance of electroreception in the feeding behaviour of these benthic sharks. *Orectolobus maculatus* has a more complex electrosensory system than *S. australis*, with a higher abundance of pores and an additional cluster of electroreceptors positioned in the snout (the superficial ophthalmic cluster). Interestingly, both species possess a cluster of pores (the hyoid cluster, positioned slightly posterior to the first gill slit) more commonly found in rays, but which may be present in all benthic elasmobranchs to assist in the detection of approaching predators.

Additional keywords: ambush feeding behaviour, ampullae of Lorenzini, Elasmobranch, electroreception, predator avoidance.

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Introduction

Electroreception is an ancient sense found in various vertebrate groups, having been lost and re-evolved several times (New 1997). Recurrent and independent evolution of the electrosensory system highlights its potential value in aquatic environments, as the bioelectric fields produced by aquatic organisms may be detectable by potential predators (New 1997; Collin and Whitehead 2004; Kempster *et al.* 2013a). Passive electroreception is found throughout the animal kingdom (Collin 2010), including elasmobranchs (Murray 1960; Kalmijn 1966), teleosts (Parker and Van Heusen 1917), amphibians (Himstedt *et al.* 1982) and even mammals (Scheich *et al.* 1986).

Electroreception in elasmobranchs serves many functions, including prey location (Kalmijn 1974; Kajiura and Holland 2002), the detection of predators (Sisneros *et al.* 1998; Kempster *et al.* 2013a) and mates (Tricas *et al.* 1995; Kempster *et al.* 2013b), social communication (Bratton and Ayers 1987;

Sisneros *et al.* 1998), and orientation to the earth's magnetic field (Kalmijn 1974, 1978; Paulin 1995). The role of electroreception within elasmobranchs also varies by species depending on their specific ecology and may range from the detection of planktonic prey in large filter feeding sharks (Kempster and Collin 2011a, 2011b) to the recognition of predators in small benthic sharks (Sisneros *et al.* 1998; Winther-Janson *et al.* 2012; Kempster *et al.* 2013a).

The variation in body morphology and ecology of elasmobranch species greatly affects how they utilise their sensory systems to live most effectively within their environment (Raschi 1986; Kajiura *et al.* 2010; Kempster *et al.* 2012). Of particular interest are the distantly related species of the orectolobid (wobbegong shark) and squatinid (angel shark) families; despite their lineages diverging roughly 350 million years ago (Heinicke *et al.* 2009), they have convergently evolved a distinctive dorso-ventrally compressed ray-like body shape to

complement their benthic lifestyle and ambush feeding behaviours (Cortés 1999; Chidlow 2007; Huveneers et al. 2007).

Unlike most benthic sharks, orectolobid and squatid species are thought to primarily ambush swimming prey from below rather than searching for prey buried in the substrate, as is common among other benthic elasmobranchs (Cortés 1999; Fouts and Nelson 1999; Motta and Wilga 2001; Chidlow 2007; Huveneers et al. 2007). This 'sit and wait' feeding strategy is unique among elasmobranchs (Last and Stevens 2009). Orectolobid species are known to feed on mostly teleost fishes, cephalopods and other chondrichthyans (Chidlow 2007; Huveneers et al. 2007). Similarly, squatid species feed primarily on teleost fishes, cephalopods and crustaceans (Cortés 1999). Until recently, sensory adaptations necessary for the ambush-style feeding method of orectolobid and squatid species were relatively unknown (Fouts and Nelson 1999). However, recent examination of the electrosensory system has begun to reveal insights into how this sensory modality may be used to facilitate ambush predation (Theiss et al. 2011). Theiss et al. (2011) examined the superficial arrangement of electrosensory pores in *Orectolobus maculatus*, and found a greater abundance of pores on the dorsal surface, an arrangement unique amongst elasmobranchs, suggesting an electrosensory role in the unique feeding behaviour of this species. However, Theiss et al. (2011) did not assess the specific clustering of electroreceptors to further evaluate the functional significance of this sensory modality.

The distinct clustering of electroreceptors in elasmobranchs is thought to facilitate the processing of multiple signals to serve different primary functions (Tricas 2001; Rivera-Vicente et al. 2011). Four discrete pairs of ampullary clusters are recognised in elasmobranchs and are named according to the major anterior lateral line nerve that they are innervated by: the superficial ophthalmic (S), buccal (B), hyoid (H) and mandibular (M) clusters (Fig. 1) (Raschi 1986; Tricas 2001; Rivera-Vicente et al. 2011; Winther-Janson et al. 2012). The S, B and H clusters project to pores on the dorsal and ventral surfaces (Raschi 1986; Winther-Janson et al. 2012; Camilieri-Asch et al. 2013) and, in some species, the S and B clusters divide into distinct subgroups (Fig. 1) (Raschi 1986; Rivera-Vicente et al. 2011). The canals of the M cluster, on the other hand, only project ventrally and are concentrated on the lower jaw near the mouth (Chu and Wen 1979; Raschi 1986).

Even though electrosensory pore abundance in elasmobranchs ranges from hundreds to thousands (Raschi 1986; Kajiura et al. 2010; Kempster et al. 2012), most studies to date have focussed on the number and distribution of pores between dorsal and ventral surfaces and related this to feeding ecology (Wueringer and Tibbetts 2008; Jordan et al. 2009; Theiss et al. 2011). However, these studies did not examine the specific clustering of electroreceptors, which is likely to be an important factor in understanding the functional significance of pore abundance and distribution in elasmobranchs. This is because central projections of electrosensory axons from different clusters project to distinct regions and retain somatotopic organisation in the brain relative to the external pore position on the skin (Bodznick and Schmidt 1984). Therefore, convergence of axons from distinct clusters may enhance directional sensitivity to electric fields, emphasising the important role of specific pore

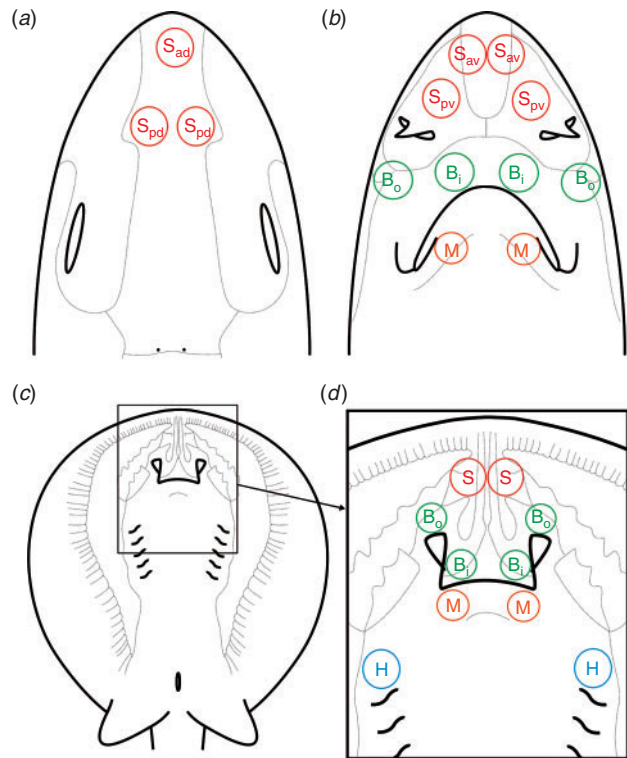


Fig. 1. Diagrams highlighting the approximate location of major electrosensory clusters in sharks (*a*: dorsal view and *b*: ventral view) and rays (*c*: ventral view and *d*: magnified ventral view). Four distinct ampullary clusters are recognised in elasmobranchs and are named according to the major anterior lateral line nerve that they are innervated by: the superficial ophthalmic (S), buccal (B), hyoid (H), and mandibular (M) clusters. The S cluster, which is located primarily around the snout, may be divided into several smaller discrete pairs of clusters named according to their anterior (a) or posterior (p) position on the ventral (v) or dorsal (d) surface. The S_{ad} cluster is the only one that lacks a distinct pair due to its central position. The B cluster may be divided into two discrete cluster pairs determined by their inner (i) or outer (o) position on the ventral surface. The M cluster pair are located on the lower jaw posterior to the mouth on the ventral surface. Finally, the H cluster pairs are located slightly anterior to the first gill slits on the ventral surface in rays.

clusters in detecting different sources of electrical stimuli (Rivera-Vicente et al. 2011).

This study compares the distribution and abundance of electrosensory pores, and also takes into account the specific clustering of electroreceptors of the spotted wobbegong shark (*Orectolobus maculatus*) and the distantly related Australian angel shark (*Squatina australis*), which appear to share similar feeding behaviours. By determining the specific clustering of electroreceptors and the spatial arrangement of their associated superficial pores, it is possible to further understand the functional importance of electroreception in these unique species of elasmobranchs.

Materials and methods

Four specimens of *Orectolobus maculatus* (2 male and 2 female; 121–132 cm total length (TL)) and eight specimens of *Squatina australis* (5 male and 3 female; 42–91 cm TL) were examined to assess the abundance and distribution of electrosensory pores

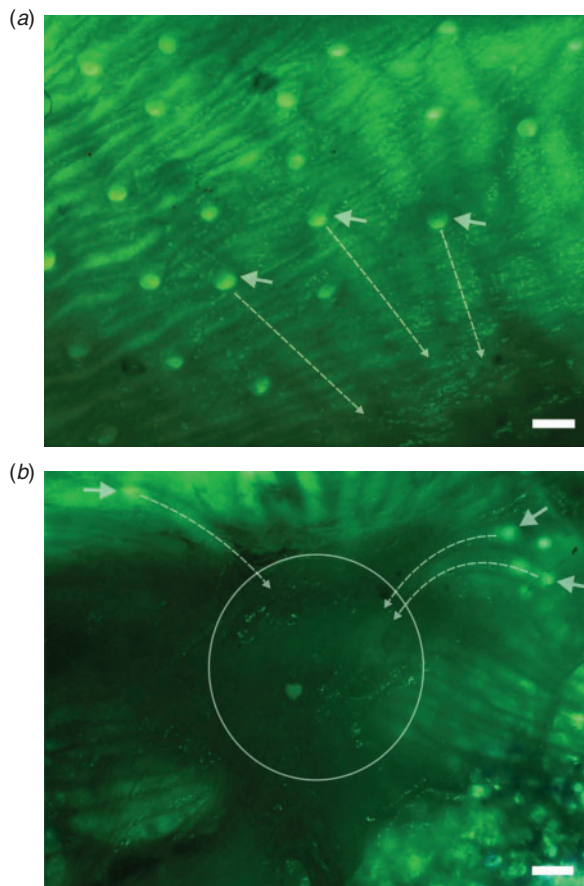


Fig. 2. Representative photographs used to produce maps of the electro-sensory system by placing dissected skins over a light box. (a) Superficial view of the skin highlighting electrosensory pores (marked by arrow heads) and their associated canals (marked by dashed arrows). (b) Internal view of the skin highlighting the external pores (marked by arrow heads) and their associated canals (marked by dashed arrows) leading to a major electrosensory cluster (outlined with a circle). Scale bar = 1 mm.

and their associated ampullary bulbs. Specimens of *O. maculatus* were collected and euthanised as part of a previous study (Theiss *et al.* 2011), and fixed in 4% paraformaldehyde in 0.1 M phosphate buffer (pH 7.2). Similarly, specimens of *S. australis* were also collected and euthanised as part of a previous study (Jones *et al.* 2010), but were instead frozen upon collection and stored before examination. As a result of the differing fixation methods between specimens, it was not possible to compare canal lengths or pore widths, primarily due to issues related to tissue shrinkage. However, canals were still visible and could easily be traced from their surface pore opening to their associated ampullary bulb within a distinct cluster (Fig. 2).

All specimens were examined for the purpose of this study following previously established protocols (Marzullo *et al.* 2011; Camilieri-Asch *et al.* 2013). To differentiate between lateral line and electrosensory pores, a methylene blue solution (~0.3% in water) was applied to the skin using slight pressure (Kempster and Collin 2011a, 2011b). This solution stained the lateral line canals blue, leaving the electrosensory canals unstained. The skin was removed from the head of each shark and placed on a light box to highlight the location of electrosensory pores in order to

count them accurately. The precise position of each ampullary pore was recorded on a transparency laid over the skin. Ampullary canals were then drawn from each pore opening to its corresponding ampullary cluster. Pore distribution maps were produced using the Corel DRAW™ graphics software (see Fig. 3) to show the location of individual pores, cluster location and associated canals. Differences in mean pore counts between individuals were statistically analysed by two-sample *t*-test using the Minitab™ statistical analysis software. Two-sample *t*-tests were used to determine statistical differences between total and dorsal and ventral pore abundance.

Results

Orectolobus maculatus has significantly more electrosensory pores (mean $572.0 \pm \text{s.d. } 7.8$) than *Squatina australis* (mean $251.3 \pm \text{s.d. } 9.8$) (two-sample *t*-test: $t_7 = -61.8$, $P \leq 0.001$) (Fig. 4 and Table S1, available as Supplementary Material on the journal website). Both species possess the majority of pores on their dorsal surface: *O. maculatus* with 93.8% (two-sample *t*-test: $t_3 = 97.7$, $P \leq 0.001$) and *S. australis* with 69.6% (two-sample *t*-test: $t_{10} = 27.7$, $P \leq 0.001$) of pores situated dorsally (Fig. 4 and Table S1).

Like rays, *Orectolobus maculatus* and *Squatina australis* possess a hyoid (H) cluster of electroreceptors (Table 1) (Chu and Wen 1979; Raschi 1986). The H cluster is located slightly anterior to the first gill slit (Fig. 3), with its associated canals and pores projecting to both the dorsal and ventral surfaces. *O. maculatus* has only 19.7% of its total number of pores associated with the H cluster, of which 74.5% are on the dorsal surface (Table 1). In contrast, *S. australis* has 73.9% of its total number of pores associated with the H cluster, of which 58.9% are on the dorsal surface (Table 1). Although the total abundance of pores associated with the H cluster differs significantly between species (two-sample *t*-test: $t_4 = 11.18$, $P \leq 0.001$), both have the majority of their H pores positioned on the dorsal surface (*O. maculatus*: mean $84.0 \pm \text{s.d. } 10.1$; *S. australis*: mean $109.3 \pm \text{s.d. } 5.5$).

The greatest abundance of pores in *Orectolobus maculatus* is found in the buccal (B) cluster (45.1%), of which just 6.8% are found on the ventral surface. In *Squatina australis*, however, only 26.1% of pores are associated with the B cluster, all of which are positioned on the dorsal surface (Table 1).

The superficial ophthalmic (S) cluster, which is not present in *Squatina australis*, accounts for 35.1% of all pores in *Orectolobus maculatus*, all of which are situated dorsally (Table 1). Additionally, both species lack a mandibular (M) cluster of pores, which is typically located posterior to the lower jaw in sharks (Figs 1, 3).

Discussion

The electrosensory systems of both *Orectolobus maculatus* and *Squatina australis* are specifically suited to their benthic life-style and unusual ambush predation style. These two species have convergently evolved a similar distribution of electrosensory pores, having the majority of pores located dorsally. This arrangement complements their ambush predation style by providing localised and directed sensory input about prey and/or predators swimming in the water column above them.

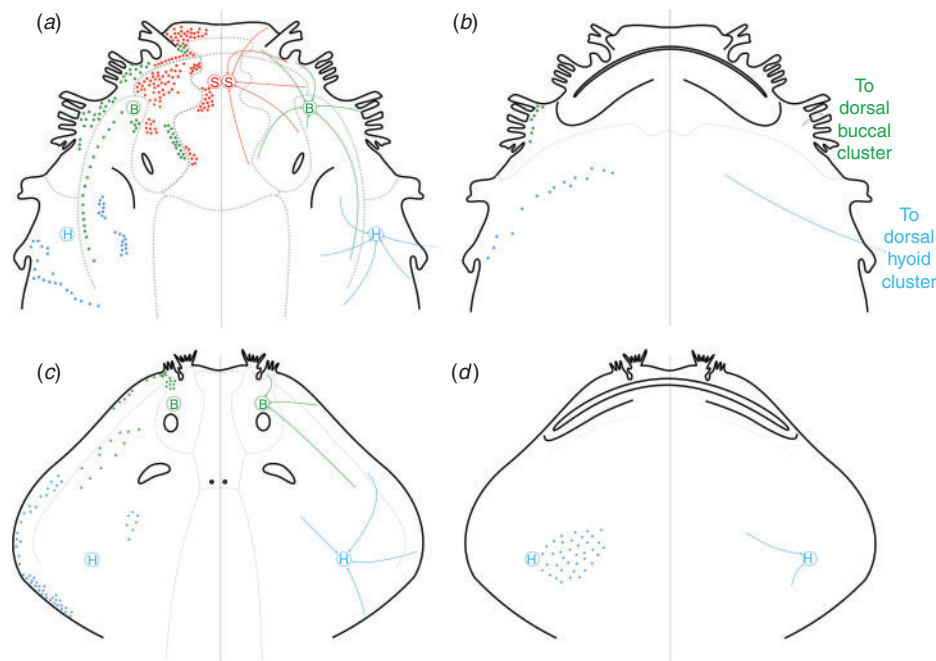


Fig. 3. Distribution pattern of electrosensory pores in *Orectolobus maculatus* (a and b) and *Squatina australis* (c and d). Approximate length and direction of canals associated with each pore cluster are highlighted (on the right side of the head) by arrows leading from the pore opening to the cluster of electroreceptors. The grey dashed line indicates the approximate position of the lateral line canals. S (red): Superficial ophthalmic cluster; B (green): Buccal cluster; H (blue): Hyoid cluster.

Most sharks are known to possess three major ampullary electroreceptor clusters: the superficial ophthalmic (S), buccal (B), and mandibular (M) clusters (Rivera-Vicente *et al.* 2011). Additionally, rays possess a fourth cluster, the hyoid (H) (Raschi 1986; Kempster *et al.* 2012). *Orectolobus maculatus* and *Squatina australis* are among the first species of sharks found to possess this H cluster of electroreceptors (Winther-Janson *et al.* 2012). The H cluster is likely to be present in most benthic sharks, but to date, most of the few studies that have examined electroreceptor clusters in elasmobranchs have focussed on pelagic shark species and benthic rays (Raschi 1986; Tricas 2001; Marzullo *et al.* 2011; Rivera-Vicente *et al.* 2011; Camilieri-Asch *et al.* 2013;).

Similar to rays, *O. maculatus* and *S. australis* may sit motionless on the benthos for extended periods of time, making them vulnerable to attack by predators from above. Given the primarily posterior and dorsal position of the H cluster in these sharks, this cluster may be useful for detecting predators approaching from behind and beyond their visual field (Fouts and Nelson 1999; Theiss *et al.* 2010; Winther-Janson *et al.* 2012), and for identifying approaching conspecifics to facilitate mating (Kempster *et al.* 2013b). Although *S. australis* possesses far fewer pores than *O. maculatus* (Fig. 4 and Table S1), both species possess a relatively similar number of dorsally located H pores, which could imply an important role in predator and conspecific detection.

Squatina australis has a greater abundance of H pores on its ventral surface than *Orectolobus maculatus*, but the role of the ventral cluster is unclear, particularly given the distinctly different distribution of these pores between species (Fig. 3).

Paulin (1995) suggested that the H cluster in rays may be used for navigation, as its posterior position on the body would seem to make it unsuitable for prey detection. Paulin (1995) went on to suggest that the development of this cluster may be correlated with an individual's tendency to move long distances through open water rather than feeding mode or phylogeny. However, given the restricted geographic range of *O. maculatus* and *S. australis* (Last and Stevens 2009) compared with more migratory shark species that lack the H cluster (for example, the white shark, *Carcharodon carcharias*; Kempster *et al.* 2012), it is unlikely that this cluster plays a significant role in navigation. Thus, at this time, the primary function of this pore cluster remains unclear.

Although these two species adopt a similar ambush predation strategy during the day, which is facilitated by the unique arrangement of their respective electrosensory systems, their nocturnal feeding strategies differ. *Orectolobus maculatus* is known to actively hunt prey at night (Compagno 1984; Compagno *et al.* 2005), while squatid species continue to utilise their sit-and-wait ambush strategy at night (Pittenger 1984; Fouts and Nelson 1999). *Orectolobus maculatus* possesses a well developed visual system adapted for nocturnal activity and scanning the water column for prey (Theiss *et al.* 2010). So, although electroreception may play a vital role in detecting fish that are swimming above the head during daylight hours, at night it may be used to actively track prey.

To assist in tracking fast-moving prey, *Orectolobus maculatus* has a higher total number of pores than *Squatina australis*. The higher total number of pores may facilitate the capture of relatively fast-moving prey through increasing the system's

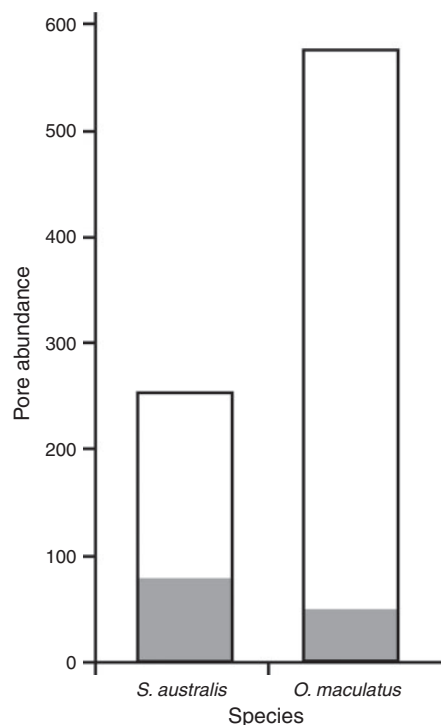


Fig. 4. Mean total abundance of electrosensory pores in *Orectolobus maculatus* and *Squatina australis*. Shaded area indicates the proportion of pores located on the ventral surface, with the remainder located dorsally. Significant differences were found between species for ventral, dorsal, and total pore abundance counts (two sample *t*-test with a *P*-value ≤ 0.001 ; see Table S1).

Table 1. Abundance of electrosensory pores associated with specific clusters in *Orectolobus maculatus* and *Squatina australis*

Data is presented as the mean number of pores \pm one standard deviation and the range. ‘*’ denotes a statistically significant difference in pore abundance between species (two sample *t*-test with a *P*-value ≤ 0.001). S, superficial ophthalmic; B, buccal; H, hyoid

Genus	Species	<i>n</i>	S	B*	H*
<i>Squatina</i>	<i>australis</i>	8	n/a	65.6 \pm 5.7	185.6 \pm 7.6
			n/a	55 – 74	171 – 195
<i>Orectolobus</i>	<i>maculatus</i>	4	200.8 \pm 1.7	258.5 \pm 9.2	112.8 \pm 11.9
			199 – 203	246 – 268	100 – 126

resolution (Rivera-Vicente *et al.* 2011). In addition, *O. maculatus* also has a more extensive electrosensory network than *Squatina australis*, as the latter lacks the S cluster, which is typically found in the snout of elasmobranchs (Raschi 1986; Rivera-Vicente *et al.* 2011) (Figs 1, 3). For *O. maculatus*, this cluster may provide greater electrosensory resolution in front of the head to assist in tracking fast-moving prey. *S. australis* has a lower abundance of pores and lacks the S cluster, which is likely because it relies more heavily on the sit-and-wait ambush predation style (Pittenger 1984; Fouts and Nelson 1999) rather than actively seeking out prey.

The M cluster of pores, which is thought to assist in directing the mouth towards prey upon the final feeding strike (Raschi

1986; Kajiura *et al.* 2010; Kempster *et al.* 2012), is absent in both *Orectolobus maculatus* and *Squatina australis*. Given their distant phylogenetic relationship, this is likely an adaptation to their specific feeding behaviour rather than a phylogenetic trait. The lack of an M cluster has only been documented in one other shark species, the basking shark (*Cetorhinus maximus*) (Kempster and Collin 2011b). This is thought to be related to their unique feeding behaviour, which is also likely to be the case for *O. maculatus* and *S. australis*.

Unfortunately, it was not possible in this study to assess the widths and lengths of ampullary canals due to the differing specimen preservation methods (see Materials and methods). However, it is likely that variations in the specific morphology of ampullary canals will influence the sensitivity and resolution of the electrosensory system, which may reveal more about the specific feeding behaviours of these two unusual species.

The simultaneous evolution of a dorsally dominated distribution of electroreceptors in two distantly related shark species emphasises the importance of considering the spatial distribution of peripheral electrosensory pores when interpreting interspecific differences in behaviour. Although *Orectolobus maculatus* and *Squatina australis* appear to have evolved a similar electrosensory system, by looking beyond the superficial arrangement of pores, significant differences are revealed in the way they are arranged by discrete clusters. Convergence of electrosensory pores into distinct clusters may enhance directional sensitivity to specific electrical stimuli, which may indicate cluster specific roles in prey detection, predator avoidance and mate selection. Only by determining the specific clustering of electrosensory pores is it possible to understand the functional significance of their superficial distribution.

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