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NOTE

Electrosensory pore distribution and feeding in the megamouth shark *Megachasma pelagios* (Lamniformes: Megachasmidae)

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ABSTRACT: The megamouth shark *Megachasma pelagios* is a rare, large filter-feeding shark. Little to nothing is known of its sensory biology, particularly in relation to its feeding behaviour. We describe the abundance and distribution of ampullary pores over the head and propose that both the spacing and orientation of electrosensory pores enables *M. pelagios* to use passive electroreception to maximise feeding efficiency.

KEY WORDS: Ampullae of Lorenzini · Electroreception · Filter feeding · Megamouth shark

INTRODUCTION

Electroreception is an ancient sense that has evolved independently across the animal kingdom in multiple groups, including agnathan (lampreys), cartilaginous (chimaeras, sharks, skates/rays) and bony fishes (lungfish, coelacanth, polypterids, chondrosteans, teleosts), some amphibians and mammals (Scheich et al. 1986, Collin & Whitehead 2004, Jorgenson 2005). The multiple and independent evolution of electroreception emphasises the importance of this sense in a variety of aquatic environments (Collin & Whitehead 2004). The electrosensory system of sharks is comprised of a series of electroreceptors, known as the ampullae of Lorenzini, distributed over almost the entire surface of the head anterior to the first gill slit. It is thought that the major role of the electroreceptors is in the detection of prey (Kalmijn 1971, Raschi et al. 2001, Kajiura et al. 2010), but other functions include the detection of predators, the facilitation of social behaviours (Sisneros et al. 1998) and the ability to orient to and navigate within the earth's magnetic field (Kalmijn 1974, 1978, 1982, Paulin 1995, Montgomery & Walker 2001).

The megamouth shark *Megachasma pelagios* is a rare species of shark (Last & Stevens 2009) and is classified as the sole member of the Family Megachasmidae. Since its discovery in 1976, only a small number of *M. pelagios* sharks have been observed worldwide, with 50 specimens caught or sighted as of 2010. Unlike other planktivorous sharks such as *Cetorhinus maximus* (basking shark) and *Rhincodon typus* (whale shark), *M. pelagios* is thought to adopt a unique method of filter feeding. Instead of swimming continuously with its enormous mouth wide open, filtering water for plankton and jellyfish, *M. pelagios* is thought to attract prey with a bioluminescent strip along its upper jaw (Taylor et al. 1983) — although this has not yet been supported with histological evidence (Nakaya et al. 2008) — and then engulf it in a single motion, similar to the feeding mechanism of some baleen whales (Compagno 1990, Nakaya et al. 2008). This active method of ingesting prey is thought to be due to the restricted internal gill openings and jaw morphology of *M. pelagios* sharks (Compagno 1990, Nakaya et al. 2008). It is thought that swimming with its mouth open would create a negative pressure,

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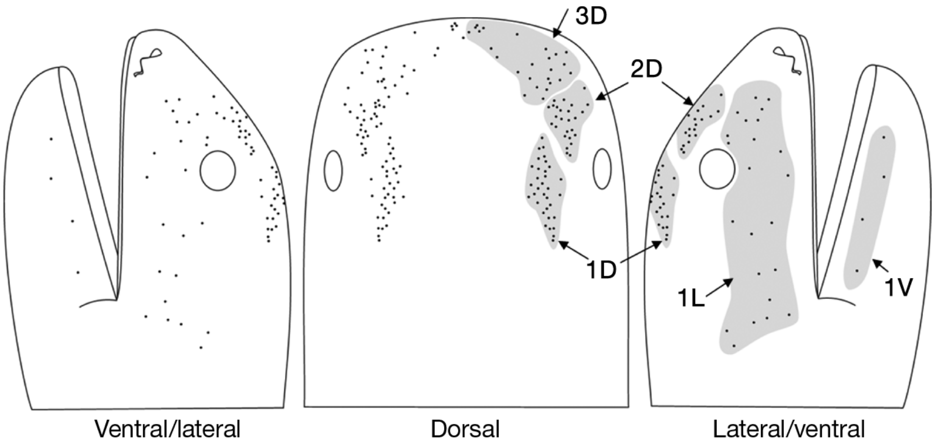

Fig. 1. *Megachasma pelagios.* Electrosensory pore distribution map for the megamouth shark. D: dorsal; L: lateral; V: ventral

whereby water and prey would be pushed aside, due to its densely packed papillose gill rakers and relatively small internal gill rakers (Compagno 1990).

M. pelagios tracked off the coast of California performed vertical migrations with the onset of sunrise and sunset (Nelson et al. 1997). This crepuscular migration allowed *M. pelagios* to consistently sample the water column at a specific level of illumination, with the shark staying at shallow depth at night (12 to 25 m) and in the deep during the day (120 to 166 m), but still well above the sea bed, which is at 700 to 850 m (Nelson et al. 1997). *M. pelagios* was thought to be following an isolume of 0.4 lux, the same light cue used by its vertically migrating prey (Nelson et al. 1997). As a result, a correlation was found between the diel depth distribution of *M. pelagios* and the vertically migrating krill *Euphausia pacifica*, which is common in southern California waters (Nelson et al. 1997). The highest night-time concentration of adults and juveniles of *E. pacifica* was reported to be between the surface and 40 m, with a deeper adult daytime peak located at 200 m (Brinton 1962, Nelson et al. 1997).

MATERIALS AND METHODS

A specimen of *Megachasma pelagios* (referred to as Megamouth 3) 5 m in length was stranded in Mandurah, Western Australia, in 1988 (Berra & Hutchins 1990). Access to the shark was given during its relocation from the Museum of Western Australia to the Western Australian Maritime Museum in Fremantle. The specimen had been fixed in 70% ethanol for 22 yr and, although it was apparent that some degree of tissue shrinkage had occurred, the ampullary pores were easily distinguishable from the lateral line pores, given the obvious size difference. Due to limited access to the specimen during this time, the lateral line pores could not be counted and/or their distribution mapped. No dissection of the ampullary pores was allowed, negating any chance of histological analysis. Pores were counted *in situ*, and photographs were used to produce the pore map presented here, with the aid of a CorelDRAW graphics suite (Fig. 1).

RESULTS

A total of 225 ampullary pores were present on the head of *Megachasma pelagios* (Fig. 1), with significantly more pores (75%) located on the dorsal (D) surface of the head than the ventral (V, 4%) and lateral (L, 21%) surfaces combined (25%; see Table 1). Ampullary pores were found in the most dense assem-

Table 1. *Megachasma pelagios*. Summary of morphometric data for the specimen Megamouth 3. Ampullary pore abundance for the dorsal (D), lateral (L) and ventral (V) surfaces

	Megamouth 3
N	1
Sex	Male
Total length (cm)	515
Body mass (kg)	690
Ventral pore number	**8**
1V Left	4
1V Right	4
Lateral pore number	**48**
1L Left	23
1L Right	25
Dorsal pore number	**169**
1D Left	33
1D Right	32
2D Left	28
2D Right	26
3D Left	25
3D Right	25
Total pore number	**225**

blages parallel (1D left and 1D right) and anterior (2D left and 2D right) to the eyes on the dorsal surface, with these fields each containing from 25 to 28 pores (Table 1). Pore fields located near the snout (3D left and 3D right) occupied a larger surface area than the previous 2 fields, but contained a similar number of pores (33 pores; see Table 1). Thus, the pore density of the 3D left and 3D right fields is much reduced. Pore fields occupying the lateral surface of the head (1L left and 1L right) run from behind the posterior margin of the nares, between the eye and jaw line, to just behind the posterior margin of the jaw. The lateral pore fields also contain a similar number of pores to the fields on the dorsal surface (23 to 25 pores; see Table 1), although, as they cover the largest spatial area of the head, they show the lowest pore density of any pore field. Finally, below the jaw line on the ventral surface lie 2 lines of ampullary pores (1V left and 1V right) that follow the edge of the jaw on the right and left sides of the head and contain the lowest number of pores of any field (4 pores; see Table 1).

DISCUSSION

Megachasma pelagios shows the lowest ampullary pore abundance of any shark species currently described and is the only pelagic shark currently known to have almost no pores on its ventral surface (Fig. 1, Table 1). We suggest that the terminal position of the mouth accounts for this unique trait. Most shark species possess sub-terminal mouths and generally do not possess many pores posterior to the lower jaw (Compagno et al. 2004, Cornett 2006). Thus, the lack of pores in this region is not uncommon for sharks, a finding which is also true for the closest living relative of the Megachasmidae, the thresher sharks (Alopidae) (Compagno 1990, Cornett 2006). Taking into account the shape and orientation of the head, with its sloping and rounded surfaces, most of the pore fields are positioned so that they are facing forward, in the direction that *M. pelagios* would be moving. This pore arrangement would allow for the detection of planktonic organisms around the head as the shark swims through the water (horizontally and vertically).

Planktonic prey produce bioelectrical fields of up to 1 mV cm^{-1}, and other species, such as paddlefish, actively hunt for plankton using passive electroreception (Wojtenek et al. 2001). Given that some species of sharks detect electrical fields as weak as 1 nV cm^{-1} (Kalmijn 1978, 1982, Kajiura & Holland 2002), *Megachasma pelagios* may use passive electroreception to determine the presence, and to some degree the abundance, of planktonic prey around its head. In view of the unique feeding mechanism thought to be used by *M. pelagios*, it would be beneficial to determine how efficient each feeding event will be before expending the energy to ingest what may possibly just be water with no energetic reward. Therefore, if *M. pelagios* sharks do possess a bioluminescent strip across the upper jaw (Taylor et al. 1983), they would be able to attract planktonic prey and, subsequently, detect their presence with the use of passive electroreception. Each pore receives and processes electrical stimuli independently. Therefore, the signal strength detected at each pore at any given moment would give an indication of the relative concentration and/or location of planktonic prey around the head.

On the other hand, *Megachasma pelagios* is able to follow migrating prey items (Nelson et al. 1997), a behaviour that could be mediated solely using passive electroreception, potentially negating the need to rely on bioluminescent signals to attract prey. With each scenario presented here, once a desired level of electrosensory stimuli has been achieved, ingestion of prey would then follow using a gulp- and suction-feeding mechanism (Nakaya et al. 2008) to consume all the available planktonic prey in the vicinity of the head, thereby maximising the efficiency of each feeding event.

As the results presented here are based on a single specimen, further work is required to unravel the unique nature of this species' use of electroreception in filter feeding. Given the very sparse and unpredictable availability of *Megachasma pelagios* specimens, it may be prudent to also focus our attention on the electrosensory systems of more widely available filter-feeding sharks such as *Rhincodon typus* and *Cetorhinus maximus*.

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