

NOTE

Electrosensory pore distribution and feeding in the basking shark *Cetorhinus maximus* (Lamniformes: Cetorhinidae)

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ABSTRACT: The basking shark *Cetorhinus maximus* is the second largest fish in the world, attaining lengths of up to 10 m. Very little 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 *C. maximus* to use passive electroreception to track the diel vertical migrations of zooplankton that enable the shark to meet the energetic costs of ram filter feeding.

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

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INTRODUCTION

Electroreception is an ancient sensory modality that has evolved independently across the animal kingdom in multiple groups (Scheich et al. 1986, Collin & Whitehead 2004). Repeated independent evolution of electroreception emphasises the importance of this sense in a variety of aquatic environments, where electric fields produced by both living and inanimate sources are numerous (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. The major role of the ampullae of Lorenzini is thought to be for the detection of prey (Kalmijn 1971, Raschi et al. 2001, Kajiura et al. 2010). However, other functions have been suggested, including the detection of predators, the facilitation of social behaviours (Sisneros et al. 1998) and the ability to orientate to and navigate within the earth's magnetic field (Kalmijn 1974, 1978, 1982).

The basking shark *Cetorhinus maximus* is the second largest extant species of fish, attaining lengths of up to 10 m (Compagno 1984). These sharks inhabit temperate coastal waters worldwide and feed upon tiny zooplankton. *C. maximus* is 1 of only 3 extant filter-feeding sharks; the other 2 species are the whale

shark *Rhincodon typus* and the megamouth shark *Megachasma pelagios*, which can attain lengths of up to 14 and 6 m, respectively (Compagno 1984). These 3 filter-feeding sharks are among the largest living marine vertebrates (Compagno 1984) and yet they are all able to meet their energetic costs through the consumption of tiny zooplankton. *R. typus* and *M. pelagios* primarily utilise suction feeding, a strategy that allows them to draw high concentrations of zooplankton across their filter apparatus without the need for strong forward swimming speeds (Compagno 1990). *C. maximus*, on the other hand, capture zooplankton by filtering prey from the passive water flow over their gills using bristle-like rakers situated on the gill arches, a strategy known as ram filter feeding (Sims 2000). Therefore, regulation of efficient filtration of zooplankton relies heavily upon the ability of *C. maximus* to select appropriate swimming speeds so that the energetic reward exceeds, or at least meets, the energetic cost of ram filter feeding.

Filter-feeding sharks are faced with a unique problem for prey detection given the extremely heterogeneous distribution and abundance of zooplankton worldwide (Greene et al. 1998). Oceanic and inner-shelf fronts support high abundances of zooplankton and are known to be principal feeding areas for *Cetorhinus maximus* (Sims & Quayle 1998). However, it is

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the response of these filter-feeding sharks to the vertical migrations of zooplankton that is relatively unknown. The daily change in vertical abundance of zooplankton, known as diel vertical migration (DVM), is a widespread behavioural phenomenon among marine and freshwater zooplankton species (Hays 2003) that influences foraging patterns of vertebrate predators (Sims et al. 2005). Zooplankton populations typically remain in deep water during the day, principally to avoid visually orientating predators (Bollens & Frost 1989), and migrate to the surface at dusk to feed before returning to depth at dawn. *Megachasma pelagios* has been shown to exhibit DVM, which was previously thought to be a strategy to maintain a constant level of ambient light rather than to orient to higher zooplankton abundance (Nelson et al. 1997). However, if filter-feeding sharks use a DVM strategy based solely on light level, this may render them less able to respond to short- and long-term changes in the vertical distribution of zooplankton (Sims & Quayle 1998). Fortunately, sharks have an advantage over most other marine predators, as they possess the ability to orient towards the bioelectric fields of their prey (Kalmijn 1974). Passive electroreception has been identified as a possible mechanism for *M. pelagios* to orientate towards and follow zooplankton populations through their DVM (Kempster & Collin 2011), negating the need to follow ambient light cues, as previously suggested (Nelson et al. 1997). In the present paper we describe the abundance and distribution of ampullary pores on a *C. maximus* specimen and discuss how this may enable the shark to track the DVM of zooplankton.

MATERIALS AND METHODS

A specimen of *Cetorhinus maximus* was obtained from the elasmobranch collection at the Museum of Western Australia. The specimen of ~325 cm in length was collected off the coast of Busselton, Western Australia, in 1969 and has been preserved in 70% ethanol for 42 yr. Although it was apparent that some degree of tissue shrinkage had occurred, the ampullary pores were still clear and easily distinguishable from the lateral line pores. Given the rarity of this species worldwide and that this was the only specimen of its kind in this collection, no dissection of the ampullary pores was permitted, negating any chance of histological analysis. Pores were counted *in situ* using transparencies that were laid over the surface of the head, on to which the position of individual pores were marked. Multiple photographs were taken of the head and relative pore region positions, which were later used to assist in producing the pore map presented here, with the aid of a CorelDRAW® graphics suite (see Fig. 1).

RESULTS

A total of 301 ampullary pores were present on the head of *Cetorhinus maximus*, with all pores located on the protruding snout, anterior to the upper jaw margin (Fig. 1). Most pores were located on the lateral (L, 59%) and dorsal (D, 35%) surfaces of the head, with very few on the ventral surface (V, 6%; Table 1). Ampullary pores were found in the greatest numbers parallel (1D left and 1D right) and anterior (1L left and 1L right) to the eyes on the dorsal and lateral surfaces, with these fields each containing between 52 and 68 pores (Table 1, Fig. 1). Pores located towards the anterior edge of the snout (1L left and 1L right) are spread across a narrow strip that widens towards the posterior margin to surround the anterior edge of the nares (Fig. 1). Posterior to each naris is a small region of pores (2L left and 2L right) located in front of the eye that may in fact be a continuation of the pore regions anterior to each nare (1L left and 1L right). For the purposes of the present investigation these regions (1L left and 1L right; 2L left and 2L right) have been split to allow a better interpretation of pore distribution. Regions with the lowest pore abundance (3L left and 3L right; 1V left and 1V right) were found posterior to the nares, between the eye and upper jaw margin, and did not extend much further back than 1 eye length from the posterior margin of the eye (Table 1, Fig. 1).

DISCUSSION

Cetorhinus maximus is the only shark species currently described with no electrosensory pores on the lower jaw, in the mandibular pore region (Fig. 1). This region of the head in sharks is generally characterised by low pore abundance and is thought to assist in guiding the mouth towards suitable prey during the final phase(s) of the feeding strike (Chu & Wen 1979, Cornett 2006). The unique morphology of the mouth and the fact that *C. maximus* is a ram filter feeder would negate any need for mandibular pores. The large gape created between the mandibular pore region and the anterior pore regions of the snout during ram filter feeding can be as much as 1 m (Matthews & Parker 1950) and would render mandibular pores ineffective; *C. maximus* would not be able to determine a relative prey concentration throughout this space, given the weak bioelectric fields of zooplankton and the effective range of the ampullae of Lorenzini being only ~30 cm (Kajiura & Holland 2002).

All organisms produce bioelectric fields, which in zooplankton can be up to 1 mV cm⁻¹, and species such as the paddlefish have been shown to actively hunt for zooplankton using passive electroreception (Wojtenek

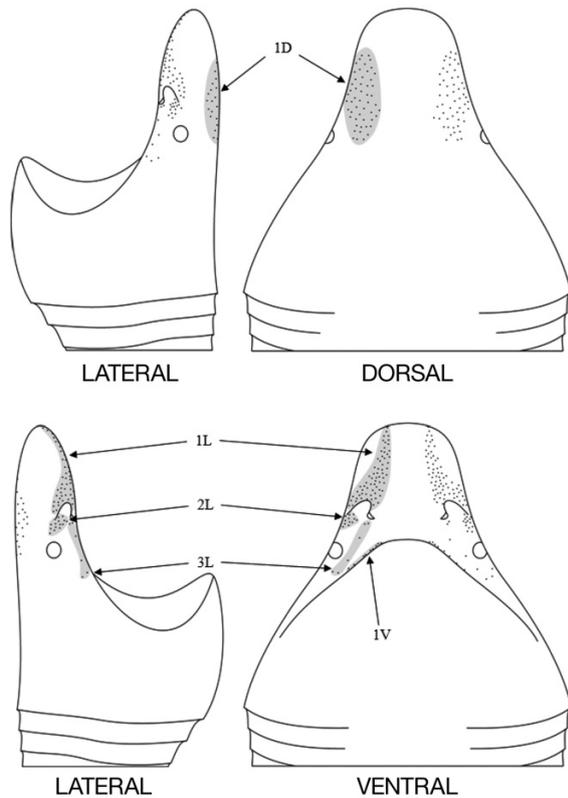


Fig. 1. *Cetorhinus maximus*. Electroreceptive pore distribution map. D: dorsal; L: lateral; V: ventral

Table 1. *Cetorhinus maximus*. Morphometric data for the basking shark specimen. Ampullary pore abundance on the ventral (V), dorsal (D) and lateral (L) surfaces, and in total

N	1
Sex	Unknown
Total length (cm)	325
No. of ventral pores	17
1V left	9
1V right	8
No. of dorsal pores	106
1D left	52
1D right	54
No. of lateral pores	178
1L left	66
1L right	68
2L left	15
2L right	15
3L left	8
3L right	6
Total no. of pores	301

et al. 2001). Sharks have been shown to detect electric fields as weak as 1 nV cm^{-1} (Kalmijn 1978, 1982, Kajiwara & Holland 2002). It is therefore possible that *Cetorhinus maximus* may use passive electroreception to determine the presence, and to some degree the abundance, of planktonic prey around its head, as we earlier proposed for *Megachasma pelagios* (Kempster &

Collin 2011). However, unlike *M. pelagios*, the snout of *C. maximus* protrudes anteriorly in front of the mouth, and is covered in electroreceptive pores (Fig. 1); the snout may act as an electroreceptive probe to guide the mouth of *C. maximus* towards dense zooplankton assemblages to increase ram filter-feeding efficiency. The arrangement of electroreceptive pores around almost the whole snout (Table 1, Fig. 1) of *C. maximus* may allow the shark to identify changes in the vertical and horizontal abundance of zooplankton. This is further supported by a decrease in swimming speed during filter feeding (Sims 2000) that may provide the conditions necessary to establish the spatial distribution of zooplankton around the snout. This would enable *C. maximus* to follow higher concentrations of zooplankton populations throughout their DVM, and thus maintain efficient filtration of zooplankton to meet the energetic costs of ram filter feeding.

All 3 extant filter-feeding shark species have independently evolved unique feeding behaviours (Wilga et al. 2007), yet similarities in the electroreceptive pore abundance of at least *Cetorhinus maximus* and *Megachasma pelagios* (Table 2) suggest that their electroreceptive systems have concomitantly evolved a similar sampling strategy for the detection of bioelectric fields of near-field prey items. The closest living relatives of *C. maximus* and *M. pelagios*, but still classified within the order Lamniformes, show a large range of electroreceptive pore abundance, in the order of 2 to 7 times greater than *C. maximus* and *M. pelagios* (Table 2). These unique differences in pore abundance have been attributed to habitat-specific conditions and species-specific differences in feeding strategy (Raschi et al. 2001, Cornett 2006). *C. maximus* and *M. pelagios* exhibit the lowest electroreceptive pore abundances of the lamniform sharks (Table 2) and also some of the lowest pore abundances of any shark species examined to date (Chu & Wen 1979, Cornett 2006, Kajiwara et al. 2010), highlighting the significance of passive electroreception in relation to their specific lifestyle and feeding mechanisms.

To further understand and confirm the potentially significant role that electroreception plays in the filter-feeding behaviour of sharks, data must be obtained for the only other filter-feeding shark, the whale shark *Rhincodon typus*. However, to truly appreciate how the electroreceptive systems of filter-feeding sharks relate to feeding behaviour, a complete histological analysis of electroreceptors is needed.

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Table 2. Ampullae of Lorenzini pore abundance for species of the order Lamniformes. No data available for Mitsukurinidae family

Lamniform family	Species (no. of replicates)	Total no. of pores ^a	Source
Alopiidae	<i>Alopias pelagicus</i> (2)	1483	Cornett (2006)
	<i>A. superciliosus</i> (1)	1338	Cornett (2006)
Pseudocarchariidae	<i>Pseudocarcharias kamoharai</i> (1)	1152	Cornett (2006)
Odontaspidae	<i>Carcharias taurus</i> (1)	1130	Cornett (2006)
	<i>Carcharias taurus</i> (2)	1030	Raschi et al. (2001)
Lamnidae	<i>Isurus paucus</i> (1)	774	Cornett (2006)
	<i>Lamna nasus</i> (2)	736	Raschi et al. (2001)
	<i>I. oxyrinchus</i> (6)	700	Raschi et al. (2001)
	<i>I. oxyrinchus</i> (1)	635	Cornett (2006)
	<i>L. ditropis</i> (1)	444	Cornett (2006)
Cetorhinidae	<i>Cetorhinus maximus</i> (1)	301	Present study
Megachasmidae	<i>Megachasma pelagios</i> (1)	225	Kempster & Collin (2011)

^aMean pore total is presented for species with multiple replicates

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