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Properties and architecture of the sperm whale skull amphitheatre

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ABSTRACT

The sperm whale skull amphitheatre cradles an enormous two-tonne spermaceti organ. The amphitheatre separates this organ from the cranium and the cervical vertebrae that lie in close proximity to the base of the skull. Here, we elucidate that this skull amphitheatre is an elastic, flexible, triple-layered structure with mechanical properties that are conjointly guided by bone histology and the characteristics of pore space. We contend that the amphitheatre will flex elastically to equilibrate forces transmitted via the spermaceti organ that arise through diving. We find that collisions from sperm whale aggression do not cause the amphitheatre to bend, but rather localise stress to the base of the amphitheatre on its anterior face. We consider, therefore, that the uniquely thin and extended construction of the amphitheatre, has relevance as an energy absorptive structure in diving.

1. Introduction

Sperm whales (*Physeter macrocephalus*) are the largest of the Odontoceti (toothed whales) and frequently dive between 400 and 1200 m (Papastavrou et al., 1989; Watkins et al., 1993; Amano and Yoshioka, 2003; Watwood et al., 2006), though they have also been reported to submerge at depths below 2 km (Ponganis and Kooyman, 2006). This cetacean is equipped with a gargantuan oil resevoir on the dorsal side of its beak known as the spermaceti organ. The spermaceti organ may have multiple functionality in buoyancy control (Clarke, 1978a,b,c), in echolocation (Galler and Koenig, 1970) or as the shock absorbing element of sperm whale collision (Carrier et al., 2002). The spermaceti organ is located above its melon, which is another massive oil carrying vessel (the junk), and is contained by an amphitheatre-like bony plate on the dorsal side of the sperm whale skull. Behind the skull amphitheatre and the cranium is the atlas (the first cervical vertebra), which is followed by six fused cervical vertebrae (James and Soundararajan, 1981). Temperatures drop and pressures rise on diving descents. These in turn change the density of the spermaceti oil (Clarke, 1978a,b,c) and cause mechanical deformation of soft tissues (Kooyman and Ponganis, 1998). Presumably these changes reverse either on ascent, or through physical equilibration during the bottom-dwelling lag-phase (Watwood et al., 2006). As such, there is a repeat cycle of deformation and relaxation of bodily components throughout the life of the whale. Sperm whales descend more slowly (ca. 1-1.45 m/s) than they ascend (ca. 1.3-1.6 m/s) (Miller et al., 2004; Watwood et al., 2006). Swimming velocities increase during descent with respect to depth, and on ascent the velocities fluctuate dramatically. As such there is a constant variation (Miller et al., 2004) of acceleration and normal forces felt upon the nose of the whale that must be equilibrated by the materials of the body of the whale.

Mature female sperm whales are approximately two-thirds the size of mature males, with males averaging 15.8 m and females averaging 11 m (Nishiwaki et al., 1963). Nevertheless, sperm whales have been shown to have similar ratios of body length to amphitheatre height (termed: occipital bone height) regardless of their gender (Kato, 1995; Nakamura et al., 2013). Moreover, the amphitheatres of the specimens measured by Nakamura et al. (2013) are similarly thick (ca. 1-3 cm) regardless of gender (G. Nakamura, personal communication regarding amphitheatre thickness of undamaged sperm whale skulls measured by Nakamura et al. (2013)). The thin extended amphitheatre distinguishes sperm whales from other odontocetes (Huggenberger, 2003; McKenna et al., 2012), as does its spermaceti organ (Huggenberger et al., 2014). Though several other species use head butting for food capture (Best, 1999), and in both intra- and

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interspecific aggression (Heyning, 1984; Visser, 1999; Visser et al., 2010; Rosso et al., 2011; Robinson, 2014), none of these animals have an extended thin amphitheatre (Huggenberger, 2003). Typically, odontocete melons are situated upon the rostrum (McKenna et al., 2012), as is the junk of a sperm whale. The spermaceti organ, however, only connects to the skull at the amphitheatre via a 10-12 cm thick case (Clarke, 1978a,b,c) containing fibrous soft tissue. Head butting may also more seldomly be used by females in defending juvenile calves, or as a self-defence tactic against attacks and harassment by orcas, pilot whales or other sperm whales. Hooker, for example (Hooker, 1998), reports signs of frontal scarring on the nose of a sperm whale, which was identified as either a mature female or a juvenile male. Nevertheless, the most typical defense tactic of female sperm whales is the formation of a marguerite around calves (Pitman et al., 2001).

Sperm whales can reach weights of 57,000 kg and are thus more than five times heavier than the next largest odontocetes (*Berardius bairdii* and *Orcinus orca*) (May-Collado et al., 2007). Forces experienced from dives and ramming are indubitably going to be higher for such a large creature than for any other odontocete colliding at similar velocities and accelarating at similar rates. At present, there are no reports to correlate the structure of the amphitheatre with its function. The research presented herein aims to elucidate the architecture and properties of the sperm whale skull amphitheatre with respect to function.

2. Materials and methods

2.1. Sperm whale skull samples

A sperm whale skull (dorsal segment only) was dredged from the ocean floor in South African waters in April 2013. The amphitheatre was intact and sections were cut from it using a hand saw and drill from approximately the centre of the skull amphitheatre on its dorsal side.

2.2. Pore space characterisation

Digital images of the anterior, mid and posterior layers (4 of each) were converted to 8-bit binary images in Image J (Abramoff et al., 2004). Prior to 8-bit conversion, the image threshold was adjusted manually for each image to separate the pores from the bone. Statistical data on the pore geometries was then obtained using in-built Image J algorithms for determining the geometrical characteristics of pores. We used four optical microscope images at magnifications up to ×400 to capture as large a size distribution of pores as possible. The images were taken using a Nikon DS-Fi2 and the microscopy was performed using an Olympus BX60.

2.3. Histological analyses

A fragment of the amphitheatre bone wall was embedded in a polyester resin (Struers Epoxy; Struers, Ballerup, Denmark) and thin sections were prepared in the transverse direction according to standard petrographic methodologies (Ray et al., 2005). The sections were examined using a Nikon E200 polarising microscope, and photomicrographs were taken using a Nikon DS Fi1 camera and examined with the image analysis software NIS Elements version 3.0.

2.4. Raman spectroscopy

The structural analysis of the different layers of the sample was performed using a confocal Raman microscope (alpha300; WITec, Ulm, Germany) equipped with a 488 nm laser source and a ×20 objective lens. An integration time of 0.7 s and acquisition time of 60 s were used for collecting the spectra. The collected spectra were smoothed and plotted using OriginPro 9.0 (OriginLab, Northampton, MA, USA). Data was collected from a single amphitheatre cross section.

2.5. Mechanical testing

The anterior, middle and posterior layers were separated and tested in a water-saturated state using an Instron 8872 (Instron, Norwood, MA, USA) at a rate of 1 $\text{mm}\cdot\text{min}^{-1}$. Initial tests were conducted in compression in the anterior-posterior direction. In this direction, tensile tests are difficult to perform because the pores are wide perpendicular to the loading direction (for structure preservation the full pores should be included) and the gauge length is tiny (<5 mm, Fig. 1); so we only performed tests in compression in the anterior-posterior direction. Water-saturated layers were then tested in tension in the dorso-ventral direction. Compressive tests are difficult to perform in this direction since the pores are long in the dorso-ventral axis (for structure preservation the full pores should be included) but the width of each layer is small (<5 mm), which means that the samples, if compressed, would be geometrically unstable and prone to buckling. Dorso-ventral tests were hence carried out in tension at a crosshead rate of $1\text{mm}\cdot\text{min}^{-1}$. A total of eight samples were mechanically tested for each layer.

2.6. Nanoindentation testing

To probe the mechanical properties of the different layers of the skull, a TriboIndenter TI-950 (Hysitron, Eden Prairie, MN, USA) was used. The machine was equipped with a standard 2D transducer and a cube corner tip. A 5s-2s-5s loading-holding-unloading load function with maximum load 1200 μN was used. The tip was calibrated using a standard fused quartz sample for required contact depths. More than 50 indentations were made for each layer.

2.7. Finite element models: stress distribution across the dorsal face of the skull

We used finite element software (Comsol Multiphysics; Comsol, Stockholm, Sweden) to simulate the effects of collision and deep sea diving on the skull amphitheatre. The sperm whale geometry was approximated from detailed anatomical descriptions found in the literature (Wall, 1890; Lydekker, 1893; Galler and Koenig, 1970; James and Soundararajan, 1981; Lockyer, 1991; Cranford, 1999; Huggenberger et al., 2006; Nakamura et al., 2013). We considered the plane stress formulation as the basis for simulations of solid state material in the whale (Equations (1) and (2)). In these equations, E is the elastic modulus, σ is stress, ϵ is strain, ν is Poisson's ratio and the subscripted numbers $_{1-3}$ represent orthogonal Cartesian axes. The soft tissues are not simple linear elastic materials, but rather the elastic modulus, E, of soft tissue in marine mammals rises as a function of the imposed stress, σ (Soldevilla et al., 2005). We thus incorporated the following relationship, $E=\alpha\sigma^{\beta}+\gamma$ into our models approximating the constants α, β and γ from detailed empirical data available from Soldevilla et al. (2005). All soft tissue is considered incompressible with Poisson's ratio, ν, set at just below 0.5. For simplicity, we modelled the bony matter as compact isotropic material with a Poisson's ratio of 0.6 (Whiting and Zernicke, 2008) and an elastic modulus based on our own experimental data (nanoindentation tests). The spermaceti organ and the junk were modelled with both solid material and viscous fluid properties since they are essentially comprised of soft tissue cavities that contain the sperm and junk oils, respectively. We modelled the dynamic pressures of impact at the anterior side of the spermaceti organ, on the outer surface essentially, of the sperm whale's nose, which is coincident with several reported observations of head