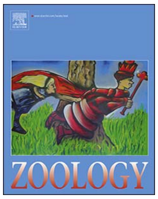
Zoology xxx (xxxx) xxx–xxx

Contents lists available at ScienceDirect

Zoology

journal homepage: www.elsevier.com/locate/zool



Stiff and tough: a comparative study on the tensile properties of shark skin

Shelby B. Creager, Marianne E. Porter*

Department of Biological Sciences, Florida Atlantic University, Sanson Science Building, 777 Glades Road, Boca Raton, FL 33431, USA

ARTICLE INFO

Keywords:
Shark skin
dermal denticles
mechanical properties
ultimate strength
stiffness
toughness

ABSTRACT

In sharks, the skin is a biological composite with mineralized denticles embedded within a collagenous matrix. Swimming performance is enhanced by the dermal denticles on the skin, which have drag reducing properties produced by regional morphological variations and changes in density along the body. We used mechanical testing to quantify the effect of embedded mineralized denticles on the quasi-static tensile properties of shark skin to failure in four coastal species. We investigated regional differences in denticle density and skin properties by dissecting skin from the underlying fascia and muscle at 10 anatomical landmarks. Hourglass-shaped skin samples were extracted in the cranial to caudal orientation. Denticle density was quantified and varied significantly among both regions and species. We observed the greatest denticle densities in the cranial region of the body for the bonnethead, scalloped hammerhead, and bull sharks. Skin samples were then tested in tension until failure, stress strain curves were generated, and mechanical properties calculated. We found significant species and region effects for all three tensile mechanical properties. We report the greatest ultimate tensile strength, stiffness, and toughness near the cranial and lateral regions of the body for all 4 of the coastal species. We also report that denticle density increases with skin stiffness but decreases with toughness.

1. Introduction

Shark skin has many proposed biomechanical functions. Previous studies have shown that dermal denticles found on shark skin reduce drag during swimming (Motta, 1977; Reif, 1985; Meyer and Seegers, 2012; Motta et al., 2012; Oeffner and Lauder, 2012; Díez et al., 2015). Shark skin is hypothesized to act as an external tendon with a direct connection to muscle and stiffen the body to transmit force to the caudal peduncle during swimming (Motta, 1977; Wainwright et al., 1978; Long et al., 1996; Naresh et al., 1997; Meyer and Seegers, 2012; Szewciw and Barthelat, 2017). Shark skin may also provide protection from predators, interactions with prey, and during mating (Tricas and LeFeuvre, 1985; Pratt and Carrier, 2001; Whitenack and Motta, 2010). These studies have investigated some of the functional aspects of skin; however, little is known about the composite effects of embedded mineralized dermal denticles on skin mechanics.

Shark skin is a biological composite composed of a matrix containing collagen fibers with embedded mineralized dermal denticles (Motta, 1977). Composites consist of two or more materials that may be stiffer and stronger than either material alone (Enos, 2012). The cartilaginous skeletons of sharks and rays are often investigated as a composite material; where the presence of a mineralized component increases the stiffness of the structure (Summers et al., 1998; Porter et al., 2006, 2007; Macesic and Summers, 2009). For example, doubling the amount of mineral results in a doubling of stiffness in cartilaginous vertebrae (Porter et al., 2007).

In shark skin, a network of collagen fibers varies between 45–70° in alternating layers of right- and left-handed helices, and fiber angle changes as the skin stretches from left to right during body undulation (Motta, 1977; Wainwright et al., 1978; Naresh et al., 1997). Collagen fiber arrangement has been shown to contribute significantly to the mechanical behavior of the skin in eels, bats, teleosts, and sharks (Hebrank, 1980; Long et al., 1996; Swartz et al., 1996; Naresh et al., 1997). For example, Naresh et al. (1997) found significant regional differences in diagonally oriented skin samples in the spadenose shark (*Scoliodon laticaudus*). Near the tail, skin had increased collagen fiber bundle thickness, decreased fiber angles, and increased stiffness compared to the mid-body (Naresh et al., 1997).

In addition to the collagen fiber network, dermal denticles are an integral component to the dermis layer of shark skin. Dermal denticles are tightly anchored to fibers in the lower stratum compactum layer of the dermis (Motta, 1977; Meyer and Seegers, 2012). Each denticle is covered in a layer of enamel and dentine and has a longitudinally-oriented pattern of riblets aligned in rows in the direction of water flow (Motta, 1977; Reif, 1985; Meyer and Seegers, 2012). Previous studies have shown that denticles vary in morphology, flexibility, density, and size (Reif, 1985; Raschi and Tabit, 1992; Lang et al., 2011; Motta et al., 2012; Oeffner and Lauder, 2012; Díez et al., 2015). For example, Motta

---

* Corresponding author.
E-mail address: me.porter@fau.edu (M.E. Porter).

https://doi.org/10.1016/j.zool.2017.10.002
Received 29 December 2016; Received in revised form 6 October 2017; Accepted 8 October 2017
0944-2006/

et al. (2012) noted differences in the morphology and flexibility of denticles between the fast swimming shortfin mako (*Isurus oxyrinchus*) and slower blacktip (*Carcharhinus limbatus*) sharks. Blacktip denticles are larger and broader compared to the shortfin mako, which have longer crowns and larger angles are measured relative to the surface of the skin (Motta et al., 2012). They proposed that the larger angles contribute to the range of denticle flexibility, especially in the flank region, and larger angles are hypothesized to control flow separation, reduce drag, and facilitate rapid burst swimming (Raschi and Tabit, 1992; Lang et al., 2008, 2011, 2012a,b, 2014; Motta et al., 2012). These studies investigated the variation in dermal denticle hydrodynamic function and morphology along the body and among species of varied swimming speeds, but the impact of denticles on skin mechanics has yet to be quantified.

In this comparative study, we aim to test the impacts of varying dermal denticle density on the mechanical properties of shark skin, a biological composite containing mineralized inclusions embedded within the collagenous matrix. Denticle density and morphology vary across the body and among species (Reif, 1985; Raschi and Tabit, 1992; Lang et al., 2011; Motta et al., 2012; Oeffner and Lauder, 2012; Díez et al., 2015). Composite materials, made of at least two different materials, can be stiffer, stronger, and tougher than an individual material alone (Enos, 2012). We hypothesize that increasing denticle density will increase the tensile mechanical properties (stiffness, strength, and toughness) of the skin. We quantify denticle density (number of denticles mm^{-2}) and quasi-static mechanical properties to failure: ultimate strength (units), yield strength (units), stiffness (units), and toughness (units) at ten anatomical landmarks from each shark. Here we focus on quasi-static tensile tests to failure to quantify the upper limits of shark skin mechanical properties (Naresh et al., 1997; Porter et al., 2006, 2007). With these data, we (1) compare differences regionally within individuals of the same species, (2) compare regions among species, and (3) correlate denticle density with mechanical properties.

2. Materials and methods

2.1. Study species

We obtained skin samples from juvenile sharks of two orders and three families ranging in total length from 56 to 85 cm: Carcharhiniformes (Carcharhinidae – blacktip, *Carcharhinus limbatus* (n = 3, 72–84.5 cm TL (total length)); Sphyrnidae – scalloped hammerhead, *Sphyrna lewini* (n = 2, 56–58 cm TL); bonnethead, *Sphyrna tiburo* (n = 3, 59.5–63 cm TL)) and Lamniformes (Lamnidae – shortfin mako, *Isurus oxyrinchus* (n = 1, 77.5 cm TL)). The blacktip, scalloped hammerhead, and bonnethead specimens were incidental mortalities collected from gill nets in Pine Island Sound, FL by Mote Marine Laboratory (survey FWC-SAL-13-0041-SRP). NOAA collected one shortfin mako specimen from long-line fishing in La Jolla, CA. We also obtained term bull shark embryos (*Carcharhinus leucas,* n = 4, 61–70 cm TL) from fishermen in the Florida Keys. Bull shark embryos are born between 60–80 cm, which encompasses the size range used in this study (Clark and von Schmidt, 1965; Dodrill, 1977 Castro, 2011). Though the bull sharks in this study were term embryos, their TL was similar to or greater than the juveniles tested here in other order Carcharhiniformes species. All species caught in FL are found in near shore waters while the mako is primarily an oceanic species (Castro, 2011).

2.2. Tissue preparation and dermal denticle density

Sharks were stored freshly frozen. We dissected skin samples from thawed sharks at 10 anatomical landmarks across the body (Fig. 1), where we hypothesized the tensile properties may differ regionally due to the differences in denticle morphology and density across the body (Motta et al., 2012; Díez et al., 2015). We dissected each skin sample in approximately a 2 × 2 cm square. However, if the size of the individual did not permit the 2 × 2 cm, we dissected a smaller square with the largest area possible. We used a scalpel to remove the skin with at least 1 cm of muscle attached and then removed the underlying muscle carefully. A thin layer of connective tissue remained attached to the skin, preserving the integrity of the sample and preventing damage to the hypodermis from the scalpel. The thin connective tissue was removed from a small subset of samples to determine if that layer impacted mechanical properties. An important caveat to note: the sharks for this study have been frozen for two years and freezing may impact mechanical properties reported herein. However, freezing effects will be consistent among species, and previous studies have shown that freezing and thawing does not affect the stiffness of soft vertebrate skeletal tissues such as mammalian tendon and articular cartilage (Szarko et al., 2010; Jung et al., 2011).

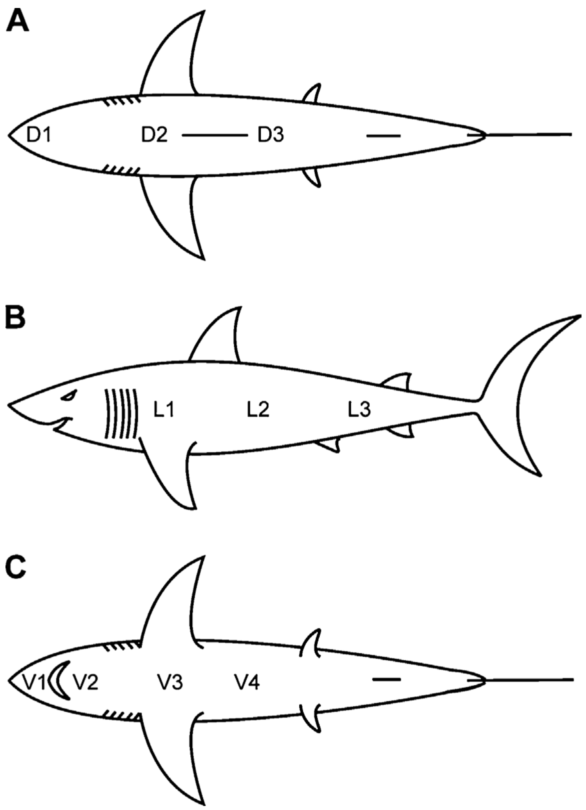


Fig. 1. Abbreviations denoting sampling regions. (A) Samples taken from dorsal midline regions: most anterior dorsal portion of head (D1), anterior to first dorsal fin (D2), and directly posterior to first dorsal fin (D3). (B) Samples taken from left mid-lateral regions: before dorsal (L1), after dorsal (L2), and posterior to pelvic fin (L3). (C) Samples taken from midline ventral regions: ventral area of snout (V1), immediately posterior from mouth (V2), pectoral girdle (V3), and abdominal region (V4).

Using a Leica EZ4W dissecting microscope (Wetzlar, Germany), we digitally photographed each skin sample three times in different areas and denticle density mm^{-2} was quantified using ImageJ (Schneider et al., 2012). We took averages of the three denticle density counts. We also photographed the deep surface of the dissected skin to determine the collagen fiber angle in the dermis along the length of the sharks and among species. However, we were not able to easily view these fibers, even after applying some stains, in the young sharks on the dissecting scope used in this study. These data may be obtained using more sophisticated imaging or perhaps the fibers are difficult to see in the skin of young sharks.

To dissect skin samples for tensile testing, we placed each sample on a cutting board and used a hydraulic press with an hourglass-shaped punch, which pressed against the skin in the cranial to caudal direction, the direction of biological relevance to lateral undulation (Naresh et al.,