Extreme mechanical strength of the cuttlebone in *Sepia officinalis*

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A main defining feature of cuttlefish (phylum Mollusca) is the presence of a cuttlebone, an internal biomineralized shell that serves as a buoyancy tank. Buoyancy is regulated by the concentration of salt ions within the cuttlebone, which influences osmotic pressure. Buoyancy adjustments can be made by the discharge of fluid from the cuttlebone, meaning that cuttlebone must be highly porous. Additionally, cuttlefish species inhabit a variety of depths down to 600m, which requires cuttlebone to sustain high hydrostatic pressure. Cuttlebone is highly damage resistant and can withstand high water pressures despite its ultra-lightweight structure, and cuttlebone morphology differs between species in relation to the depth of their habitat (Sherrard 2000). Therefore, it is suggested that there are trade-offs associated with the demands of buoyancy and strength for cuttlebone morphology (Sherrard 2000). Previous studies have shown that cuttlefish are capable of surviving with partially damaged cuttlebones, despite the intrinsic brittleness of the aragonite of which cuttlebone is primarily composed. Yang et al. (2020) examined the structure of cuttlebone and analyzed the failure process when cuttlebone is damaged.

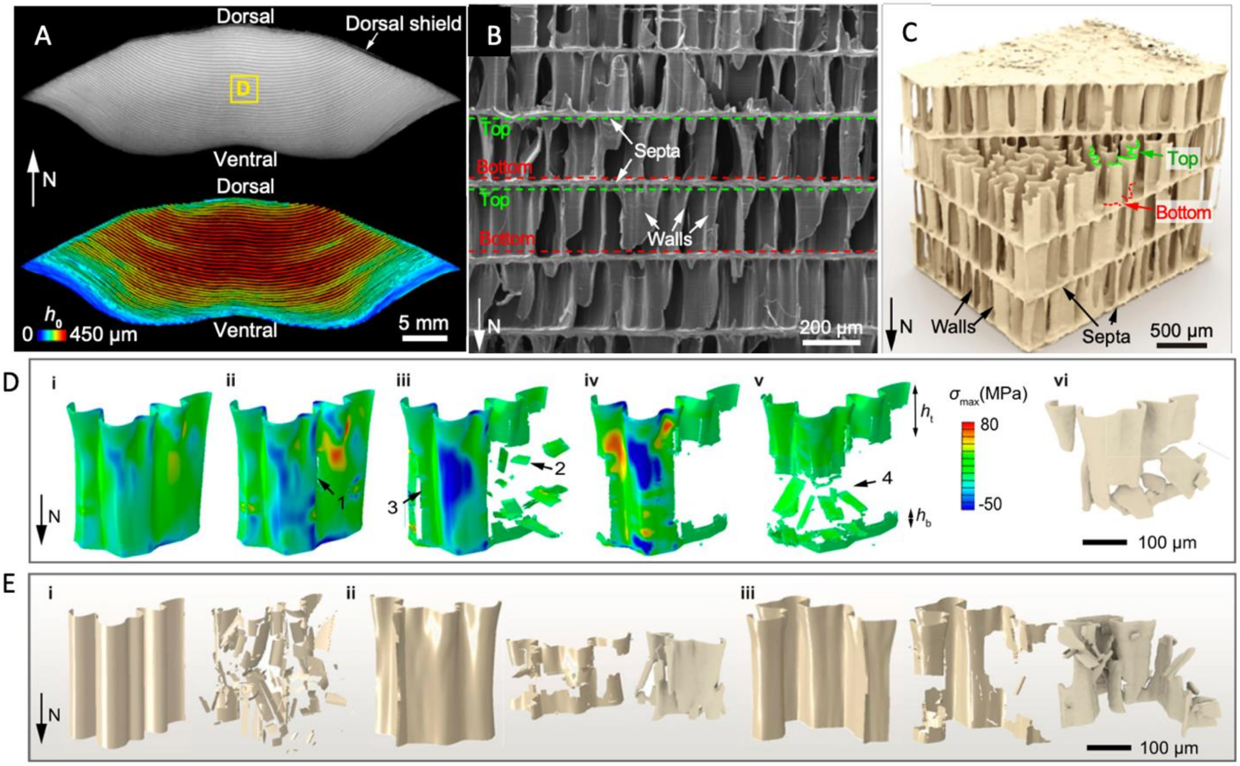
To assess the structural trade-offs of cuttlebone, Yang et al. (2020) conducted mechanical and compression tests, as well as simulations comparing different cuttlebone morphologies. Cube shaped samples (both 10 mm and 2 mm in size) were dissected from frozen adult cuttlefish (*Sepia officinalis*) and used to analyze cuttlebone morphology as well as to conduct mechanical tests. The authors used scanning electron microscopy (SEM) to visualize the structure of cuttlebone vertical walls and horizontal septa ("floors," which serve to divide cuttlebone into layers of chambers). For the compression tests, researchers applied load perpendicular to cuttlebone septa using a stepper motor and used a microscope camera to capture the failure process. Additionally, Yang et al. (2020) used X-ray imaging to visualize the results of the indentation test, in which a tungsten rod with a flat punch applied to cuttlebone induced localized deformation. To compare the relative strength of different cuttlebone morphologies--specifically, straight and wavy walls--vertical wall geometries were modelled using tomography data, and computer software was used to conduct simulations of the mechanical response of cuttlebones under compression.

SEM results showed that the horizontal septa of the cuttlebone separate it into individual chambers (Focus Figure 1a) supported by numerous vertical walls forming a labyrinthine pattern (Focus Figure 1b,c). The walls within cuttlebone display a corrugated morphology, with the walls becoming wavier towards the top of the chamber (Focus Figure 1b,c). Moreover, the results of the mechanical tests indicated that the failure of individual chambers occurs progressively rather than simultaneously due to the waviness of cuttlebone walls (Focus Figure 1d). Straight walls had higher stiffness in comparison to wavy walls, which caused straight walls to fail in a more catastrophic manner (Focus Figure 1e). Further, it was found that the stress of failure decreased with increasing wall waviness. Wavy geometry caused uneven stress distributions throughout the cuttlebone, leading to a more progressive failure system where the areas under highest stress fractured first (Focus Figure 1d). The results of this study showed that cuttlebone morphology allows for a graceful failure of cuttlebone.

Through the examination of the failure process, the authors identified three important stages of cuttlebone failure. The first stage is characterized by local penetrations of the individual deforming chamber and the creation of multiple high-strain regions within the chamber, and the second stage begins when such penetrations expand. The third failure stage is defined by a densification process, where the walls in the damaged chamber become gradually compacted and eventually come in contact with each other.

Yang et al. (2020) concluded that cuttlebone gains high energy absorption and damage tolerance from its unique wavy structure. Wavy walls reduce stress on both the septa and wall ends of the cuttlebone, but raise stress in the middle of the walls, which improves septa integrity, limits damage to a specific location, and facilitates asymmetric wall failure of the cuttlebone. Although Yang et al. (2020) found that wavier walls displayed more progressive failure overall, simulations revealed that the efficiency of walls degraded once a specific waviness threshold was reached. These results suggest that there is an optimal wall waviness that allows for cuttlebone to fail gracefully.

The analysis of cuttlebone morphology and its failure system conducted by Yang and colleagues provides insight into how cuttlefish are able to survive at greater depths and maintain their structural integrity despite high amounts of pressure associated with increased depth. Future studies could explore differences in optimal wall waviness levels between cuttlefish species that inhabit shallow waters and species that inhabit greater depths. This comparison may provide insight into the extent to which hydrostatic pressure influences the waviness of the cuttlebone. Additionally, it is not yet known how wall waviness influences the flow of water through the cuttlebone, and ultimately the efficiency of buoyancy regulation.



Focus Figure 1. Influence of waviness on cuttlebone fracture process. Sections A, B, and C display the morphology of cuttlebone. Section A shows a transverse view of the cuttlebone that displays the chamber height. Sections B and C illustrate the difference in waviness between top and bottom portions of the walls, with top portions observed as wavier than bottom portions. Sections D and E show simulation results of stress areas during the fracture process (D) and the fracturing of straight and wavy walls (E). Section D displays the stress levels measured in MPa for different areas of the cuttlebone wall during the fracture process and marks the fracture sequence numerically. This portion of the figure highlights that the bottom of the cuttlebone fails first, which is the straighter portion of the walls. Section E displays the results of a simulation comparing the failure process of straight (i) and wavy walls (ii and iii). The straight walls are observed to fracture more catastrophically into tiny pieces, while the wavy walls fracture gradually into larger pieces.

Additional Literature Cited

Sherrard, K. M. 2000. Morphology limits habitat depth in eleven species of *Sepia* (Cephalopoda: Sepiidae). *Biological Bulletin*. 198:404-414. https://www.jstor.org/stable/1542696