Composite model of the shark's skeleton in bending: A novel architecture for biomimetic design of functional compression bias

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A B S T R A C T
Much of the skeleton of sharks, skate and rays (Elasmobranchii) is characterized by a tessellated structure, composed of a shell of small, mineralized plates (tesserae) joined by intertesseral ligaments overlaying a soft cartilage core. The typical adult chordate skeleton is made up of bones with cartilaginous elements serving as bearing surfaces, but the elasmobranch (sharks, skates and rays) fishes are unusual in having skeletons of only mineralized and unmineralized cartilage. This skeletal design is counterintuitive since cartilage, unlike bone, cannot self-heal [1]; and yet elasmobranch fishes lead particularly dynamic lifestyles. They are some of the fastest and largest animals in the oceans, and many feed on prey larger than themselves or as hard and tough as mollusk shell. We hypothesize that a key component of the high level of performance of their skeletons is the unique arrangement of tissue: much of the axial skeleton and the entire appendicular skeleton is made of tessellated cartilage, a composite of mineralized hydroxyapatite blocks (tesserae) over a core of uncalcified cartilage (Fig. 1) [2–6].

Adjacent tesserae are adjoined by stout intertesseral ligaments that apparently allow for movement of tesserae relative to one another: either separation when the tesseral mat is loaded in tension or abutting when under compression (Fig. 2). Both of these situations can occur in bending of a skeletal structure (e.g. a beam of uncalcified cartilage sheathed in tiles) where an applied nonaxial load produces a maximum tensile stress in the tesseral layer farthest from the axis of bending and a maximum compressive stress in the contralateral layer. This differential loading would result in starkly different intertesseral joint volume fractions from one side of the element to the other; the intertesseral joints must therefore influence the stress distribution of tessellated cartilage in bending. Since external surfaces are typically more susceptible to fatigue crack initiation, bending is particularly detrimental because the particularly damaging maximum tensile stresses are localized to one of the surfaces of the skeletal element. Further, shear stresses are also produced in bending that are proportional, albeit smaller in amplitude, to the maximum tensile or compression stresses. Hence, it is reasonable that tessellated cartilage loaded in bending (a particularly common mode for a swimming or biting fish) is in serious danger of fatigue and fracture. This risk is particularly poignant for cartilage since, having essentially no vascular system, it cannot readily repair itself.

The multiple interacting constituents of tessellated cartilage tissue increase the difficulty of predicting its mechanical behavior, particularly when it is subjected to multiaxial stresses such as those associated with bending. To address this complexity, we developed an idealized dynamic numerical model to gain a better understanding of the bending behavior of tessellated cartilage as depicted schematically in Fig. 2.

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The purpose of the present work was three-fold: 1) to develop a model that it is reasonably realistic in terms of geometry and mechanical properties but also provides insightful and easily interpretable predictions of bending behavior; 2) to predict the bending behavior of the tessellated structure for different elastic moduli of intertesseral joints (for which empirical data are lacking) to determine how the value of this property affects the distribution of stresses; and 3) to gain a better understanding of shark skeletal tissue under bending loads, which are common and often repeated under physiological loading conditions. The limited healing capacity of cartilage suggests that the tessellated design imparts some resistance to fatigue damage, a typical failure mode for man-made structures loaded in bending. The present model was therefore also intended to yield qualitative insights as to how the morphology of tessellated cartilage tissue might affect its susceptibility to damage from excessive or repeated bending loads.

### 2. Elastic moduli and composite geometry

Tessellated cartilage is comprised of three distinct tissue phases: unmineralized cartilage, mineralized cartilage, and fibrous joint tissue. The elastic properties and dimensions used in the present model were derived from representative measured values. We imagined a simple cross-sectional slice of a tessellated beam, with a solid uncalcified cartilage block sandwiched between upper and lower tessellated layers. Each tissue component was treated as a linear elastic element in the present model. While this simplification does not completely capture the nonlinear behavior of the soft tissue components, it was useful for providing tractable and insightful descriptions of the role that the overall structure has in determining the stress distribution in bending. The elastic modulus for mineralized tessera, $E_T$, has been found to be approximately equal to 3 GPa in recent nanoindentation tests [7]. A representative elastic modulus of approximately 3 MPa was used for the uncalcified cartilage sandwiched between the tessellated layers; this value is also supported by this recent experimental work. There are no empirical data for intertesseral fibers. Depending on the elastin to collagen ratio and strain rate, the elastic modulus of the joints between the tesserae can realistically lie somewhere in the range of 3 MPa to 1 GPa [8]. Accordingly, the present model was exercised with different values for the joint modulus within this range.

The dimensions of each mineralized tessera in the outer layers of the tissue was approximated at 0.7 mm thick by 1 mm wide and the size of the joints was set at 20 mm wide in the $y$ direction and 0.7 mm between the tessera based on anatomical measurements [9–12]. These estimates give an unloaded joint volume fraction, $f_J$, of 0.02 within each of the tessellated layers. The uncalcified cartilage was assigned a representative thickness of 10 mm. The dimensions used in the present model are all within the typical ranges of values observed in cartilaginous fishes. Whereas these dimensions can vary with species and skeletal location [e.g. 4,11], the understanding gained in executing the present models should be qualitatively relevant for most tessellated tissues.

### 3. Composite behavior of the tessellated layer

Our model approximates a skeletal cross section, represented by a monolithic block of uncalcified cartilage sandwiched between two external tessellated layers (mats of tesserae adjoined by intertesseral fibers). The effective elastic modulus of each of the external tessellated layers, $E_{ext}$, can be approximated by the Reuss (isostress) description of composite behavior given by

$$E_{ext} = \left[ f_I E_I + \left(1 - f_I\right) \frac{E_T}{1 + \left(\frac{E_T}{E_I} - 1\right) f_I} \right]^{-1}$$

where $f_I$ is the volume fraction of intertesseral joint phase, $E_I$ is the elastic modulus of the intertesseral joint phase, and $E_T$ is the elastic modulus of the tesserae. We note that there are also joints running parallel to the stress direction in a three-dimensional tessellated structure as illustrated in Fig. 3. The isostain relation governing their contribution to the composite modulus would be

$$E_{ext} = f_I E_I + \left(1 - f_I\right) E_T.$$

Considering this equation and the fact that the volume fraction of parallel joints is approximately 0.02 and would not change, it is safe to assume that the effect of parallel joints on the overall composite modulus is negligible. By contrast, it can be seen that the value of $E_I$

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**Fig. 1.** Uncalcified and mineralized phases of tessellated tissue, depicted as a schematic of the inset cross sectional BSE image.

**Fig. 2.** Schematic of the present model of a tessellated composite inspired by the tissue in Fig. 1 in both (a) unloaded and (b) bending configurations. The thickness of the tessera and curvature in (b) are exaggerated for the purposes of illustration.
could have a significant effect on $E_{eq}$ in Eq. (1) if it is sufficiently smaller than $E_t$ even for $f_J$ values as low as 0.02. Accordingly, the effect of joints running perpendicular to the stress direction needs to be considered in the present model. By not including the parallel joints, we assume that all of the stress in these joints is transferred to the tesserae and perpendicular joints in series. This assumption is not only consistent with the low value of $f_J$ in Eq. (2) but also the relatively low modulus of the joint phase.

Constraint on the joint by the much stiffer tesserae requires that straining the intertesseral joint in the plane of the tesserae is accompanied by a change in its volume fraction within the tessellated straining the intertesseral joint in the plane of the tesserae is low modulus of the joint tissue, $\varepsilon_T$.

Therefore, the external force on the $E_T$ material is altered to

$$dF_{T2} = \frac{(nE_T)\gamma}{\rho} dA = E_T \frac{\gamma}{\rho} (nb_1 dy) \text{ where } n = \frac{E_T}{E_{eq}}.$$  

Thus, the equivalent cross section width of the beam is

$$b_{eq} = b_2 = \frac{E_2}{E_1} b_1$$

in the section where the modulus is $E_2$, and $b_{eq} = b_1$ in the section with modulus $E_1$.

The stress in the equivalent cross section in bending is then given by

$$\sigma_{eq} = \frac{M_y y}{(I_{eq})_{y}}$$

where $M_y$ is the applied bending moment and $(I_{eq})_{y}$ is the moment of inertia for the equivalent cross section area, $A_{eq}$. The equivalent cross section moment of inertia is given by

$$I_{eq} = \int y^2 dA = \int y^2 b_{eq} dy.$$
As shown in Fig. 4, \( \sigma = \sigma_{\text{ecs}} \) at locations in which the elastic modulus is \( E_1 \). Stresses at locations that correspond to the greater elastic modulus, \( E_2 \), are transformed according to

\[
\sigma = \frac{E_2}{E_1} \sigma_{\text{ecs}}.
\]

**4. Equivalent cross section for calcified cartilage**

The calcified cartilage structure shown in Fig. 2 is a typical section through an elasmobranch skeletal element, and contains two layers of greater modulus, one at the top and one at the bottom. However, because of the intertesseral joints, the modulus of each of these layers depends on the stress and loading regime (tension or compression) imposed in each. Substituting the relation for \( E_{\text{ext}} \) in Eq. (7) for \( E_2 \) in Eq. (15) leads to the following equivalent cross section width for the external tessellated layers in Fig. 2:

\[
b_{\text{ext}} = \frac{E_{\text{ext}} b_1}{E_u} = \frac{E_2 b_1}{E_u \left[ 1 + \left( \frac{1}{T} - 1 \right) f_1 \right]}
\]

where \( E_u \) is the modulus of the uncalcified cartilage sandwiched between the two external tessellated layers, and \( b_1 \) is the actual cross section size of the composite structure. For convenience, \( b_1 \) was assigned a value of unity in the present model.

The transformation from the composite cross section to equivalent cross section is illustrated schematically in Fig. 6. Once \( b_{\text{ext}} \) is determined for both tessellated layers, \( I_{\text{z}}_{\text{ecs}} \) can be calculated using Eq. (14). We note that the equivalent cross section of the tensile side is smaller than the compressive side when loaded due to the increase in volume of the soft tissue joints in tension and the decrease in joint volume in compression. In addition, the equivalent external layers have the shape of isosceles trapezoids as opposed to rectangles due to the gradient in stress, and therefore elastic modulus, in these regions. We also note that the shape of the present equivalent cross section varies with changes in bending moment as intertesseral joints compress or stretch from their resting states. In particular the width of the regions corresponding to the tessellated layers change significantly as the bending moment increases or decreases.

The present model begins its determination of the stress distribution from the unloaded state. Substituting the unloaded joint volume fraction, 0.02, into Eq. (7) gives \( \left( E_{\text{ext}} \right)_u = 131 \text{ MPa} \) and \( \left( b_{\text{ext}} \right)_u \) is then equal to 44 mm for both external layers. According to Eq. (14), the initial unloaded value for the equivalent second moment of inertia is \( 1.84 \times 10^{-3} \text{ m}^4 \). Starting with these values, the stress distribution for the composite cartilage was then determined for an incrementally small increase in the bending moment. Based on Eqs. (13) and (15), this incremental change in stress with a small change in bending moment is given by

\[
\Delta \sigma_{\text{ext}} = \frac{E_{\text{ext}} I_{\text{z}} y}{E_u (I_{\text{z}})_{\text{ecs}}} \Delta M_z
\]

in the external tessellated layers while

\[
\Delta \sigma_u = \frac{M_z y}{(I_{\text{z}})_{\text{ecs}}}
\]

holds for the internal uncalcified cartilage. Taken together, Eqs. (17) and (18) can be used to determine the change in stress at vertical positions, designated by \( y \), through the entire composite cross section for an incremental increase in the bending moment. The total stress at a position \( y \) can then be determined from

\[
\sigma_{\text{ext}} = \frac{1}{E_u} \sum E_{\text{ext}} \frac{\Delta M_z y}{(I_{\text{z}})_{\text{ecs}}}
\]

and

\[
\sigma_u = \sum \frac{\Delta M_z y}{(I_{\text{z}})_{\text{ecs}}}
\]

We note that \( (I_{\text{z}})_{\text{ecs}} \) is not constant during loading as a result of the variation in \( b_{\text{ext}} \). Accordingly, the value of \( y \) for a given position in the composite also changes during bending as a result of a shift in the neutral axis as \( (I_{\text{z}})_{\text{ecs}} \) changes. Eqs. (19) and (20) were solved numerically by incrementally increasing the bending moment by \( 1 \times 10^{-5} \text{ Nm} \) from 0 to 0.4 Nm. This increment in bending moment was sufficiently small to avoid significant error. For each iteration, the calculated stress distribution was used in Eq. (7) to update the modulus in each tessellated layer. New values of \( b_{\text{ext}} \) and then \( (I_{\text{z}})_{\text{ecs}} \) were then also determined using the updated \( E_{\text{ext}} \). These values were
then used in the subsequent iteration to calculate the stress distribution for the next incremental increase in bending moment. The predictions were limited to bending moments that correspond to a maximum applied stress of approximately 300 MPa in the tessellated layer under compression, which is approximately an order of magnitude greater than the ultimate compressive strengths measured for vertebral calcified cartilage from elasmobranch species [14]. This is a reasonable limit due to the fact that stresses are transferred from the uncalcified cartilage to the stiffer tessellated cartilage and that the thickness of the uncalcified regions is approximately 10 times greater than that for the tessellated layers.

5. Results

The composite elastic modulus calculated using Eq. (7) is plotted in Fig. 7 for different values of joint modulus, $E_J$, and as a function of stress. These results demonstrate a pronounced and abrupt change in composite modulus under compressive stresses for the lowest joint moduli. This trend is due to the change in volume fraction of joint tissue that can decrease to very low values for applied compressive stresses and substantially increase under tension. This difference in joint volume gives rise to a very high modulus in compression and a relatively low modulus in tension. As $E_J$ decreases, the compressive and tensile composite moduli of the tessellated layer are increasingly dominated by the mechanical behavior of the separate hard and soft tissues, respectively, resulting in strikingly different composite moduli under different loading conditions. Conversely, the moduli in compression and tension approach the same value as $E_J$ increases in value.

Predicted stress distribution for applied bending moments of 0.01, 0.04 and 0.4 Nm are plotted in Fig. 8. Several features are worth noting in this figure. First, the magnitudes of the maximum stresses in the tessellated layers becomes more different as the bending moment increases, with the compressive layer exhibiting much larger maximum stresses. From the lowest to the highest bending moments, the maximum compressive stresses increase over 200-fold, whereas maximum tensile stresses only increase by about a factor of 10. Second, the stresses in the uncalcified cartilage (central plots) are relatively low in amplitude, remaining less than 0.03 MPa in compression and 8 MPa in tension (red) even though the stress amplitude in the tessellated layer under compression (blue) exceeds 300 MPa. By comparison, the stress in the tessellated layer under tension reaches a value slightly less than 14 MPa. Finally, the neutral axis in the tissue (where the stress transitions from tension to compression) migrates, with increasing bending moment, toward the compression side of the tissue until it enters the tessellated layer there.

Neutral axis migration is plotted for multiple values of the joint modulus in Fig. 9 as a function of bending moment. It can be seen in this figure that this migration is more pronounced for the lower values of $E_J$ and occurs at lower bending moments. For $E_J \geq 100$ MPa, neutral axis migration is negligible. These results demonstrate how stress redistribution becomes less prominent as joint modulus increases. We note that for $E_J = 3$ MPa the neutral axis shifts into the tessellated layer under compression at a relatively low bending moment of about 0.04 Nm. Comparison with Fig. 8 indicates that this migration into the tessellated layer corresponds to the formation of a discontinuity in stress distribution at the interface between the uncalcified cartilage and the tessellated layer.

Maximum tensile stress in the upper tessellated layer is plotted as a function of bending moment in Fig. 10 (a). With increasing joint stiffness, stress increases more rapidly in the tensile tessellated layer and reaches a larger maximum stress. As before, changes in joint stiffness have less of an effect at $E_J \geq 100$ MPa. It can be seen that the tensile stress reaches about 57 MPa for $E_J \geq 100$ MPa and an applied bending moment of 0.4 Nm. By comparison, the maximum tensile stress for $E_J = 3$ MPa is less than 14 MPa for a bending moment of 0.4 Nm as also shown in Fig. 8. Thus, reducing $E_J$ from 1000 to 3 MPa results in a 75% decrease in maximum tensile stress.

Maximum compressive (most negative) stress in the lower tessellated layer is plotted against bending moment for different values of $E_J$ in Fig. 10 (b). The amplitude of this stress exceeds 300 MPa under a bending moment of 0.4 Nm for $E_J = 3$ MPa indicating an extreme bias towards compression compared with the corresponding maximum tensile stress in Fig. 10. As noted above, changes in joint stiffness have a relatively small effect on the compressive stress in the lower tessellated layer.
stiffness above $E_J \geq 100$ MPa have negligible effect on predicted stresses. Whereas compressive stresses are much higher for cartilage complexes with lower joint stiffness values, for $E_J \geq 100$ MPa, stresses in the tessellated layers are more symmetrically balanced such that both maximum compressive and tensile stresses approximate an absolute value of 57 MPa under a bending moment of 0.4 MPa (Figs. 10 and 11).

Maximum tensile stress in the uncalcified cartilage layer is plotted versus bending moment in Fig. 11 (a). As shown in Fig. 8, this maximum stress exists at the interface with the upper tessellated layer. The greatest stress at a bending moment of 0.4 Nm is exhibited for $E_J = 3$ MPa while lower values are obtained for higher values of $E_J$. Stress versus bending moment at the center of the uncalcified cartilage (central axis) is plotted in Fig. 11 (b) to examine the likelihood of the development of fatigue damage there. This central axis corresponds to cartilage tissue that is exactly in the middle between the two tesseral mats and furthest away from the fibrous perichondrium that wraps skeletal elements (Fig. 1). This region is therefore likely to have the lowest access to nutrients that diffuse in from the surrounding vascularized tissue and as a result would have the lowest capacity for repairing any fatigue damage that develops under repeated bending. Fig. 11 (b) shows that the only significantly finite stresses are tensile by nature as in the cases of $E_J = 3, 10,$ and 30 MPa. The greatest tensile stresses were predicted for $E_J = 3$ MPa but reach a value slightly less than 4.2 MPa for a bending moment of 0.4 Nm.

Maximum compressive stress in the uncalcified layer, plotted versus bending moment, is illustrated in Fig. 11 (c). The greatest stress amplitude at a bending moment of 0.4 Nm is exhibited for $E_J = 100$ MPa while lower values are obtained for higher values of $E_J$. The absolute values of these stresses are about an order of magnitude less than those for maximum tension shown in Fig. 11 (a). Larger
differences between maximum compression and tension stresses were predicted for the lower $E_J$ values. For $E_J = 3$ and 10 MPa, compressive stresses in the uncalcified cartilage are eliminated with increasing bending moment as a result of the migration of the neutral axis into the lower tessellated layer. Despite this absence of compressive stress, the maximum tensile stress within the uncalcified layer remains extremely low compared to the compressive stresses that develop in the adjacent tessellated mat. While the tessellated structure assures low tensile stresses, it can result in the broad distribution of tension throughout the structure due to the migration of the neutral axis. The possibility exists that this widely distributed low-level tension is advantageous. For example, it could be hypothesized that the resulting hydrostatic tension throughout most or all of the uncalcified core layer could increase the presence of nutrients that diffuse from the vascularized perichondrium under compression. More work is needed to explore this possible advantage.

6. Discussion

The present model predicts that significantly more stress will be borne by the tessellated layer on the compressive side compared to the core and the tensile tessellated layer for a bending skeletal element with joint tissue stiffness less than 100 MPa ($E_J < 0.01E_T$). This result is consistent with the fact that the tesseral mat more closely behaves as a homogenous layer when the joints stiffness approaches that for the tesserae. The predicted functional bias towards compression also becomes more pronounced when the composite bears a larger bending moment. Based on a comparison of Figs. 10 (a) and (b), the maximum compressive stress could be over two orders of magnitude greater than the maximum tensile stress in the tessellated...
The similarity between the stress redistribution in bending predicted in the present work for tessellated cartilage and that observed earlier for bone is worth noting. In the case of bone, migration of the neutral axis towards the side under compression also occurs as a result of asymmetric yielding due to the formation of microcracks under tension [17–19]. We surmise that this yielding behavior is sustainable under moderate loading amplitudes for two reasons. First, the observed neutral axis migration keeps the tensile stresses low. Second, bone can repair the microcrack damage relatively quickly by remodeling processes [20]. A beneficial migration of the neutral axis also occurs in tessellated cartilage but as a result of an asymmetric and repeatable contribution of the joint ligaments that does not require the formation of microcracks. This difference in facilitating a bias towards compressive stresses appears to be essential because calcified cartilage tissue, unlike vascularized bone, cannot readily repair microcrack damage.

7. Conclusion

A numerical model was used to gain insight into the functional characteristics of tessellated cartilage found in elasmobranch species. The results indicate that tessellation serves to manage bending loads in a way that can increase resistance to damage by distributing the highest stresses to the tissues and loading regimes best able to bear them. The stresses produced in the external tessellated layers can be well over an order of magnitude greater than those in the internal uncalcified cartilage. The model also demonstrates how the external tessellated layers can produce much lower tensile stresses compared to the corresponding compressive stresses in bending. This functional bias towards compression was also observed for bone in bending but with the formation of microcracks in the regions under greatest tension. By contrast, the same functional bias can be achieved in a tessellated cartilage structure if the modulus of the soft tissue joints is less than about 1% of the modulus of the tesserae, a reasonable range for soft tissue ligaments. The predicted functional bias towards compression is accompanied by a migration of the neutral axis from the midpoint of the tissue so that more of the uncalcified tissue is periodically under relatively low tensile stresses. The tessellated structure modeled here could provide guidance for manufactured biomimetic materials in which a low modulus core is overlaid with a jointed or tiled high modulus layer. We show that soft tissue joints in this outer layer are a key feature to this design, one that allows for neutral axis migration and the associated shifting of stresses to the less damaging compressive regime.

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