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PAPER

3D-printing a ‘family’ of biomimetic models to explain armored grasping in syngnathid fishes

Michael M Porter\(^1\)\(^2\) and Nakul Ravikumar\(^1\)

\(^1\) Department of Mechanical Engineering, Clemson University, Clemson, SC 29634, United States of America
\(^2\) Zucker Family Graduate Education Center, Clemson University, North Charleston, SC 29405, United States of America

E-mail: mmporte@clemson.edu

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Abstract

Seahorses and pipehorses evolved at least two independent strategies for tail grasping, despite being armored with a heavy body plating. To help explain mechanical trade-offs associated with the different designs, we created a ‘family’ of 3D-printed models that mimic variations in the presence and size of their armored plates. We measured the performance of the biomimetic proxies across several mechanical metrics, representative of their protective and prehensile capacities. Our results show that the models mimicking the tails of seahorses are the best all-around performers, while those of the distal-most, prehensile region of pipehorses are more flexible, but less protected. The comparison also reveals that different adaptive strategies provide different task-specific performance advantages, which could be leveraged for the design of armored manipulators or other bio-inspired technologies.

1. Introduction

Many biological systems evolve different structures to perform similar functions [1, 2], resulting in a natural design space rich with a diversity of time-tested strategies for bio-inspiration [3–6]. However, identifying which designs to explore for inspiration can be challenging because adaptive modifications often involve changes across multiple anatomical parts [7, 8]. Also, biological structures usually evolve to perform biologically-relevant functions that could be nonessential for the bio-inspired applications of interest. For that reason, biomimetic models are often used as experimental proxies of the natural designs [9–12], so that individual traits can be released from their evolutionary constraints, artificially modified, and systematically tested in controlled laboratory environments. Some recent examples of this strategy are demonstrated in studies that investigate the mechanics of bio-inspired articulated and multi-material structures [13], including some fish scale-like [14–16] and abalone nacre-like [17–19] structures. With this approach, synthetic models (which are often simplified or idealized mockups of the natural systems they mimic) can be directly compared to reveal how structure-function relationships elicit performance trade-offs. The models can also be modified to explore alternative designs that lie outside the natural design space, allowing for comparisons of the natural versus hypothetical [20].

To demonstrate this comparative strategy, we explore the biomechanics of a common seahorse and pipehorse tail using 3D-printed proxies as idealized models of the natural systems. These fishes, belonging to the family Syngnathidae, have flexible prehensile tails covered by dermal armors of articulated bony plates [21–26]. The ancestral syngnathid condition is represented by a pipefish, which has a non-prehensile tail and a caudal fin (see figure 1(A)) [25, 26]. Interestingly, seahorses and pipehorses lost the caudal fin and evolved at least two, and possibly up to nine or more [27], parallel strategies for tail prehension [25, 26]. Two known strategies are: (i) a partial or complete loss of plates towards the distal tip of the tail that allows for less constrained mobility, as seen predominantly in some pipehorses (figure 1(B)); and, (ii) a reduction in plate size that provides increased articulation space (spatial freedom for the plates to slide and rotate), as seen predominantly in seahorses (figure 1(C)).

In addition to facilitating prehension (in pipehorses and seahorses), the armored plates also provide body support, control mobility, and protect against predatory attacks. Overlapping joints at the ring mid-seCTIONS absorb energy when crushed to protect the
vertebral column from damage [23]. Peg-and-socket joints at the ring corners connect adjacent segments and permit high degrees of flexibility in bending, yet restrain against over-twisting [20]. Together, with their square cross-sections, these joints also provide a shape restitution mechanism that allows the structures to snap back to their resting positions upon relaxation [20]. Whereas the organization (square cross-sections) and articulation (overlapping and peg-and-socket joints) of the tail rings are fairly similar among the different species [25], there are a few distinct structural variations in the bony plates that influence their mechanics; notably, the length of the pegs relative to the overall length of the plates [26]. Pipefishes generally have the widest plates with peg-to-length ratios of ~0.1–0.3, while the peg-to-length ratios of pip- ehores (of various genera) range from ~0.2–0.5 and of seahorses from ~0.3–0.6 [26]. These adaptations, along with a loss of plates in some pipehorses (see figure 1(B)), are likely the reason why seahorses and pipehorses exhibit a much greater tail bending capacity than pipefishes [25, 26]. But, how do these adaptations affect other functions like twisting, protection and prehension?

To answer these questions, we created a ‘family’ of 3D-printed models that mimic the different tail skeletons of a seahorse and a type-II pipehorse (see [25] for reference to type-I versus type-II pipehorses; for brevity, we refer to the type-II pipehorse, Syngnathoides biaculatus, investigated here as a pipehorse). However, rather than making direct replicas of the natural designs, we use morphological data extracted from several fishes [20–26] to build idealized models of the natural systems, as well as representative intermediates of those with averaged forms of the different designs (which also resemble the proximal and middle regions of some pipehorse tails; see figure 1(B)). The combination of both the idealized models and their averaged intermediates allow us to directly measure how distinct modifications in the armored plates affect their mechanical performance across several bending, twisting, and crushing experiments. Then, we compare the models’ resulting behaviors to explain how the skeletal armors of these syngnathid fishes may facilitate or impede different functions, without the need for animal testing. Finally, we suggest that designs most closely mimicking a seahorse tail are best fit for armored grasping applications; the presence of armored plates with a reduced size not only provides adequate protection, but also aids in grasping functions.

2. Materials and methods

2.1. Animal procurement and micro-computed tomography (CT)

The syngnathid fishes—Syngnathus leptorhynchos, S. biaculatus, Hippocampus reidi, and Hippocampus kuda—were donated by the Birch Aquarium at Scripps Institute of Oceanography after they died due to natural causes and were subsequently stored frozen. Prior to micro-CT scanning, the fishes were thawed and preserved in 70% isopropanol, as previously described [20, 23, 24]. Micro-CT images of their tails, as well as a single bony plate and vertebra excised from the proximal end of a mature seahorse tail (H. kuda) [23], were scanned with a Skyscan 1076 scanner (Kontich), inside custom Styrofoam molds and plastic tubes, like that previously described [20, 23, 24]. Rendered models of the tails and bones were developed using Skyscan’s CTVox software. Representative measurements between selected landmark points on the bony plate and vertebra were recorded using Skyscan’s Dataviewer software. All images of the syngnathid tails were color-masked using Adobe Photoshop CC (Adobe Systems) to distinguish the bony plates from the vertebral columns.

2.2. Computer-aided design (CAD) and 3D-printing

The plates and vertebrae of the models were created with a CAD software (SolidWorks, Dassault Systemes), then fabricated on a multi-material 3D-printer (Connex 350, Stratasys). Figure 2 illustrates the biomimetic design process. First, selected landmark points (blue dots) on the plate and vertebra extracted from a seahorse tail (H. kuda) were scaled-up and sketched as symmetric, idealized cross-sections into four parallel planes. Then, the solid models of each part were formed by lofting between the four cross-sections

Figure 1. Skeletal organization of three representative syngnathid tails. Micro-computed tomography images of the tails of: (A) a non-prehensile pipefish (S. leptorhynchos), (B) a prehensile pipehorse (S. biaculatus), and (C) a prehensile seahorse (H. reidi). For clarity, the plates and vertebrae are colored gray and magenta, respectively. The animal silhouettes highlight the different species. Each tail cross-section is approximately 10 mm wide.
and smoothed with fillets into their final shapes. The plate sizes were modified by changing their peg-to-length ratios:

$$\lambda = \frac{\ell_p}{\ell_w + \ell_p}$$

(1)

where $\ell_w$ and $\ell_p$ are measurements between the planes that form the plate wings and pegs, respectively. The peg-to-length ratios for models I–III (see figure 2) were designed to be 0.167, 0.333, and 0.500, respectively, encompassing a range observed within the natural morphospace [26]. The vertebrae were designed in a similar manner, but further modified to be quadraxially symmetric and accommodate ball-and-socket joints, similar to [20]. In addition, four holes surrounding the central column of the vertebrae were added for the future integration of internal actuators (not discussed here). All plates and the central regions of the vertebrae were printed with a relatively rigid material (VeroWhite®, Stratasys), while the four orthogonal struts of each vertebra were printed with a more flexible material (TangoPlus®, Stratasys) in order to mimic the vertebrae’s deformable nature [23]. The overlapping plates of each segment were connected to the vertebrae with 1.0 mm diameter elastic bands (Bead Landing™, Michaels), and seven identical segments for each model were strung together at the ball-and-socket joints with 8.0 mm diameter glass beads (Bead Gallery®, Michaels) and 0.5 mm diameter fishing line (Mill Ends 25lb Filament Line, Mason Tackle), similar to our established procedure [20]. Glass beads were used instead of plastic balls for the ball-and-socket joints in this study to reduce vertebral friction, which was neglected throughout our analyses. Also, the overlapping plates of each segment were connected in an alternating sequence, similar to [20].

2.3. Material characterization

Relevant mechanical properties of the various materials used to construct the models were matched to the natural materials [28] to best of our ability using the resources available [29], following a similar procedure to that of [20]. The material properties were measured via tension tests of three to five samples each on a universal materials testing system equipped with a 50 kN load cell (AGS-X, Shimadzu) at a displacement rate of 0.10 mm s$^{-1}$. The measured elastic moduli (average ± standard deviation) of each material are: 455 ± 92 MPa for VeroWhite® (plates and vertebral column), 0.25 ± 0.01 MPa for TangoPlus® (vertebral struts), 1.1 ± 0.1 GPa for the fishing line (ball-and-socket joints), and 15.1 ± 0.7 MPa for the elastic bands (overlapping joints) [20]. The 3D-printed materials were measured using three dog-bone samples each with gage lengths of 10 mm and cross-sections of 7.6 mm$^2$. The fishing line and elastic bands were measured using five individual strands cut to lengths of ~126 mm (fishing line) and one strand each of ~10, 30, and 60 mm (elastic bands), respectively.
2.4. Structural measurements

Figure 3 shows schematics of the parameters used to measure the armored coverage and grip contact of the models; it also shows the five models after ink-stamping (described below). Armored coverage represents the approximate fraction of plates covering the vertebral column, where $A_p$ and $A_m$ are the respective areas of the plates and model profiles measured from their unbent and untwisted silhouettes (see figure 3(A)):

$$AC = \frac{A_p}{A_m}.$$  \hspace{1cm} (2)

We measured these areas from pictures of the models using ImageJ (National Institutes of Health). Grip contact represents the extent to which the exterior surfaces of the models contact an object of maximum allowable curvature, where $\kappa_{\text{max}}$ is the maximum curvature of a cylindrical object that the models could theoretically fully wrap around, and $A_c$ is the approximate surface contact area of the models that touches a flat surface when unbent and untwisted (see figure 3(B)):

$$GC = \kappa_{\text{max}} \left( \frac{A_c}{A_m} \right).$$  \hspace{1cm} (3)

In this case, the maximum curvature of a cylindrical object that the models could theoretically grab is equal to the inner curvature of the models when bent to their passive capacities ($\kappa_{\text{max}} = \kappa_i$), which is greater than the curvature of the central vertebral column ($\kappa_i > \kappa$). We measured this parameter from pictures of the models bent to their maximum passive capacities, using ImageJ. The surface contact areas of the models ($A_c$) were measured by an established ‘ink-stamping’ method [30], where we lightly stamped the models on a felt water-based ink pad (Shiny Stamp) and measured the relative areas of contact with the pad when unbent and untwisted, also using ImageJ (see figure 3(C)). Note, for comparative purposes we measured the approximate contact area of model V (and the non-plated side of model IV) to be equal to the total cross-sectional area of its seven vertebral struts; even though, model V is likely to ‘grasp’ objects such that the sides/corners of two struts per segment contact objects along a plane oriented 45° between its struts.

2.5. Bending and twisting experiments.

Figure 4 shows images of the five models bent and twisted to their maximum passive capacities, which were measured as the average angular deflection per segment when no force was required to hold them in their respective positions. In addition, a handheld force gauge (FGV-XY, Shimpo) was used to measure the perpendicular forces required to bend or twist the models beyond their passive capacities. In both tests, one end of the seven-segmented models was fixed to a rigid support frame, while their free end was attached to the force gauge (refer to figure 7). In bending, the support frame was a simple wood 2 × 4 beam, with holes drilled into its side, where the terminal segment of each model was fixed with zip ties. In twisting, the models were fixed into a custom frame made from large steel brackets, and a rigid copper rod (1.25 mm diameter) was strung through the models’ vertebral columns to keep them from bending during the torsion tests. In both tests, a 120 mm long steel wire (1.50 mm diameter) was attached between the force
gauge and the free end of each model, perpendicular to the vertebrae. In bending, the wire was fixed to the central column; in twisting, it was fixed to the end of a strut. The models’ free end and the tip of the force gauge were positioned along predetermined guidelines in bending to ensure that the applied load was perpendicular to the vertebral column and parallel to the force gauge during all tests. The guidelines also served as predetermined measurements of the different moment arms for each test, which were calculated from simple geometric relations of the models bending angle and position of the force gauge. In twisting, the force gauge was attached to a rigid swing arm to keep the moment arm of the applied force constant during all tests. Overhead pictures of the models were taken to measure their total angular deflection and applied load (converted to an applied moment) in each position. All tests were conducted on a smooth horizontal plane surface in order to neglect gravitational and frictional effects due to the vertebrae. In bending, the cross-sections of the models, which were strung together with elastic bands, began to expand at loads >4.0 N; we stopped the tests at this point such that tension in the fishing line could be neglected. In twisting, the cross-sections of the models, which were strung together with fishing line, began to stretch at loads >4.0 N; we stopped the tests at this point such that tension in the fishing line could be neglected. In addition to pure bending and pure twisting, we also conducted combined bending and twisting tests to observe the overall shape restitution response of the models subject to manual manipulations (refer to figure 5 and Movie 1 (stacks.iop.org/BB/12/066007/mmedia)). The models were (i) bent then twisted, (ii) twisted then bent, or (iii) simultaneously bent and twisted in different orientations (e.g. bent and twisted to the right, bent to right and twisted to the left, or vice versa). Although these tests were also conducted on a smooth horizontal plane surface, the combined loading trials showed a non-negligible dependence on gravity and contact friction.

2.6. Crushing experiments

Compression tests were run on the five models at a constant displacement rate of 0.10 mm s⁻¹ up to –6 mm (~10% of their original width) on a universal materials testing machine equipped with a 500N load cell (AGS-X, Shimadzu) (refer to figure 8). The apparent crushing stiffnesses and resiliencies of the models were calculated from recorded load-displacement data. The stiffness was measured as the slope of the curves from 0–0.6 mm (0–1% displacement). The relative resilience was measured as the total area under the curves from 0–5 mm (empirically determined to be within the models’ elastic regime). Also, the inflection points at which the models began to ‘yield’ (discussed below) were determined from the plots to be ~1.6 mm for model I, ~1.3 mm for model II, and ~1.0 mm for models III and IV (plated side).

3. Results and discussion

For clarity, we refer to the five biomimetic models created here as models I–V, corresponding to the colored numerals shown in figures 3 and 4. Upon comparison of figure 1 with figures 3 and 4, and with literature data [26], it is seen that model I is most representative of a pipefish tail, while models III and V are most representative of the prehensile regions of common seahorse and pipehorse tails, respectively. Models II and IV represent averaged intermediates of models I + III and III + V; they also closely resemble the morphologies of other pipehorse tails [25, 26]. Although the models are not identical to their natural counterparts, the biomimetic structures were modified from an idealized model of a seahorse...
Table 1. Experimental measurements of the mechanical metrics of the biomimetic models with respect to their number of plates per segment, peg-to-length ratios, total mass, and plate mass.

<table>
<thead>
<tr>
<th>Biomimetic models</th>
<th>I</th>
<th>II</th>
<th>III</th>
<th>IV</th>
<th>( i )</th>
<th>( ii )</th>
<th>( iii )</th>
<th>( iv )</th>
<th>V</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plates per segment (n)</td>
<td>4</td>
<td>4</td>
<td>4</td>
<td>2</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>0</td>
</tr>
<tr>
<td>Peg-to-length ratio (λ)</td>
<td>0.167</td>
<td>0.333</td>
<td>0.500</td>
<td>0.500</td>
<td>—</td>
<td>—</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total mass (g)</td>
<td>215</td>
<td>178</td>
<td>144</td>
<td>78</td>
<td>—</td>
<td>13</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Plate mass (g)</td>
<td>7.2</td>
<td>5.9</td>
<td>4.7</td>
<td>4.7</td>
<td>—</td>
<td>—</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Armored coverage (%)</td>
<td>100</td>
<td>96</td>
<td>74</td>
<td>43</td>
<td>—</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grip contact (m(^{-1}))</td>
<td>0.4</td>
<td>1.9</td>
<td>4.7</td>
<td>3.7</td>
<td>—</td>
<td>1.9</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bending capacity (degrees)</td>
<td>12.8</td>
<td>13.0</td>
<td>18.8</td>
<td>45.0</td>
<td>—</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Twisting capacity (degrees)</td>
<td>172</td>
<td>165</td>
<td>156</td>
<td>—</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Shape restitution (N · mm · rad)</td>
<td>197</td>
<td>172</td>
<td>135</td>
<td>71</td>
<td>—</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Bending energy (N · mm · rad)</td>
<td>45</td>
<td>71</td>
<td>99</td>
<td>93</td>
<td>—</td>
<td></td>
<td></td>
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<tr>
<td>Twisting energy (N · mm · rad)</td>
<td>377</td>
<td>268</td>
<td>219</td>
<td>117</td>
<td>—</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Compressive resilience (N · mm(^{-1}))</td>
<td>46.9</td>
<td>35.3</td>
<td>28.6</td>
<td>7.6</td>
<td>—</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Crushing stiffness (N · mm(^{-1}))</td>
<td>12.2</td>
<td>2.9</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td></td>
<td></td>
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</tr>
</tbody>
</table>

a The values listed for model IV are either direct measurements or averages of those taken from the column to the right, when different sides/orientations yielded different results: i.e. \((i + ii + iii)/4\) or \((i + ii)/2\).

b The measurements \((i–iii)\) of model IV were taken from the positions shown in figure 4(A), corresponding to the inner concave sides of the model.

c The measurements \((i, ii)\) of model IV were taken from the positions shown in figure 8(B), corresponding to the orientations where the model was loaded (i) parallel and (ii) perpendicular to its overlapping plates.

tail [20]. Keeping the vertebral columns equivalent in all models, we increased the size of the plates (I–III) or removed them (III–V) to systematically compare the effects of the armor on the tail-inspired systems. However, because the models are not true replicas of the natural systems (an intentional design), we do not make claims that they provide true representations of the organisms’ behaviors. Instead, analogical comparisons of the biomimetic ‘family’ allow us to approximate their biomechanics and reveal the bio-inspired potential of each design.

Table 1 lists the mechanical responses of the five models across all metrics measured here. Reported values are those averaged from measurements taken across all four orthogonal orientations (parallel to the four sides of their square cross-sections). Except for model IV, all models were designed to be quadraxially symmetric, such that their mechanical properties and behaviors are equivalent in all four orientations. Model IV exhibits different results due to its lateral symmetry, in which two or three of the four orientations for some metrics are different (refer to figures 3, 4, 7 and 8); the two columns of reported values in table 1 are those of the individual metrics (e.g. \((i, ii, iii)\)) and their averages (e.g. \((i + ii + iii)/4\)).

3.1. Structural properties

Figure 3(D) shows the average grip contact and armored coverage measurements versus the weight of the five models. Clearly, adding plates and increasing their size increases their weight and results in a greater armored coverage. Conversely, their grip contact increases upon adding plates and decreasing their size, leading to model III having the greatest grip contact. Thus, adding plates increases both metrics, but increasing the plate size results in a performance trade-off: improving the models’ protective function, but diminishing their prehensile ability. This is because the grip contact metric is dependent on the bending capacity of the models, which decreases as the plates are enlarged.

3.2. Bending and twisting response

Figure 4 shows the models bent and twisted to their passive capacities. Clearly, they increase in both bending and twisting as the plates decrease in size.
(I–III) or as they are removed from the vertebral column (III–V). Note, however, that for comparative purposes we do not consider the models’ bending capacities when their vertebral struts are offset from the horizontal plane because the plates of models I–IV largely restrict these offset modes; such an offset would increase the capacity of model V, but decrease that of the other four models. With this in mind, model IV exhibits some interesting behaviors (see figure 4(A)): (i) when bent such that the overlapping plates are on its concave side, its capacity is ~12.8°, which is slightly more than that of model III; (ii) when bent in the plane parallel to the overlapping plates, its capacity is ~13.0°, which is slightly more than that of orientation (i); (iii) when bent such that the overlapping plates are on its convex side, its capacity is ~18.8°, which is slightly less than that of model V. These behaviors suggest that the peg-and-socket joints along the outer convex side of the models (not only the inner concave side) play a minor role in bending. Likewise, the twisting capacity of model IV is also slightly less restricted than model III due to its lack of plates on one side. This transition of armor from full-coverage (model I) to no-coverage (model V) can be seen in the middle region of some pipehorse tails (refer to figure 1(B)). It likely enhances their bending capacity in the ventral direction, which is better suited for grasping, without a major sacrifice of their dorsal armor.

According to a detailed geometric analysis (figure 5), we found that the bending and twisting capacities of models I–III are primarily dependent on their plate morphologies and joint properties, respectively. Their passive bending capacities follow a nonlinear trend, in which the plate wing width ($\ell_w$) can be expressed as a function of the models’ bending capacity per segment ($\ell$) and several geometric constants:

$$\ell_w = f(\theta) = \frac{(h - w)(2v - s \sin \theta)}{2h - w - s \cos \theta};$$

where $h$ is the overall height of the models (60 mm), $w$ is the width at the intersection of the plate wings and the base of the pegs (48 mm), $s$ is the distance between the sockets (55 mm), and $v$ is the distance between adjacent segments or the ball-and-socket joints (18 mm). Equation (4) is plotted numerically in figure 5(B), where the derived relationship (dashed line) fits well to the experimental data (colored dots). This confirms that the morphology of the plate wings and pegs on the inner concave surface of the models (as derived) is the primary factor that constrains bending. Similarly, the models’ passive twisting capacities per segment ($\phi$) can be expressed as:

$$\phi = \frac{\pi}{4} - \cos^{-1}\left(\frac{\sqrt{2}}{2}\left(\frac{s + 2a}{t}\right)\right);$$

where $s$ is the distance between sockets (55 mm), and the geometric parameters $t$ and $a$ are described as follows: $t$ is the width of the segments at the location coincident to the sockets, where the pegs of the anterior segments contact the sockets of the posterior ones in the unbent condition. It can be expressed as a piecewise function:

$$t = \begin{cases} 
  w + \frac{\ell_w - v}{\ell_p}(w - p), & \ell_w \leq v; \\
  2h - w - \frac{2v}{\ell_w}(h - w), & \ell_w \geq v;
\end{cases}$$

Figure 5. Geometric kinematics of pure bending and twisting. (A) and (C) Schematics of models I–III illustrating the geometric parameters used to derive the analytical bending and twisting capacities shown in equations (4)–(7). Note that the bending capacity ($\theta$) and the peg-to-length ratio ($\lambda$) are both dependent on the width of the plate wings and pegs ($\ell_w$, $\ell_p$) and several geometric constants only, while the twisting capacity ($\phi$) is dependent on the perpendicular distance ($a$) added to the length of the sockets ($s$), which is a function of the relative plate rotation allowed by the overlapping joints ($\gamma$). (B) and (D) Plots of the analytical (black lines) and experimental (colored dots) bending and twisting capacities ($\theta$ and $\phi$) versus the plate peg-to-length ratio ($\lambda$). Note that the bending relationship $\ell_w = f(\theta)$ was plotted numerically, and the twisting relationships depend on the plate rotations, $\gamma = 0^\circ$ (dotted line) and $\gamma = 3^\circ$ (dashed line).
where \( h, w, v, \) and \( \ell_w \) are the geometric constants described above, \( p \) is the distance between the tips of the pegs (42 mm), and \((\ell_w + \ell_p) = 30\) mm, in this case. Using these relationships, equation (5) is plotted in figure 5(D) when \( a = 0 \) (the condition where there is no plate rotation due to the overlapping joints; i.e. \( \gamma = 0^\circ \)). Clearly, this relationship (dotted line) underestimates the actual measured twisting capacities of the models (colored dots). That is because, when twisted, the overlapping joints are subject to some rotation \((\gamma > 0^\circ)\), which increases the articulation freedom of the peg-and-socket joints. To account for this increased torsional freedom, we include the adjustment parameter \( a \), which is defined as the perpendicular distance between the edges of the sockets in their non-rotated positions relative to that of their rotated positions (see insets in figure 5(C)):

\[
a = \frac{s}{2} \left( \cos \gamma + \frac{1}{2} \sin 2\gamma - 1 \right) + \frac{s}{4} \sin \gamma \left( \frac{\ell^2}{2} - 8 \sin \gamma + 2 \cos 2\gamma - 6 \right)
\]

(7)

where \( \gamma \) is the relative plate rotations at the overlapping joints. The influence of this parameter is shown in figure 5(D), where equation (5) is plotted for the two distinct cases: \( \gamma = 0^\circ \) (dotted line) and \( \gamma = 3^\circ \) (dashed line). From this empirical comparison, it is clear that the pegs must exert minor outward forces on the sockets causing the rings to expand when twisted, thereby increasing their articulation freedom. This cross-sectional expansion depends on the stiffness of the overlapping joints, which are tied together with elastic bands (with a modulus of \( \sim 15\) MPa). Thus, figure 5 proves that, although the overlapping joints do not play a major role in the bending capacity of the models, they do increase the models’ twisting capacity considerably. While the stiffness of the overlapping joints of syngnathid tails are not known, there is some evidence that these joints are mobile under large deformations [23]. Although it is beyond the scope of this study, it is plausible that the overlapping joints of some syngnathid tails might experience a similar expansion when forcefully twisted, like that observed when they are crushed [23].

3.3. Shape restitution

In addition to pure bending and twisting, we subjected the models to combined bending and twisting to observe their overall shape restitution behaviors. Interestingly, the sequence of events of (i) bending followed by twisting, (ii) twisting followed by bending, or (iii) simultaneous bending and twisting resulted in slightly different behaviors for models I–IV; their restorative responses also varied according to their plate size and exclusion. In contrast, the vertebral column (model V) exhibited no restorative response to any sequence of combined loading. Figure 6 and Movie 1 show representative responses observed in model III when subject to manual manipulations, then released. In multiple trials, the models consistently returned to a relaxed state slightly offset from their initial straightened positions (red lines). When bent, then twisted the models fell short of their initial positions upon release (see figures 6(A) and (B)); conversely, when twisted, then bent (and when simultaneously bent and twisted) the models returned to a relaxed state beyond their initial positions (see figures 6(C) and (D)). That is because, in these cases, segments closer to the fixed base of the models store more energy in the overlapping joints due to segmental torsion (white arrows), which increases their restorative potential and causes the models to ‘overshoot’ their initial positions upon release. This difference in shape restitution is also an artifact of the experimental setup. Contact between the models with the plane surface (where gravity is directed into the page) causes the models to snap back to their initial resting positions more quickly than would be expected in an aqueous medium of free-space, like that of the natural habitats of syngnathid fishes. Also, when twisted in opposition of their natural ‘rolling’ motion (e.g. twisted to the left, but bent to the right), frictional contact between the models and the plane surface restricts shape restitution, holding the models in their deformed positions. Thus, to approximate this general restorative behavior (independent of gravity), we measured the models’ overall shape restitution as the collective elastic energy stored in the models when subject to pure bending and pure twisting.
In these experiments, we bent or twisted the models beyond their passive capacities up to the critical loads of 4.0 N and 2.5 N, respectively (see materials and methods). Figure 7 shows the experimental setups used to measure their responses to the different loading events, as well as the recorded moment/torque versus angular deflection data. From this, we quantified the collective energy stored by the models, which represents their ability to snap back to their relaxed shape upon extensive deformation, similar to the ‘external tendon’ effect observed in the skins and scales of many fishes [31–34]. We refer to this behavior as the shape restitution energy:

$$U_t = \int M d\theta_t + \int T d\phi_t$$

(8)

where $M = F_B x$ and $T = F_T y$ are the respective bending and twisting moments due to the perpendicular applied forces ($F_B$ and $F_T$) and moment arms ($x$ and $y$), and $\theta_t$ and $\phi_t$ are the cumulative bending and twisting angles of the seven-segmented models (refer to schematics). More simply, equation (8) is a measure of the added areas under the curves from the two plots, calculated from the respective trend lines fit to each data set. All trends for models I–IV exhibited strong exponential correlations ($R > 0.9$), while those of model V were constant and nearly zero, suggesting that the vertebral column plays a minimal role in energy storage. For comparative purposes, we added the bending and twisting energies together, even though the models exhibited distinctly different responses to the different loading events. That is, the bending and twisting energies of models I–III respectively decrease and increase with decreasing plate size, but when added together their total energies are nearly equivalent (see table 1). Conversely, when the plates are removed, as in models III–V, both their bending and twisting energies decrease. This restorative response, which is seen in the more heavily-armored models I–III, has been suggested to facilitate tail relaxation in seahorses [20]. Likewise, pipefishes might use their plates to store and release energy when swimming; although no experimental evidence exists on pipefishes, similar mechanisms are observed in other heavily-armored fishes [33].

A comparison of the trend lines in figure 7 reveals some interesting relationships. In bending, models I–III follow the equation, $M(\theta_t) = A_1 e^{B_1 \theta_t}$, where the exponent $B_1 = 0.03$ for all three models, but the constant $A_1$ varies from 48.0, 20.5, and 8.5, respectively. In twisting, models I–III follow a similar equation, $T(\phi_t) = A_2 e^{B_2 \phi_t}$, where the constant $A_2 = 10$ for all three models, but the exponent $B_2$ varies from 0.025, 0.016, and 0.012, respectively. Thus, the constant $A_1$ is likely dependent on the plate morphologies (peg-to-length ratios), which play a more dominant role in the models’ bending behaviors (see equation (4)). Similarly, the exponent $B_1$ is likely dependent on the joint properties (stiffness of the overlapping joints), which play a more dominant role in the models’ twisting behaviors (see equations (5)–(7)). Also, model IV
displays trends that further support our conclusions. In bending, its constant $A_1 = 0.75$ and its exponent $B_1$ varies depending on its orientation from 0.048, 0.042, and 0.037, corresponding to (i–iii) shown in figure 4(D). In twisting, the trend line fit to model IV has an equivalent exponent to that of model III ($B_2 = 0.012$), but its constant $A_2 = 4.5$. These differences can be attributed to its lack of plates on one side, which effect both the plate morphology and joint properties, represented as $A_i$ and $B_i$, respectively.

### 3.4. Compressive resistance

As seen in figure 8, we transversely crushed the models up to ~6 mm (~10% of their original width). From the resulting load-displacement data, we measured the resilience and stiffness of the models (see table 1). Models I–III and IV (top curve; when its overlapped plates are parallel to the applied load) exhibit notable changes in their linear-elastic behaviors at ~1–2 mm, whereas models V and IV (ii) (bottom curve; when its overlapped plates are perpendicular to the applied load) exhibit changes in their elastic behaviors at ~5 mm. These inflection zones (or changes in the slopes) occur when models I–III and IV (i) begin to ‘yield’ due to an initial buckling and bulging of their struts, subsequent rotation of their vertebrae, and consequent separation of their overlapping plates, as shown in figures 8(C)–(E). In contrast, models V and IV (ii) display different behaviors, which primarily depend on the response of the vertebrae (described in more detail below). Note, however, that the materials that make up the models never actually yield, because they never undergo plastic deformation in the tests. For that reason, we compare the models’ resilientities up to an equal displacement of 5 mm (when the vertebral column ‘yields’) and their stiffnesses from 0–0.6 mm (0–1% of their original width). Adding plates and increasing their size enhances both properties. As such, the vertebral column seems to play a less important role in models I–III and model IV (i) because the plates (and overlapping joints) actively resist deformation.

Evidently, there are significant plate–plate interactions that occur at the overlapping joints oriented parallel to the applied load during initial loading. Different from previous work [20], the plates in this study were printed with a softer, rougher material (VeroWhite®, rather than ABSplus® [29]), which increases friction at the overlapping joints such that it can no longer be neglected, as it was in previous work. Thus, to account for friction, we introduce an empirical correction factor ($C_p$) to the theoretical force-displacement relationship:

$$P = 7(C_v + n_hC_h + n_vC_v)\delta + n_pC_p$$

(9)
where the multiplier 7 accounts for the seven segments that are compressed, the integers $n_i$ describe the number of horizontally-oriented struts ($n_h$), elastic connections ($n_e$), and plate–plate contact interactions ($n_p$) per segment that are involved in supporting the compressive loads, and the first three constants $C_s$ can be defined, according to previous work [20], as:

\[
C_s = \frac{k_s}{2} = \frac{E A_s}{2 L_s};
\]

\[
C_h = \frac{3 \beta_h}{L_s} = \frac{3 E J_s}{L_s};
\]

\[
C_e = 2 \kappa_e = \frac{2 E e A_e}{L_e};
\]

such that $C_s$ and $C_h$ respectively describe the behavior of the vertebral struts in compression (those oriented vertically) and bending (those oriented horizontally), and $C_e$ describes the behavior of the elastic bands (two per joint) that connect the overlapping joints and vertebral struts together. Note, the geometries and material properties of the models’ different components are listed here: $C_s = E A_s/2L_s$ depends on the modulus ($E_s = 0.25$ MPa), moment of inertia ($I_s = 10.49$ mm$^4$), and length ($L_s = 10$ mm) of the vertebral struts in compression; $C_h = 3E J_s/L_s$ depends on the modulus ($E_s = 0.25$ MPa), moment of inertia ($I_s = 10.49$ mm$^4$), and length ($L_s = 10$ mm) of the vertebral struts in bending; $C_e = 2E e A_e/L_e$ depends on the modulus ($E_e = 15$ MPa), moment of inertia ($I_e = 0.79$ mm$^4$), and length ($L_e = 60$ mm) of the elastic bands in tension. The empirical correction factor $C_p$ was found to scale with the width of the plate wings ($\ell_w$) and displacement ($\delta$), accounting for the stresses accumulated in the plate material at the overlapping joints, which are caused by contact friction at the plate–plate interface. It is expressed as:

\[
C_p = K \ell_w((1 - H(\delta - \delta_0))\delta + H(\delta - \delta_0)\delta_0)
\]

where $K = 10^3$ is an empirically-derived scaling factor dependent on the contact geometry, coefficient of friction, and relative stiffness of the plates and elastic bands [35, 36], and $H(\delta - \delta_0)$ is the Heaviside step function, which activates at a critical displacement ($\delta = \delta_0$) when the models begin to ‘yield’ due to slight rotations of the vertebral columns. At this critical inflection point, the overlapping plates separate from each other (see figures 8(C)–(E)), touching only at a line contact [35] of length $\ell_w$, so that $C_p$ switches from a linear function ($C_p = K \ell_w \delta$) when $\delta < \delta_0$, in which quasi-static contact stresses accumulate in the plate material, to a constant ($C_p = K \ell_w \delta_0$) when $\delta \geq \delta_0$, in which only sliding contact stresses remain.

As seen in figure 8(B), our linear approximation in equation (9) predicts the compressive behaviors of the biomimetic models quite well, with a few exceptions. When models I–III and IV (i) begin to yield, their theoretical slopes adjust according to the correction factor $C_p$ (see dotted lines), such that they become nearly equal when $\delta \geq \delta_0$ (where $\delta_0$ was empirically evaluated; see materials and methods). However, the theoretical relationship predicted for model I clearly underestimates its actual behavior. That is likely because the plates of model I are so large that they do not markedly separate from each other when loaded beyond a critical displacement of ~1.6 mm. Thus, when $\delta \geq \delta_0$ the close contact of the overlapping plates in model I causes wear (confirmed through observation). The apparent friction in this case could be the result of plate–plate sliding over an interfacing layer of wear detritus [36], or alternatively, due to the nonlinear nature of friction [37]. Another observation is that the theoretical relationships predicting the behaviors of model IV (ii) and V also underestimate their true compressive behaviors (see dotted lines). In these theoretical relationships, equation (9) reduces where $n_p = n_e = 0$ for both models and $n_h = 0$ for model V. The constants $C_s$ and $C_h$ which describe the behavior of the vertebrae, are dependent on their initial engineering properties; they do not account for any geometric changes when loaded. In reality, the vertebral struts bulge, warp, and buckle when crushed, which changes their apparent cross-sectional areas ($A_h$) and inertias ($I_h$), respectively. Therefore, we conclude that as the plates get larger more contact between them at the overlapping joints amplifies the friction opposing the compressive load, which depends on the plates’ size ($\ell_w$). Model IV really exemplifies this behavior, where the top (i) and bottom (ii) curves in figure 8(B) show the cases where its overlapping plates are aligned vertically, exhibiting linear sliding such that $C_p = f(\delta - \delta_0)$, and horizontally, exhibiting no interaction such that $C_p \to 0$.

As observed in the crushing response of a seahorse tail [23], deformation of its skeleton is primarily controlled by the linear sliding of its armored plates, which is a result of its square-like morphology [20]. Similarly, the initial linear sliding that occurs in models I–V is the result of their square-like architectures. However, when the natural (or biomimetic) structures experience larger deflections, linear-elastic tensile loads in the connective tissues (or elastic bands) at the overlapping joints are transferred to the ‘skeletal’ components, which likely undergo nonlinear deformations (due to bending and compressive loads), and may even fracture (at displacements $\geq 10\%$). Depending on the material properties and geometries of the constituent bones versus photopolymers), these nonlinear responses may cause softening or stiffening effects, as observed in the compression and contortion (bending and twisting) experiments, respectively. Comparable effects have been described for a prismatic beam reinforced with biomimetic scales [38] and a whole teleost fish [39]. Furthermore, the natural bony armors and vertebrae of syngnathid fishes are organized into hierarchical structures across several length scales [23]. Such a hierarchy, which is common among many
natural materials [40, 41], but not included in the biomimetic models, could further improve the toughness and overall performance, while also decreasing the weight, of these articulated structures.

3.5. Multifunctional performance comparison

Table 1 lists the averaged measurements of all metrics recorded for models I–V. Figure 9 plots their normalized performances \( \bar{P} = P_i/\max(P_i) \) where \( P_i \) is the average measured performance of each i metric) across the seven mechanical metrics of interest. The animal silhouettes in figure 9 illustrate where the ‘bio-inspiration’ for models I, III and V was derived, while models II and IV closely resemble the proximal and middle regions of some pipehorse tails. As seen in the plot, model I exhibits the greatest armored coverage and resistance to crushing (stiffness and resilience); model III exhibits the greatest grip contact; and model V exhibits the greatest flexibility (bending and twisting capacity). Interestingly, the two intermediate models (II and IV) are not top performers across any of the measured metrics, suggesting that the structures proxied by models I, III and V are ‘optimal’ designs for specific tasks—armor, grasping and flexibility. Note that because the effect of gravity is small in the underwater habitat of syngnathid fishes, we generally ignore the weight of the models in these comparisons.

As seen in figure 9, three distinct trade-offs can be visualized where the performance lines intersect. Two trade-offs occur around grip contact for models I–III (between armored coverage and grip contact) and for models III–V (between bending capacity and grip contact). This is because model III is the top performing gripper of the biomimetic ‘family’; it also happens to be most representative of a seahorse tail, suggesting that this design is optimal for grasping (within the tested group). However, the combined attributes of models IV and V, which closely mimic the middle and distal regions of a pipehorse tail (refer to figure 1(B)), could provide advantageous qualities for grasping as well. This is especially true if we consider other biological design features, such as internal muscles and external skins. If included in the biomimetic models, added muscle and skin would have at least one obvious effect—they would increase the apparent grip contact of models IV and V without significantly changing that of the others. As noted, similar morphologies to model IV are also observed in the middle and/or distal regions of some pipehorse tails [25, 26], indicating that trade-offs between armored and grasping functions exhibit some interspecific variation.

The third trade-off revealed in figure 9 lies at the point where the performance lines of all models intersect between shape restitution and bending and twisting capacities. This suggests that adding plates and increasing their size limits flexibility, but enhances the models’ restorative response to contortions (and crushing). Note that our definition of shape restitution in equation (8) is an emergent property of the models’ bending and twisting response. The collective metric also accounts, in part, for the fact that syngnathid tails would rarely experience pure bending or pure twisting in nature; it more accurately describes their behaviors in a biologically-relevant context. Thus, the plates, regardless of their size, are responsible for the restorative behaviors of syngnathid tails because the averaged shape restitution energies of models I–III are nearly equivalent.

4. Concluding remarks

By comparing a ‘family’ of biomimetic models inspired by the tails of syngnathid fishes, we found that three representative designs are best fit to perform different tasks. The different plate morphologies and joint properties of the designs independently control their behaviors in bending, twisting, and crushing. Our results suggest that the bony plates of a pipefish tail (c.a., model I) provide protection against crushing via frictional contact between its overlapping joints; the loss of plates in the distal part of a pipehorse tail (c.a., model V) permit considerable flexibility due to the unrestrained mobility of its vertebral column; and, the plates of a seahorse tail (c.a., model III) strike an optimal balance of performance best suited for armored grasping via a combination of its

Figure 9. Multifunctional performance comparison. Plot of the normalized average performance of models I–V across the seven performance metrics measured. The bars show the relative performance of each model, while the lines highlight changes in their performance; trade-offs are located at the intersection of the performance lines, as indicated. The animal silhouettes indicate the respective species tails’ that models I, III and V mimic.
Reduced plate size and augmented peg-and-socket joints. With these structure-function relationships in mind, it is possible to conceive different bio-inspired designs for human applications. For instance, long slender structures requiring ample protection from contortions and crushing, yet limited mobility (e.g. submerged cables) could be informed by pipefish tails; devices requiring ample flexibility, yet little protection (e.g. catheters) could be informed by pipehorse tails; and, armored manipulators intended to grasp objects in hazardous environments (e.g. bomb disposal robots) could be informed by seahorse tails.

The motivation behind the use of biomimetic models to investigate biological design is simple: engineered systems are well controlled (they are constrained by set tolerances), whereas biological systems are not (they are constrained by evolution and other natural processes [9–13]). In other words, engineered models can be designed (and redesigned) with high precision, and structural modifications can be introduced to one component at a time, keeping all others constant; such models also allow researchers to test designs that lie outside the natural morphospace [20]. Still, biomimicry has its limitations. Most modern design and manufacturing technologies are unable to replicate bulk mechanical components with the hierarchical and heterogeneous complexity observed in many natural materials and joints [42]. As a result, several assumptions and simplifications are usually necessary when designing biomimetic systems for comparative testing. In this study, for example, we scaled up the 3D-printed designs and simplifications are usually necessary when designing biomimetic systems for comparative testing.

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