

Research



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Swimming and defence: competing needs across ontogeny in armoured fishes (Agonidae)

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Biological armours are potent model systems for understanding the complex series of competing demands on protective exoskeletons; after all, armoured organisms are the product of millions of years of refined engineering under the harshest conditions. Fishes are no strangers to armour, with various types of armour plating common to the 400–500 Myr of evolution in both jawed and jawless fishes. Here, we focus on the poachers (Agonidae), a family of armoured fishes native to temperate waters of the Pacific rim. We examined armour morphology, body stiffness and swimming performance in the northern spearnose poacher (*Agonopsis vulsa*) over ontogeny. As juveniles, these fishes make frequent nocturnal forays into the water column in search of food, while heavily armoured adults are bound to the benthos. Most armour dimensions and density increase with body length, as does body stiffness. Juvenile poachers have enlarged spines on their armour whereas adults invest more mineral in armour plate bases. Adults are stiffer and accelerate faster than juveniles with an anguilliform swimming mode. Subadults more closely approximate adults more than smaller juveniles, with regards to both swimming and armour mechanics. Poacher armour serves multiple functions over ontogeny, from facilitating locomotion, slowing sinking and providing defence.

1. Introduction

Armour can serve many roles, including protection, display, and as a physiological reservoir for calcium and phosphorus. The evolutionary history of fishes is rich in both armoured species and diversity of armour types [1]. The earliest jawless and jawed fishes were well armoured—for example, extinct placoderms had large, ornate head shields [2] and ostracoderm head shields are among the most visually arresting of ancient fish fossils. Recent fishes like bichirs (Polypteridae) and gars (Lepisosteidae) retain robust armour in the form of interlocking ganoid scales, and many other lineages have convergently evolved armour of interesting, and sometimes enigmatic design [3–6]. Over evolutionary time armour has changed from large, rigid plates with few joints in the jawless fishes and placoderms, to the flexible, imbricate squamation, clad in enamel and dentine, of ancient actinopterygians [7]. Most recent teleosts have reduced squamation (exceptions outlined below), without heavily mineralized coatings like enamel, instead they have thinner layers of less dense tissue like elasmoid [7]. However, some lineages like sticklebacks, pipefishes, pufferfishes and even piranhas, have independently evolved robust armour composed of heavy dermal plates [7–9]. These dermal armours, plates and scutes are homologous with elasmoid scales, but are histologically distinct

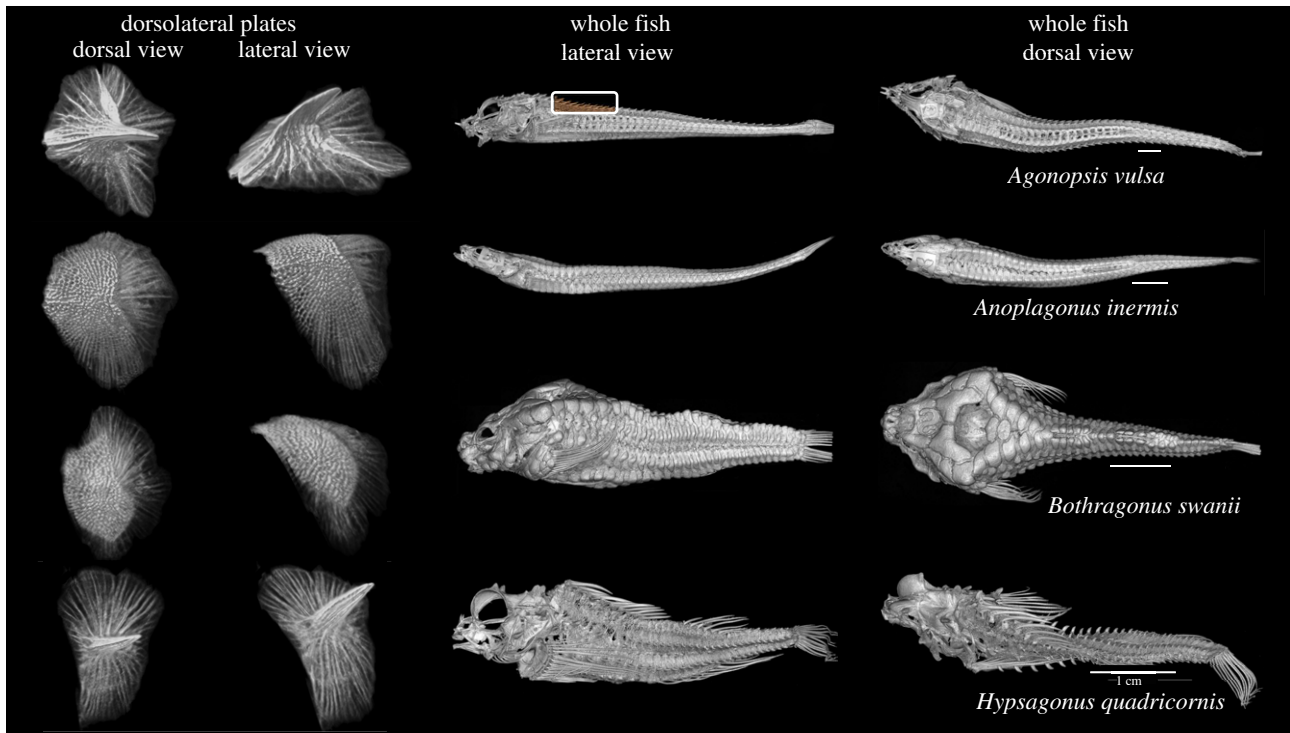


Figure 1. Morphological diversity of poacher (Agonidae) species and their armour plates. From top to bottom: north spearnose poacher, *Agonopsis vulsa*; smooth alligatorfish, *Anoplagonus inermis*; rockhead poacher, *Bothragonus swanii*; fourhorn poacher, *Hypsagonus quadricornis*. Left side images are the same armour plate, left dorsolateral scute in dorsal and lateral view. Circle on spearnose poacher (top middle) shows the region from which scale renders were taken (dorsolateral row; [27]).

from the scales of other recent fishes in that they are composed exclusively of bone, i.e. having lost hypermineralized coatings like elasmidine [7,10,11].

As armour morphologies changed over the evolutionary history of fishes, so presumably did armour function. Armour's presumed primary function is to protect fishes from predators [12], but earlier, heavier armours served multiple functions, either as ion reservoirs [13,14] or means of producing lift while negatively buoyant [15,16]. Armour in the bichir *Polypterus* even functions as an elastic recoil mechanism for aerial breathing [17]. More recent, segmented armour demonstrates a dual function of protection and flexibility [18]; consider, for example, the prehensile nature of seahorse tails [19,20] or the trunk armour of *Corydoras* and other callichthyid catfishes [21]. These are extreme examples however, as even the majority of fishes benefit from some degree of protection and flexibility lent by typical ctenoid or cycloid scalation [22]. Segmented plate armour has an added benefit, that if individual plates become damaged or even lost, the effect is localized to a small region [23]. Moreover, remodelling and healing in bony plates means these armours can regenerate if damaged [9,24]. The transition from large, immobile plates of the earliest armoured fishes to the segmented armour that has evolved many times in ray-finned fishes, allows us to study the trade-offs and opportunities presented by inter-plate mobility.

The poachers (Agonidae) are a useful system for looking at trade-offs in armour function. They are cottoid fishes, related to sculpins, greenlings and other formerly 'scorpaeniform' fishes, but differ from their relatives in that all agonids have imbricating bony armoured plates similar to seahorses and sticklebacks, but with more complete body coverage reminiscent of pipefishes and pipehorses ([11,25,26]; figure 1). However, unlike armoured pipefishes or seahorses, poachers lack the extreme exoskeletal dexterity that seahorses use to

grasp substrates [19,28]. Like many other cottoids, poachers inhabit cooler marine intertidal and subtidal habitats, living on littoral slopes according to substrate preferences [29–35]. Though poachers are almost all benthic as adults, they start life as pelagic larvae, and many have pelagic juveniles [36,37]. Since poachers have a buoyant life-history stage suited for life in the water column [38], a drastic ontogenetic shift occurs as they age and settle to the benthos.

The aims of this study are fourfold: (1) generate a detailed description of how armour morphology (plate shape, size and number) changes with increasing size in the common northern spearnose poacher, *Agonopsis vulsa*, (2) determine how changes in armour morphology affect the flexural stiffness of the fish, (3) relate body stiffness to swimming performance and (4) explore how armour form relates to armour function in other poacher species. We predict that adults will have more robust armour than juveniles, based on them being larger and thereby more conspicuous to predators. Adult armour will be made of larger and denser overlapping plates than juveniles and smaller adults, which will make larger individuals stiffer and less manoeuvrable than smaller individuals. Moreover, we expect denser, heavier armour in benthic adults, relative to less dense armours in younger poachers, as suggested by the pelagic and semi-pelagic ecologies of poacher larvae and juveniles, respectively.

2. Methods

2.1. Specimen collection

Adult and subadult *Agonopsis vulsa* [39] specimens ($n = 22$; 7.0–19.0 cm) were obtained from bottom otter trawling on the R/V *Centennial* in the Spring and Summer months (2017) in San Juan Channel, east of San Juan Island and Friday Harbor Laboratories (48.5460° N, 123.0130° W). To complete the lower end of the size

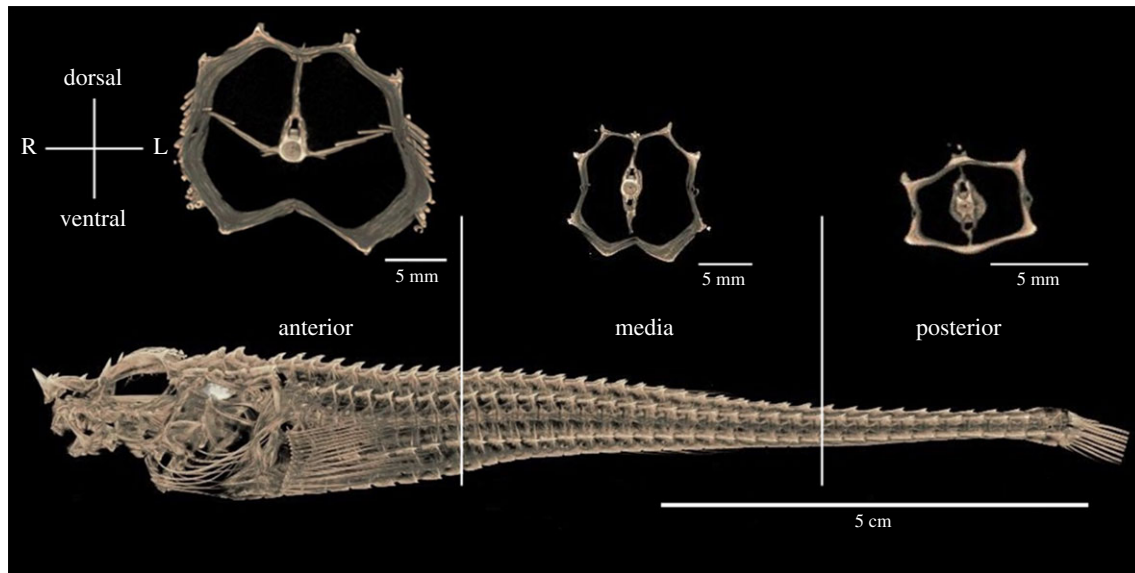


Figure 2. Body regions (cross-sections) from a μ CT reconstruction and volume render of an adult spearnose poacher, *Agonopsis vulsa*.

series, juvenile *A. vulsa* specimens ($n=9$; 2.6–6.8 cm) were collected from the Friday Harbor Laboratories docks using a night-light and dipnet or obtained through the University of Washington (UW) Burke Museum collections. Specimens were kept in flow-through aquaria and were fed a diet of brine shrimp and pieces of spot prawn (*Pandalus* sp.) daily prior to experimentation. Specimens, after experimentation, were euthanized with tricaine methanesulfonate (MS-222), fixed in buffered formalin, and preserved in 70% ethanol. All animals were collected and housed under IACUC protocol 4238-03. For interspecific comparisons of armour morphology among agonids, we contrasted *A. vulsa* to the rockhead poacher (*Bothragonus swanii*, Steindachner 1876), a subtidal poacher with unusual cranial armour (having a cavernous fossa on the dorsal surface of the cranium), the smooth alligatorfish (*Anoplagonus inermis*, Günther 1860) a subtidal to deep-water poacher with smooth, robust armour plating along its entire body, and the fourhorn poacher (*Hypsagonus quadricornis*, Valenciennes 1829), a subtidal to deep water poacher with ornate, spiny plates and a laterally compressed bauplan (figure 1).

2.2. CT scanning, image refinement, and morphometry

Formalin-fixed specimens were scanned using the Bruker Skyscan 1173 micro-computed tomography (μ CT) scanner (Bruker microCT, Kontich, Belgium) with the parameters of 65 kV, 123 μ A, and 1175 ms exposure. X-ray projections were captured with a 2240 $\times$ 2240-pixel, charge-coupled device (CCD), with resolutions ranging from 7.0 to 35.3 μ m. Raw CT image stacks were reconstructed, and individual specimens were digitally isolated using Bruker DataViewer software, and these new image stacks were converted to dicom format using Bruker DicomConverter software.

Horos (<http://www.horosproject.org/>) software was used to volume render, digitally segment and measure specimens. We measured how individual plate dimensions varied with length in poachers, as well as how plate size and mineralization change over ontogeny. Plate morphology changes from anterior to posterior in *Agonopsis*, so we divided the body into three regions: anterior (post-cranial to end of first dorsal fin), medial (end of first dorsal fin to end of second dorsal fin) and posterior (end of second dorsal fin to caudal peduncle) (figure 2). We measured three linear metrics of plate size: (1) the length of the bony plate, measured by the latitudinal axis of the plate, (2) the width of the bony plate, measured by the longitudinal axis of the plate intersecting at the base of the spine and (3) the height of the plate, measured perpendicular from the base of

the plate to the tip of the spine (figure 3d). These measures were repeated three times for each individual, that is, at 15%, 45% and 85% of each specimen's standard length.

We used reduced major-axis (RMA) regression to determine how armour morphometrics change with respect to standard length (SL) over ontogeny (v. 1.7.3, *lmodel2* package in R; Legendre, 2018). To determine if plate length, width or height scaled disproportionately with respect to body length, we compared the experimental slope of these variables relative to a predicted isometric slope ($=1$). Since we measured plate dimensions along each plate row, dimensions from each row at a given body region were averaged together for further analyses. If the regression between an armour dimension and body length produced a slope which fell above or below the predicted slope's 95% confidence interval, we considered this to be indicative of positive or negative allometry. All measurements were log-transformed prior to analyses.

2.3. Swimming kinematics and analyses

We filmed an ontogenetic series of spearnose poachers ($n=16$; 40–16.2 mm) swimming freely around a track, to gauge how differences in size equated to differences in swimming performance. We filmed trials using a single GoPro Hero4 Black camera (<https://gopro.com/en/us/>) at 60 frames per second using the 'narrow' setting on the camera to minimize warping from the fisheye lens.

Fish were transferred to the trial tank and allowed to acclimate for several minutes before trials began. We controlled the camera using the GoPro App (v. 4.2.1) and recorded as the fish swam around the track. Fish were not held in the trial tank for more than a 30 min. We continued trials over several days until five usable videos were gathered from each individual. A trial was designated as 'usable' if the fish swam more than three tailbeats without the aid of its pectoral fins. Though these fish swim at slower speeds with just their pectoral fins we limited the kinematic study to caudal locomotion since this swimming mode involves axial bending.

Before analysis, we removed the fisheye distortion from the videos using GoPro Studio. Videos were then analysed in MATLAB using midline analysis software modified from [40], github.com/CDonatelli/PoacherArmorMechanics. We measured several kinematic variables: swimming speed (in body lengths, specifically BL s^{-1}), tail beat frequency (Hz), tail beat amplitude (BL) and stride length (BL). Tail amplitude is the distance (expressed relative to the body length or BL) the tail tip travelled, from left or right, relative to the midpoint of the fish's swimming cycle. Similarly, stride

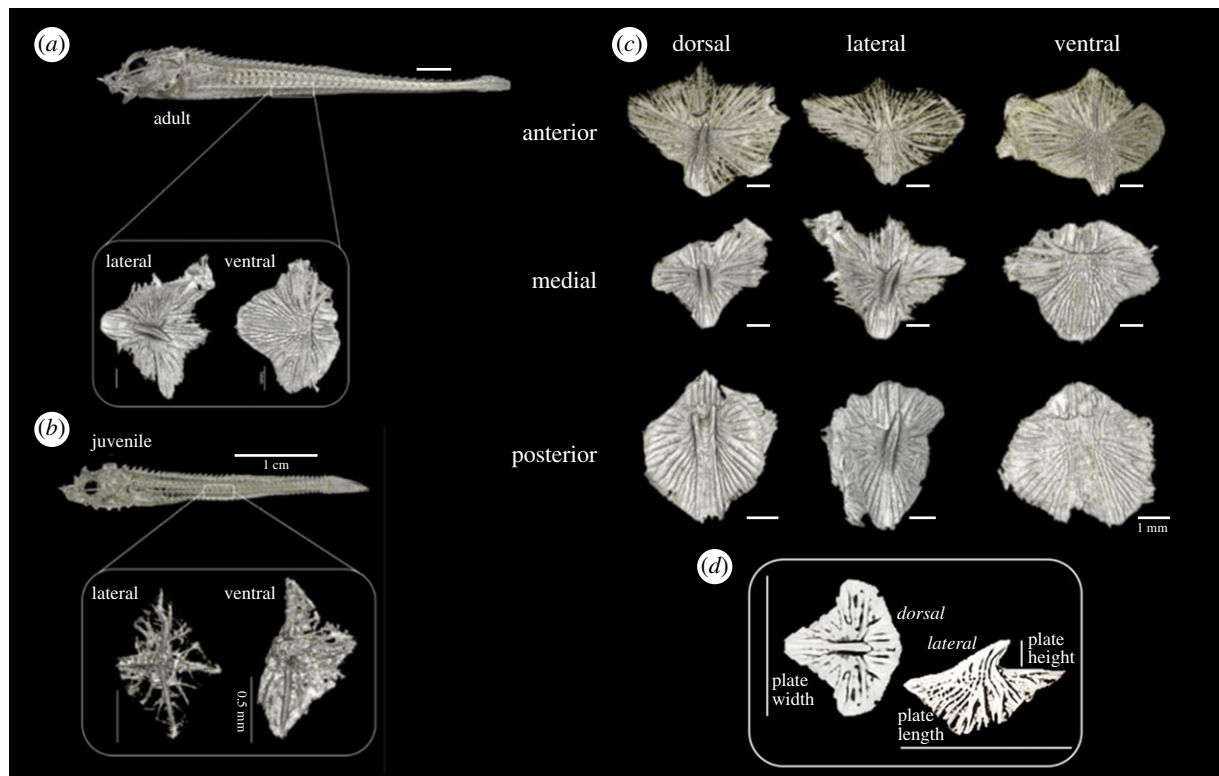


Figure 3. Comparison of plate morphology among dorsal, lateral and ventral rows in juvenile and adult spearnose poachers using μ CT volume renders. Note the extreme difference in mineralization between adults and juveniles, as well as the non-overlapping nature of plates in juveniles. (a) Adult poacher, (b) juvenile poacher, (c) comparison of plates among different body regions in the adult poacher, (d) diagram of plate morphometrics. Isolated scales on right side of figure are rotated 90° anticlockwise from their natural orientation for a better appreciation of their shape. Following Busby [27], ‘dorsal’ plates are from the left-sided, dorsolateral row; ‘lateral’ plates are from the left-sided, supralateral row; ‘ventral’ rows are ventrolateral position.

length is also expressed relative to BL to correct for absolute differences in size among study organisms. For comparative analyses, fish were assigned a size class: juveniles were 1–10 cm, transitions were 10–13 cm and adults were 13 cm and longer, based on natural breaks in the data and differences in ecology (semi-pelagic juveniles versus entirely benthic adults) and morphology (total plate ossification approx. 5–10 cm; see [27] figures 5 and 6). We also analysed these data with body size (standard length) treated as a continuous variable (see below). Mechanical and kinematic data were merged in R, then analysed using non-parametric permutational multivariate analysis of variance (permMANOVA) and the pairwise extension of this method (*pairwise.perm.manova* function, RVAide-Memoire package; [41]), with 500 permutations each (*adonis* function, vegan package).

2.4. Armour mechanical properties and analyses

Using the same individuals from swimming trials, we measured the passive bending mechanics of *Agonopsis* using a Material Testing System (MTS Synergie 100 - MTS System Corp., Eden Prairie, MN). Recently euthanized (less than 40 min before testing) specimens were placed in a custom bending rig, and the force it took to bend regional segments was measured down the length of the body at as many points, separated by 1 cm, as could fit before the head. From these measurements, we calculated bending stiffness (F/A) (Nm^2), mechanical stress (F/d) (Pa) and Young’s modulus (Pa) (stress/I) along the length of the body.

To determine how plate mineralization changed over ontogeny, we estimated relative bone mineral density by comparing greyscale values across a subset of our *Agonopsis* ontogenetic series ($n = 11$; 30–160 mm SL). These specimens were scanned with hydroxyapatite phantoms; cylinders of known density (hydroxyapatite of 0.25 and 0.75 g cm^{-3} respectively), to allow

standardization of greyscale profiles among different scans. We then used 3DSlicer (v. 4.10.1, www.slicer.org [42]) to measure average greyscale values of the 19th, 20th and 21st plates in the dorsal-most row and the row just dorsal to the lateral line. We converted these measured armour greyscale values to relative bone mineral densities (BMD) by regressing the 0.25 g cm^{-3} and 0.75 g cm^{-3} standards against their measured greyscale values. BMD fit normality assumptions, but standard length (SL) did not; all analyses were subsequently log-transformed. We used RMA regression (*lmodel2* package, [43]) to determine the scaling relationship of log-transformed BMD relative to standard length, with a predicted isometric slope of zero (see [44] for BMD scaling expectations).

3. Results

3.1. General armour morphology

The bony plates in spearnose poachers are irregularly shaped, four to six-sided polygons with two primary components, a wide trapezoidal base and a single posteriorly swept spine projecting from the central region of the base. The base of the plate is the first to form during ontogeny, with the spine arising from the middle of the plate. This spine, even early in ontogeny, is denser and more mineralized than the base (figure 3). The plate surface is porous, made of intertwining bony trabeculae (figure 3). Like boxfish armour plating, there are raised struts that extend from the margins of the plate to the spine base [45].

Bony plates in *A. vulsa* are organized into eight longitudinal rows or ridges that cover the entire trunk region, starting just posterior to the cranium and ending after the second

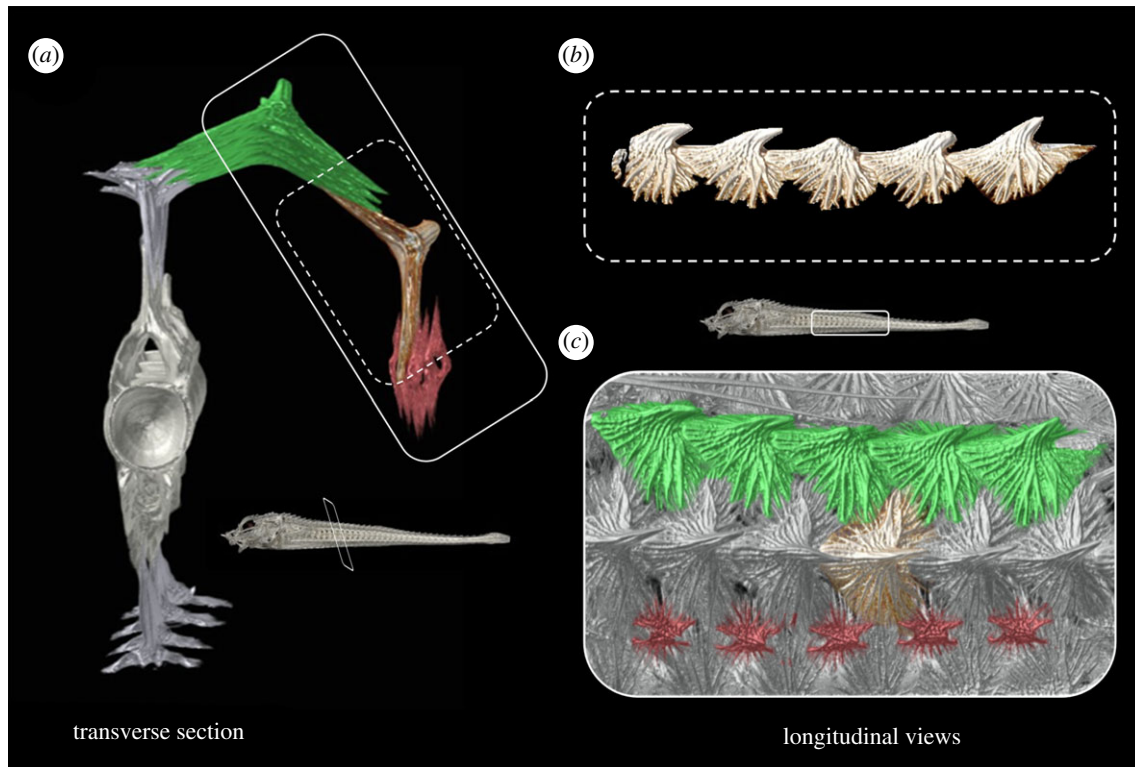


Figure 4. Variation in plate morphology by row and plate overlap among rows, from a μ CT volume render of an *Agonopsis vulsa*. Select plate rows were false-coloured during rendering for ease of identification: green, dorsolateral row; orange, supralateral row, red, lateral line canal (follows [27]). (a) Transverse section through the torso of an adult spearmose poacher; note the overlap among the three plate rows. (b) A single dorsal scale row; note the worn or damaged spines. (c) *In situ* overlap of the highlighted plate rows relative to their neighbours; note the lack of any spaces between plates. Inset images of whole *Agonopsis* show where the expanded images were taken. The interaction between two plate rows form the lateral line scale pattern: the lateral line canal actually begins as two distinct spines, which curve towards the midline of the fish, eventually encircling the lateral line itself (see also: [27, p. 7]).

dorsal fin. From cross-sectional slices through the body, we find these plates are arranged transversely around the body axis in an octagonal shape, with each side of the eight sides represented by its own scale row. A pair of plate rows lies on either side of the dorsal fins, and a pair of rows lie either side of the anal fin on the ventral surface. Laterally, there are two rows down each side, one above the lateral line and one below (figure 2). There are separate plates associated with the lateral line that do not lie adjacent to each other but are spaced along the side of the fish with a foramen for the lateral line. The ridge pairs are continuous for the entire length of the body, except for the ventral pair, which narrow towards the tail and then fuse together. The dorsal ridge pairs also fuse in the caudal region, but unlike the ventral plates, retain two distinct spines, so the body has a hexagonal cross-sectional shape in the caudal region. An additional, truncated series of bony plates surround the cloaca. Since the number of plates does not change over ontogeny, then any changes in body stiffness must be explained by changes in either plate dimensions, mineral composition or overall stiffness.

Plate overlap increases over ontogeny from nearly non-existent to considerable, in accordance with findings by Busby [27] (figure 4*a,b*). Lateral plate margins fit within the space created between the two flanking plates, i.e. plates from adjacent rows are arranged in a staggered or alternating pattern. Plates from the same ridge pair overlap only along their anterior and posterior sides, whereas lateral overlap is generally restricted to adjacent plates from another ridge pair. For this reason, lateral overlap of a focal plate is typically

skewed, meaning there is chirality to which side of the plate shows more overlap (figure 4*b,c*). This also suggests that neighbouring plates might ‘slide’ against each other laterally, lending built-in ‘give’ to the plates when compressed. The lateral line lies in between the lateral paired ridges, atop where these plates meet (but do not overlap). At this intersection, the lateral line runs through a central canal formed by bridge-like structures (plate spines) which emerge from the plate base (figure 4*c*).

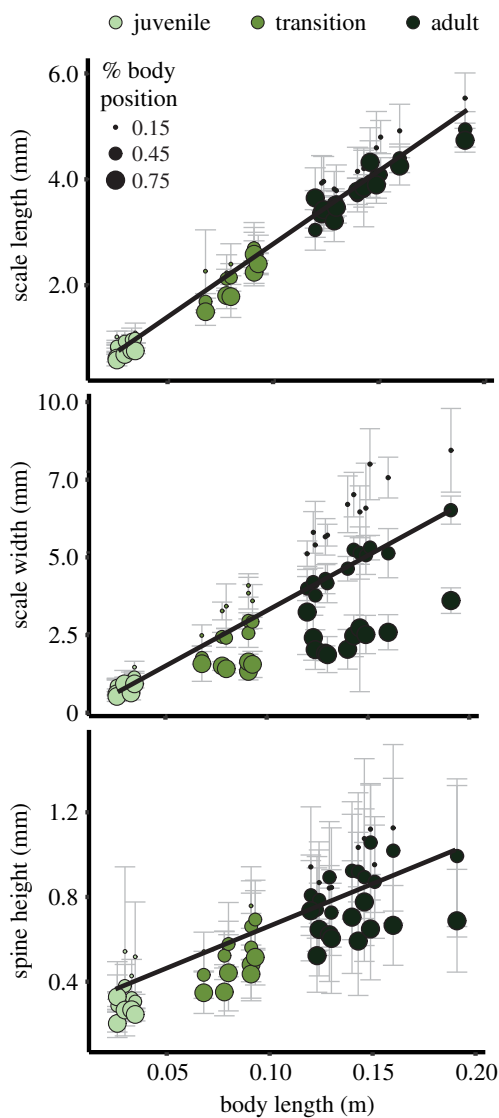
3.2. How does armour plate morphology change over ontogeny?

Within each ridge the fixed number of plates remains constant over ontogeny. Since plates are not lost or gained except in cases of damage, increases in plate size are roughly commensurate with increases in body size (see below for more details; table 1). Plate (i.e. spine) heights are proportionately taller in juveniles (slope = 0.60; CI = 0.52–0.70, figure 5) and juvenile ventral plates have spines similar to other ridge pairs; however, ventral spines are lost in adults, resulting in a smooth ventral surface. Plate length scaled isometrically with respect to SL (slope = 0.98; CI = 0.94–1.03), while plate width scaled with slight positive allometry over ontogeny (slope = 1.08; CI = 1.0–1.16).

ANOVA results indicated that there is a significant relationship between bone mineral density (BMD) and standard length ($p < 0.001$), size class ($p < 0.001$), and the interaction of size class and SL ($p = 0.012$). Armour BMD also scaled with positive allometry relative to body size

Table 1. Scaling of poacher plate morphometrics and material properties. For scaling scenario: P denotes positive allometry, N for negative allometry and I for isometry.

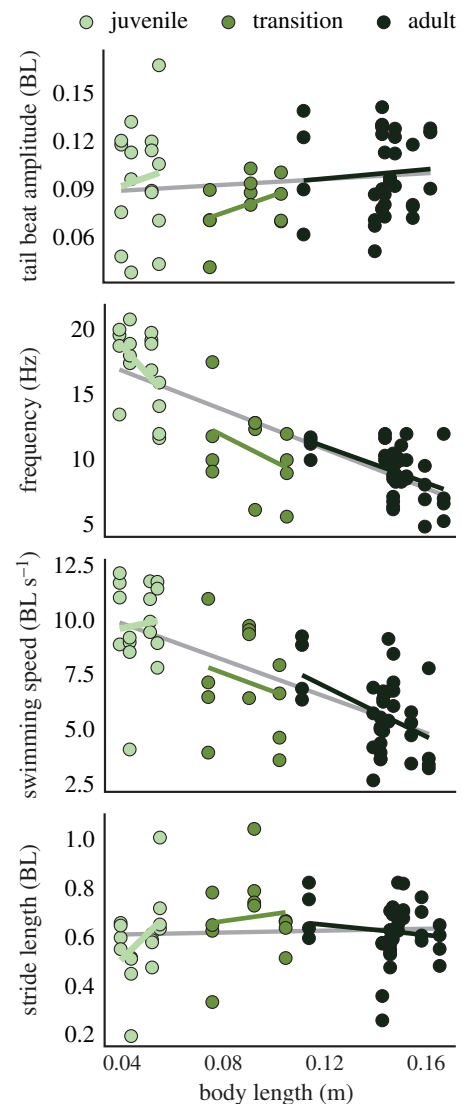
independent variables	r^2	isometric slope	intercept (a)	slope (b)	CI	p -value	scaling scenario
armour plate length (mm)	0.98	1	-1.25	0.98	0.94–1.03	<0.01	I
armour plate width (mm)	0.97	1	-1.34	1.08	1.00–1.16	<0.01	P
armour spine height (mm)	0.89	1	-1.88	0.60	0.52–0.70	<0.01	N
armour plate density (g mm^{-3})	0.32	0	1.20	0.26	0.20–0.33	0.003	P

**Figure 5.** Plate dimensions over ontogeny in *Agonopsis vulsa*. Light green represents the smallest size class, darker green is for subadults, and black represents adult data points and trendlines. Size of the circles represents size of the scale relative to the position along the body, at 15%, 45% and 75% standard length (*sans* skull).

(slope = 0.26, CI = 0.20–0.33; table 1). Considering our largest individual as an outlier (given its high BMD values) and excluding it from scaling analyses did not affect the pattern of BMD changes over ontogeny, which still scales with positive allometry (slope = 0.18, CI = 0.14–0.23).

3.3. Swimming performance and body mechanics

Differences in both stride and amplitude were critical in distinguishing swimming performance patterns among size

**Figure 6.** Spearnose poachers (*Agonopsis vulsa*) swimming kinematics over ontogeny. Grey trendline is for all data combined, light green is for the smallest size class, darker green is for subadults, and black represents adult data points and trendlines. Tail amplitude is the distance (expressed relative to the body length or BL) the tail tip travelled, from left or right, relative to the midpoint of the fish's swimming cycle. Similarly, stride length is also expressed relative to BL to correct for absolute differences in size among study organisms.

classes, which suggest a transition from more anguilliform swimming to more carangiform swimming. According to our permMANOVA results, there were significant differences in kinematics among size classes and length in general ($p = 0.001$) as well as bending mechanics ($p = 0.001$). Juveniles had significantly faster tail beats ($p < 0.05$; figures 6 and 7) and swam faster, in body lengths per second ($p < 0.05$;

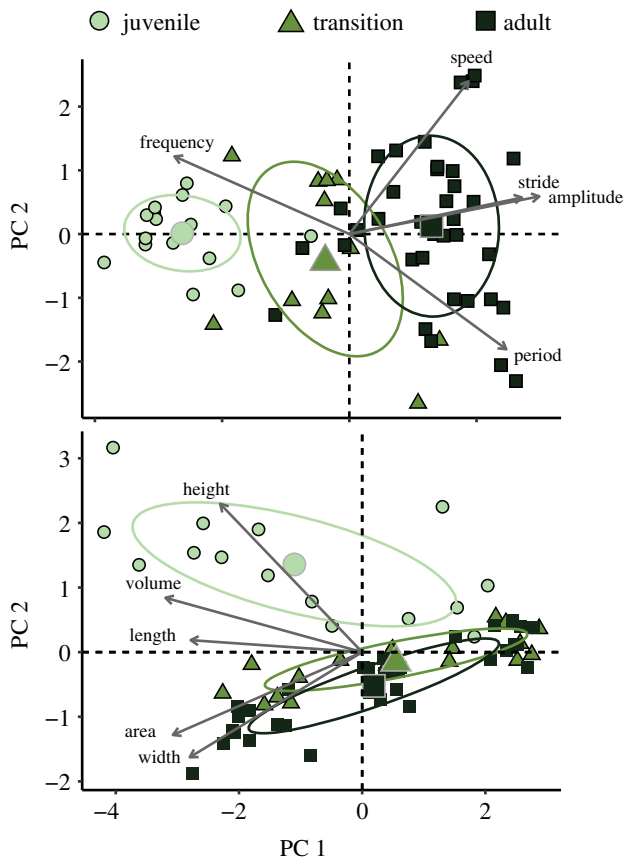


Figure 7. Comparison of juvenile versus adult plate morphology and kinematics (PCAs) in *Agonopsis vulsa*. Morphological trait correlations presented in the top plot, whereas kinematic data are shown in the bottom. Light green represents the smallest size class, darker green is for subadults, and black represents adult data points and trendlines.

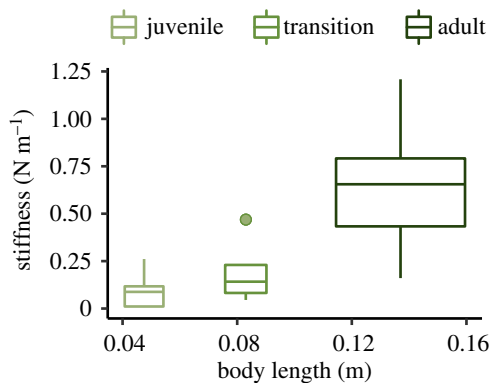


Figure 8. Stiffness increases over ontogeny across an ontogenetic subset of spearnose poachers, *Agonopsis vulsa*. Light green represents the smallest size class, darker green is for subadults, and black represents adult data points and trendlines.

figures 6 and 7), than subadult and adult individuals. In general, while amplitude and stride length increased over ontogeny, tail-beat frequency and swimming speed decreased (figures 6 and 7). Our principal component analysis shows subadults and adults can be distinguished from juveniles (with minimal overlap) according to their stride and tail beat amplitude, as well swimming speed and frequency (figure 7). There is a decline in stiffness from anterior to posterior in all groups, though adults are significantly stiffer overall compared to the other two size classes ($p < 0.05$;

figure 8) and thus endure greater stresses as the tail is bent away from the midline ($p < 0.05$; figure 5).

3.4. Comparative armour morphology

Though the plates of *Anoplagonus inermis*, *Bothragonus swanii* and *Hypsagonus quadricornis* are quite different from *Agonopsis vulsa*, all poacher species share the arrangement of eight longitudinal rows. In spearnose poachers, there is a small cusp at the centre of each bony plates, while in the fourhorn (*Hypsagonus*), this cusp is very long and recurved (figure 1), while both the rockhead (*Bothragonus*) and smooth alligatorfish (*Anoplagonus*) bear smooth plates (figure 1) [46]. Armour rows in *Bothragonus* are arranged in a loosely octagonal manner, but the postcranial skeleton is extremely laterally compressed, so the dorsal ridges are present only as distinct rows when flanking the dorsal fins. The convex plates in *Bothragonus* result in thicker armour-plating than *Agonopsis*. *Anoplagonus* armour plates are flat relative to the other three species, and there is fusion of the ventral and dorsal ridges at the termination of the first dorsal fin (figure 1). The cross-sectional shape of *Hypsagonus* is octagonal transitioning to hexagonal as ventral and dorsal ridge pairs fuse, around plate 20–21 versus plate 26–27 in *Anoplagonus*, 26 in *Agonopsis* and 20–21 in *Bothragonus*. *Hypsagonus* is strongly laterally compressed along its entire body (figure 1). And, there are reduced and somewhat laterally projecting spines on the ventral series. The two ventral rows fuse post anal fin. When captured, our *Hypsagonus* had profuse growths of epibionts on the spines, this included red and brown algae, sponges and bryozoans as reported previously [47].

4. Discussion

4.1. Changing roles of armour through ontogeny

In adult poachers, increased body stiffness correlates with greater armour mineral density and changes to plate morphology, i.e. increased plate width and plate overlap relative to juveniles. In addition to these morphological changes, swimming behaviour also shifts from the whole-body axial undulation of juveniles to the caudally oscillating locomotion of adults (see [48]). This shift in morphology and mechanics coincides with two modes of locomotion in adults. They use their pectoral fins to navigate around substrates like other cottoids [49,50]. Poachers only switch to an undulatory gait when moving somewhere quickly. A more rigid, imbricate armour not only protects these fish from predators but its higher stiffness may also increase the fish's ability to sprint away from harm, as a stiffer body allows for higher accelerations over a longer period of time [51,52].

Just as different lineages of fishes have different uses for their armours, as the northern spearnose poacher grows, the demands on their bony plates change as well. While juveniles have lighter, spinier armour, adults have denser, robust armour that stiffens the whole body. The changing role of armour in a single species highlights the complementary and even competing functions of armour when considered as a multifunctional organ. The less stiff skeleton of juveniles allows a more energetically efficient anguilliform swimming mode. Juveniles make frequent forays from the benthos up into the water column at night, where they feed on pelagic plankton. By contrast, adults spend most of their

time along the benthos foraging for prey like amphipods and cumaceans [53–55].

The increased stiffness of adult poachers could be due to changes in the mineralization of the armour or characteristics of internal soft tissues that we could not document using radiological methods. Alternatively, increased stiffness could come from connective tissue between armour plates or an integrated whole-body hydrostat [56]. We cannot definitively discriminate among these causative factors or rule out the contribution of soft tissues or endoskeleton (e.g. vertebral column) influencing whole-body stiffness. In fact, we expect that these factors do play some role in whole body stiffness. However, it is unlikely that the role is significant given the thin material between plates and the modest vertebral column. For point of comparison, the mineral investment in the vertebral column is less than 20% the mineral investment in the armour itself [26].

4.2. What goes up, comes back down... slowly. A natural history explanation for spinous armour?

Juvenile poachers make nocturnal ventures from the benthos into the water column to feed, then slowly sink while curled into an S-shape ([27]; MA Kolmann, CM Donatelli, AP Summers 2014, personal observations). This S-shaped hydrofoil conformation while sinking, after slow, anguilliform locomotion on their ascent may allow juveniles to frequent the 'twilight' zone between Reynolds regimes (inertial-dominated versus viscous dominant) (figure 9). We propose that armour plates in the northern spearnose poacher may shift from parachute to protection. The proportionately longer spines in juvenile poachers serve the same function as enlarged spines in invertebrate zooplankton: slowing the rate of descent while sinking [57–59]. As juveniles recruit to the benthos, the early exaggeration of the spine (i.e. the negative allometry of plate height) relative the rest of the plate over ontogeny, reflects a change from a hydrodynamic to a defensive function. This hypothesis can and should be tested with physical models and/or computational fluid dynamics.

Juvenile *Agonopsis*, like some slowly sinking plankton, are at an awkward stage between flow forces dominated by viscosity and inertia. If juvenile poachers do not swim, their bodies sink with their negative buoyancy resisted by friction (Stokes) drag. This puts a premium on spiky excrescences such as the spines on their armour, because they increase the profile of the fish. Once juvenile poachers start thrashing their tail and swimming, they shift to an inertial regime where both drag and lift are more complex. Similar paradigms are present in aquatic organisms like *Daphnia*, which can show shifts in armour morphology based on turbulence and defensive impetus [60,61]. Juvenile poachers navigate a habitat shift and a paradigm shift in the properties of their surroundings.

4.3. All or nothing? Different ways to avoid predation in poachers

At all life-history stages, armour in poachers serves some role as camouflage, as spines break up the outline of the fish against its background. Juveniles make nocturnal forays into the water column, while during the day these fishes remain motionless and rely on camouflage to hide from predators (MA Kolmann, CM Donatelli, AP Summers 2014, personal observation; [53]). There is a further role for

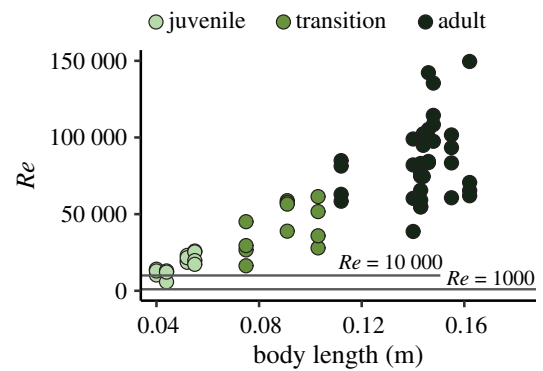


Figure 9. Reynolds number comparison among a size series of *Agonopsis vulsa*. Note that juveniles cross the arbitrary $Re = 10\,000$ point between regimes starting around 40 mm standard length. Light green represents the smallest size class, darker green is for subadults, and black represents adult data points and trendlines.

armour in camouflage; in *Hypsagonus*, like seahorses, spines serve as substrate for epibionts which further muddle the profile of the animal against its habitat [62]. Whereas in other poachers, such spines might serve a role in adults for sexual display [26].

Crypsis is not 100% effective, poachers are consumed by other fishes, particularly larger demersal and pelagic flatfishes (Pleuronectiformes). Poachers are swallowed whole and observed as articulated corpses in gut contents [63,64]. It is notable that these predatory fishes are large relative to their poacher prey. Pacific halibut (*Hippoglossus stenolepis*), Kamchatka flounder (*Atheresthes evermanni*) and Greenland halibut (*Reinhardtius hippoglossoides*) are easily 100–250 cm standard length and their prey (e.g. *Sarritor*, *Aspidophoroides*) are a tenth that size (20–27 cm; see [54] for data on Atlantic poachers, otherwise see [63,64]).

Poacher armour does not serve as protection against larger predators with large gapes. We have found no records of sablefishes or lingcod (*Ophiodon*) for example, eating adult poachers, presumably because these predators have smaller gapes. We suppose poachers are consumed by large Dungeness and red rock crabs (*Cancer* spp.) and the marine analogues to army ants, *Pandalus* shrimp. As with armoured sea turtles, which are vulnerable to myriad predators at smaller sizes, but eventually outgrow predation except by the largest, most tenacious predators like tiger sharks [65], poacher armour is no invulnerable aegis, but perhaps a deterrent to the most mundane of predators. However, something that predators like lingcod and crabs have in common, relative to predators like halibut, is that they pierce or crush prey [66], rather than swallow it outright. The armour of adult poachers would appear particularly robust to such puncture-related attacks [26].

4.4. The macroevolution of armour in fishes

Research into armoured fishes has investigated hypotheses in isolation; for example, [67] covers the protective potential of arapaima scales, whereas Bruet *et al.* [5] propose the potent providence of *Polypterus* plates. The former study is fascinating because it proposes a fictional/dubious situation where the selective pressure on armour is predation by piranhas, except that the 'prey' in this case, the largest fish in the Amazon, *Arapaima gigas*, are 4–10 times larger than even their largest 'predators' (most large piranhas are approx.

20 cm long; most arapaima are approx. 240 cm long). These authors propose that the microstructure of scales in these fishes are models for biomimetic armour, but they miss the wider application of these multifunctional structures. Understanding the complex selective demands on phenotype requires acknowledgement that all biological structures are inherently multifunctional [68].

This tendency to consider armour function in a vacuum lends itself to open interpretation as to whether similarities among armoured lineages represent parallelism, convergence or equifinality (but see [69,70]). Albeit, the deep phylogenetic divisions among these lineages strongly indicate patterns of either convergence or equifinality, and presumably parallelism within each lineage. Are these armours serving the same function or just similar ones, especially in poachers? Like boxfishes (Ostraciidae), poacher armour is bony, roughly six-sided, and has raised trusses on the surface [45]. Unlike boxfishes, in which plates are sutured together at their margins, poacher scales overlap. Overlapping plates like these are found in fishes like alligator gar, loriciid catfishes, pegasid seamoths and the regrettably-named 'armoured pipefish,' which while armoured are not pipefish nor related to them (i.e. *Indostomus* spp.; [7,8,71]). Unlike catfishes or gar, poachers, syngnathids, and indostomids have armour made solely from bone, rather than bone capped in a hypermineralized material like hyaloine, or ganoine [7]. Poachers have armours most like seahorses and pipefishes, with overlapping armour plates [19]. These two lineages, agonids and syngnathids, have potential for exploring armour form and function within each diverse armoured clade, as well as among these clades. However, while seahorses and their allies number in the hundreds of species worldwide and have correspondingly broad ecological diversity, perhaps poachers are a more tractable system, as there are less than 50 agonid species found in cold waters throughout the northern hemisphere.

5. Conclusion

Poacher armour serves several functions, including actively aiding in locomotion, perhaps passively increasing drag, providing defence against predators, and is even used as a substrate for epibionts that increase crypsis. From the earliest thoughts on armoured fishes [4,12] to more recent ruminations regarding model systems like sticklebacks [72], defence from predators has preoccupied notions regarding the function of armour [6,71]. However, the role of armour is not restricted to defence according to well-documented,

but infrequently invoked, alternative explanations for armour form and function [13–17]. Here, we demonstrate that not only does armour serve multiple functions, but that these functions change in the same species over ontogeny. In parallel with these changes in armour function are changes in armour form. Moreover, these changes in armour phenotype do not necessarily indicate trade-offs as simplistic as 'more armour equal slower fishes,' but rather that a fish can have dense, protective armour and still swim effectively too (at least at sprint speeds). Complex phenotypes like armour are often the product of competing functional demands [68] and in the poacher's case armour must defend, add stiffness, assist in camouflage, and likely act as a signal of mate quality [26].

Ethics. We collected fish from San Juan Islands and housed these fishes in the flow-through system at Friday Harbor Laboratories according to the University of Washington Institutional Animal Care and Use Committee (IACUC) protocol (4238-03). Following swimming trials, fishes were anaesthetized and then euthanized with an overdose of buffered tricaine methanesulfonate (MS-222).

Data accessibility. Armour morphometrics, bending rig data, BMD, and analyses as well as the data and code are available from the Dryad Digital Repository: <https://dx.doi.org/10.5061/dryad.v41ns1rsf> [73].

Authors' contributions. All authors contributed to conceiving and designing the study. T.P., C.D. and J.P. collected the data. M.K. and C.D. analysed the data. M.K. and C.D. drafted the initial version of the manuscript. All authors contributed to later versions of the manuscript.

Competing interests. We declare we have no competing interests.

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