© 2024. Published by The Company of Biologists Ltd | Journal of Experimental Biology (2024) 227, jeb247544. doi:10.1242/jeb.247544

RESEARCH ARTICLE

Biphasic burrowing in Atlantic hagfish (*Myxine limosa*)

Douglas S. Fudge*, Joshua Lee, Kennedy Guillen, Cassandra M. Donatelli, Andrew Lowe, Luke Arnold, Keolani Kahale-Lua, Christian Quinteros, Peter Ly, Larissa Atkins, Noah Bressman and Charlene L. McCord

ABSTRACT

Myxine limosa is a burrowing species of hagfish that occurs in the western North Atlantic in areas with muddy substrate and at depths generally greater than 100 meters. Burrowing of *M. limosa* has been observed from submersibles, but little is known about the behavior of these animals within the substrate or the biomechanical mechanisms involved. Here, we investigated burrowing in *M. limosa* by observing individuals as they burrowed through transparent gelatin. A photoelastic setup using crossed polarizers allowed us to visualize stress development in the gelatin as the hagfish moved through it. We found that *M. limosa* created U-shaped burrows in gelatin using a stereotyped, two-phase burrowing behavior. In the first ('thrash') phase, hagfish drove their head and their anterior body into the substrate using vigorous sinusoidal swimming movements, with their head moving side-to-side. In the second ('wriggle') phase, swimming movements ceased, with propulsion coming exclusively from the anterior, submerged portion of body. The wriggle phase involved side-to-side head movements and movements of the submerged part of the body that resembled the internal concertina strategy used by caecilians and uropeltid snakes. The entire burrowing process took on average 7.6 min to complete and ended with the hagfish's head protruding from the substrate and the rest of its body generally concealed. Understanding the burrowing activities of hagfishes could lead to improved understanding of sediment turnover in marine benthic habitats, new insights into the reproductive behavior of hagfishes, or even inspiration for the design of burrowing robots.

KEY WORDS: Biomechanics, Bioturbation, Burrowing, Hagfish, Internal concertina, Photoelasticity

INTRODUCTION

Hagfishes (Myxini) are a group of eel-like craniates that are found in deep (>100 m) benthic habitats around the world. They are well known as scavengers, with baited camera studies showing they are often some of the earliest animals to arrive when carrion reaches the seafloor (Zintzen et al., 2011; Smith, 1985). In addition to scavenging, burrowing seems to be an important aspect of the hagfish lifestyle. Multiple observations of hagfishes burrowing in the wild suggest that most if not all hagfishes are capable of burrowing into soft sediments. The western Atlantic hagfish (*Myxine limosa*) and the inshore hagfish (*Eptatretus burgeri*) have both been observed burrowing in the wild (Fernholm, 1974; Martini, 1998). A study from New Zealand observed a predatory hagfish (likely from the genus *Neomyxine*) disappearing into a burrow of the teleost *Cepola haastii*; while this is not evidence for hagfish making burrows, it does indicate that this species can readily enter and move through a pre-existing burrow. Other evidence of hagfish burrowing comes from stomach content data, which reveals a significant part of the hagfish diet consists of infaunal invertebrates such as polychaete worms (Martini, 1998), as well as from excavation of hagfish burrows using a suction device (Foss, 1968). In captivity, Pacific hagfish (*Eptatretus stoutii*) consistently squeeze into PVC pipes provided for enrichment, and *Myxine limosa* will burrow into sand when available. A lab study showed that hagfishes are adept at squeezing through tight spaces as small as half their body width, which is thought to be related to their ability to burrow into carcasses for feeding, or into substrate for protection from predators and/or for reproduction (Freedman and Fudge, 2017).

The burrowing habits of hagfishes and their large population densities in some areas suggest that they may be significant drivers of substrate turnover in muddy habitats (Martini, 1998). Despite the clear importance of burrowing to the hagfish lifestyle and possibly to global bioturbation processes, little is known about the mechanics of how hagfish burrow through sediment. Observations of hagfishes in the wild provide a rough sketch of the process. Burrowing begins with the animal swimming vigorously downward using high amplitude undulatory movements, while its head is in contact with the substrate. Swimming movements continue until a portion of the anterior body is submerged, after which the animal stops thrashing, and the exposed part of its body noticeably relaxes. Progress continues, however, with the animal gradually entering the substrate until its entire body is submerged. During this final stage of burrowing, forward motion is clearly generated by movements within the substrate, as the exposed part of the body remains relaxed (Martini and Heiser, 1989; Martini, 1998). Finally, the hagfish terminates burrowing movements when the head re-emerges from the sediment at a distance, suggesting completion of a U-shaped burrow. Observations of *M. glutinosa* burrows by divers using a suction device revealed that hagfish burrows might be more complex than a simple U-shape and might have multiple entrances and/or branches (Foss, 1968), although some of the secondary structures might have been created by opportunistic burrowing invertebrates.

While the initial phase of hagfish burrowing has been observed in wild hagfishes, we wished to learn more about how a hagfish continues to move into the sediment after its initial swimming movements cease. We were especially interested in two specific processes – creation of the burrow and locomotion through it. Burrow extension in elastic substrates has been best studied in polychaete worms, which create tongue-shaped cracks in which the animal is compressed dorsoventrally (Dorgan et al., 2008). In these animals, muscular and hydraulic mechanisms at the anterior end of the worm are used to propagate the crack and extend the burrow. We wanted to test whether hagfishes use similar mechanisms to move through elastic substrates. Regarding mechanisms of locomotion through the burrow, other burrowing animals provide several

Schmid College of Science and Technology, Chapman University, 1 University Drive, Orange, CA 92866, USA.

*Author for correspondence (fudge@chapman.edu)

Received 16 February 2024; Accepted 3 May 2024

Journal of Experimental Biology (2024) 227, jeb247544. doi:10.1242/jeb.247544

possibilities. Many burrowing invertebrates use a peristaltic mechanism that involves anchoring via local expansion coupled with forceful elongation of the body anterior to an anchor point (Dorgan, 2018). Peristalsis often involves a hydrostatic skeleton that can transduce the forceful shortening of longitudinal and circumferential muscles into body expansion and elongation (Quillin, 1998). Hydrostatic mechanisms are relatively rare in vertebrates, with some burrowing caecilians being an exception (O'Reilly et al., 1997). Lampreys are the closest living relatives of the hagfishes, and lamprey larvae are known to move within substrates using alternating sharp bends of their body (Paggett et al., 1998). Another possible mechanism, which is far more common in elongate vertebrates such as snakes and caecilians, is a concertina strategy in which the body undergoes alternating phases of bracing against burrow walls with wavelike bends and elongating by straightening out those bends. In the most highly specialized burrowers, the concertina movements all take place within a loose and baggy skin, a condition known as 'internal concertina'. Hagfishes have been shown to possess a flaccid body design that would make an internal concertina mechanism possible (Uyeno and Clark, 2020; Boggett et al., 2017).

Until now, how hagfish create burrows, how they move within them, and the final structure of the burrows have been enigmatic because the opacity of sediment obscures a clear view. Researchers studying other infaunal animals have overcome this problem by using transparent substrates such as the mineral cryolite, which has the same optical density as seawater and provides a window into how animals move through sandy substrates (Josephson and Flessa, 1972; Dorgan, 2018). Transparent hydrogels made from solubilized collagen (i.e. gelatin) have properties that more closely approximate those of mud, which has substantial elasticity owing to the adhesive forces among its mineral and organic components (Johnson et al., 2002). Gelatin has been most extensively and successfully employed to observe the burrowing behavior of invertebrates such as polychaete worms (Dorgan et al., 2005, 2007; Che and Dorgan, 2010; Dorgan et al., 2013). Here, we used custom transparent chambers containing gelatin to observe hagfishes creating and moving through burrows for the first time.

MATERIALS AND METHODS

Animals and care

Myxine limosa Girard 1859 were collected east of the Isles of Shoals by staff at the Shoals Marine Laboratory using traps set at a depth of approximately 100 m and were held under IACUC protocol 210503. Forty live hagfish were shipped overnight to Chapman University and housed in a 1000 liter chilled (11°C) saltwater (34‰) tank where they were fed monthly on a diet of frozen squid and live nereid worms.

Burrow chambers

Three separate acrylic burrowing chambers were constructed and used for these experiments. The first chamber we used had internal dimensions of 35.5×6.5×74.6 cm and a wall thickness of 6.1 mm. The second chamber had internal dimensions of 35.5×6.5×51 cm with a wall thickness of 61 mm. The largest chamber had internal dimensions of 50.5×7.5×61.5 cm with a wall thickness of 1.12 cm. The protocol for gelatin preparation was modified from Dorgan et al. (2005), with a final concentration of 156 g of gelatin l^{-1} of seawater. Gelatin was solubilized by heating in artificial seawater (ASW; Instant Ocean, 34‰) and added to the chamber in a liquid state until it was ∼40% full. We strived to keep the material properties of the gelatin consistent between trials, but there were several factors that influenced the stiffness of the gel. Time in the cold room was the most important source of variability, with longer setting times leading to stiffer gels up to a point. After a day or two, gelatin stiffness declined over time, presumably due to bacterial digestion of the collagen. In some trials, the hagfish had difficulty creating a burrow and it wasn't until the following day, when the gel was softer and weaker, that we could get a successful trial. To encourage burrowing, a hole in the gelatin was created near each lateral wall using two 15 ml conical tubes that were placed partway into the molten gelatin, and removed after it had set overnight in a cold room at 4°C. The mean hole depth for 25 trials was 5.4±0.3 cm (s.e.m.). Once the gelatin was set, chilled ASW was added on top to fill the chamber. In some trials, settling of the gelatin after setting led to the formation of cracks, which was something that we were not able to completely avoid.

Burrowing trials

In total, we collected and analyzed video of 25 hagfish burrowing into gelatin. Some of the trials were likely done with the same hagfish, as animals were randomly selected out of a tank of approximately 40 hagfish and returned to the same tank after the trial was complete. Sixteen of these trials were illuminated from the front and side with white light and nine of them were filmed in a photoelastic setup in which the gelatin was illuminated from behind and viewed through two crossed circular polarizers on either side of the chamber. Lighting was provided using two VidPro LED-312 Varicolor light sources and burrowing behavior was filmed using a digital video camera (GoPro Hero8 Black) mounted on a tripod and oriented perpendicular to the plane of the chamber. Video was collected at a frame rate of 60 frames s^{-1}. We also conducted photoelasticity trials, which allowed us to visualize where and how hard the hagfish pushed on the gel as they moved through it (Full et al., 1995). For the photoelasticity trials, we covered the back surface of the burrowing chamber with a circular polarizer film (American Polarizers, APNCP42-008T-RH) and another circular polarizer was mounted on the GoPro camera (Cinema CPL Filter, Sandmarc). Crossing the polarizers resulted in little light passing through both filters, even with an intense, uniform 43×60 cm LED array light source behind the chamber (HSK model A3). Deformation of the gelatin by a burrowing hagfish created a bright spot, caused by strain-induced changes in the birefringence of the gelatin due to partial alignment of the collagen molecules within it, allowing some light to pass through the second filter. Photoelastic trials therefore provided detailed information about when, where, and how hard a burrowing hagfish pushed on the gelatin, with brightness varying positively with gel strain. After a hagfish was added to the burrowing chamber, a lid was fastened to the top to prevent the hagfish escaping. If a hagfish showed no signs of voluntary burrowing behaviors after 20 min, it was removed and replaced. Hagfish were filmed until the animal completed its burrow and its head broke through the surface of the gelatin, or after a total of 30 min after burrowing behaviors started, whichever came first.

Burrow morphometrics

From videos of hagfish burrowing, we extracted information about burrow morphometrics and the time spent in different burrowing modes. We quantified the following parameters using frames from the video: total burrow distance, transition depth, transition distance, maximum depth, tail exposure, horizontal distance and hole depth (from conical tube) (Fig. 1). Each of these measurements was made by analyzing individual video frames using ImageJ (v. 2.14.0/1.54f). Total burrow distance was measured as the traced

Journal of Experimental Biology (2024) 227, jeb247544. doi:10.1242/jeb.247544

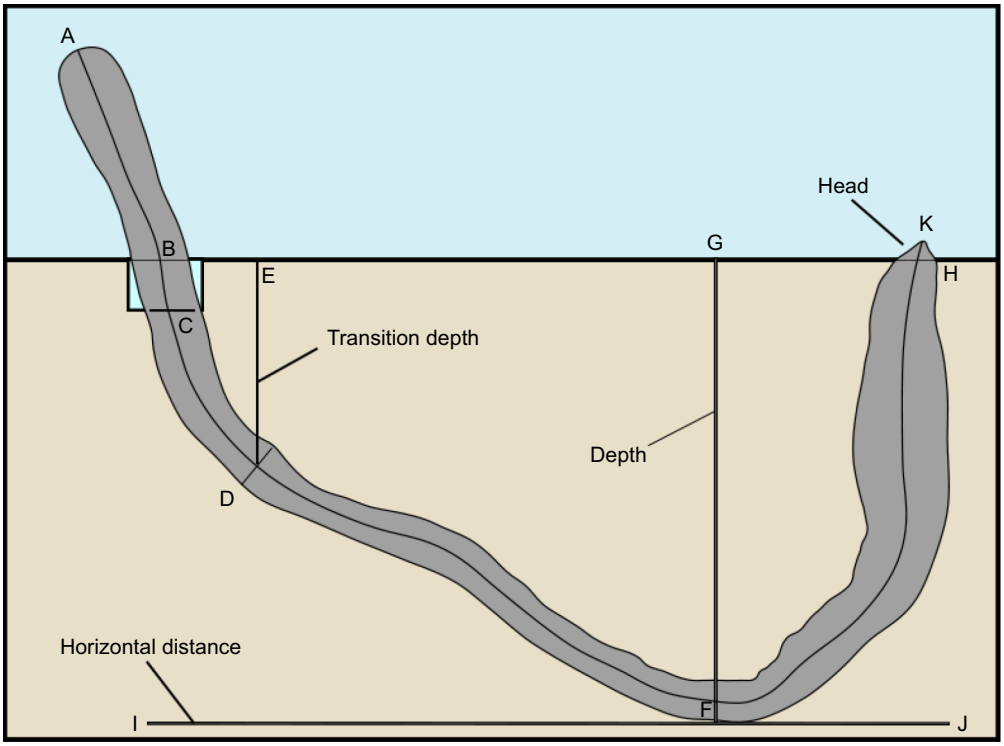

Fig. 1. Outline of a hagfish in a completed burrow showing how various burrow morphometrics were measured. Smoothed line down the hagfish's midline was used to measure the hagfish length (A–K), with burrow distance being only the parts of the hagfish length within the gelatin (B–H) minus the hole depth (B–C). The transition point used for the calculation of transition distance (B–D) and transition depth (E–D) was the location of the tip of the hagfish's head at the end of thrash phase burrowing (D), i.e. when vigorous swimming motions of the anterior end ceased. Tail exposure was measured from the tip of the tail to the surface of the gelatin (A–B), with positive values indicating an exposed tail and negative values indicating the distance of the tip of the tail below the gelatin–water interface.

distance from the initial point in which the hagfish started burrowing to the point where its head broke through the gelatin to complete the burrow. These values were then adjusted by subtracting the hole depth. Transition depth was measured as the shortest distance between the lowest point of the body (usually the head) and the surface of the gelatin at the time the hagfish transitioned from the vigorous swimming (i.e. 'thrash' phase) to the submerged (i.e. 'wriggle' phase), which corresponded with the moment the exposed part of the body ceased swimming movements and became relaxed. Transition distance was defined as the length of the hagfish within the gelatin at the time of this transition minus the hole depth. Maximum depth was measured from images of complete burrows as the shortest distance from the lowest point of the hagfish burrow to the surface of the gelatin. Horizontal distance was measured from complete burrows as the distance between two lines perpendicular to the gelatin surface denoting the leftmost and rightmost positions of the hagfish. Tail exposure was measured as the length of the tail above the substrate (not in the burrow) when the burrow was complete, with positive values indicating an exposed tail and negative values indicating the distance of the tip of the tail below the gelatin–water interface.

Burrow duration and velocities

We quantified three time-specific variables including: thrash phase duration, wriggle phase duration and total burrow duration. Thrash duration was the time from the moment the hagfish began burrowing with vigorous swimming motions to the transition when its tail stopped thrashing. Wriggle duration was the time from the transition point to the end of the burrowing event (when the hagfish's head broke through the surface of the gelatin). Total burrow duration was calculated as the sum of the thrash and wriggle durations. The average burrowing velocity over the thrash phase for a given hagfish was calculated by dividing the transition distance by the duration of the thrash phase. The average velocity over the wriggle phase was calculated by dividing the wriggle phase distance by the wriggle time. Wriggle phase length was calculated by subtracting the transition distance from the burrow distance.

Midline analysis

Midline traces were generated using a script inspired by Donatelli et al. (2017). We digitized each frame manually by clicking an arbitrary but dense number of points along the length of the fish from a thresholded image, being sure to include the anterior most point of the head and posterior most tip of the tail. After manually clicking points for each frame, we used the interparc function in MATLAB (https://www.mathworks.com/matlabcentral/fileexchange/34874-interparc) to generate the midline of the thresholded image of the hagfish defined by 21 evenly spaced points along the body with 0 at the head and 21 at the tail. Code is available at https://github.com/CDonatelli/HagfishBurrowing.

Photoelasticity trial analysis

Four photoelasticity trials were used to measure how much of the body engaged in active locomotion during the wriggle phase. For each video, nine timepoints were selected, with each representing a different amount of progress into the gelatin. By scrubbing back and forth from each timepoint in the video, the farthest anterior position showing evidence of active pushing was marked and a screenshot taken. Screenshots were analyzed using FIJI to measure the length of the hagfish, the length of the body within the gelatin and the length of the body engaging in active pushing movements.

RESULTS

Most *M. limosa* that were placed in the burrowing chamber explored the bottom of the chamber and approximately one-third of them began stereotyped burrowing behavior within minutes. It is notable that all hagfish that burrowed started their burrows in one of the two holes that we provided for them; no hagfish attempted to burrow into the flat surface of the gelatin between the two holes.

Journal of Experimental Biology (2024) 227, jeb247544. doi:10.1242/jeb.247544

General description of burrowing behavior in *M. limosa*

Detailed observations of 25 hagfish burrowing events in gelatin revealed a predictable sequence of behaviors associated with burrow formation (Movie 1). Burrowing typically was preceded by searching behavior, with the hagfish moving along the gelatin surface with its head down. Discovery of one of the holes in the gelatin often led to exploration of the hole and insertion of the hagfish's head. Commitment to burrowing typically appeared as the commencement of vigorous undulatory swimming movements with the head inserted in a hole. With vigorous swimming movements driving the animal downward, the head exhibited regular side to side movements. These mostly lateral movements of the head appeared to break up the gel. This 'thrash' phase of the burrowing sequence, with vigorous swimming coupled with side-to-side head movements, continued until approximately one-fifth [22.8±1.3% (mean±s.e.m.)] of the hagfish's body was submerged in the substrate. A second 'wriggle' phase of burrowing took over at this point, with the exposed portion of the body ceasing swimming movements, and often relaxing to the point of flopping over and resting on the surface of the gelatin. Side to side movements of the head continued during the wriggle phase, with forward progress appearing to be powered by the submerged part of the body. Movement through the gel continued in this way until the burrow was complete and the hagfish's head protruded out of the gelatin into the seawater above (Fig. 2). We found that once a hagfish entered the wriggle phase in a successful burrow, it never restarted the thrash phase. Photoelastic trials failed to show any obvious single crack in the gelatin in front of the hagfish's head, but instead suggested that the gelatin got broken up into pieces by movements of the head (Fig. 2; Movie 2). One consequence of burrowing was that the anterior portion of the hagfish that was submerged in the gelatin appeared wrung out and wrinkled, while the remainder of the animal got progressively swollen (Fig. 3).

Burrow morphometrics

The generally U-shaped burrows produced by the hagfish in our trials were usually the result of two overall changes in burrowing direction. Burrowing direction was vertical at the start of a burrow, with progress becoming more horizontal as the hagfish turned away from the nearest wall. Progress often continued in the horizontal direction until a second change in direction was performed, this time with the hagfish turning upward toward the gelatin surface. In some cases, contact with the wall coincided with this final turn, but this was less frequent in the widest burrowing chamber, with the turn often occurring well before the far wall was approached. In other cases, hagfish encountering the wall performed a 180 deg turn and continued in a horizontal direction before making their final upward turn (Fig. 2). We should note that in some cases the burrowing trajectory was more tortuous and traced a path more complex than a U-shape (Fig. 4).

Morphometrics of completed burrows were quantified for 25 burrows (Table 1, Fig. 4). The mean (±s.e.m.) burrow distance (45.2±2.4 cm) plus the mean hole depth (5.4±0.3 cm) was shorter than the mean hagfish length (61.6±1.7 cm), meaning that several hagfish had substantial portions of their tails exposed after the burrow was complete (mean tail exposure 13.0±3.6 cm; head

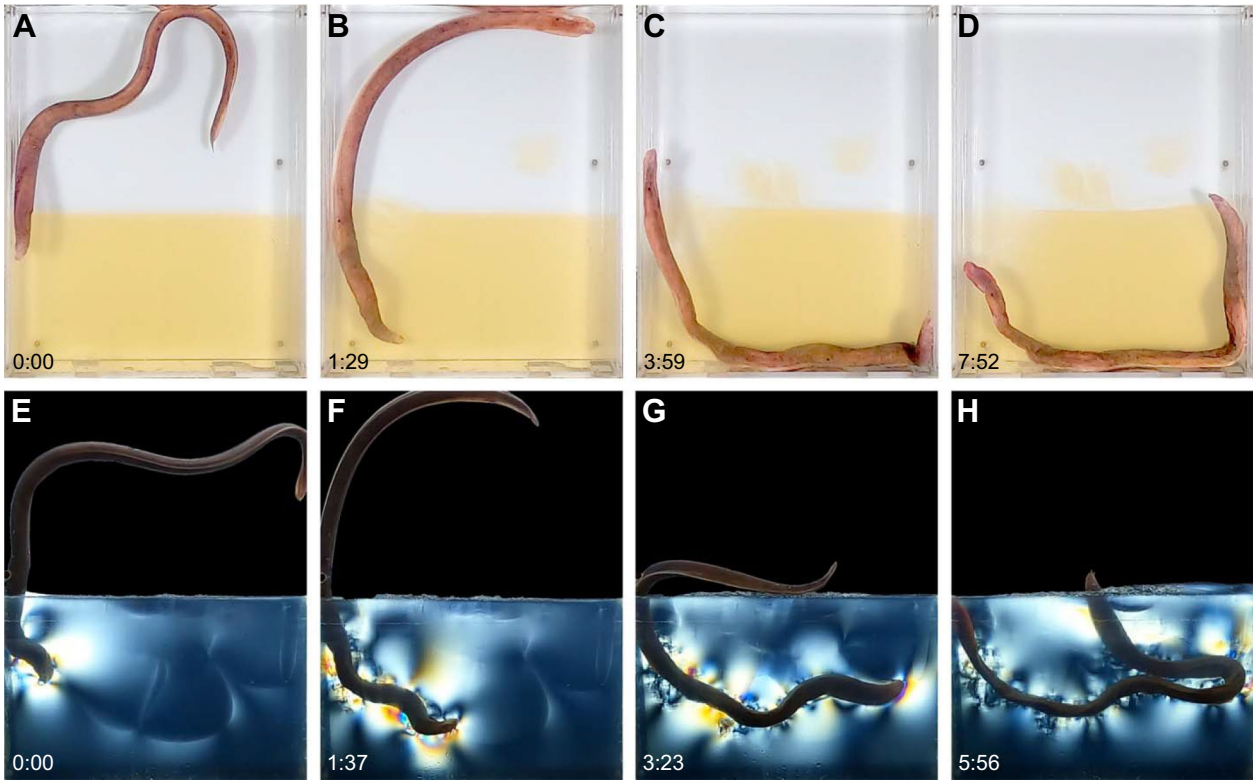

Fig. 2. Burrowing sequences for *Myxine limosa* in gelatin. (A–D) Still images from video filmed with conventional lighting. (E–H) Still images from a photoelastic setup that makes it possible to visualize stress development in the gelatin. Burrowing started with the hagfish driving its head into the gelatin using vigorous swimming movements (A,E). Once one-fifth of the hagfish's body was submerged, swimming movements ceased, the exposed part of the body relaxed, and further progress was driven exclusively by movements within the gelatin (B,C,F,G). Burrowing movements stopped when the hagfish's head re-emerged from the substrate (D,H). Both trials were filmed in a 50.5 cm wide chamber. In panels E–H, the seawater-filled area above the gelatin has been made pure black to minimize distraction. Timestamps are in min:s format.

Journal of Experimental Biology (2024) 227, jeb247544. doi:10.1242/jeb.247544

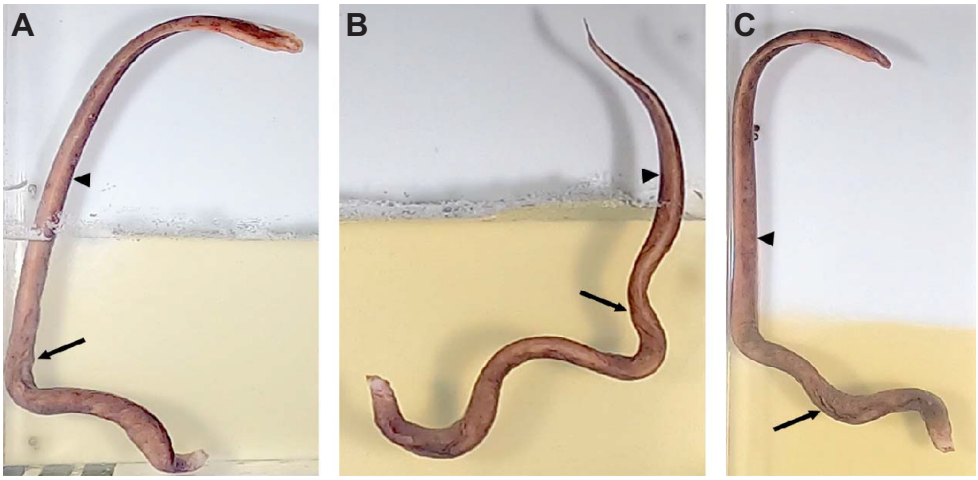

Fig. 3. Burrowing in *M. limosa* results in redistribution of subcutaneous blood. (A–C) Burrowing leads to a wrinkled appearance in anterior regions within the gelatin (arrows), with posterior regions looking inflated and slightly turgid (arrowheads). Inflation also often causes an initially flopped-over tail (A,C) to stand up straight (B).

exposure was typically minimal). This was likely the result of the physical constraints of the burrow chambers, as tail exposure was less common in the widest burrow chamber. From the five trials in the widest burrowing chamber, the mean tail exposure was −1.2 cm, with negative values indicating distances below the gelatin surface. For the two narrower burrowing chambers, the mean tail exposure was +16.6 cm. These data suggest that hagfishes probably avoid tail exposure in the wild. The average depth where hagfish transitioned from thrash to wriggle was 10.3±0.5 cm, which was approximately two-thirds of the average maximum depth of burrows (15.2±0.8 cm), suggesting that most hagfish continued to move deeper during the wriggle phase. The average horizontal distance of burrows was 28.2±1.5 cm, or approximately half the length of the hagfish on average.

Midline analysis

Burrowing kinematics were visualized by tracing midlines of a burrowing hagfish at three different times (Fig. 5). These analyses provided a simple way to capture which parts of the hagfish's body were moving and by how much at different times. At the start of a burrowing bout (i.e. thrash phase), the hagfish generated large amplitude sinusoidal swimming movements with most of its body, with only its head in the gelatin (Fig. 5A). At this stage, the head was also quite active and moving side to side (Fig. 5B). About halfway through the burrowing process (i.e. well into the wriggle phase), the tail was no longer moving sinusoidally, but in some cases stood up straighter as anterior blood appeared to be squeezed into an ever-smaller posterior subcutaneous sinus that was outside the gel (Fig. 5C). Near the end of a burrowing bout (i.e. near the end of wriggle phase), most if not all the body was immersed in the gelatin, and the most obvious movements were at the anterior end (Fig. 5D). In the trial shown in Fig. 5, measured head movements were underestimated by the midline traces because the movements were mostly oriented perpendicular to the plane of the burrowing chamber.

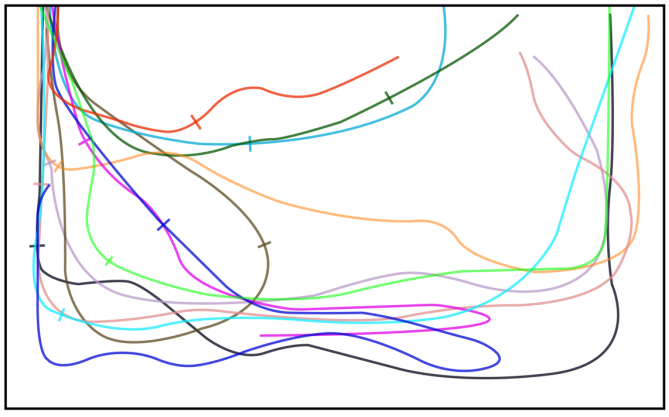

Fig. 4. Burrow shapes for *M. limosa* in gelatin. Each line denotes the final posture of a hagfish within the gel after it had completed its burrow in a 35.5 cm wide gelatin chamber and was generated by tracing the midline of the completed burrow. All burrows started at one of the pre-made holes in the gelatin on either side of the burrow chamber and most of them ended with the hagfish's head emerging on the other side of the chamber, forming an approximately U-shaped burrow. To visualize similarities and differences, traces starting on the right have been flipped so that all traces start at the left side of the tank. Short lines perpendicular to each trace denote the location where the hagfish transitioned from the thrash phase to the wriggle phase (*N*=14).

Photoelasticity

Midline analysis was able to capture large body movements, such as the large amplitude undulations of the body during the thrash phase or the persistent side-to-side movements of the head throughout a burrowing bout (Fig. 5). However, midline analysis was not sensitive enough to detect moments when the hagfish pushed on the walls of the burrow by creating subtle bends in its body. Fortunately, these moments were visible in photoelastic trials, with areas of high gelatin stress showing up as bright spots as the hagfish pushed (Movie 2). In four trials, we were able to quantify the proportion of the hagfish's body that was actively engaged in burrowing movements over a substantial portion of the burrowing bout. These data show that as more of the body penetrated the

Table 1. Hagfish lengths and morphometrics of burrows made by *M. limosa* in gelatin

	Mean±s.e.m.
Hagfish length (cm)	61.6±1.7
Burrow distance (cm)	45.2±2.4
Transition depth (cm)	10.3±0.5
Transition distance (cm)	14.0±0.9
Burrow depth (cm)	15.2±0.8
Tail exposure (cm)	13.0±3.6
Horizontal distance (cm)	28.2±1.5

Measurements were made by analyzing video screenshots using ImageJ. See Fig. 1 for a visual explanation of terms. *N*=25.

Journal of Experimental Biology (2024) 227, jeb247544. doi:10.1242/jeb.247544

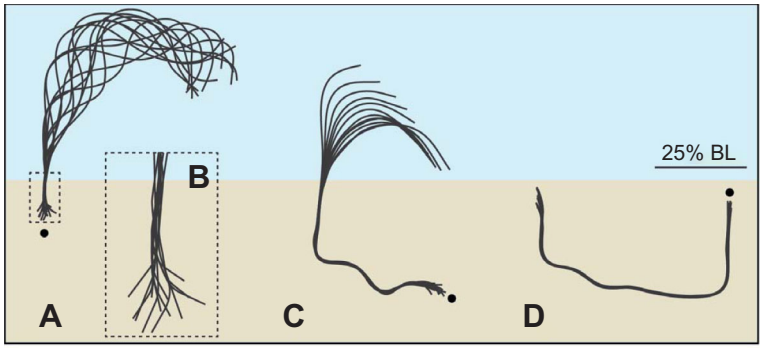

Fig. 5. Hagfish body movements during burrowing. Black lines show 12 midline traces from three parts of a burrowing trial, with the tan box representing the gelatin gel. (A) Typical thrash phase behavior, with the hagfish driving its head into the gelatin using vigorous sinusoidal swimming motions of its body and its head moving side to side. (B) A 4× zoomed view of the head movements in A. (C) Body movements during the wriggle phase, i.e. after sinusoidal swimming motions have ceased. (D) End of wriggle phase. Dots in A, C and D indicate the position of the head. Subtle movements along the body that are detectable using photoelasticity are not obvious with this method. Head movements in D are underestimates because most of the movements were perpendicular to the plane of the figure. Midline traces in A, C and D are separated by 0.30, 1.00 and 0.91 s, and represent 3.6, 12.0 and 11.0 s, respectively.

gelatin, a larger portion of the body engaged in generating active burrowing movements (Fig. S1). In one trial, it appears that the curve starts to level off, implying that after a certain amount of the body is submerged, a constant length of the anterior body is used to power burrowing, with the posterior portion getting passively dragged along.

Burrow time course and velocities

The mean total burrow duration for 25 analyzed trials was 445±97 s (±s.e.m.), with a mean for the thrash phase of 38±7 s and mean for the wriggle phase of 401±97 s (Table 2). Based on the thrash and wriggle durations, the transition distance and the total burrow distance, we calculated the velocity for thrash and wriggle phases as well as the average velocity for the entire burrowing event. The mean thrash phase velocity was 24.7±5.5 cm min^{-1} and the mean velocity for the wriggle phase was 11.5±2.2 cm min^{-1}. The average velocity for the entire burrow duration was 11.4±1.7 cm min^{-1}. The average wriggle phase velocity was considerably lower than for the wriggle phase burrowing bout shown in Fig. 6 (Movie 3). The difference can be explained by the fact that the burrowing shown in the figure was for a short period when the hagfish was actively burrowing for the entire duration, whereas the wriggle phase velocities in Table 2 include periods of inactivity when the hagfish was not actively burrowing (i.e. when velocity=0). These pauses during burrowing were not infrequent (they occurred in 12 out of 25 trials), but overall pause behavior was quite variable. In thirteen trials, there were no pauses, in eight trials, there was a single pause, in two trials two pauses, in one trial three pauses, and in one trial four pauses. The longest pause lasted for over 13 min. We discerned no obvious pattern of when the pauses occurred, other than the fact that they all happened during the wriggle phase.

DISCUSSION

Our observations of hagfishes burrowing within gelatin are consistent with observations of hagfishes burrowing in the wild.

Table 2. Temporal measurements of burrowing behavior in *M. limosa*

	Mean±s.e.m.
Thrash phase duration (s)	38±7
Wriggle phase duration (s)	401±97
Total duration (s)	445±97
Thrash phase velocity (cm min^{-1})	24.7±5.5
Wriggle phase velocity (cm min^{-1})	11.5±2.2
Mean burrow velocity (cm min^{-1})	11.4±1.7

Thrash phase was defined as the interval when the hagfish was actively thrashing with its body to drive its head into the substrate. Wriggle phase was defined as the interval when burrowing was powered exclusively by movements within the substrate. *N*=25.

Similarities include an initial phase in which the hagfish drove its head into the substrate via vigorous undulatory swimming movements (thrash phase), followed by a submerged phase where the exposed part of the body was relaxed, with progress into the substrate proceeding steadily (wriggle phase) (Martini, 1998). Based on the distance between the head and tail of burrowed hagfishes in the wild, it was suspected that *M. limosa* make U-shaped burrows. Hagfish in our trials also made U-shaped burrows, with their head appearing at a distance about half the length of the animal away from the initial burrow opening. These similarities suggest that the behaviors of hagfishes we observed within transparent media are an accurate representation of how hagfishes are creating and moving within burrows in the wild. It is possible that the constraints of the chambers we used affected the observed burrow shapes, with the narrow thickness of the chambers (a necessity for clear optics) possibly making the burrow trajectories more planar, and the left and right walls possibly making the sides of the 'U' straighter than they might be in the wild. It is also possible that hagfish in the wild add new secondary structures to their burrows over time (as suggested by Foss (1968), which we could not have captured in our short-term experiments.

Hagfish in our burrow chambers took more than 7 min on average to complete their burrows, which at first glance seems like a long time. Indeed, some fishes burrow much faster than this. Sand lance of the genus *Ammodytes* burrow into sand in ∼1 s (Gidmark et al., 2011) and sand diving in the slippery dick (*Halichoeres bivittatus*) is also fast, taking 1–3 s (Tatom-Naecker and Westneat, 2018). The burrowing eel, *Pisodonophis boro*, also burrows quickly through sand, taking 2–3 s to translocate its entire body length while submerged (Herrel et al., 2011; Herrel & Adriaens, 2024). These extremely rapid burrowing events are likely only possible in sand, which can be fluidized via high frequency undulations, as seen in the terrestrial 'sandfish' lizard (Baumgartner et al., 2008), or by non-slipping wave locomotion, as seen in the sand lance (Gidmark et al., 2011). In contrast, the adhesive forces between mineral particles and organic material in mud preclude fluidization or non-slipping wave locomotion strategies. Indeed, other fishes that burrow into mud do so over much longer timescales. In the red band-fish (*Cepola rubescens*), burrow formation in mud occurs via excavation using the mouth. In one study of burrowing in captive individuals, burrowing to a depth of 50% body length took 45 min on average, with complete burrow construction and maintenance lasting hours to days (Atkinson and Pullin, 1996). Another consideration is that hagfishes protect themselves from predators using defensive slime, which makes them less vulnerable to predators during the burrowing process than other fishes would be (Lim et al., 2006; Zintzen et al., 2011; Bressman and Fudge, 2021). In most hagfish species, the slime glands at the posterior end of a

Journal of Experimental Biology (2024) 227, jeb247544. doi:10.1242/jeb.247544

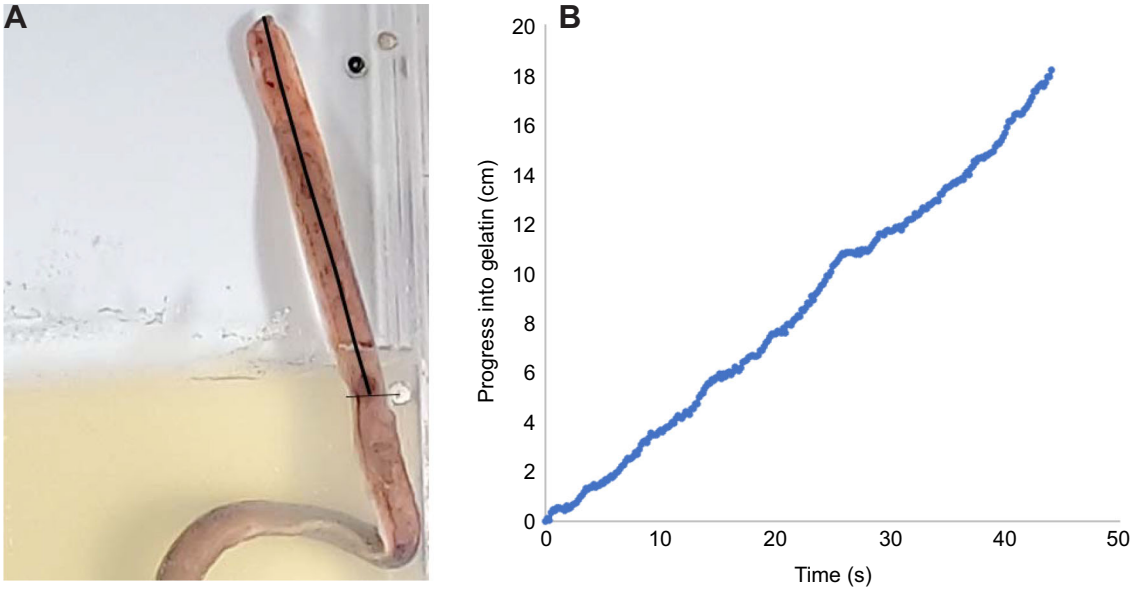

Fig. 6. Progress into gelatin during wriggle phase burrowing in *M. limosa*. (A) Progress into gelatin was estimated for one fortuitously oriented hagfish by measuring the length between the tip of the tail and a fixed location on the burrow chamber (middle of the silver dot with the thin horizontal line) every 167 ms for 44 s. (B) For this interval, the average burrowing speed was 24 cm min^{-1}. Video can be viewed in Movie 3.

hagfish appear to be larger than the glands on other parts of the body, which may be related to the fact that the tail is exposed for the longest amount of time during the burrowing process.

Mechanism of burrow creation

One of the main challenges of burrowing is creating an opening in a solid substrate through which the animal can move. This process has been best studied in polychaete worms, who have been shown to propagate and follow cracks in sediment, presumably as a means of reducing the energetic costs of burrowing (Dorgan et al., 2005, 2007). In gelatin, polychaetes tend to create and elongate a tongue-shaped crack that is oriented laterally, with the animal compressed dorsoventrally. On one hand, our observations from the onset of burrowing are consistent with the idea that hagfishes exploit cracks to extend their burrows. At the beginning of a trial, hagfishes showed obvious interest in areas where the gelatin was uneven or where we had created a hole. In fact, all burrows started in one of these holes, with not a single animal attempting to burrow in an area where the gelatin was flat and smooth. This is consistent with observations of hagfishes entering pre-existing burrows in the wild, which surely results in energetic savings compared with creating a completely new burrow. This is also consistent with the behavior of hagfishes feeding on carcasses, which they are known to enter via existing openings (e.g. mouth or anus) or weaknesses in the body created by other scavengers (Martini, 1998). On the other hand, we did not see strong evidence of an obvious crack or crack propagation in front of a hagfish's head, which should have been obvious in the photoelasticity videos if they were present. Instead, it appeared that

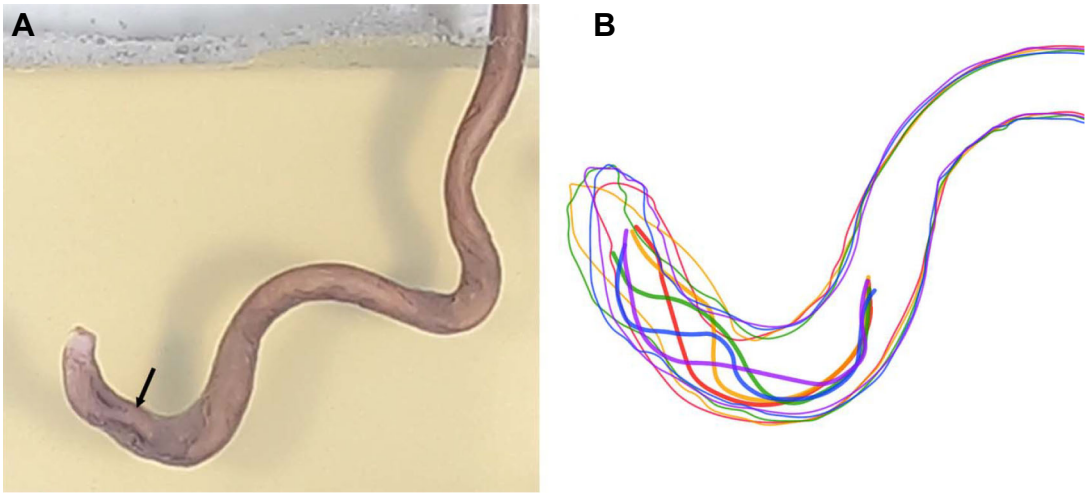

Fig. 7. Example of *M. limosa* exhibiting behavior consistent with an anterior internal concertina burrowing strategy. (A) The anterior body musculature behind the head is highly curved within the loose skin (arrow). The long wavelength curves in more posterior parts of the body are a consequence of the burrow path through the gelatin and are not part of the concertina movements. (B) Body outlines (thin lines) from same video shown in A and traces of body musculature midline (thick lines) are shown using sequential color (red–orange–green–blue–purple) for five video frames spanning 3.12 s of burrowing.

Journal of Experimental Biology (2024) 227, jeb247544. doi:10.1242/jeb.247544

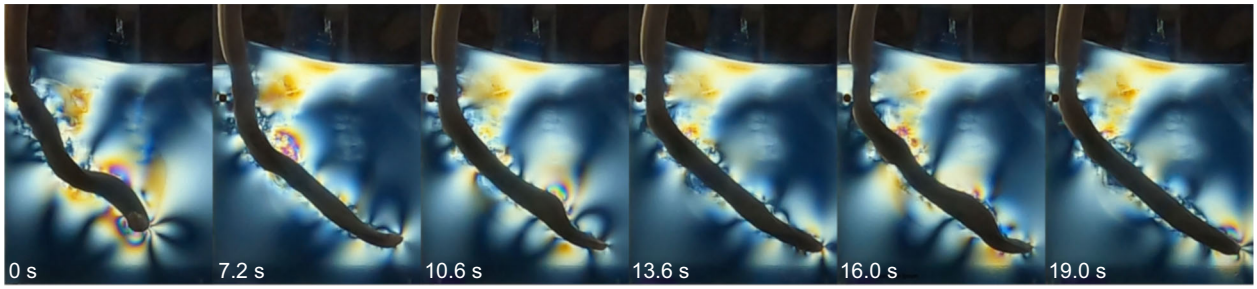

Fig. 8. Stills from photoelastic videos showing evidence for an internal concertina burrowing strategy by *M. limosa*. Photoelasticity allowed us to visualize the location and relative magnitude of the stresses generated by the hagfish as it burrowed through the gelatin. Consistent with a concertina strategy, hagfish pushed laterally on the gel by throwing the anterior part of their body into waves, which created bright spots in the gel corresponding to areas of high stress. These moments of body curvature and high gel stress alternated with moments of lower gel stress when the hagfish pushed forward by straightening its anterior body. Shown here are three cycles of bending and straightening over a 19 s period. Times provided are relative to the first panel. Video can be viewed in Movie 2.

the hagfish disrupted the gelatin in front of it by moving its head from side to side, which resulted in the gelatin getting chopped up into pieces. Although we did not quantify it, we noticed that some hagfish appeared to use a twisting motion of their head, which likely assisted in chopping up the gelatin. We should note that although gelatin and marine sediments both possess significant elasticity, there are important differences in their material properties, especially in their fracture behavior (Dorgan et al., 2007). It is therefore unwise to extrapolate too much from our observations in gelatin about the precise fracture mechanisms that hagfishes use in the wild to create their burrows.

Locomotion through burrows

During the thrash phase, the forces driving the hagfish forward appear to come from vigorous swimming movements, with side-to-side movements of the head likely serving to chop up the gel. During the wriggle phase, however, it was less obvious how the hagfish generated the forces that drive it forward. One possible mechanism is a concertina strategy, which has been well-described in snakes (Gray, 1946; Jayne, 1986, 2020). Concertina movements are commonly used by snakes to move in a controlled and stable way through narrow passages and burrows. Like the peristaltic strategy used by annelid worms, concertina movements involve forceful elongation of the body as well as lateral forces exerted on the walls for bracing and for widening the burrow. In annelid peristalsis, these forces are typically generated by antagonistic circumferential and longitudinal muscles, which cause elongation and shortening of each segment, respectively. In vertebrates like snakes, a rigid spine that resists body elongation and shortening makes peristaltic movements untenable. Instead, these animals shorten their bodies by throwing them into a wave, which allows them to exert lateral forces on the sides of a burrow, with straightening the body used to achieve forceful elongation. A snake using concertina movements will make steady progress through a narrow channel or burrow by alternating waves of elongation and shortening.

Concertina movements assume that the width of the channel or burrow is wider than the animal traversing it, but what about animals like hagfishes that create and move within tight burrows? Such a scenario has been described in burrowing uropeltid snakes and the legless amphibians known as caecilians (Gans, 1973; Gans et al., 1978). Within tight burrows, both groups have been shown to use a strategy called ‘internal concertina’, which resembles concertina, but the accordion-like movements of the body occur within the animal’s loose skin (Gans, 1973; Summers and O’Reilly, 1997). Like uropeltid snakes and caecilians, hagfishes possess loose skin and a flaccid body design that makes an internal concertina mechanism possible (Uyeno and Clark, 2020; Boggett et al., 2017). Our observations of hagfishes burrowing within gelatin are consistent with their use of an internal concertina burrowing strategy. The concertina part of the hypothesis predicts that hagfishes should exhibit alternating waves of body bending and elongation as they make progress through substrate, and a peak in lateral force generation during periods of maximum bending. The internal part of the hypothesis predicts that substantial amounts of body bending should occur within the loose skin. Evidence for these kinds of movements and stress production are provided in Figs 7 and 8. If the loose skin of hagfishes facilitates their use of an internal concertina strategy, this provides another functional use of loose skin in this group, in addition to knot-tying and defense against biting predators (Uyeno and Clark, 2020; Haney et al., 2020).

A possible alternative to an internal concertina mechanism is a hydrostatic one. Annelid worms use a hydrostatic skeleton to transduce forces generated by circumferential and longitudinal muscles and there is some evidence that fossorial caecilians employ hydrostatic mechanisms (O’Reilly et al., 1997; Quillin, 1998). The large subcutaneous sinus of hagfishes, and the fact that it contains up to a third of their blood volume might suggest that hydrostatics could be contributing to burrowing in hagfishes (Forster, 1997). However, the flaccid body design mentioned above would seem to preclude such a mechanism. Boggett et al. (2017) showed that the subcutaneous sinus in hagfishes can accommodate a lot more fluid than it contains (~40% of the hagfish’s body volume) without any increase in pressure. This means that the sinus is rarely pressurized, which would make it a poor candidate for a hydrostatic skeleton. Another possibility is that a hagfish’s body musculature acts as a muscular hydrostat, similar to a human tongue, an elephant’s trunk, or a squid’s tentacle (Kier and Smith, 1985). Whether such a mechanism would be possible depends on the orientation of muscle fibers as well as the mechanical properties of the hagfish notochord, which would need to be able to shorten and elongate without excess resistance (Long et al., 2002).

Muscular basis of burrowing in hagfishes

The movements we report here raise interesting questions about the muscles that hagfishes use to power burrowing. While it is clear that the body swimming movements during thrash phase are powered by the parietal muscles, it is less clear which muscles power the regular side to side head movements during the thrash and wriggle phases. The anterior musculature of a hagfish is complex and dominated by the lingual muscles associated with feeding (Clark and Summers,

2007). It is known that the lingual muscles are responsible for protraction and retraction of the tooth plates during feeding, but it is not known if these muscles contribute to the side-to-side head movements and the internal concertina movements during burrowing that we describe here. Generating bending of the head with these muscles would require an ability to activate and shorten one side at a time, while the other side remains relaxed, as is seen in the axial muscle of fishes during swimming. Further investigations of the functional morphology of the hagfish lingual apparatus and anterior musculature are clearly needed to determine which muscles are used to power these behaviors.

Influence of body size on burrowing

While we did not systematically explore the effects of body size on the burrowing behavior and performance of *M. limosa*, it appeared to us that larger hagfish were more likely to initiate and complete a U-shaped burrow. One possible explanation is that the gelatin in our burrowing chambers was stiffer and/or tougher than the sediment they typically enter and therefore only large hagfish were strong enough to break up the gel and burrow through it. While this pattern may not hold in the wild, especially in areas with loose, soft sediments, it does raise the possibility that certain size classes of hagfishes might prefer areas where sediments are less compact and easier to penetrate. We should also note that, among burrowing animals, hagfishes are on the large end of the spectrum. Benthic ecologists classify animals living in sediment according to two size classes, meiobenthos and macrobenthos, which are defined as animals between 0.1 mm and 0.5 mm, and those that are larger than 0.5 mm, respectively. These size classes are indicative of the small size that is typical among infaunal invertebrates (Warwick and Clarke, 1984). Burrowing fishes, in contrast, tend to be much larger and can generate burrows that penetrate 0.5 m into the sediment (Atkinson and Pullin, 1996). With body sizes up to a meter in length, hagfishes are orders of magnitude larger than most burrowing invertebrates. Future research on the burrowing performance of hagfishes as a function of body size and substrate types might reveal interesting patterns that could explain the geographical and demographic distribution of some hagfish species.

Ecological implications

The burrowing activities of hagfishes are likely to have substantial effects on substrates in the regions where they live (Martini, 1998). In our burrow chambers, hagfishes burrowed to an average depth of 15 cm, which is clearly an underestimate given that some hagfishes burrowed to the bottom of the chamber and likely would have gone deeper in a larger chamber. At any rate, 15 cm is considerably deeper than the average mixed layer depth of ∼10 cm for global sediments (Boudreau, 1994). Hagfish burrowing will therefore likely have important effects on sediment turnover, and, through ventilation of their burrows, on the redox chemistry of the sediment. Sediment near a hagfish burrow that might otherwise be anoxic might contain substantial amounts of oxygen, thus altering the kinds of organisms that can live there. Polymer casts of the burrows made by *C. rubescens* in the wild reveal that other organisms, likely crustaceans, build secondary offshoot burrows from the passageways of their generally Y-shaped burrows (Atkinson and Pullin, 1996). While it is not clear how long hagfish occupy their burrows in the wild, it is likely that they are transient structures and that they create many burrows in their lifetimes (Martini, 1998). In areas where population densities are high, hagfishes could have dramatic effects on sediment structure and even might be considered ‘ecosystem engineers’ in those areas (Darwin, 1892; Woodin et al., 2010).

Summary and future work

This work represents the first comprehensive study of burrowing in hagfishes and provides an initial window into the behavior of hagfishes within sediment. Our observations show that hagfishes create U-shaped burrows by employing a biphasic strategy that involves vigorous swimming of the exposed body followed by internal concertina-like movements within the substrate. While the burrow chambers we used were ideal for getting a clear picture of hagfish movements, wall effects might have affected the behavior of the hagfish or the shape of the burrows they made. For this reason, these experiments should be repeated using sediments obtained from *M. limosa*’s natural habitat. To visualize movements in these sediments, X-ray videography of burrowing hagfishes implanted with radiopaque markers will be needed. Future research should investigate the effects of body size and substrate type on burrowing performance in hagfishes, as well the differences in burrowing behavior and performance among the six genera and 90 species of described hagfishes. Further exploration of the mechanisms used by hagfishes to burrow might also reveal principles that could be useful for the design of effective soft burrowing robots.

Acknowledgements

We are grateful to the staff of the Shoals Marine Lab for collection of hagfishes and especially to the SML Investigative Marine Biology Laboratory classes of 2021 and 2022 for pushing this project forward. This is contribution #205 of the Shoals Marine Laboratory. Matt Snyder built the burrow chambers and Kelly Dorgan provided advice on encouraging animals to burrow in gelatin.

Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: D.S.F., A.L., N.B., C.L.M.; Methodology: D.S.F., J.L., K.G., C.M.D., A.L., L. Arnold, K.K.-L., N.B., C.L.M.; Software: C.M.D.; Validation: C.L.M.; Formal analysis: D.S.F., J.L., C.M.D., L. Arnold, L. Atkins, C.L.M.; Investigation: D.S.F., J.L., K.G., L. Arnold, K.K., C.Q., P.L., L. Atkins, N.B., C.L.M.; Resources: D.S.F.; Data curation: D.S.F., J.L., K.G., C.M.D., K.K.-L., C.Q., P.L., C.L.M.; Writing - original draft: D.S.F., J.L.; Writing - review & editing: D.S.F., J.L., C.M.D., A.L., N.B., C.L.M.; Visualization: D.S.F., J.L., C.M.D., C.L.M.; Supervision: D.S.F., C.L.M.; Project administration: D.S.F., C.L.M.; Funding acquisition: D.S.F.

Funding

C.Q. and P.L. were supported by a REPS supplement and K.G. by an RET supplement for a National Science Foundation grant to D.S.F. (IOS-1755397). C.L.M. was supported by a Grand Challenges Initiative fellowship at Chapman University.

Data availability

All data are available in Fudge (2024): https://doi.org/10.5061/dryad.np5hqc028

References

Atkinson, R. J. A. and Pullin, R. S. (1996). Observations on the burrows and burrowing behaviour of the red band–fish, *Cepola rubescens* L. *Mar. Ecol.* **17**, 23-40. doi:10.1111/j.1439-0485.1996.tb00487.x

Baumgartner, W., Fidler, F., Weth, A., Habbecke, M., Jakob, P., Butenweg, C. and Böhme, W. (2008). Investigating the locomotion of the sandfish in desert sand using NMR-imaging. *PLoS One* **3**, e3309. doi:10.1371/journal.pone.0003309

Boggett, S., Stiles, J. L., Summers, A. P. and Fudge, D. S. (2017). Flaccid skin protects hagfishes from shark bites. *J. R. Soc. Interface* **14**, 20170765. doi:10.1098/rsif.2017.0765

Boudreau, B. (1994). Is burial velocity a master parameter for bioturbation? *Geochim. Cosmochim. Acta* **58**, 1243-1249. doi:10.1016/0016-7037(94)90378-6

Bressman, N. and Fudge, D. (2021). From reductionism to synthesis: the case of hagfish slime. *Comp. Biochem. Physiol. Part B: Biochem. Mol. Biol.* **255**, 110610. doi:10.1016/j.cbpb.2021.110610

Che, J. and Dorgan, K. M. (2010). It’s tough to be small: dependence of burrowing kinematics on body size. *J. Exp. Biol.* **213**, 1241-1250. doi:10.1242/jeb.038661

Clark, A. J. and Summers, A. P. (2007). Morphology and kinematics of feeding in hagfish: possible functional advantages of jaws. *J. Exp. Biol.* **210**, 3897-3909. doi:10.1242/jeb.006940

Darwin, C. (1892). *The Formation of Vegetable Mould, Through the Action of Worms, With Observations on Their Habits*. p. 326. J. Murray.
Donatelli, C. M., Summers, A. P. and Tytell, E. D. (2017). Long-axis twisting during locomotion of elongate fishes. *J. Exp. Biol.* **220**, 4745. doi:10.1242/jeb.173823
Dorgan, K. M. (2018). Kinematics of burrowing by peristalsis in granular sands. *J. Exp. Biol.* **221**, jeb167759. doi:10.1242/jeb.167759
Dorgan, K. M., Jumars, P. A., Johnson, B., Boudreau, B. P. and Landis, E. (2005). Burrow extension by crack propagation. *Nature* **433**, 475. doi:10.1038/433475a
Dorgan, K. M., Arwade, S. R. and Jumars, P. A. (2007). Burrowing in marine muds by crack propagation: kinematics and forces. *J. Exp. Biol.* **210**, 4198-4212. doi:10.1242/jeb.010371
Dorgan, K. M., Arwade, S. R. and Jumars, P. A. (2008). Worms as wedges: effects of sediment mechanics on burrowing behavior. *J. Mar. Res.* **66**, 219-254.
Dorgan, K. M., Law, C. J. and Rouse, G. W. (2013). Meandering worms: mechanics of undulatory burrowing in muds. *Proc. R. Soc. B* **280**, 20122948. doi:10.1098/rspb.2012.2948
Fudge, D. (2024). Data from: Biphasic burrowing in Atlantic hagfish (*Myxine limosa*) [Dataset]. *Dryad* https://doi.org/10.5061/dryad.np5hqc028
Fernholm, B. (1974). Diurnal variations in the behaviour of the hagfish *Eptatretus burgeri*. *Mar. Biol.* **27**, 351-356. doi:10.1007/BF00394371
Forster, M. E. (1997). The blood sinus system of hagfish: its significance in a low-pressure circulation. *Comp. Biochem. Physiol. Part A Physiol.* **116**, 239-244. doi:10.1016/S0300-9629(96)00215-0
Foss, G. (1968). Behaviour of *Myxine glutinosa* in natural habitat investigation of the mud biotope by a suction technique. *Sarsia* **31**, 1-14. doi:10.1080/00364827.1968.10411105
Freedman, C. R. and Fudge, D. S. (2017). Hagfish Houdinis: biomechanics and behavior of squeezing through small openings. *J. Exp. Biol.* **220**, 822-827. doi:10.1242/jeb.151233
Full, R., Yamauchi, A. and Jindrich, D. (1995). Maximum single leg force production: cockroaches righting on photoelastic gelatin. *J. Exp. Biol.* **198**, 2441-2452. doi:10.1242/jeb.198.12.2441
Gans, C. (1973). Locomotion and burrowing in limbless vertebrates. *Nature* **242**, 414-415. doi:10.1038/242414a0
Gans, C., Dessauer, H. C. and Baic, D. (1978). Axial differences in the musculature of uropeltid snakes: the freight-train approach to burrowing. *Science* **199**, 189-192. doi:10.1126/science.199.4325.189
Gidmark, N. J., Strother, J. A., Horton, J. M., Summers, A. P. and Brainerd, E. L. (2011). Locomotory transition from water to sand and its effects on undulatory kinematics in sand lances (Ammodytidae). *J. Exp. Biol.* **214**, 657-664. doi:10.1242/jeb.047068
Gray, J. (1946). The mechanism of locomotion in snakes. *J. Exp. Biol.* **23**, 101-120. doi:10.1242/jeb.23.2.101
Haney, W. A., Clark, A. J. and Uyeno, T. A. (2020). Characterization of body knotting behavior used for escape in a diversity of hagfishes. *J. Zool.* **310**, 261-272. doi:10.1111/jzo.12752
Herrel, A. and Adriaens, D. (2024). Burrowing in fishes: anatomy, physiology, function and ecology. In *Encyclopedia of Fish Physiology*, 2nd edn (ed. S. Alderman and T. Gillis), pp. 649-653. Elsevier.
Herrel, A., Choi, H. F., Dumont, E., De Schepper, N., Vanhooydonck, B., Aerts, P. and Adriaens, D. (2011). Burrowing and subsurface locomotion in anguilliform fish: behavioral specializations and mechanical constraints. *J. Exp. Biol.* **214**, 1379-1385. doi:10.1242/jeb.051185
Jayne, B. C. (1986). Kinematics of terrestrial snake locomotion. *Copeia* **1986**, 915-927. doi:10.2307/1445288
Jayne, B. C. (2020). What defines different modes of snake locomotion? *Integr. Comp. Biol.* **60**, 156-170. doi:10.1093/icb/icaa017
Johnson, B. D., Boudreau, B. P., Gardiner, B. S. and Maass, R. (2002). Mechanical response of sediments to bubble growth. *Mar. Geol.* **187**, 347-363. doi:10.1016/S0025-3227(02)00383-3
Josephson, R. K. and Flessa, K. W. (1972). Cryolite: a medium for the study of burrowing aquatic organisms. *Limnol. Oceanogr.* **17**, 134-135. doi:10.4319/lo.1972.17.1.0134
Kier, W. M. and Smith, K. K. (1985). Tongues, tentacles and trunks: the biomechanics of movement in muscular-hydrostats. *Zool. J. Linn. Soc.* **83**, 307-324. doi:10.1111/j.1096-3642.1985.tb01178.x
Lim, J., Fudge, D. S., Levy, N. and Gosline, J. M. (2006). Hagfish slime ecomechanics: testing the gill-clogging hypothesis. *J. Exp. Biol.* **209**, 702-710. doi:10.1242/jeb.02067
Long, J. H., Jr, Koob-Emunds, M., Sinwell, B. and Koob, T. J. (2002). The notochord of hagfish *Myxine glutinosa*: visco-elastic properties and mechanical functions during steady swimming. *J. Exp. Biol.* **205**, 3819-3831. doi:10.1242/jeb.205.24.3819
Martini, F. H. (1998). The Ecology of Hagfishes. In *The Biology of Hagfishes* (ed. J. M. Jørgensen J. P. Lomholt R. E. Weber and H. Malte), pp. 57-77. Springer Science.
Martini, F. H. and Heiser, J. B. (1989). Field observations on the Atlantic hagfish, *Myxine glutinosa*, in the Gulf of Maine. *Am. Zool.* **29**, A38-A38.
O'Reilly, J. C., Ritter, D. A. and Carrier, D. R. (1997). Hydrostatic locomotion in a limbless tetrapod. *Nature* **386**, 269-272. doi:10.1038/386269a0
Paggett, K. C., Gupta, V. and McClellan, A. D. (1998). Adaptive variations of undulatory behaviors in larval lamprey: comparison of swimming and burrowing. *Exp. Brain Res.* **119**, 213-223. doi:10.1007/s002210050335
Quillin, K. J. (1998). Ontogenetic scaling of hydrostatic skeletons: Geometric, static stress and dynamic stress scaling of the earthworm, *Lumbricus terrestris*. *J. Exp. Biol.* **201**, 1871-1883. doi:10.1242/jeb.201.12.1871
Smith, C. R. (1985). Food for the deep sea: utilization, dispersal, and flux of nekton falls at the Santa Catalina Basin floor. *Deep Sea Res. Part A Oceanogr. Res. Papers* **32**, 417-442. doi:10.1016/0198-0149(85)90089-5
Summers, A. P. and O'Reilly, J. C. (1997). A comparative study of locomotion in the caecilians *Dermophis mexicanus* and *Typhlonectes natans* (Amphibia: Gymnophiona). *Zool. J. Linn. Soc.* **121**, 65-76. doi:10.1111/j.1096-3642.1997.tb00147.x
Tatom–Naecker, T. A. M. and Westneat, M. W. (2018). Burrowing fishes: kinematics, morphology and phylogeny of sand-diving wrasses (Labridae). *J. Fish Biol.* **93**, 860-873. doi:10.1111/jfb.13789
Uyeno, T. A. and Clark, A. J. (2020). On the fit of skins with a particular focus on the biomechanics of loose skins of hagfishes. *Can. J. Zool.* **98**, 827-843. doi:10.1139/cjz-2019-0296
Warwick, R. M. and Clarke, K. R. (1984). Species size distributions in marine benthic communities. *Oecologia* **61**, 32-41. doi:10.1007/BF00379085
Woodin, S. A., Wethey, D. S. and Volkenborn, N. (2010). Infaunal hydraulic ecosystem engineers: cast of characters and impacts. *Int. Comp. Biol.* **50**, 176-187. doi:10.1093/icb/icq031
Zintzen, V., Roberts, C. D., Anderson, M. J., Stewart, A. L., Struthers, C. D. and Harvey, E. S. (2011). Hagfish predatory behaviour and slime defence mechanism. *Sci. Rep.* **1**, 131. doi:10.1038/srep00131