

RESEARCH ARTICLE

Locomotory transition from water to sand and its effects on undulatory kinematics in sand lances (*Ammodytidae*)

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SUMMARY

Sand lances, fishes in the genus *Ammodytes*, exhibit a peculiar burrowing behavior in which they appear to swim rapidly into the substrate. They use posteriorly propagated undulations of the body to move in both water, a Newtonian fluid, and in sand, a non-Newtonian, granular substrate. In typical aquatic limbless locomotion, undulations of the body push against water, which flows because it is incapable of supporting the static stresses exerted by the animal, thus the undulations move in world space (slipping wave locomotion). In typical terrestrial limbless locomotion, these undulations push against substrate irregularities and move relatively little in world space (non-slipping wave locomotion). We used standard and X-ray video to determine the roles of slipping wave and non-slipping wave locomotion during burrowing in sand lances. We find that sand lances in water use slipping wave locomotion, similar to most aquatic undulators, but switch to non-slipping waves once they burrow. We identify a progression of three stages in the burrowing process: first, aquatic undulations similar to typical anguilliform locomotion (but without head yaw) push the head into the sand; second, more pronounced undulations of the aquatic portion of the body push most of the animal below ground; third, the remaining above-ground portion of the body ceases undulation and the subterranean portion takes over, transitioning to non-slipping wave locomotion. We find no evidence that sand lances use their body motions to fluidize the sand. Instead, as soon as enough of the body is underground, they undergo a kinematic shift and locomote like terrestrial limbless vertebrates.

Key words: *Ammodytes*, burrowing, anguilliform locomotion, serpentine locomotion.

INTRODUCTION

Sand lances (Family *Ammodytidae*) are a group of fishes that employ anguilliform locomotion during pelagic swimming, and exhibit a peculiar behavior of actively swimming into sandy substrates as a refuge (Dick and Warner, 1982). This burrowing behavior is associated with hibernation during the winter, daily migrations into the sand after dark and predator avoidance (Winslade, 1947a; Winslade, 1947b; Girska and Danilov, 1976). The burrowing behavior of sand lances presents a good opportunity to investigate the mechanics of both locomotion within and transitions between different environments.

Seawater behaves as a Newtonian fluid and will flow continuously when a shear stress is applied, whereas a sand–water mix may act as a non-Newtonian fluid, because of both sand–sand and sand–water interactions. Settled wet sand is a hybrid material with some solid and some fluid properties, and it will generally support some shear stress. The precise mechanics of particle interaction remains unclear, although similar ‘frictional fluid’ sand–air mixtures have been studied (Maladen et al., 2009).

During terrestrial locomotion, snakes and other limbless vertebrates use undulatory locomotion whereby they apply force to discrete, non-moving points on the ground *via* a posteriorly propagating wave (Gray, 1946). In the ideal case, where these points are immobile, the animal’s propulsive undulations travel caudally

along the body, maintaining a velocity equal, though oppositely oriented, to the animal’s forward progress (Jayne, 1986). Consequently, all points along the axis of the body will follow the same trajectory: the undulatory wave, which, while propagating posteriorly along the animal’s body, will not move in a world-based coordinate system (Jayne, 1986). We will refer to this mode of locomotion as ‘non-slipping wave’ locomotion.

By contrast, animals using aquatic undulatory locomotion do not have discrete push points available because they are exerting force onto a fluid for propulsion. Because water continuously deforms under shear stress, the water will flow as the body of an animal pushes against it. Also, because flow results in undulatory waves that move in a world-based coordinate system, all points along the body’s axis will not follow the same trajectory (Grillner and Kashin, 1976; Gillis, 1998). In this case, the undulatory waves move posteriorly with respect to both the body and the world. We will refer to this mode as ‘slipping wave’ locomotion. In a study comparing the mechanics of undulatory locomotion on land and in water, Gillis (Gillis, 1998) studied kinematic differences in the eel, *Anguilla rostrata* (Lesueur 1817). Effectively, eels traveling on land locomote using nearly non-slipping wave locomotion (more like other terrestrial vertebrates), whereas those same individuals engage in slipping wave locomotion in an aquatic environment (Fig. 1).

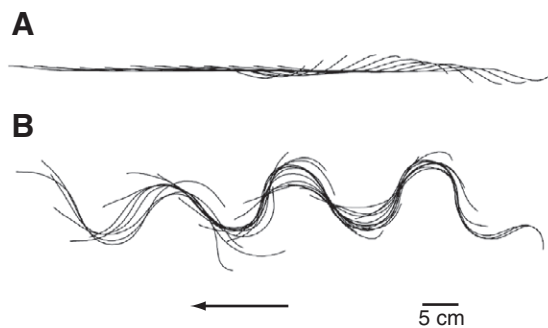


Fig. 1. Sequential midlines from an individual *Anguilla rostrata* traveling at the same speed (0.4 body lengths per second) during locomotion in (A) water and (B) on land. Anterior is to the left. The arrow denotes direction of movement. Modified from Gillis (Gillis, 1998).

This dichotomy between the mechanics of non-slipping wave and slipping wave locomotion raises the issue of how an animal transitions from one medium to another, as when sand lances transition from aquatic to subterranean locomotion. Given the higher viscosity and heterogeneity of the sand–water mix, we hypothesize that buried sand lances will exhibit kinematics more closely resembling those of terrestrial snakes (i.e. we predict that they will employ non-slipping wave locomotion). Furthermore, any portion of the animal not buried will move with kinematics more closely resembling those of aquatic eels (i.e. we predict that they will employ slipping wave locomotion).

We filmed sand lances burrowing using standard high-speed video and X-ray video to quantify their kinematics. We use these data to qualitatively and quantitatively examine the progression of kinematic behavior throughout the burrowing process in these fishes. Then, we compare our findings with the available data on terrestrial snakes, aquatic and terrestrial eels, and other animals that exhibit undulatory locomotion. Finally, we develop a model to explain the observed movements, and determine whether the environmental transition happens either as a gradient [or intermediate gait (*sensu* Ashley-Ross and Bechtel, 2004)] or as an abrupt change in kinematics at some critical threshold.

MATERIALS AND METHODS

Specimens

Two sets of specimens were used in this project (Table 1). The first set of specimens ($N=10$) were Pacific sand lance, *Ammodytes hexapterus* (Pallas 1814), collected using a mesh bag seine off the shoreline of San Juan Island, WA, USA. These fish were fed mysid shrimp and maintained in tanks in a flow-through seawater system at the Friday Harbor Laboratories (FHL), University of Washington. All experiments with these specimens were conducted at FHL in accordance with the University of Washington animal health and welfare policies.

The second set of specimens ($N=10$) was a mixture of the American sand lance, *A. americanus* (DeKay 1842) and the Northern sand lance, *A. dubius* (Reinhardt 1837). These fishes were caught

using a custom bottom trawl off the coasts of Rhode Island and Massachusetts, USA. They were maintained in the Kauffman lab at Boston University (Boston, MA, USA), on a diet of *Artemia* spp. Fishes were transported to Brown University, where they were used in cinefluoroscopy experiments. Specimens were difficult to classify to species while alive, and so were used for experiments while alive and then subsequently killed for species identification by lateral scale counts. All work using these specimens was conducted in accordance with both Brown University and Boston University animal health and welfare policies.

The *A. hexapterus* individuals in the FHL dataset ranged from 66 mm to 104 mm standard length (*SL*), whereas the *A. dubius* and *A. americanus* specimens in the Brown dataset ranged from 126 to 142 mm and 105 to 123 mm *SL*, respectively. This size difference was not relevant to the study because comparisons between above- and below-ground locomotion are exclusively qualitative and all quantitative comparisons are made within a size class. Interspecies comparisons or scaling issues are not addressed using these datasets.

Videography

High-speed videos of the FHL specimens was used to characterize the above-sand portion of sand lance burrowing kinematics. A high-speed video camera (Motionscope, Redlake Imaging, Tallahassee, FL, USA) recorded animals at 125 frames s^{-1} with an exposure time of 2 ms. The filming tank was approximately $20 \times 45 \times 10$ cm (height \times length \times width), filled with 10 cm of sand with 10 cm of water above it. The camera was positioned so that activity in the tank could be recorded in lateral view. A mirror was positioned at a 45 deg angle above the tank to provide a dorsal view using the same camera. The filming tank was illuminated by fiber-optic and incandescent lights. Each individual *A. hexapterus* was placed into the tank and filmed while burrowing until it was completely underground. After a 15 min recovery period, each fish was removed from the substrate and allowed to burrow again. Three to five burrowing sequences were recorded for each of ten individuals, for a total of 36 burrowing sequences. The clearest video sequence of each individual was used for further analysis.

The fish studied at Brown University (Brown specimens) were filmed using three synchronized Photron Fastcam 1024 PCI high-speed video cameras (Intronix Imaging Technologies, Westlake Village, CA, USA) at a frame rate of 125 frames s^{-1} . Two of the cameras were connected to retrofitted C-arm fluoroscopes (Radiological Imaging Services, Hamburg, PA, USA) to provide X-ray videos of burrowing behaviors in lateral and dorsoventral views. During burrowing the fish displaced sand, thus allowing the body to be viewed as a negative X-ray image. X-ray energies varied somewhat between sequences, but were generally set at 20 mA and 100–120 kVp. The third camera was positioned to collect standard (not X-ray) videos of the fish swimming in the water above the sand. Aquaria of various sizes and shapes were used so that lateral and dorsoventral X-ray and standard high-speed video images could be obtained. Because of the X-ray density of the water and sand, combined with the need to provide the animals with enough space to perform natural behaviors, we were not able to collect satisfactory lateral and dorsoventral X-ray movies simultaneously. In the end,

Table 1. Summary of specimen use

Species	Dataset	<i>N</i> (size range; mm)	Standard views	X-ray views	Data in figures
<i>Ammodytes hexapterus</i>	FHL	10 (85.3±19)	2	0	3, 4
<i>A. americanus</i>	Brown	7 (118.9±13.5)	1	1	4, 5, 7
<i>A. dubius</i>	Brown	3 (133.8±8)	1	1	2, 4, 7

all of the quantitatively analyzed data were collected in oblique lateral standard camera perspective and dorsoventral X-ray camera perspective. The aquarium was 20×20 cm square and 23 cm deep. It was filled to a depth of 5 cm with Arag-Alive aragonite reef sand (Carib Sea, Inc., Fort Pierce, FL, USA), with a depth of 8 cm of water above the sand. This aquarium sand has a manufacturer-specified grain size of 0.2–2.2 mm.

Camera views and synchronization of data

The FHL dataset provided three-dimensional (3-D) kinematics for the portion of the body that remained above ground. These 3-D data were crucial because the above-ground portion of the studied behavior is not planar. The Brown dataset could not resolve three-dimensional motion. However, no animals burrowed deeper than 5 cm in sand, despite availability of greater depths in several trials. Moreover, during burrowing, animals typically remained upright (dorsal side up, ventral side down), with little deviation from horizontal pitch. For analysis purposes, we assumed that no dorsoventral movement occurred in burrowed animals. Following this assumption, we used the standard video camera from the Brown dataset to align time points of above-ground kinematics with those from X-ray videos of below-ground kinematics. We used the dorsoventral X-ray camera to quantify subterranean movements.

Kinematic analyses

Using a custom script in MATLAB 7.4 (MathWorks, Inc., Natick, MA, USA), we digitized a midline for every frame of selected sequences ($N=20$; 10 from FHL and 10 from Brown). Each sequence was from a different individual. FHL sequences were analyzed from the time the nose touched the substrate (nose-touch) until the time the tail could no longer be seen by the above-ground camera. The FHL videos were analyzed in both lateral and dorsal views, but the Brown X-ray videos were analyzed in dorsal view only.

For each frame of video, enough points were digitized to accurately depict above-ground body position in each camera view. This ranged from roughly twenty points at the beginning of a burrowing sequence when most of the body was exposed to two points at the end of a sequence when most of the body was underground. Registration was accomplished by first fitting a spline to the 2-D data from each view. The tangent of these splines in 2-D space was used to calculate the tangent of the midline in 3-D space. By stepping posteriorly through the midline points and calculating the 3-D tangent of each segment, it was possible to map the positions on one midline to positions on the second midline.

With all the positions on one midline registered to corresponding positions on the other midline, a 50-point 3-D midline was reconstructed. These animals have between 70 and 75 vertebrae, so each segment of the midline spanned approximately 1.5 vertebrae.

To measure body curvature, we used each sequential point triplet (1, 2, 3; 2, 3, 4; etc.) to define a circle, rendering 48 circles defined at each frame. We calculated instantaneous curvature values by taking the inverse of the radius of each circle and averaging these values across the entire body, resulting in one measurement for each frame. Because this metric still contained a strong noise component, we averaged across 15 frames from each stage of burrowing for statistical comparison (see Results for a description of these three stages of burrowing). We tried breaking the data up into two and three sections – i.e. one analysis of just the anterior *versus* posterior half of the exposed portion of the body, and anterior, middle and posterior thirds. Neither showed patterns of curvature changes longitudinally within a stage, suggesting that lumping values longitudinally is a valid approach.

Inter-dataset comparisons

The two datasets examined herein are largely non-overlapping. Therefore, the FHL dataset is chiefly used for a qualitative description of above-ground kinematics, with quantitative data being used to examine differences between stages of burrowing. The Brown dataset is used as a descriptor of below-ground kinematics, with quantitative data comparing stages of subterranean locomotion within this dataset. The timing variables measured in both datasets are linked by the standard camera view, which is used to determine the time of nose-touch, the end of the burrowing sequence and the stage divisions.

RESULTS

Above-ground kinematics

We observed a sequence of three distinct stages during burrowing in every trial for every individual. The progression involves a sudden increase in above-ground movements, when undulations become more pronounced and increased in frequency. This is followed by a sudden halt in movement, when the tail ceases undulation and appears to glide effortlessly into the sand. In all stages undulations that occur above ground have a slipping wave pattern. Burrowing sequences (measured from the time of the nose touching the substrate until the tail can no longer be seen above ground) lasted approximately 1 s. The shortest recorded burrowing event lasted 0.55 s and the longest lasted 1.75 s. Each of the three stages lasted approximately one third of the sequence.

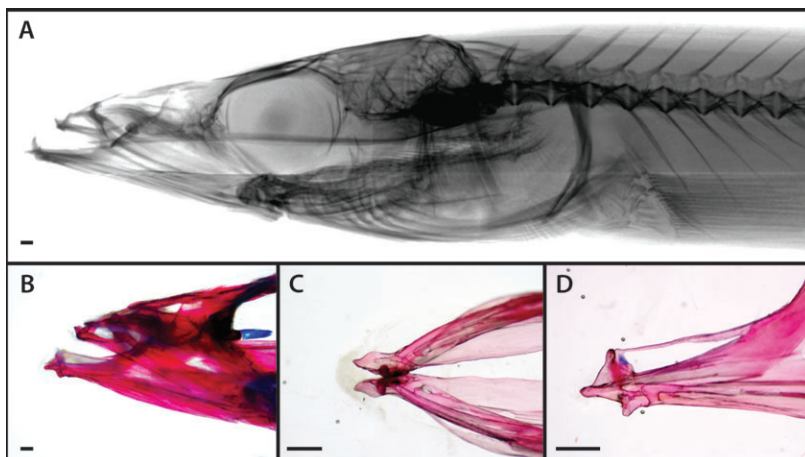


Fig. 2. Cephalic morphology of *Ammodytes dubius*. (A) A lateral radiograph, demonstrating the overall cone shape of the head. (B–D) Anatomy of other *A. dubius* after clearing and staining. (B) Whole head. (C) An isolated lower jaw in dorsal view, highlighting anterior projections protruding from the dentary. (D) A lateral view of an isolated left lower jaw. Anterior to the left in all panels. Scale bar, 0.1 cm in all panels.

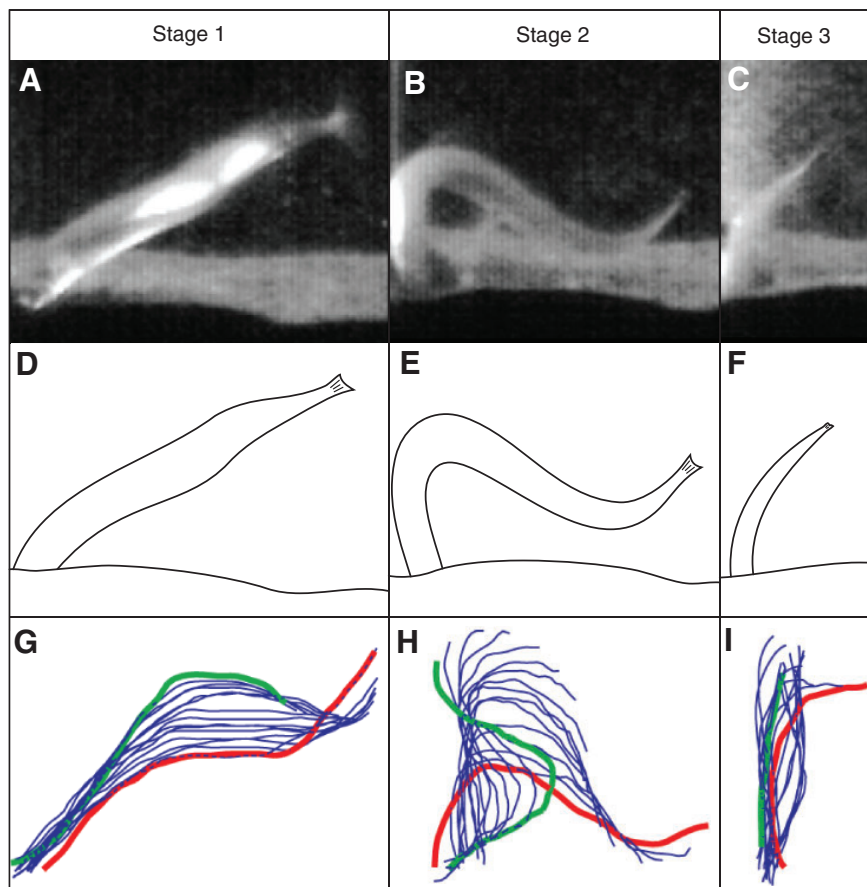


Fig. 3. Representative sequence of the above-ground undulatory movements during burrowing. Top row (A–C): selected standard video frames of Stages 1, 2 and 3, respectively. Middle row (D–F): drawings of the standard video frames. Bottom row (G–I): reconstructed midlines of fifteen consecutive frames. First frame shown in red, final frame in green and remaining frames in blue. Stage 1 of burrowing is shown in A, D and G; Stage 2 in B, E and F; Stage 3 in C, F and I. Frame rate was $125 \text{ frames s}^{-1}$.

Initially, when burrowing commences, the animal uses conventional slipping wave locomotion, in which the body continues to undulate as if not encountering the resistance of the sand, although the fish has already engaged the substrate. The sand lance uses these undulations to drive its pointy, cone-shaped head into the sand (Fig. 2). This kinematic phase is qualitatively similar to swimming observed before the nose touches the substrate, except for the lack of head yaw, which is due to the rostrum being embedded in the sand. We term this portion of the burrowing sequence ‘Stage 1’ (Fig. 3A,D,G).

Stage 2 is characterized by more pronounced body undulations, in which the tail often makes contact with the substrate (Fig. 3B,E,H). The body undulations also attain higher curvatures than in Stage 1 (Fig. 4; $P=0.0028$ in a paired t -test, $N=10$). The frequencies and amplitudes of the tail tip do not vary between Stages 1 and 2, remaining at approximately 0.7 Hz and 6 cm, respectively. These more pronounced undulations drive approximately two-thirds of the body into the substrate.

Stage 3 is marked by a sudden halt in above-ground undulation, and the above-ground portion of the tail typically straightens (Fig. 3C,F,I). We term the beginning of this stage ‘tail stop’. Undulations observed during Stage 3 are less curved than those at Stage 2 (Fig. 4; $P=0.0008$ in a paired t -test, $N=10$). The two outliers (marked by open circles) in Fig. 4 are data for fish with their tail bent over and resting on the sand. In both cases, the tail was no longer undulating.

Comparison with below-ground kinematics

During Stage 1, the underground portion of the animal does not undulate and thus enters the sand in a straight line (Fig. 5A,D,G).

At the onset of Stage 2 (denoted by the increase in curvature and amplitude in the single standard camera view), the buried portion of the animal typically makes a 90 deg lateral bend, and the head begins traveling in a direction orthogonal to its entry trajectory (Fig. 5B,E,H). At the onset of Stage 3 (denoted by the offset of undulations in the above-ground portion of the body in the standard

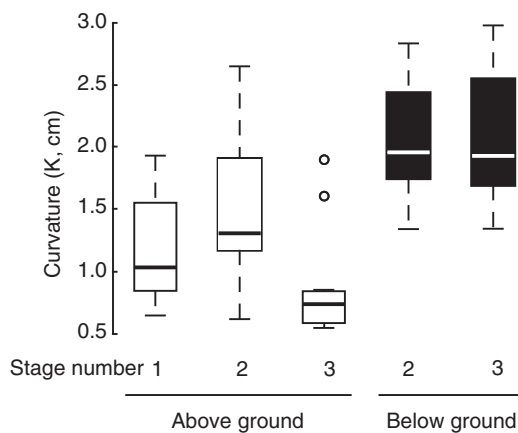


Fig. 4. Average body curvature at different stages of burrowing, averaged over 15 frames for each stage. Open boxes are above-ground data (FHL dataset), solid boxes on below-ground data (Brown dataset). All pair-wise comparisons are statistically significantly different ($P<0.05$), with the exception of the two below-ground stages ($P=0.6222$). Bold lines indicate median; boxes encompass 25th percentile to 75th percentile; whiskers indicate range. Statistical outliers indicated with open circles.

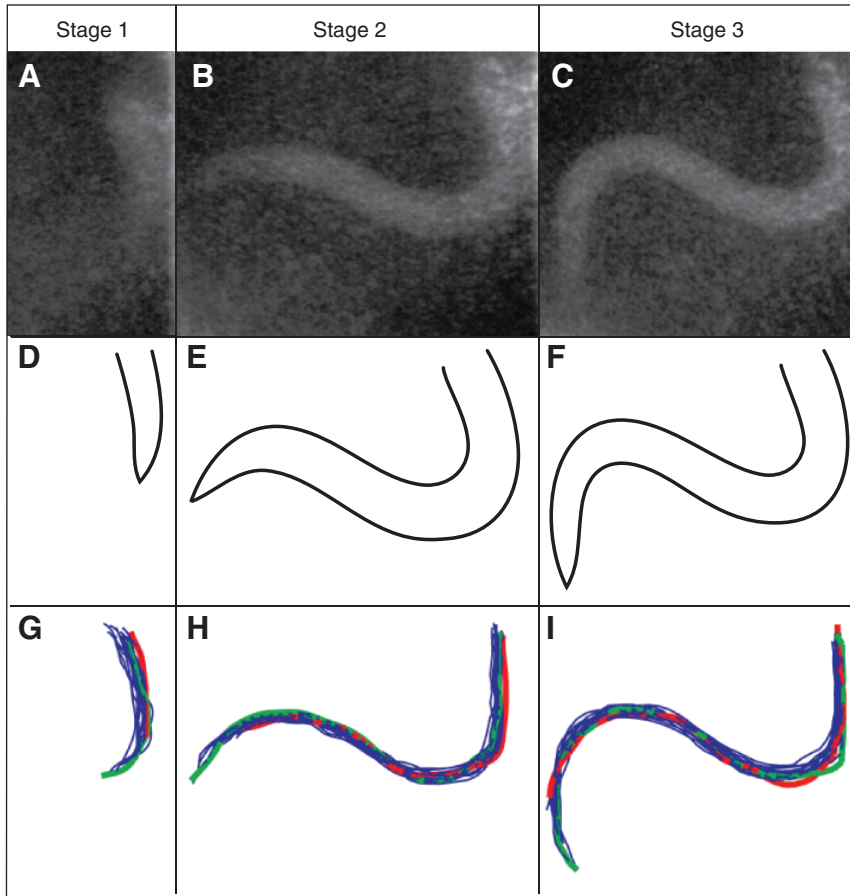


Fig. 5. Dorsoventral projection of below-ground undulatory movements in a representative burrowing sequence. Panels are organized as in Fig. 2, but are in dorsal view. Top row (A–C): selected X-ray frames. Middle row (D–F): drawings of the frames in the top row. Bottom row (G–I): reconstructed midlines of fifteen consecutive frames in the same lateral view. First frame shown in red, final frame in green, and remaining frames in blue. Stage 1 of burrowing is shown in A, D and G; Stage 2 in B, E and F; Stage 3 in C, F and I. Frame rate is 125 frames s^{-1} .

camera view), the animal makes a second lateral 90 deg bend in the opposite direction, pointing its head back in the original orientation of movement (Fig. 3C,F,I). The frequency of undulation is also greatly reduced (Fig. 5G,H,I) from that of the above-ground portions of the body (Fig. 3, same panels). Underground, Stages 2 and 3 are indistinguishable from each other on the basis of radius of curvature of the fish (Fig. 4; $P=0.6222$ in a paired t -test, $N=10$) and are more curved than above-ground portions of the body in all stages (Fig. 4, $P=0.001$ in a standard t -test, $N=20$). In all stages the undulations below ground, have a non-slipping wave pattern.

Kinematic timing

Synchrony can be identified by comparing the relative timing of kinematic events (Fig. 6). Nose-touch is the principal kinematic event of the burrowing process (we use nose-touch as the initiation point of the burrowing sequence and the point at which the tail is completely submerged in sand as the end of the burrowing sequence) and is followed by the first subterranean lateral bend after a variable delay. The second subterranean bend is likewise variable in its timing (paired t -test of first bend *versus* second bend timing; $P=0.0001$, $N=10$) and the tail stop is also significantly different in timing from the first lateral bend (paired t -test, $P=0.0001$, $N=10$). The only kinematic events that occur reliably in concert are the second lateral bend and the ceasing of tail movement (paired t -test, $P=0.2796$, $N=10$). These two variables always occur within 0.1 s of each other, although their relative order varies.

DISCUSSION

We have shown that sand lances exhibit different modes of undulatory locomotion depending on the environment with which

they are in contact. Furthermore, the change in locomotor kinematics occurs abruptly at a specific point during the burrowing process, before which aquatic thrust, by way of the tail, is the predominant mode of propulsion. Once enough of the body is underground, the anterior portion of the body takes over, and the tail ceases force-generating movements. While swimming, sand lances maintain the stereotypical anguilliform mode in which the undulatory wave travels faster posteriorly along the body than the animal itself travels anteriorly – the hallmark of slipping wave locomotion. Once

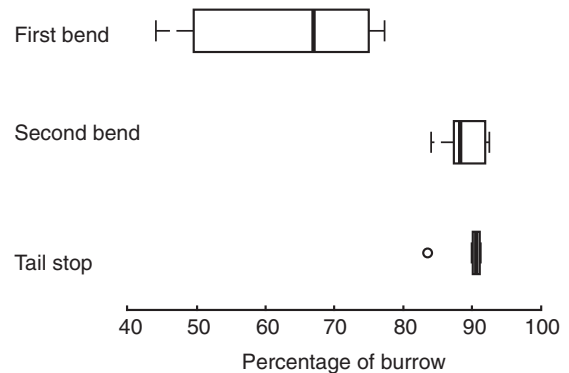


Fig. 6. Timing variables of kinematic events during burrowing of the Brown fish. Lateral (subterranean) bends were identified using the cinefluoroscope; tail stop identified using the standard camera. The timing of the second lateral bend and tail stop are not statistically significantly different (paired t -test, $P=0.2796$). Bold lines indicate the median; boxes encompass 25th to 75th percentile, whiskers indicate the range of the data. Statistical outlier indicated with an open circle.

subterranean propulsion has commenced, however, the observed kinematics change, becoming more snake like. Similarly, eels that leave water and travel terrestrially also locomote in a snake-like manner (Gillis, 1998), though they do slip somewhat on any substrate.

Aquatic locomotion and burrow initiation

In their burrowing sequence, sand lances are initially only capable of aquatic locomotion, yet they must propel themselves into a sand–water mix, which is more viscous and supportive of shear stress than water. We hypothesize two adaptations for burrowing in such a situation: (1) a pointed head with a bony projection from the dentary and (2) behavioral increases in undulation frequency and amplitude. Equipped with these morphological and behavioral attributes, the sand lance is able to propel itself into the sand water mix.

During Stages 1 and 2, the above-ground portion of sand lances exhibit slipping wave locomotion (Fig. 3, first two columns). This is not surprising because these animals are pushing off against water, rather than solid, non-moving points, to propel themselves forward. In Stage 2, the increases in amplitude and frequency become evident, indicating a more dedicated ‘push’ into the substrate. One important way that this mode of locomotion is different from typical eel-like locomotion is the nearly complete lack of head yaw (Fig. 3G,H). This is the result of the head being planted into the substrate and may serve to more directly orient propulsive forces into the sand.

Once the animal is approximately two-thirds submerged in the substrate – i.e. at the beginning of Stage 3 – it abruptly and fundamentally changes its mode of locomotion. The previously important undulations of the non-buried portion of the body cease, suggesting the tail’s uselessness as a propulsive organ in the final stage of the burrowing sequence.

Underground locomotion

Subterranean undulatory kinematics of sand lances resemble terrestrial snake locomotion in having a non-slipping wave pattern. During terrestrial locomotion, snakes rely on surface irregularities in the substrate – such as pebbles, tufts of grass, or asperities in the ground – and frictional anisotropy of the scales to push themselves forward (Jayne, 1986; Hu et al., 2009). Some snakes are capable of locomotion with a single peg fastened to a low-friction floor, although having multiple points of substrate contact in a zig-zag configuration can aid in cancellation of lateral forces, which can allow for faster and more effective locomotion (Moon and Gans, 1998). These idealized zig-zags and the two sequential 90 deg bends observed underground in this study bear a striking resemblance to an experimental apparatus used by Gray and Lissmann to study snake locomotion, which is redrawn in Fig. 7 (Gray and Lissmann, 1950). In the tunnel, each wall registered forces acting normal to it. Snakes were allowed to travel voluntarily from point X to point Y. Although all walls were force sensitive, only walls F, D and B registered forces. Forces applied to wall D greatly exceeded those of walls F and B. Thus, the majority of propulsion as a result of lateral undulation in this apparatus is only possible after the snake completes two lateral bends and can push back against wall D, propelling itself forward. It should also be noted that prior to the second lateral bend, the snakes used concertina locomotion rather than typical undulatory locomotion.

For successful underground locomotion, sand lances must push against the sand to propel themselves forward. Given the experimental results of Gray and Lissmann and our observations of abruptly ceasing tail movements, we hypothesize that sand

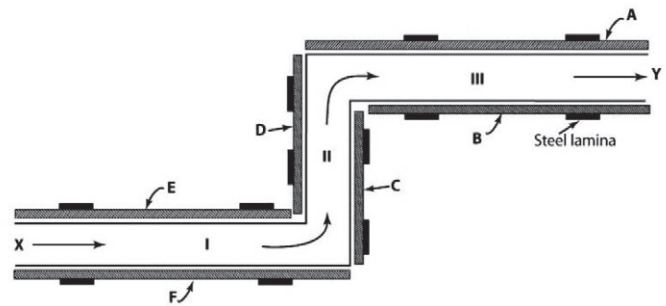


Fig. 7. Dorsal view of the experimental set up used by Gray and Lissmann. A–F are vertical force-sensitive walls supported by steel lamina. Snakes were released head-first into the tunnel at point X, passed through corridors I, II and III, then exited through opening Y. Redrawn from Gray and Lissmann (Gray and Lissmann, 1950).

lances are only able to impart forces onto the substrate underground once they have completed the second lateral bend (Gray and Lissmann, 1950). Prior to this, an alternative mode (i.e. augmented undulation of the aquatic portion of the tail) is needed to propel the animal into the substrate. After the second lateral bend, there is a section of the body that is normal to the desired direction of travel. It is with this segment that the sand lance is able to push posteriorly against sand – the analog of Gray and Lissmann’s wall D. The fact that this perpendicular region of the body does not move in world space (although it does travel posteriorly on the fish’s body), suggests that the sand posterior to that segment is capable of resisting static shear stress, and thus provides the equivalent of a ground reaction force to propel the animal forward. The fish’s 90 deg bends, we postulate, allow for stabilization and direction of that force in an analogous way to Gray and Lissmann’s walls F and B.

The point at which the sand lance has this ability (the time point of the second lateral bend) coincides with the time point of cessation in tail undulatory movements (Fig. 6). We hypothesize that this transition between Stages 2 and 3 marks the point of switching from an aquatic to a terrestrial propulsive mode. We did not directly measure muscle activity in this study, but we envision two possible scenarios for patterns of muscle activation in the transition from Stage 2 to Stage 3. First, the pattern of muscle activation could remain constant and the material property of the environment could be responsible for the observed change in kinematic pattern. Second, this kinematic shift could be the result of a different pattern of muscle activity – one more suited to subterranean locomotion. Our finding that the aquatic tail undulations cease (Fig. 3C,F,I), and that the tail passively glides into the sand during the final stage of burrowing, suggests that the wave of muscle activity passing down the body is not continuous from head to tail. We hypothesize that the shift between Stages 2 and 3 is the result of a shift in motor pattern. This new motor pattern may only require activation of the anterior portion of the axial musculature, allowing the tail portion of the body to follow passively.

Sand–body interactions

The same morphological adaptation that allows these animals to push off water and propel themselves through sand could explain why they are able to push off and through the sandy substrate without slipping. In an aquatic medium, despite having a pointed nose,

animals pushing on water induce flow, resulting in anguilliform kinematics. However, once completely buried, the sand lance is still pushing against and through the same medium – this time a sand–water mix – without observable flow of that medium. We explain this as an irregularity in how the substrate responds to stresses (Maladen et al., 2009). In a frictional fluid such as the sand–water mix, changes in weight distribution or areas where large surfaces are pushing (such as the side of the body or the tail) would be more supportive of shear stress than those where forces are concentrated – such as the nose. By taking a cone-shaped head and further supporting the pointed nose with a bony projection (Fig. 2), stresses could become even more concentrated, while, at the same time remaining fortified. Interestingly, Horner and Jayne showed that increasing the viscosity of an aquatic medium results in increased slipping of undulatory waves in lungfish, which have a less pronounced point at the anterior of the rostrum (Horner and Jayne, 2008). This underscores the importance of sand particle interactions beyond simple increases in viscosity, as well as the importance of stress concentration to sand lance locomotion mechanics. The mechanical explanation of exactly how the substrate responds to this projection is beyond the scope of this paper, but warrants further research.

One way for a sand lance to make its burrowing less energetically expensive might be to fluidize sand by rapid vibration of its head. This could change the water/sand ratio immediately around the head, which is an important parameter in defining how such an environment responds to forces exerted by an animal (Maladen et al., 2009). However, we see no evidence that the sand directly contacting the body of these fish is in any way fluidized, as the outline of the fishes in our X-ray sequences did not become blurred at the initial stages of burrowing. We also see no head yaw during slipping wave locomotion (Fig. 3H). The head of the sand lance, once buried, moves much more slowly than the above-ground portion of the body, and during Stage 1 it only translates anteriorly. The rapid, high-undulation movements of the non-buried portion of the body must be sufficient to propel the animal forward into the sand.

Comparison of air–sand transitions with water–sand transitions

Many vertebrates must modulate their locomotor strategies in response to the specific physical nature of their environment. Several species of legged lizards dig or burrow to escape from predators, heat and other adverse conditions. One such group is the iguanid genus *Uma*, which inhabit sandy deserts. These animals do not travel underground, but instead they use these burrowing events to cover themselves in sand. The kinematic progression of *Uma* burrowing bears a striking resemblance to that of sand lances – summarized below, based on accounts in Stebbins (Stebbins, 1944) and Jayne and Daggy (Jayne and Daggy, 2000). During surface locomotion, the lizards use typical four-limbed undulatory locomotion. At the start of a burrowing sequence, the anteriorly extended limbs are retracted to force the head into the ground using the inertia of the body. As the head is thrust downward into the sand, it undulates laterally at the neck, with quick, low-amplitude oscillations. Next, the forelimbs are pressed flat against the body and the hind limbs begin a vigorous push to submerge the majority of the animal. Following this, the (non-undulating) tail is vibrated to finish the burying task. Analogs of the lateral undulations of the head and vibration of the tail in lizards are not observed in sand lances. However, the progression begins with inertial thrusting of the head into the sand (i.e. Stage 1 in the sand lance's burrowing sequence) followed by a propulsive stage (i.e. Stage 2) and

subsequently a retraction of the propulsive tools (legs and tail in *Uma* and the tail in *Ammodytes*) into the substrate. The similarity in progression of burrowing events in *Uma* and *Ammodytes* is remarkable.

The sandfish – a member of the genus *Scincus* – is another lizard that exhibits sand burrowing. The burrowing behavior of these animals was recently investigated using NMR and X-ray imaging (Baumgartner et al., 2008; Maladen et al., 2009). Unlike other lizard species such as those mentioned above, sandfish fluidize the sandy bed by high-speed undulations and capitalize on the low viscosity of the air–sand mix to ‘swim’ using their limbs. The limbs are thought to be used to modulate local compaction, thus providing a local, ephemeral push point onto which the animal can exert force (Baumgartner et al., 2008). Other investigators of sandfish locomotion have found that arms are not used, but rather large amplitude undulations are sufficient (Maladen et al., 2009). Maladen et al. found, in contrast to the present study, that sandfish undulatory locomotion involves slipping wave locomotion (Maladen et al., 2009).

Concluding remarks

We have shown that a sand–water mix can respond differently to different parts of the sand lance's body; the pointed nose pushes through sand, whereas the body pushes against sand. One avenue that requires further exploration is experimental variation of the resistance to shear stress of the substrate. Sand lances operate in one manner in water and another in an undisturbed and settled sand–water matrix. However, these effects may be due to local variation in compaction, the viscosity of the substrate, a combination of the two, or other aspects of the media. Experiments that manipulate the rate of water flow through the sand separately from sand density could help distinguish the relative roles of these effects.

Substrate heterogeneity is another interesting avenue of research that deserves exploration. Despite substrate homogeneity, we have shown heterogeneity in the substrate's reaction to forces exerted by the sand lance. It is unclear whether this is a passive attribute of the substrate or actively modulated by the sand lance to optimize metabolic efficiency (or some other variable). Also, we have not been able to examine whether sand lances are able to modify their locomotion to take advantage of larger particles (pebbles and stones) or heterogeneous substrates that would inevitably be present in their natural environment.

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