

ENVIRONMENTAL EFFECTS ON UNDULATORY LOCOMOTION IN THE AMERICAN EEL *ANGUILLA ROSTRATA*: KINEMATICS IN WATER AND ON LAND

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Summary

Historically, the study of swimming eels (genus *Anguilla*) has been integral to our understanding of the mechanics and muscle activity patterns used by fish to propel themselves in the aquatic environment. However, no quantitative kinematic analysis has been reported for these animals. Additionally, eels are known to make transient terrestrial excursions, and in the past it has been presumed (but never tested) that the patterns of undulatory movement used terrestrially are similar to those used during swimming. In this study, high-speed video was used to characterize the kinematic patterns of undulatory locomotion in water and on land in the American eel *Anguilla rostrata*. During swimming, eels show a nonlinear increase in the amplitude of lateral undulations along their bodies, reaching an average maximum of $0.08L$, where L is total length, at the tip of the tail. However, in contrast to previous observations, the most anterior regions of their bodies do not undergo significant undulation. In addition, a temporal lag (typically 10–15% of an undulatory cycle) exists between maximal flexion and displacement at any given longitudinal position. Swimming speed does not have

a consistent effect on this lag or on the stride length (distance moved per tailbeat) of the animal. Speed does have subtle (although statistically insignificant) effects on the patterns of undulatory amplitude and intervertebral flexion along the body. On land, eels also use lateral undulations to propel themselves; however, their entire bodies are typically bent into waves, and the undulatory amplitude at all body positions is significantly greater than during swimming at equivalent speeds. The temporal lag between flexion and displacement seen during swimming is not present during terrestrial locomotion. While eels cannot move forwards as quickly on land as they do in water, they do increase locomotor speed with increasing tailbeat frequency. The clear kinematic distinctions present between aquatic and terrestrial locomotor sequences suggest that eels might be using different axial muscle activity patterns to locomote in the different environments.

Key words: locomotion, swimming, kinematics, behavior, eel, *Anguilla rostrata*.

Introduction

Transitions between aquatic and terrestrial environments have occurred repeatedly during the course of vertebrate evolution and also occur regularly during the life history of a number of vertebrate taxa. While such a transition presents respiratory and osmotic challenges to an organism (Little, 1983; Dejours *et al.* 1987), moving from the viscous, buoyant medium of water into the less-viscous, gravity-dominated terrestrial environment is also likely to present biomechanical challenges for the musculoskeletal system of an organism (Martinez, 1996). Often, as during the ontogeny of many amphibian taxa, drastic changes in locomotor morphology and/or mode occur in concert with the environmental transition in order to overcome such biomechanical problems (Duellman and Trueb, 1986). In contrast, however, there are also vertebrate taxa that undertake transitions between aquatic and terrestrial environments (typically over a shorter time scale) and do not undergo any morphological changes before doing so. For example, elongate vertebrates (e.g. many snakes and

various fish taxa) can often move about both in water and on land using axial-based locomotion to propel themselves in both environments (Jayne, 1988; Gordon and Olson, 1995).

Axial-based undulatory aquatic locomotion is common to many fishes, amphibians and reptiles, and the patterns of undulatory movement used by such taxa during swimming have received much recent attention from organismal biologists (Videler and Hess, 1984; Jayne, 1985; Wassersug and von Seckendorff Hoff, 1985; Graham *et al.* 1987; Dewar and Graham, 1994; Jayne and Lauder, 1995; D'Aout and Aerts, 1997; Gillis, 1997). Additionally, numerous kinematic analyses of axial bending during terrestrial locomotion in amphibians and reptiles have also been performed over the last 15 years (Jayne, 1986; Gans and Gasc, 1990; Ritter, 1992; Ashley-Ross, 1994; Gans and Fusari, 1994). However, very little work has been carried out comparing axial undulatory movements between aquatic and terrestrial environments either among different species or within the same species (see Jayne,

1988; Frolich and Biewener, 1992, for exceptions). This lack of work might be due to assumed similarities between axial undulatory locomotion in water and on land (Gray, 1946, 1968). Yet studies examining lateral undulatory locomotion on land in snakes suggest that all parts of the body tend to follow the same general path of travel, implying that undulatory movements should be of similar amplitude along the length of the body. This is in marked contrast to the typical pattern of increasing amplitude observed along the body of swimming fishes. Thus, if we are to test whether the axial musculoskeletal system of a laterally undulating organism functions differently on land from in water, we first need quantitative data on the patterns of movement used in both environments by that organism.

Undulatory locomotion in American freshwater eels *Anguilla rostrata* provides an excellent system with which to address questions regarding axial movements in both aquatic and terrestrial environments for several reasons. First, anguillid eels are known to make short-term transitions between water and land in the wild (Gray, 1968; Tesch, 1977; Lindsey, 1978), so brief bouts of terrestrial locomotion are natural behaviors in this species. Second, unlike many tetrapods that can use their axial and/or appendicular musculoskeletal systems to locomote in water or on land, eels exclusively use their axial musculoskeletal system to move about in both environments, affording the opportunity to examine how physical differences between environments affect locomotion without confounding effects due to the use of different morphological systems. Furthermore, although previous studies of swimming in eels have been integral to our current understanding of the mechanics and muscle activity patterns used by fish during swimming (Gray, 1933; Grillner and Kashin, 1976), a quantitative analysis of eel swimming kinematics has yet to be performed.

Therefore, in the following study, I examine the patterns of movement used by the American freshwater eel *Anguilla rostrata* during undulatory locomotion in both an aquatic and a terrestrial environment. My three goals are (1) to describe the kinematics of swimming in eels over a twofold range of speeds, (2) to describe the axial movements used during terrestrial undulatory locomotion by eels, and (3) to compare the movements used by eels during swimming with those used during terrestrial locomotion. Specifically, it will be of interest to examine whether eels use movements similar to terrestrially undulating snakes while on land (i.e. all parts of the body follow a similar path of travel and have similar degrees of lateral displacement), but use the movements more typical of a swimming fish when in water (different regions of the body follow different paths, with lateral amplitude increasing posteriorly).

Materials and methods

Animals

Kinematic data were collected from four *Anguilla rostrata* (LeSueur) [34.5–39.0 cm total length (L), mean 35.9 cm]

obtained from Anguilla Fish Farm, South Carolina, USA. Animals were housed individually in 40 l aquaria and provided with 30–40 cm pieces of polyvinyl chloride tubing used for hiding during daylight hours. Eels were fed a maintenance diet of earthworms (*Lumbricus* sp.) twice weekly. Water temperature within aquaria was kept at $19.5 \pm 1.5^\circ\text{C}$, and a photoperiod of 12 h:12 h L:D was established and maintained.

Aquatic kinematic data collection

Methods used for video-taping swimming eels are described in more detail in Gillis (1997). Briefly, eels were video-taped from a ventral view (Fig. 1) at 250 fields s^{-1} swimming in a flow tank (working section 28 cm \times 28 cm \times 78 cm) at three velocities: 0.4, 0.7 and 1.0 total lengths per second ($L\text{s}^{-1}$) using a NAC high-speed video system. Owing to the lengthy process of analyzing swimming movements, only two swimming speeds were used to address kinematic patterns and to test for obvious speed effects on swimming kinematics (0.4 and 1.0 $L\text{s}^{-1}$). These two speeds largely encompass the range of speeds obtained during terrestrial undulatory sequences used for analysis (described below). The third speed (0.7 $L\text{s}^{-1}$) was used only to help characterize the relationship between swimming speed and tailbeat frequency.

Flow speed within the flow tank was calibrated using dye injections 0.5–1.0 cm above the bottom of the tank. As in

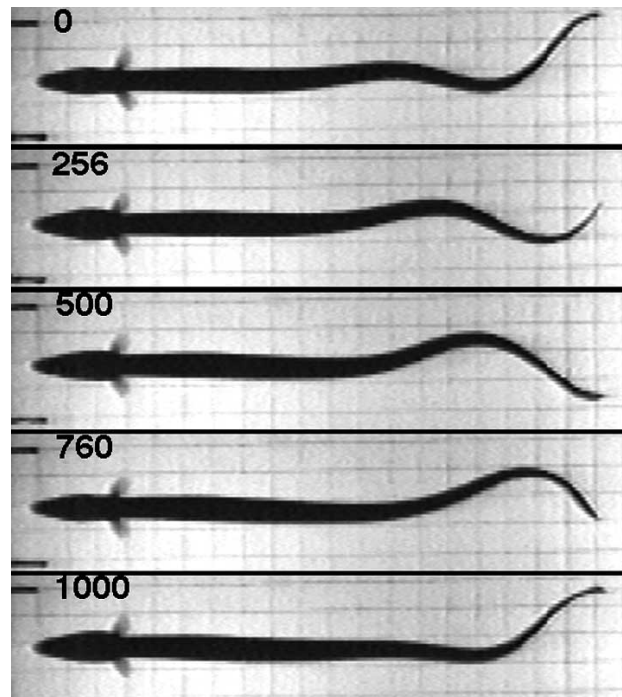


Fig. 1. A series of video images (ventral view) showing one complete tailbeat cycle from a 39 cm total length (L) individual swimming at $0.4 L\text{s}^{-1}$. The numbers in the upper left-hand corner of each image represent the time elapsed, in milliseconds, relative to the top image. Note that only the posterior half of the animal undergoes lateral undulations during swimming at this speed. The scale of background grid is 2 cm \times 2 cm.

previous experiments (Gillis, 1997), animals usually swam at the bottom of the flow-tank, and only sequences in which animals were swimming in this position were used for analysis. Gap:span ratios were calculated for all swimming trials (Webb, 1993). Values of the average gap (harmonic mean of the distances of the tailtip from the side walls of the flow tank at its lateral extremes and at midbeat) ranged from 10.8 to 12.4 cm. Values of the span (depth of the tail near its tip) ranged from 1.5 to 2.0 cm. Hence, all gap:span ratios were greater than 3.0, implying that the side walls of the tank were probably not influencing the swimming behavior of the animals (Webb, 1993).

Four tailbeat cycles were video-taped for each individual at each swimming speed. Twenty video fields evenly spaced in time were captured (Video Blaster; Creative Labs, Inc.), downloaded and analyzed within each tailbeat cycle, in addition to five video fields before the start of the first cycle and five video fields after the end of the last cycle.

Terrestrial kinematic data collection

Using a NAC high-speed video system, eels were video-taped from a dorsal view at $250 \text{ fields s}^{-1}$ undulating across wet, packed sand in a circular, inflated plastic wading pool (1.3 m diameter). To make the terrestrial substratum, sand and water were mixed with a 3:1 volume ratio and then packed by hand into the wading pool to a depth of 1 cm. Sand was then smoothed and flattened using a straight edge. Sand grain size ranged from 0.06 to 6.78 mm^3 ($0.95 \pm 1.22 \text{ mm}^3$, mean \pm S.D., $N=40$). Movement of eels across the substratum tended to create indentations in the sand; therefore, eels were typically allowed to perform only three locomotor sequences in a row before the sand environment was smoothed and repacked for the next set of sequences.

Average forward velocity for a terrestrial sequence was calculated as the total straight-line distance moved by a point at $0.40L$ (approximated center of mass of eels based on data from Webb and Weihs, 1994, for *Anguilla anguilla* of similar size) from the beginning to the end of a sequence, divided by the time required to move that distance. Although locomotor direction and speed could not be controlled, sequences were subsequently chosen for analysis in which the animal was moving steadily in one direction and speed was at least

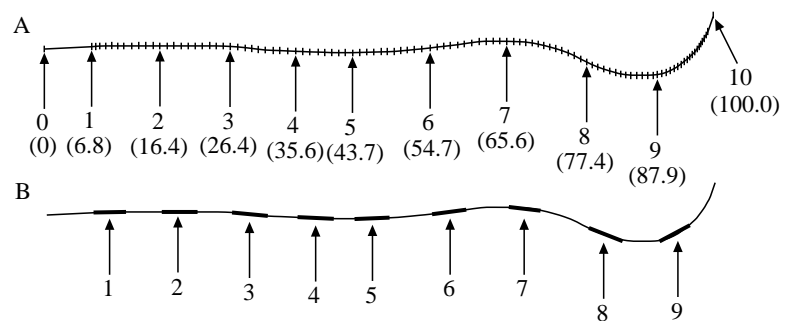
$0.3Ls^{-1}$ (to allow comparable speeds to be examined across environments). Speeds from terrestrial locomotor sequences used for analysis ranged from 0.3 to $0.6Ls^{-1}$ (the fastest recorded) and averaged $0.44Ls^{-1}$.

Four tailbeat cycles were video-taped and analyzed for each individual in the terrestrial environment. However, because the animal typically moved out of the field of view of the camera after approximately 2.5 tailbeat cycles, two video sequences (each consisting of at least two tailbeat cycles) were used for each individual. Twenty video fields evenly spaced in time were captured (Video Blaster; Creative Labs, Inc.), downloaded and analyzed within each tailbeat cycle, in addition to five video fields before the start of the first cycle and five video fields after the end of the last cycle.

Image analysis

Eel outlines (from ventral view during swimming and from dorsal view during terrestrial locomotion) were digitized from each of the video fields downloaded from all locomotion sequences. Ninety points were digitized around the animal's body, and a custom-designed computer program (described in detail by Jayne and Lauder, 1993, 1995) was then used to create a smooth eel outline and to construct the midline of that outline. To divide the midline into segments approximating axial skeletal elements, X-ray photographs were taken of four eels of similar size (36–39 cm total length). Absolute lengths of all skeletal elements were then measured for each of these four individuals and converted to relative lengths per individual. Individual vertebral counts varied from 102 to 106, but longitudinal variation in vertebral size was consistent across individuals. An 'average' eel midline, consisting of a skull, 104 vertebrae, and a small segment corresponding to the convergence of the dorsal and anal fins posteriorly, was then calculated and used to divide the constructed midlines into 106 axial segments (Fig. 2A). All axial segments are defined as straight lines, and the flexion between any two consecutive elements is known. To investigate movements along the entire length of the animal's body (at approximately $0.1L$ increments), 11 midline points were subsequently analyzed for each locomotor sequence: the tip and base of the skull (points 0 and 1), and nine points approximately evenly distributed ($0.08\text{--}0.12L$ between any two points) along the rest of the body

Fig. 2. (A) Constructed eel midline divided into segments representing elements of the axial skeleton (the relative lengths of these elements were derived from X-ray photographs of four individuals of similar length). The kinematics of 11 points (0–10) distributed longitudinally along the body were analyzed. Below the number of each point is the proportionate distance of the point from the tip of the snout (in % total length, L). Note the proportionate increase in the number of vertebrae per unit length in the distal tail region. (B) The same midline as in A divided into nine linear segments (each $0.05L$) used to analyze the lateral velocity, path angle and orientation of different regions of the eel's body.



(Fig. 2A). In addition, an analysis of the orientation and movements of nine linear segments along the length of the body, each $0.05L$ and originating from midline points 1–9, was performed (Fig. 2B).

Kinematic variables

Maximum lateral displacement (z_{\max}) of the 11 midline points was calculated for all tailbeat cycles as the average distance traveled between the extreme lateral excursions of each cycle, divided by two (to account only for excursions from the midline to one lateral extreme). Maximum flexion (B_{\max}) between the vertebrae (or between the skull and the first vertebra) was calculated for the intervertebral joints located at points 1–9 (Fig. 2A) as the average maximum angular excursion at a joint, divided by two (to account for the fact that excursions encompass flexion to both the left and the right). The phase lag (z – B lag) between maximum displacement to one side and maximal flexion concave to the opposite side was also calculated. All phase lags were calculated as a proportion of a tailbeat cycle. A positive z – B lag indicates that maximum displacement occurred prior to maximum flexion, whereas a negative lag indicates that flexion occurred before displacement.

Maximum lateral velocity, path angle and orientation were calculated for nine linear body segments (Fig. 2B) for one individual swimming at both swimming speeds and for one individual undulating on land. Each segment's lateral velocity was determined between all consecutively sampled video fields as the lateral distance traveled by the midpoint of the segment divided by the time that elapsed between fields. The path of each segment was defined as the straight line connecting the midpoint of that segment between each pair of sampled video fields, and the path angle was then calculated as the angle subtended by the path relative to the animal's direction of forward travel. The orientation of each segment was calculated for each video field as the angle subtended by the segment relative to the animal's direction of forward travel. For a more detailed description of how path angle and orientation are defined and calculated, see Fig. 4 and associated text in Gillis (1997).

Average tailbeat cycle time was calculated as the average time required for the tip of the tail to move through one undulatory cycle. Tailbeat frequency was then calculated as the inverse of tailbeat cycle time.

For all aquatic sequences, the speed of the mechanical wave traveling along the body was calculated. For sequences at $0.4Ls^{-1}$, average wave speed was calculated from $0.6L$ to $1.0L$ by dividing the distance along the body between these sites by the time lag between maximum lateral displacement at these sites. At this low speed, wave speed could not be calculated anterior to $0.6L$ because lateral undulations were too small (or nonexistent) to measure consistently anterior to this point. For sequences at $1.0Ls^{-1}$, wave speed was calculated as described above but from $0.4L$ to $1.0L$ (wave velocity along the additional 20% of the body could be determined accurately at the higher speed due to increased lateral undulations

anteriorly). To examine whether wave speed changed with longitudinal position, wave speed was also calculated in $0.2L$ increments at each speed (0.6 – $0.8L$ and 0.8 – $1.0L$ at the low speed and 0.4 – $0.6L$, 0.6 – $0.8L$ and 0.8 – $1.0L$ at the high speed).

In addition, for a single, representative individual, propulsive wavelengths were calculated during all cycles for both swimming speeds. Following Webb *et al.* (1984), half-wavelengths were measured by superimposing the x coordinates of the tip of the snout from eel midlines 180° out of phase. The length of each half-wave along the body was then multiplied by two to estimate the propulsive wavelength.

To describe further the patterns of movement used during terrestrial undulatory locomotion, velocity profiles of three longitudinal sites (3, 6 and 8; Fig. 2A) were calculated from four terrestrial locomotor sequences (two from each of two individuals). Following Jayne's (1986) work using quantitative, graphical definitions of terrestrial undulatory locomotor modes in snakes, velocities in the x (V_x) and y (V_y) dimensions were calculated at each site between every pair of sampled images by determining the distance moved by that site in the x and y dimensions, respectively, and dividing that by the time interval between sampled images. In addition, resultant velocities (V_r) were calculated by summing the x and y vectors.

Statistical analyses

In addition to the calculation of basic statistics (mean and standard error) for the kinematic variables described above, analyses of variance (ANOVAs) were performed to test for the effects of individual, swimming speed, longitudinal position or environment on all variables for which data were collected from all individuals (thus excluding the analyses of propulsive wavelength and segment lateral velocity, path angle and orientation, which were determined for only one individual). For aquatic sequences, the effects of swimming speed, body position and individual on maximal displacement (z_{\max}), maximal flexion (B_{\max}) and their timing relative to one another (z – B lag) were tested using three-way mixed-model ANOVAs (Sokal and Rohlf, 1981). Similarly, the effects of speed, position and individual on the traveling wave speed were also tested using a three-way mixed-model ANOVA. A two-way mixed-model ANOVA was used to analyze the effects of speed and individual on tailbeat period and frequency. For terrestrial sequences, two-way ANOVAs were used to determine the effects of longitudinal position and individual on z_{\max} , B_{\max} and z – B lag. Finally, one-way ANOVAs were used to determine the effects of environment on z_{\max} , B_{\max} and z – B lag by comparing all terrestrial sequences (mean velocity $0.44Ls^{-1}$; mean tailbeat period 927 ms) with aquatic sequences at $0.4Ls^{-1}$ (mean tailbeat period 982.5 ms).

For all ANOVAs, the fixed effects (speed, longitudinal position and environment) were tested over their respective interaction mean square (fixed effect \times individual) and the random effect (individual) was tested over the residual mean square. Interactions among variables were also tested over the appropriate mean square (Zar, 1984). To account for multiple simultaneous ANOVAs, the level of statistical significance was

adjusted (within a particular ANOVA model) within columns using the sequential Bonferroni technique described by Rice (1989).

Results

Aquatic kinematics

Eels swim by passing undulatory waves posteriorly along their bodies at a higher velocity than that at which they are swimming forwards. The amplitude of these undulatory waves is significantly affected by longitudinal position (Table 1), increasing nonlinearly from zero in the anterior regions of the body to near $0.08L$ at the tip of the tail (Fig. 3A). Speed has no significant effect on the amplitude of lateral displacement ($P=0.08$, Table 1). However, while it is clear that between 0.4 and $1.0 L s^{-1}$ speed does not affect the undulatory amplitude of the most anterior ($0-0.2L$) and posterior ($0.9-1.0L$) regions of the body, there is a tendency for the remaining portion of the body ($0.2-0.9L$) to undergo greater amplitude undulations at the higher swimming speed (Fig. 3A).

Longitudinal position also has a significant effect on intervertebral flexion (Table 1). Flexion increases from 0° at the base of the skull to a maximum of approximately 4° near $0.80L$ (Fig. 3B). Flexion then decreases along the rest of the tail as the number of vertebrae begins to increase per unit of tail length. Flexion, like undulatory amplitude, tends to be reduced at the lower speed over much of the body, although this effect was not significant after Bonferroni correction ($P=0.02$; in this case, P needs to be less than 0.017 to be significant after Bonferroni correction).

At a given longitudinal position, maximum lateral displacement and maximal flexion do not coincide in time. The temporal lag between flexion and displacement generally ranges from -0.1 to -0.2 cycles (flexion leading displacement in time) with no obvious consistent effect of longitudinal position or swimming speed, despite the high F -value for the speed effect (Tables 1, 2).

In the one individual for which variables associated with body segments were calculated, maximum lateral velocity,

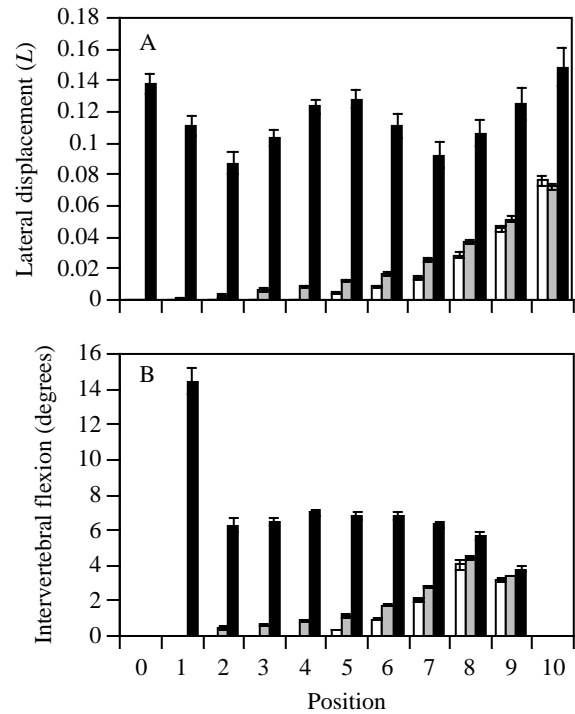


Fig. 3. Bar graphs of (A) average maximum lateral displacement (undulatory amplitude) and (B) intervertebral flexion at 11 and 9 positions along the body respectively (see Fig. 2A) for all individuals swimming in water at 0.4 and $1.0 L s^{-1}$, where L is total length, or undulating on land between 0.3 and $0.6 L s^{-1}$ (mean $0.44 L s^{-1}$). Vertical bars represent $0.4 L s^{-1}$ aquatic (white), $1.0 L s^{-1}$ aquatic (grey) and $0.3-0.6 L s^{-1}$ terrestrial (black) from left to right. Values are means + S.E.M. Amplitude and flexion are clearly greater along the entire body during terrestrial sequences. Note that eels show very little undulatory movement in the anterior regions of their body when swimming, particularly at the slow swimming speed. Each bar represents data from four individuals (four undulatory cycles per individual).

path angle and orientation of body segments all tend to increase along the length of the body (Fig. 4). In addition, each of these

Table 1. Three-way ANOVA results of the effects of longitudinal position (site), speed and individual on maximum lateral displacement z_{max} , maximum flexion B_{max} and the temporal lag between maximum displacement and flexion $z-B$ lag

| Variable | Site | Speed | Individual | Site × speed | Site × individual | Speed × individual | Site × speed × individual |
|-----------|---------------------|----------------|---------------------|-------------------|---------------------|--------------------|---------------------------|
| z_{max} | 203.6** (10, 30) | 7.0 (1, 3) | 124.4** (3, 264) | 6.2** (10, 30) | 13.4** (30, 264) | 32.3** (3, 264) | 4.4** (30, 264) |
| B_{max} | 153.6** (8, 24) | 22.7 (1, 3) | 75.6** (3, 216) | 2.6 (8, 24) | 11.3** (24, 216) | 21.3** (3, 216) | 6.6** (24, 216) |
| $z-B$ lag | 2.1 (7, 4) | 16.9 (1, 3) | 0.5 (3, 145) | 2.6 (4, 11) | 3.2** (19, 145) | 0.05 (3, 145) | 2.3 (11, 145) |

Data are from swimming eels only (four individuals, four cycles per individual at each speed).

Table entries are F -values, degrees of freedom are in parentheses.

**Significant at $P=0.005$, using the sequential Bonferroni method described in Rice (1989).

Table 2. Mean phase lags (proportion of a tailbeat cycle) between maximum lateral displacement (z) and maximum flexion (B) for different longitudinal body positions (see Fig. 2A) for eels moving in both aquatic and terrestrial environments

| Longitudinal position | Aquatic | | Terrestrial |
|-----------------------|---------------|---------------|-------------|
| | 0.4 Ls^{-1} | 1.0 Ls^{-1} | |
| 1 | | | -0.06±0.02 |
| 2 | | -0.24±0.02 | -0.04±0.02 |
| 3 | | -0.08±0.03 | -0.01±0.02 |
| 4 | | -0.14±0.02 | 0.02±0.02 |
| 5 | -0.15±0.04 | -0.13±0.02 | 0.02±0.01 |
| 6 | -0.13±0.02 | -0.12±0.01 | 0.03±0.01 |
| 7 | -0.20±0.01 | -0.08±0.01 | 0.01±0.02 |
| 8 | -0.13±0.01 | -0.10±0.01 | -0.02±0.02 |
| 9 | -0.12±0.01 | -0.14±0.01 | 0.01±0.03 |

Values are means ± S.E.M.

Note that empty cells are present because of the lack of displacement or flexion at some sites.

Data are from four locomotor cycles from each of four individuals in either environment or at either speed.

L , total body length.

Table 3. Mean tailbeat period, stride length, traveling wave velocity (overall mean and for three longitudinal portions of the body) and slip (swimming velocity/traveling wave velocity) for swimming sequences only

| Variable | 0.4 Ls^{-1} | 1.0 Ls^{-1} |
|--|---------------|---------------|
| Tailbeat period (ms) | 982.5±30.7** | 402.5±6.9 |
| Stride length (L) | 0.39±0.01 | 0.40±0.01 |
| Wave velocity (Ls^{-1}) | 0.50±0.01** | 1.27±0.02 |
| Wave velocity at 0.4–0.6 L (Ls^{-1}) | | 1.34±0.04 |
| Wave velocity at 0.6–0.8 L (Ls^{-1}) | 0.48±0.02** | 1.24±0.03 |
| Wave velocity at 0.8–1.0 L (Ls^{-1}) | 0.52±0.01** | 1.25±0.02 |
| Slip (dimensionless) | 0.82±0.02* | 0.79±0.01 |

Data are from four individuals, four cycles per individual per speed. Values are means ± S.E.M.

* indicates significant difference between speeds at $P=0.05$;

** indicates significant difference between speeds at $P=0.001$.

Note that the empty cell is present because of a lack of displacement anteriorly at the slow speed.

L , total length.

variables also tends to increase with swimming speed at all locations (Fig. 4). The average maximum path angle is greater than the average maximum orientation, and all segments tend to reach their maximum path angle slightly after they have reached their maximum orientation (but coincident with reaching their maximum lateral velocity).

Tailbeat period decreases significantly with increased

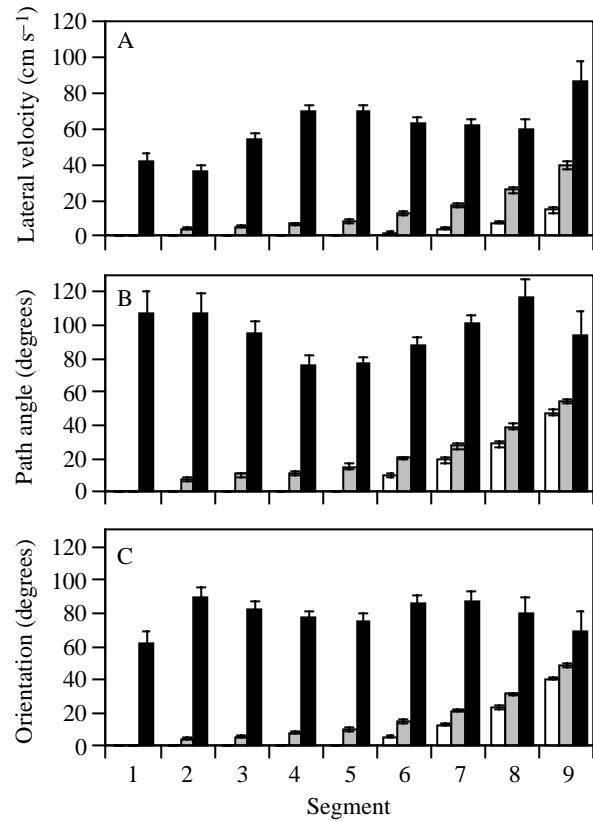


Fig. 4. Average maximum lateral velocity (A), path angle (B) and orientation (C) of nine longitudinally distributed linear segments (see Fig. 2B) of an eel moving in water at 0.4 and 1.0 Ls^{-1} or on land at 0.3–0.6 Ls^{-1} . Vertical bars represent 0.4 Ls^{-1} aquatic (white), 1.0 Ls^{-1} aquatic (grey) and 0.3–0.6 Ls^{-1} terrestrial (black) from left to right. Values are means + S.E.M. Lateral velocity, path angle and orientation are all greatest during terrestrial locomotion and also tend to increase with swimming speed. Note that these data are from four undulatory cycles of a single individual in each environment.

swimming speed and, as a result, tailbeat frequency increases significantly with swimming speed (Table 3). Although only three swimming speeds were examined, the relationship between tailbeat frequency f and swimming speed U (Ls^{-1}) can be approximated by $f=2.43U+0.042$ ($r^2=0.94$, $P<0.0001$; Fig. 5). Clearly this relationship might change with the inclusion of data from additional swimming speeds.

Swimming speed has a significant effect on the speed of the undulatory wave traveling posteriorly along the body, which averages $0.5±0.01 Ls^{-1}$ at the slow speed and $1.27±0.02 Ls^{-1}$ at the faster speed. There is no statistically significant effect of longitudinal position on traveling wave velocity ($P=0.09$). However, while wave velocity at a given swimming speed does not change between 0.6 and 1.0 L , at the faster swimming speed wave speed tends to be higher between 0.4 and 0.6 L than between 0.6 and 1.0 L (Table 3). The ratio of forward swimming speed to average mechanical wave speed (slip) averaged approximately 0.8 for both swimming speeds, though it is significantly higher at the slower speed (Table 3).

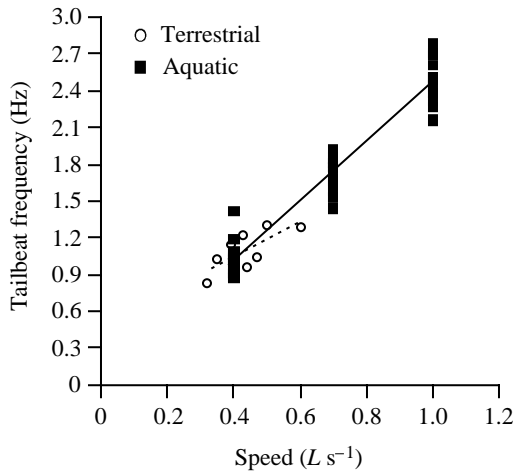


Fig. 5. Plot of tailbeat frequency as a function of locomotor speed for eels undulating in water (filled squares, solid line) and on land (open circles, dotted line). Note that points from terrestrial sequences show the same general relationship as those from aquatic sequences, with tailbeat frequency increasing with speed. Regression equations are given in the text.

Using only half-waves, propulsive wavelength varied from $0.4L$ to $0.64L$ across both speeds, averaging $0.48L$. Using full waves at the higher speed, propulsive wavelength varied from 0.44 to $0.54L$, averaging $0.49L$. Full waves were observed and could be measured at the higher swimming speeds because more anterior regions of the body also experienced lateral displacement. Although propulsive wavelength was similar for both speeds, fewer waves (between 0.5 and 1) were present along the body at any given instant at the slow speed since the

anterior one-third of the body underwent no lateral undulations and therefore formed no portion of a propulsive wave.

Terrestrial kinematics

Eels can locomote across a terrestrial substratum in a directional, coordinated manner in which their entire body undergoes high-amplitude undulatory movements (Fig. 6). All points on the body move in a wave-like fashion and follow a relatively similar path of travel (although some regions may occasionally deviate drastically from the path; Fig. 7). There is a significant effect of longitudinal position on maximum lateral displacement (Table 4; $P=0.014$), and Figs 3A and 7 suggest subtle variation in the amplitude of undulatory movements longitudinally. Specifically, regions near $0.16L$ and $0.66L$ show reduced undulatory amplitude, while the tip of the snout and tail tend to show increased undulatory amplitude.

Longitudinal position also has a significant effect on flexion (Table 4). Flexion is highest ($14-15^\circ$) between the skull and first vertebra, then decreases to $6-7^\circ$ along most of the rest of the body, finally decreasing to less than 4° along the distal region of the tail (Fig. 3B).

The temporal lag between maximum lateral displacement and flexion is not significantly affected by longitudinal position ($P=0.16$, Table 4), but is affected by environment ($P<0.0001$), typically varying between -0.03 and 0.03 on land, with the exception of the joint between the skull and the first vertebra (mean -0.06). Given the oscillations of these values around zero, it is unlikely that there is any real time lag between maximum flexion and maximum lateral displacement during terrestrial locomotion, and a two-tailed *t*-test confirms that the phase lag between flexion and displacement (data from all sites

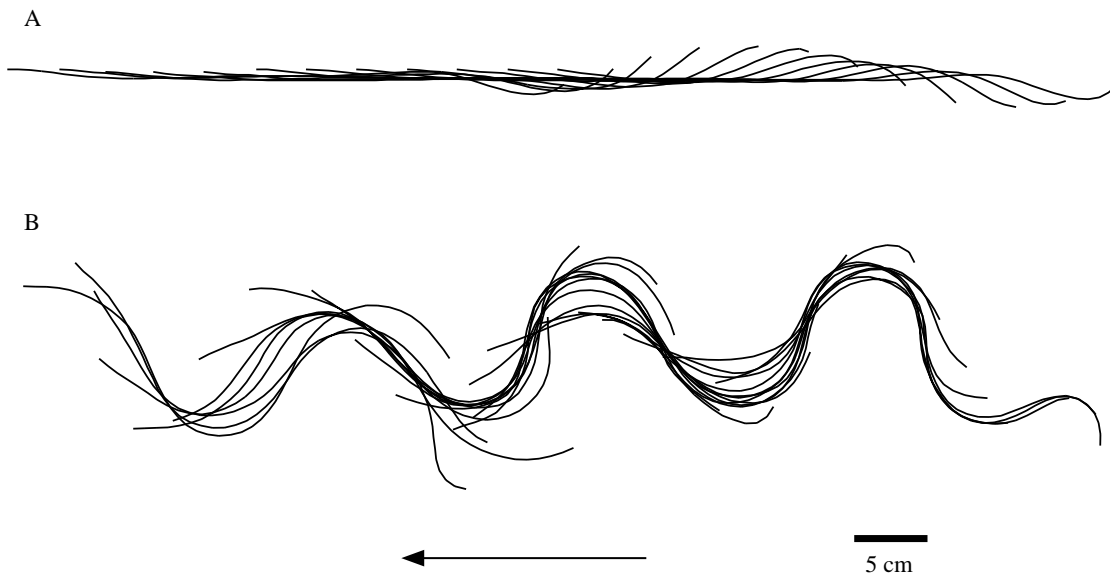
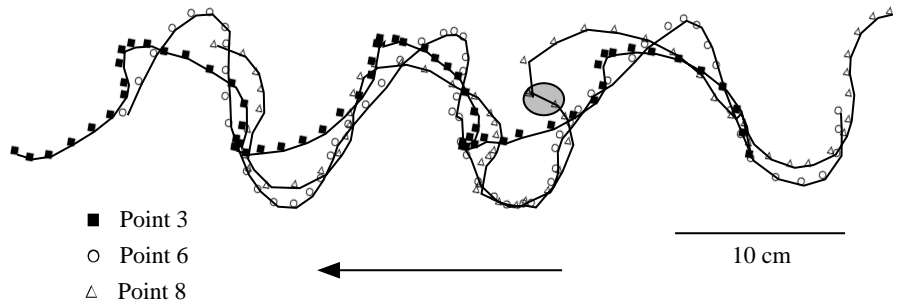


Fig. 6. A series of eel midlines derived from digitized locomotor sequences from the same individual (35 cm total length L) over several tailbeat cycles in both an aquatic (A) and a terrestrial (B) environment. The eel is moving with the same average forward velocity ($0.4L s^{-1}$) in both sequences. Note that, during the aquatic sequence, only the posterior half of the body experiences obvious undulations, while on land, the entire body is bent into a series of sinusoidal waves and traverses the environment with a number of high-amplitude undulatory cycles.

Fig. 7. Displacements of three longitudinally distributed points (see Fig. 2A) along an individual eel (point 3, filled squares; point 6, open circles; point 8, open triangles) during several terrestrial locomotor cycles. The animal has an average forward velocity of $0.5 L s^{-1}$ and is moving from right to left (40 ms between any two consecutive symbols). Note that points generally follow the same path of travel, although some differences in amplitude are present, and occasionally some points move backwards (see shaded circle for example) and/or out of the path of the others (note point 8 at the end of its first cycle, just prior to moving backwards).



and all individuals) is not significantly different from zero on land ($P=0.68$).

An analysis of body segments from one individual shows that the maximum path angle varies between approximately 80° and 120° , while the maximum orientation of body segments ranges from approximately 60° to 90° (Fig. 4). Interestingly, for several segments (4, 5 and 6), average maximum path angle and maximum segment orientation are identical, suggesting that, in this region of the body, the segments are actually oriented nearly exactly along their paths of travel, and two segments (4 and 5) appear to be following nearly the same path of travel with the same orientation. At certain sites, average maximum path angle is greater than 90° ; at these sites, the path of travel often consistently included a region in which that part of the body moved backwards relative to the overall direction of movement, producing a path angle of over 90° (see, for example, the circled portion of the path of point 8 in Fig. 7). At such sites, the body segments themselves are not oriented directly along their path of travel and instead subtend a much less extreme orientation relative to the direction of travel than does the path.

Table 4. Two-way ANOVA results of the effects of longitudinal position (site) and individual on maximum lateral displacement z_{max} , maximum flexion B_{max} and the phase lag between them z - B lag

| Variable | Site | Individual | Site \times individual |
|---------------|-------------------|--------------------|--------------------------|
| z_{max} | 2.8* (10, 30) | 3.8* (3, 132) | 2.8** (30, 108) |
| B_{max} | 41.3** (8, 24) | 15.1** (3, 108) | 3.3** (24, 108) |
| z - B lag | 1.6 (8, 24) | 1.0 (3, 108) | 1.6 (24, 108) |

Data are from terrestrially undulating eels only (four cycles from each of four individuals).

Table entries are F -values, degrees of freedom are in parentheses.

Significant at * $P=0.05$, ** $P=0.005$, using the sequential Bonferroni method described in Rice (1989).

Forward velocity during terrestrial locomotion ranged from 0.3 to $0.6 L s^{-1}$ (mean $0.44 \pm 0.03 L s^{-1}$, $N=8$), and tailbeat periods ranged from approximately 760 to $1200 \text{ ms cycle}^{-1}$ (mean $927 \pm 53 \text{ ms cycle}^{-1}$). In general, tailbeat frequency f increases with locomotor velocity U ($L s^{-1}$) according to the following equation: $f=1.37U+0.50$ ($r^2=0.53$, $P=0.04$), which is a slower rate of increase than during swimming (Fig. 5).

During the four terrestrial undulatory sequences examined for velocity profiles, the resultant velocity of three points along the body (3, 6 and 8) never fell to zero (see, for example, Fig. 8D), indicating that during terrestrial locomotion all portions of the body appear to be moving in some direction at all times. There is variation in the magnitude of the resultant velocity at each of the points throughout all cycles (Fig. 8D), with the coefficient of variation ranging from 0.22 to 0.62 in the four sequences examined for this variable. Additionally, the more anterior and posterior points (3 and 8) show consistently higher coefficients of variation for resultant velocity than does the middle point (6).

The velocity of body points in the x (V_x) and y (V_y) dimensions tends to oscillate cyclically during undulatory cycles (Fig. 8B,C). V_y oscillates around 0 (positive and negative values indicating movement to the right and left, respectively) and has a period similar to the body's undulatory period (e.g. tailbeat period) (Fig. 8C). V_x oscillates with half this period and often reaches zero or negative values, indicating that points stop moving forwards or even move slightly backwards periodically (Fig. 8B). V_x is greatest when body points are near their maximum lateral displacement, while V_y is greatest during times intermediate to this. Thus, V_x is greatest when V_y is close to zero, while V_y is greatest when V_x is close to zero (Fig. 8B,C).

Discussion

Gray (1968; p. 36–37) states in his comprehensive book on animal locomotion: 'As is well known, eels can travel long distances over land by means of movements which do not differ fundamentally from those which it exhibits when swimming freely in water'. However, as suggested by Lindsey (1978) and quantified in the present analysis, lateral undulatory amplitude in eels (and the underlying intervertebral flexion) is

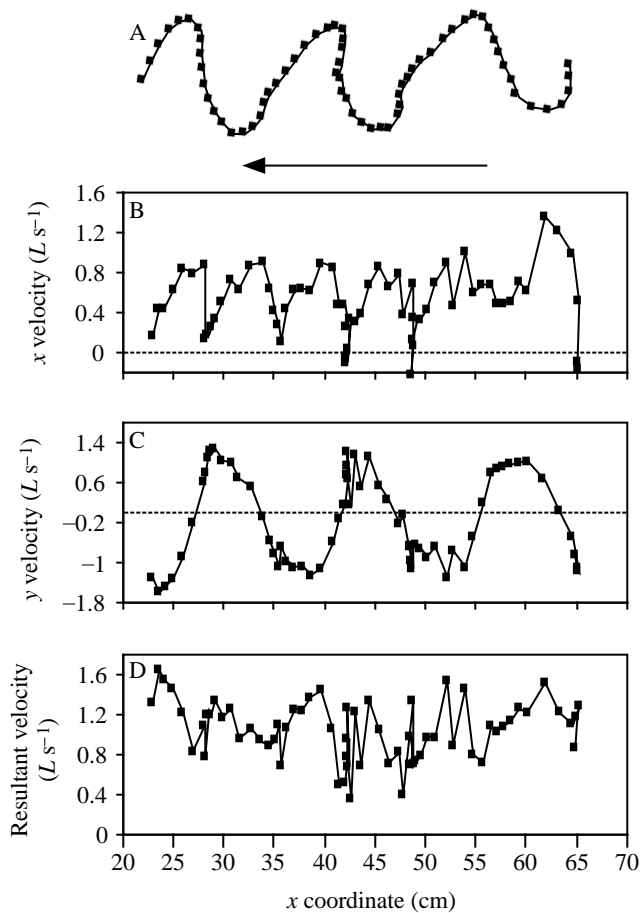


Fig. 8. (A) Plot of approximately three cycles of terrestrial undulatory displacement for one point midway along an eel's body (point 6; Fig. 2A), and the resulting calculated velocities in the x direction V_x (B) and the y direction V_y (C), and the resultant velocity V_r (D) for those cycles. Cycles are the same shown for point 6 in Fig. 7. Note that V_x and V_y oscillate together, with V_x having half the period of V_y . V_x periodically decreases to zero or negative values, while V_r never decreases to zero.

much greater on land than in water. In addition, the patterns of movement of the entire body are different on land relative to during swimming. When traversing the terrestrial environment, the eel's entire body is bent into obvious waves, and much of the body follows a similar path of travel, as is generally the case in a terrestrially undulating snake. However, in water this is not the case. Instead, the amplitude of lateral movements tends to increase along much of the body, and the path of travel of posterior portions of the body is very different from that of more anteriorly located regions. Furthermore, on land, some regions of the animal's body actually spend short periods moving slightly backwards over the course of an undulatory cycle, resulting in maximum path angles greater than 90° , while in water this is never observed (Figs 4, 7).

It is likely that these kinematic differences are not due to differences in the speed of the locomotor sequences across environments (speeds and undulatory frequencies overlapped

between environments), but rather are fundamental distinctions between the patterns of movement used in water and on land. Such fundamental distinctions may partly be the result of environment-specific axial muscle activity patterns, but this remains to be tested.

Swimming kinematics

The study of swimming in eels has played a historically important role in our understanding of axial locomotion in fishes in general. Breder (1926), for example, chose to use the genus name *Anguilla* to categorize the swimming behavior typical of flexible elongate fish (anguilliform mode). In addition, Gray's (1933) classic work on swimming in eels set a historical precedent in trying to relate the patterns of axial movements used by swimming fish to the production of forward thrust (Webb, 1975). Finally, Grillner and Kashin's (1976) work on the axial muscle activity patterns used during swimming in eels foreshadowed the growing body of recent investigations into the neuromuscular control of swimming behavior, and the role (or function) of axial muscle at different longitudinal positions in swimming fish. It is ironic that, despite such historical importance, very little quantitative information exists on the patterns of movement actually used by anguillid eels during swimming. In fact, it appears likely that our understanding of the swimming kinematics in these animals is incomplete and, in some instances, incorrect.

The general notion regarding the patterns of movement used by eels (or other anguilliform swimmers) during swimming is that undulatory waves are produced in the anterior region of the body and then passed posteriorly along the rest of the body, producing propulsive thrust. Such a notion was probably derived from and corroborated by Gray's (1933) work on swimming eels, in which his figures and photographic plates reveal *Anguilla vulgaris* swimming using large undulatory waves originating at the animal's head and passing posteriorly to the tail. The amplitude of undulatory displacement of the animal's snout is quite high, approximately one-third of the amplitude at the tip of the tail. These figures have led to the general impression in the more recent literature that eels have relatively high lateral undulatory amplitudes anteriorly and, therefore, generate thrust along their entire bodies while swimming (Williams *et al.* 1989; Wardle *et al.* 1995).

However, it is important to recognize that Gray's (1933) figures and photographs of a swimming *Anguilla vulgaris* are from a small, young individual (7 cm total length). Hence, much of our basic understanding of the patterns of movement used by eels during swimming is derived largely from the kinematic patterns of this one very small individual. Given that swimming kinematics probably changes with animal size in such a way that smaller fish tend to use movements with a higher relative amplitude than larger fish (Webb *et al.* 1984), such swimming patterns may be specific to smaller eels. In the present study, the kinematics of larger eels (35–39 cm total length) was analyzed during swimming, and the most striking result is the longitudinal pattern of undulatory amplitude along the swimming eel: undulatory amplitude is very low or

nonexistent (at the slow swimming speed) in the anterior regions of the body (Fig. 1). For example, at $0.4Ls^{-1}$, undulatory waves are not present along the body anterior to $0.4L$, and even at $1.0Ls^{-1}$ amplitude is extremely low over the anterior 20% of the body. Therefore, in these larger animals, at the two swimming speeds examined, thrust cannot be generated along the animal's entire body; in fact, at the slower swimming speed, thrust generally can only be produced over the posterior half of the body (Fig. 1). From personal observations, enhanced anterior undulations become progressively more pronounced at higher swimming speeds (greater than $1.0Ls^{-1}$) and during accelerations. During such circumstances, the animals use undulations of, and potentially generate thrust along, the entire body [i.e. use movements similar to those of the small eel depicted by Gray (1933) and a larger 36 cm European eel *Anguilla anguilla* in Grillner and Kashin (1976) although, unfortunately, the swimming speed of this larger eel was not reported].

In addition to having very low undulatory amplitude anteriorly, eels in the present study also had relatively low-amplitude undulations along their entire body, including the tip of the tail. The average maximum tailtip amplitude in this study was approximately $0.08L$ (Fig. 3A), which is substantially lower than the tailtip amplitude seen in other similarly sized elongate vertebrate swimmers such as snakes and elongate salamanders swimming at similar speeds (in which it typically ranges from 0.11 to $0.19L$; Jayne, 1985; Graham *et al.* 1987; Gillis, 1996, 1997). While many carangiform and subcarangiform swimmers tend to increase their tailtip amplitude and tailbeat frequency with increasing swimming speed across relatively slow speeds (Bainbridge, 1958; Webb, 1975), this is not the case in *Anguilla rostrata*, in which tailbeat frequency increases but tailtip amplitude remains similar at both 0.4 and $1.0Ls^{-1}$ (Figs 3A, 5). Rather than increasing tailtip amplitude, eels tend to increase the proportion of their bodies undergoing undulatory displacement and/or increase the magnitude of undulatory displacements along regions of the body other than the tip of the tail. Interestingly, this is a feature also seen during swimming in elongate salamanders (Gillis, 1997) and may be common in flexible, elongate vertebrate swimmers.

In other undulatory swimmers, swimming speed also often has effects on parameters such as stride length (distance traveled per tailbeat) and slip (ratio of forward swimming speed to speed of the traveling wave, which can be used to estimate mechanical efficiency; Lighthill, 1975). For example, in a variety of vertebrate swimmers, both stride length and mechanical efficiency tend to increase with swimming speed (at least across a range of speeds below $1-2Ls^{-1}$). However, in swimming eels, both stride length and slip show similar values for both 0.4 and $1.0Ls^{-1}$. Stride length approximates $0.4L$ per tailbeat at both speeds, while slip ratios are near 0.8 at both speeds and even decrease slightly, but significantly, with increasing speed (Table 3). It is unclear why eels do not show increases in these swimming parameters with swimming speed. It is possible that the range of swimming speeds

examined was too narrow to determine such trends, but this is unlikely since across a similar range of speeds, and using the same methodology, it was demonstrated that elongate salamanders showed the typical trend of increasing stride length and efficiency with speed common to most swimming vertebrates (Gillis, 1997).

Eels increase their tailbeat frequency with increases in swimming speed at a higher rate than some other anguilliform taxa, such as sirenid salamanders (Gillis, 1997) and water snakes (Jayne, 1985). However, only three speeds were examined in the present study, and Grillner and Kashin (1976) reported lower rates of increase in tailbeat frequency with swimming speed in *Anguilla anguilla*. In addition, unlike other anguilliform taxa examined to date, the speed of the traveling wave does not increase as it travels posteriorly along the body; instead, wave speed remains fairly constant.

Terrestrial undulatory kinematics

The movements used by eels out of water are similar to the serpentine movement (Gray, 1946) or lateral undulation (Gans, 1974) of snakes, in which the entire body is 'thrown' into a series of sinusoidal waves and all parts of the animal's body move simultaneously along a similar path of travel. However, as shown in Fig. 7, not all points move along exactly the same path of travel as would be expected in the case of true lateral undulatory behavior. Part of this difference is probably due to the inconsistency of the location of sites of lateral resistance found within the terrestrial environment used in this study. Lateral undulatory locomotion depends upon the presence of sites of lateral resistance against which the animal can push and propel itself forwards (Mosauer, 1932).

Many examinations of terrestrial lateral undulatory behavior in snakes have used pegs inserted in a pegboard to elicit lateral undulatory behavior (e.g. Bennet *et al.* 1974; Jayne, 1986). Such pegboards provide a very consistent spatial pattern of sites of lateral resistance, hence allowing for consistent and continuous thrust to be generated along most of the body (depending upon the number and spacing of the pegs). In contrast, the wet, packed-sand environment used in the present study will be much less consistent in terms of its spatial array of sites for thrust production. For example, across the sand, small, physical projections (such as vertical protrusions caused by imperfect smoothing or by mechanical interactions between the eel and the substratum prior to re-smoothing) are used by the body as sites of resistance for thrust production. Furthermore, while pegs on a smooth pegboard offer solid sites of lateral resistance and very little ventral resistance (assuming a smooth pegboard), the packed-sand environment offers relatively high ventral resistance, with fewer obvious sites of lateral resistance. Hence, an eel traversing wet, packed sand encounters spatially inconsistent sites of lateral thrust production and relatively high levels of ventral friction; as a result, the magnitude of thrust production is unlikely to be continuous along the body. In fact, the points on the body with the lowest lateral amplitude (points 2 and 7; Fig. 3A) generally also underwent periods with very low resultant velocity

(<0.25 Ls^{-1}), suggesting that these points had a greater purchase on the terrestrial substratum than did points with greater amplitudes and velocities, and may therefore be regions where relatively large levels of thrust are being produced.

In addition, owing to the eel's mucus-covered smooth surface and laterally compressed tail, it is likely that some points, particularly along the distal portion of the tail, will occasionally experience a brief failure of resistance (i.e. slip) relative to the environment. Therefore, despite the general use of a lateral undulatory mode of locomotion, it might be expected that some regions of the body would deviate from the path of travel of other regions of the body (Figs 4, 7), in addition to showing subtle differences in the amplitude of lateral displacement (Fig. 3).

Inconsistent lateral thrust production and occasional failures of resistance (especially in the distal regions of the tail) can also help to explain the variable, yet relatively low, forward velocities observed in the terrestrial locomotor trials (0.3–0.6 Ls^{-1}). It may be that eels were simply incapable of moving at higher forward speeds on this substratum. Snakes moving through pegboard arrays of appropriate spacing can move at much higher speeds (0.75–1.89 Ls^{-1} in 70–90 cm animals; Jayne, 1986), and it is possible that eels would be able to achieve higher velocities in such a pegboard array.

Jayne (1986) derived a graphical analysis of locomotor modes in terrestrially locomoting snakes. In this analysis, velocity profiles (V_x , V_y and V_r) were calculated for a point along the middle one-third of the animal's body, over several undulatory cycles. Jayne (1986) defined a sequence as lateral undulation if the coefficient of variation in V_r was less than 0.37. In examining V_r at a point near 0.5 L in four locomotor sequences from two individuals (two sequences per individual), the coefficient of variation (C.V.) in V_r was less than 0.37 in sequences in which average forward velocity was greater than 0.4 Ls^{-1} (mean C.V. 0.26), but was greater than 0.37 in sequences slower than this (mean C.V. 0.48). Therefore, only the faster sequences truly meet Jayne's (1986) definition of lateral undulatory behavior. However, the slower sequences did not meet Jayne's (1986) requirements for sidewinding or concertina locomotion (V_r never periodically reached zero), so it is unclear whether Jayne's (1986) graphical definition of lateral undulation is too restrictive or whether the eels were combining two or more locomotor modes (as suggested by Jayne, 1986, for occasions in which his criteria for defining a locomotor mode were not met).

Temporal lag between maximal flexion and displacement

It has been noted in several undulatory swimming vertebrates that the maximum intervertebral flexion at a point along the body is not coincident in time with that point's maximum lateral displacement (Jayne and Lauder, 1993, 1995, 1996; Gillis, 1997). In the present study, maximum flexion consistently occurs prior to maximum displacement at a given longitudinal position by approximately 0.1–0.2 cycles. In the terrestrial environment, however, this temporal lag between flexion and displacement is no longer present. As suggested by

Jayne and Lauder (1996), such a phase lag is not expected if the points along an undulating body all travel along the same sinusoidal path (which is at least approximated by terrestrially undulating eels).

More recently, S. L. Katz and R. E. Shadwick (in preparation) have suggested that a phase lag between maximum midline curvature and maximum lateral displacement (with flexion leading displacement in time) is a geometric result when undulatory amplitude increases along the body. The present eel data support this suggestion since eels do show such a phase lag while swimming (when amplitude increases longitudinally), but not during locomotion on land (when amplitude does not increase consistently along the body). An additional prediction from S. L. Katz and R. E. Shadwick's model is that the phase lag should increase longitudinally along the undulator's body and, while they have found this result in swimming mackerel (*Scomber japonicus*), it was not found in the present study for swimming eels nor for swimming sirenid salamanders *Siren intermedia* (Gillis, 1997), bluegill sunfish *Lepomis macrochirus* (Jayne and Lauder, 1993) or largemouth bass *Micropterus salmoides* (Jayne and Lauder, 1995). While it is clear that our methodologies are different [S. L. Katz and R. E. Shadwick measure midline curvature, while Gillis (1997, and present study) and Jayne and Lauder (1993, 1995) measure the actual flexion between axial structural elements], it is unclear why these methodological differences could have led to this discrepancy. All these results agree, however, that maximum lateral displacement and maximal intervertebral flexion or midline curvature do not occur simultaneously along an undulating swimmer with increasing amplitude along its body. Hence, maximum lateral displacement should not be used as an indicator of maximum muscle strain in studies correlating muscle activity and function with whole-body or midline kinematics.

Predictions for motor patterns and scaling of eel locomotion

Several results from this study suggest that further examination of undulatory locomotion in eels would be of interest. First, given that the kinematic patterns of locomotion on land and in water are so different, is it also the case that the underlying axial muscle activity patterns producing the axial movements are fundamentally different? If so, do muscle activity patterns differ in their temporal patterns (relative to kinematic events), in their extent of motor unit or fiber type recruitment, or both? Given that eels moving on land use large-amplitude undulations of their entire body, one would predict that the underlying sequence of muscle activation would also be distributed along the entire length of the animal's body. However, as lateral undulations are typically small or not present anteriorly during swimming, muscle activity might only be present in the posterior half to two-thirds of the body in the water. Furthermore, as a result of the effects of gravity and enhanced friction in the terrestrial environment, it is likely that eels will need to recruit red and white muscle maximally while traversing terrestrial substrata at speeds similar to those

recorded in this study ($0.3\text{--}0.6\text{Ls}^{-1}$). However, during swimming, only red muscle activity might be necessary to move at similar speeds.

Second, the kinematic patterns observed here are different from those described by Gray (1933) for much smaller eels, particularly in regard to the amplitude of the undulatory movements anteriorly. A detailed quantitative study of the scaling of locomotor kinematics in eels would help clarify how patterns of movement change with size in an anguilliform swimmer. Webb *et al.* (1984) found that, in trout, propulsive wavelength and undulatory amplitude become relatively smaller in larger fish. One could predict similar results for eels, yet it would be interesting to know whether body form and swimming mode have any effects on the nature or magnitude of the scaling relationships of kinematic parameters in swimming fish. By addressing issues such as these, we should gain a better understanding of the ways in which parameters such as the physical environment and organismal size affect the generation of undulatory movements during locomotion in elongate vertebrates.

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