Undulatory Locomotion in Elongate Aquatic Vertebrates: Anguilliform Swimming since Sir James Gray[1]

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SYNOPSIS. Anguilliform locomotion is the mode of undulatory swimming used by eels and other elongate vertebrates in which waves (of shorter length than the body of the animal) are propagated posteriorly along the length of the animal, propelling it forward. Although a broad array of vertebrate taxa convergently use this locomotor mode, much of what we know regarding the kinematics of anguilliform swimming derives from the classic work of Sir James Gray in the 1930s on the European eel, *Anguilla anguilla.* To better understand the variability within this phylogenetically widespread mode of locomotion, I have reviewed recent work on the swimming kinematics of elongate fishes, salamanders and snakes. The amplitude and relative speed of the undulatory waves propagated along the body during swimming differs among elongate vertebrate taxa, and can also vary with swimming speed. In addition, the lateral velocity and orientation of tail segments can reach their maxima at different times within a tailbeat cycle (in contrast to Gray's suggestion that these two events occurred simultaneously). Finally, the angle of attack of tail segments is negative during a consistent portion of each tailbeat cycle in the elongate salamander *Siren.* While this has yet to be examined in other anguilliform taxa, it is possible that they will also show this pattern. Hence, although Gray's descriptions of anguilliform swimming are generally accurate, gaining a broader understanding of this mode of locomotion requires the characterization of the diversity and complexity found among animals using this undulatory mode.

INTRODUCTION

Aquatic vertebrates span a broad range of shapes and sizes, and accordingly use a number of different locomotor modes to move about in their environments. Axial-based undulatory locomotion is probably the most widely used of these swimming modes and is typically organized into several categories based upon the proportion of the axial morphology involved in producing propulsive thrust (Breder, 1926; Lindsey, 1978; Webb and Blake, 1985). Across the range of axial-based swimming (from the ostraciiform mode to the anguilliform mode), animals recruit greater proportions of their bodies to propel themselves through the water (Fig. 1). Within this range, the more intermediate carangiform and subcarangiform modes have been studied most intensively.

Anguilliform locomotion deserves closer examination for several reasons. Perhaps most importantly, although most work on anguilliform swimming has focused on elongate fishes (particularly eels), elongation of the body has evolved independently in several vertebrate tetrapod taxa (Gans, 1975). Consequently, anguilliform swimming is phylogenetically widespread and is found in a variety of ecologically and morphologically divergent fishes, amphibians, and reptiles. Hence a broader understanding of anguilliform swimming will lead to a better appreciation for the kinematic vari-
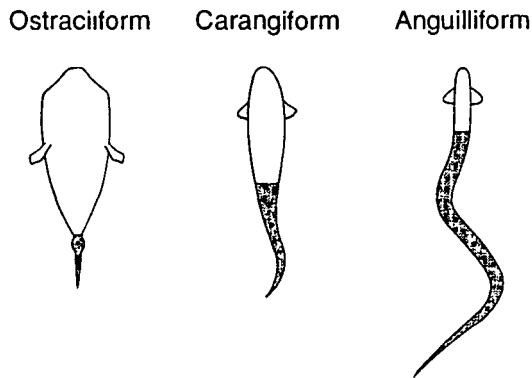
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Ostraciiform   Carangiform   Anguilliform

FIG. 1. Breder's original categorization of axial un-
dulatory modes (Breder, 1926). In ostraciiform loco-
motion, only the tail is moved from side to side to
push the animal forward, whereas during anguilliform
locomotion, most of the body is bent into waves (short-
er than the length of the animal) which are propagated
posteriorly along the length of the animal, pushing it
through the water. Carangiform locomotion is inter-
mediate to these two modes. Subcarangiform loco-
motion is a common category intermediate to the car-
angiform and anguilliform modes. Figure modified
from Gray (1968).

TABLE 1. Internal and external morphological vari-
ation across several elongate vertebrate taxa.

Taxon	Average number of vertebrae	Average tail length (% total length)	General tail shape
Anguilla	104	60	laterally compressed
Siren	95*	33	laterally compressed tapered near tip
Pelamis	186**	11	laterally compressed
Elaphe	297**	16	tapered along length

* One individual examined had only 74 vertebrae.
** Bruce Jayne (Pers. comm.).

ability among taxa which utilize this loco-
motor mode and the underlying causal bas-
es to such variation. Second, we currently
have little appreciation for how differences
in external and internal morphology influ-
ence swimming behavior and performance.
However, among taxa which utilize the an-
guilliform mode, substantial variation in
both internal and external morphological
features exists (Table 1), providing a poten-
tial framework for examining how such
variation might affect kinematics and me-
chanics during swimming. In addition, de-
tailed, quantitative comparisons of anguil-
liform swimming to the carangiform and
subcarangiform modes, should help clarify
if and in what ways elongation of the body
affects swimming movements. Third, with-
in the limited data for swimming in elon-
gate vertebrates, movements along the en-
tire body of the animal are rarely quantified
despite the fact that most of the body typ-
ically undulates and can produce useful
thrust (Lighthill, 1975). Finally, much of
what is published regarding anguilliform
swimming, particularly in textbooks or re-
views of aquatic locomotion, comes from
analyses performed by Sir James Gray in

the 1930s. Yet many modern techniques
now allow more precise quantification of
body movements and muscle activity pat-
terns during swimming, and may provide
further insight into the swimming behavior
of elongate vertebrates. It is therefore time
for a reassessment of the anguilliform lo-
comotor mode.

GRAY'S CONTRIBUTIONS TO
OUR UNDERSTANDING OF
UNDULATORY LOCOMOTION

In Gray's (1933) seminal work on un-
dulatory swimming, he analyzed films of
fishes swimming in a tank with a fixed
background grid so that movements made
by the animal could be tracked and record-
ed. His analysis of these records described
how cyclic undulatory movements of a fish
body could produce the forces required to
propel the animal through water. In addi-
tion, Gray also made several general qual-
itative conclusions that characterized the
movements used during swimming by elon-
gate fishes such as eels (Anguilla).

A number of Gray's general conclusions
dealt with the speed and amplitude of the
undulatory waves generated during loco-
motion, as well as with the transverse ve-
locity and orientation of body segments
along the fish while swimming. These con-
clusions greatly enhanced our understand-
ing of how undulatory movements of fish
lead to forward movement during swim-
ming, and therefore are found in many ex-
tended treatises on fish locomotion (see for
example, Blake, 1983; Videler, 1993;
Webb, 1975). However, despite their prev-
alence in the literature, the generality of
Gray's conclusions have yet to be tested by

detailed quantitative kinematic analyses of swimming eels (or other elongate fish) or other elongate swimming vertebrates, such as salamanders or snakes. The goal of this paper is to examine some of Gray's conclusions regarding undulatory locomotion. I use recent data from my own high-speed videos of swimming eels and salamanders, as well as data from the literature on swimming colubrid snakes (Jayne, 1985) and sea snakes (Graham *et al.*, 1987) in order to address the generality of Gray's conclusions with respect to the anguilliform swimming mode as well as the extent of variability present within this mode.

Undulatory amplitude

Gray (1933) states that "The most conspicuous features of a moving eel . . . are the waves of curvature which pass along the length of the body from head to tail." More specifically, Gray noted that during swimming, the amplitude of these waves increases longitudinally (along the rostral–caudal axis) such that undulatory amplitude is greatest at the tip of the tail. All additional studies of the kinematics of anguilliform swimming generally confirm Gray's observation; however, the nature of amplitude increase along the body can be quite variable depending upon taxon and swimming speed.

Figure 2 shows clear differences in the amplitude of undulatory excursions across a variety of anguilliform vertebrate swimmers. While the amplitude of lateral undulations tends to increase longitudinally along the body in all taxa examined, eels (*Anguilla*) generate waves of lower amplitude than similarly sized salamanders (*Siren*), colubrid snakes (*Elaphe*), and sea snakes (*Pelamis*) swimming at a similar speed. It seems likely that differences in internal and/or external morphology could be partially responsible for some of these differences. For example, internally, the total number of vertebrae (body segments) varies greatly among the taxa in Figure 2 (Table 1). However, Jayne (1985) has shown that drastic differences in the number of vertebrae between two colubrid snakes, *Elaphe* (average of 289 vertebrae) and *Nerodia* (average of 196 vertebrae), had no obvious ef-
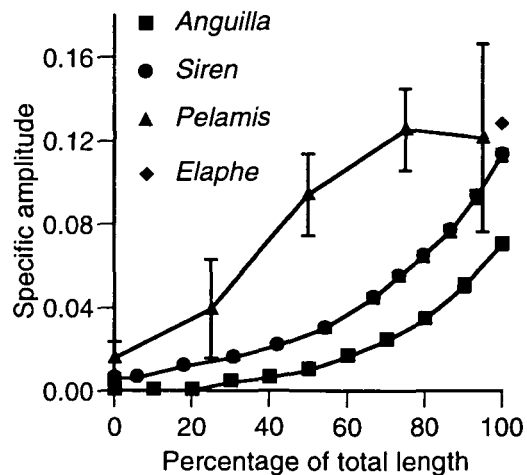

FIG. 2. Undulatory amplitude (measured as a proportion of total length) as a function of longitudinal position (0 = tip of snout, 100 = tip of tail) in a number of similarly sized elongate vertebrates swimming at comparable speeds. Amplitude is measured as half the lateral displacement between successive maximum excursions. Note that for *Elaphe*, data were based upon regression statistics (amplitude was regressed *vs.* distance along axis of forward motion, rather than distance along body), so only 1 data point is present, showing amplitude at the tip of the tail. Data from eels (*Anguilla*) are from Gillis (unpublished data) using 34–35 cm individuals swimming at 0.5 Lsec⁻¹. Data from sirenid salamanders (*Siren*) are from Gillis (unpublished data) using 33–38 cm individuals swimming at 0.6 Lsec⁻¹. Data from sea snakes (*Pelamis*) are from Graham (1987) using a 51 cm individual swimming at 0.63 Lsec⁻¹. Data from colubrid snakes (*Elaphe*) are from Jayne (1985) using a 33.5 cm individual swimming at 0.55 Lsec⁻¹.

fect on the undulatory waveform generated during swimming. Additionally, in my own work with swimming *Siren*, an individual salamander with significantly fewer vertebrae did not deviate kinematically from other individuals with more vertebrae (75 *vs.* 96–98 vertebrae, respectively). Therefore, variation in the number of vertebrae across taxa may not be related to the differences in undulatory amplitude shown in Figure 2.

Differences in external morphology, such as the size and shape of an animal's body and tail are also apparent across elongate vertebrates (Table 1). These external morphological differences can affect the nature of the propulsive forces generated during undulatory locomotion. For example, Lighthill (1975) suggests that during un-

dulatory swimming, deep, laterally compressed bodies or tails produce a greater transfer of momentum from an animal to the water (greater propulsive force) than cylindrical bodies with tapering tails. Hence, as a deep, laterally compressed tail is swept through the water, it will generate greater propulsive forces than would a similar sweep of a cylindrical tapering tail. For this reason, one would expect that animals like eels (which are laterally compressed and have increased body depth due to expanded dorsal and ventral fins along most of their body) would use slower, or less exaggerated undulatory movements than would *Siren* or *Elaphe* (which have more cylindrical bodies with tapering tails), to swim at similar speeds. However, *Pelamis*, a sea snake, is laterally compressed along much of its body, yet also shows high-amplitude undulatory excursions during swimming (Fig. 2). It is therefore likely that factors other than external body morphology can also affect the amplitude of undulatory movements used during anguilliform swimming.

For example, the depth of swimming might also affect the kinematics of these animals. While the eels and sirenid salamanders used for the kinematic data in Figure 2 always swam under water (typically at or near the bottom of the flow tank), the snakes (*Elaphe* and *Pelamis*) from which the data in Figure 2 were collected tended to swim at or near the water surface. It is possible that surface swimming utilizes different muscle activity patterns relative to subsurface swimming (as shown by Jayne, 1988) and that this, in turn, creates different kinematic patterns. In addition, forces resisting locomotion (drag forces) increase when swimming near the surface (Hertel, 1966) due to wave formation. Such increased drag might explain why *Pelamis*, despite having a deep and laterally compressed body, uses higher amplitude undulatory movements to swim at the same speed as similarly sized eels and salamanders. Therefore, differences in external morphology as well as behavior (surface *vs.* subsurface swimming) have hydrodynamic consequences and probably can account for some of the different patterns of undulatory

amplitude observed across anguilliform swimmers.

Finally, although in Figure 2 animals are swimming at relatively similar speeds, swimming speed also has a potential effect on the undulatory amplitude used during anguilliform swimming. Interestingly, these changes in amplitude with speed are not necessarily consistent across taxa. For example, Jayne (1985) found that undulatory amplitude of swimming snakes tended to decrease with increased swimming speed. In contrast, I have found in swimming *Siren* that amplitude does not change drastically across a range of speeds from 0.3–1.5 Lsec^{-1}, but further increases in speed (up to 1.85 Lsec^{-1}) lead to significant increases in amplitude (Gillis, unpublished data). Little is known about how swimming speed effects the kinematics of anguilliform swimming, however, it is clear from the examples given above that the answer is probably not simple and varies across taxa.

Speed of undulatory waves

Gray (1933) also briefly discussed how fast waves travel posteriorly along the body of an undulatory swimmer. By tracking wave crests as they were propagated toward the tail in a variety of swimming fish, Gray (along with a number of earlier workers) concluded that the speed at which these undulatory waves pass backwards was always greater than the speed at which the animal swims forward. This conclusion is generally correct. However, closer examination of wave propagation in a variety of anguilliform taxa over a range of swimming speeds reveals substantial variability in the speed at which these waves travel relative to the animal's swimming speed.

The relative speed of a backward traveling wave can be expressed as a ratio of the forward swimming speed (U) of an undulatory swimming animal to its traveling wave speed (V). Figure 3 shows that this ratio (U/V), for a variety of swimming speeds in eels, sirenid salamanders and sea snakes, is less than one. Thus, as Gray had suggested, traveling waves generally move faster backward than the animal is swimming forward [although see Jayne (1985) for an interesting exception regarding the
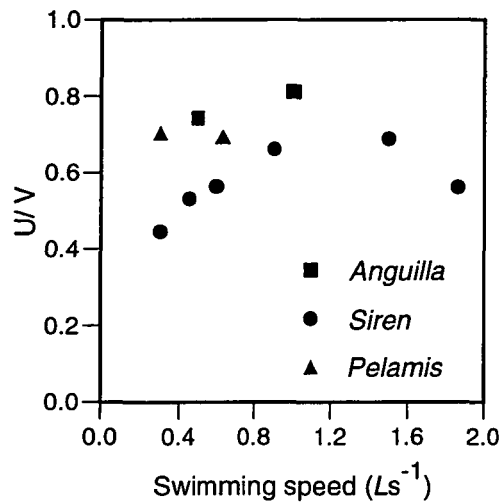
FIG. 3. Graphical representation of the forward swimming speed (U) relative to the traveling wave speed (V) across several elongate vertebrate taxa. Data are from the same animals described in Figure 2 (excluding *Elaphe*).

anterior regions of swimming snakes]. Interestingly, this ratio can vary considerably with swimming speed. For example, in sirenid salamanders swimming at low speeds (0.3 Lsec^{-1}), this ratio approximates 0.45, but as swimming speed increases, the value of this ratio increases to approximately 0.7 at a swimming speed of 1.5 Lsec^{-1}. However, the values of this ratio, and their pattern of change with speed, are not consistent across elongate vertebrates. In two other anguilliform swimmers, eels and sea snakes, the ratio of forward swimming speed to backward traveling wave speed is much higher (wave speed is relatively slower) than that of salamanders swimming at the same speed, and does not obviously increase with swimming speed.

Furthermore, the above discussion assumes that traveling wave speed remains constant along the body during anguilliform swimming. While this appears to be the case in swimming eels (Grillner and Kashin, 1976), it is not true of other elongate taxa which have been examined. For example, in swimming snakes, wave speed tends to increase along the length of the body (Jayne, 1985; Graham *et al.*, 1987). In swimming *Siren*, the pattern is even more complex because wave speed remains con-

stant during slow swimming speeds, but increases along the body at high swimming speeds (Gillis, unpublished data). A potential reason for such differences across taxa is that different species use quantitatively different patterns of axial muscle activity during swimming [*e.g.*, the speed of the wave of muscle activation increases along the body in snakes studied to date (Jayne, 1988), but moves at a constant velocity along the body in eels (Grillner and Kashin, 1976)]. In addition, internal and external morphological differences across groups may affect the way in which a wave of muscle activity is translated into a mechanical wave traveling along the body.

Transverse velocity of tail segments

While Gray was interested in the waveform of swimming animals, perhaps he is better known for developing "segmental analyses" of swimming fish. Gray suggested that much could be learned about the mechanism of undulatory propulsion by considering a swimming fish as a series of interconnected body segments, and that by analyzing the movements of individual segments, one could better understand how an undulating body was interacting with the water in a way which propelled the animal forward. In Gray's original segmental analysis of undulatory locomotion, he made the generalization that the transverse velocity of any body segment would always be greatest when that segment was crossing the axis of forward movement. In Figure 4 of a swimming eel, points 1–7 (Fig. 4A) represent positions of the tip of the tail at equally spaced time intervals during one tailbeat cycle. As the lateral distance between points 4 and 5 is greater than that between any other two consecutive points in this figure, the lateral velocity of the tail tip must also be greatest during this time interval (as it is passing the axis of forward motion), supporting Gray's generalization. However, note the coarseness of Gray's sampling in this figure. The time interval between points 4 and 5 is over 10% of the tailbeat cycle, and the displacement between these two points in time encompasses nearly ⅓ of the entire extent of the lateral displacement of the tail. Therefore, al-
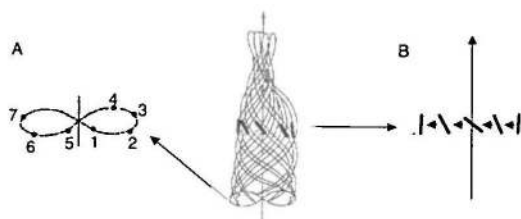
FIG. 4. A series of images of an eel swimming with its snout aligned to the same longitudinal position. A. An enlargement of the path of travel of the tail tip of the swimming eel during an undulatory cycle. The tip of the tail travels in a figure eight path. Points 1–7 are sampled at equal time intervals, so lateral distance between points is equivalent to the lateral velocity at the tail tip. Distance between points 4 and 5 is the greatest, hence, the lateral velocity of the tail tip is highest during this interval, which coincides with when the tail is crossing the axis of forward movement (thin vertical line at center of figure eight). B. An enlargement of a body segment, as it beats from right to left during an undulatory cycle. Note that it subtends its greatest angle (θ) relative to the axis of forward motion as it crosses that axis. Figure is a modification of figures 14 and 15 from Gray (1933).

though Gray suggested that the tail was moving fastest as it crossed the axis of forward movement, it could actually be moving fastest at any instant between points 4 and 5, including times slightly before or after it crossed this axis.

Few workers have empirically tested the notion that body segments reach their maximum lateral velocity as they are crossing the axis of forward movement. Using a higher sampling rate (20 video fields per tailbeat cycle) I have quantified the lateral velocities of tail segments of sirenid salamanders swimming at a variety of speeds to examine when the maximum velocity is reached. As a tail beats from right to left through half of one tailbeat cycle, the time at which the tail is crossing the axis of forward progression is at one quarter of the cycle (Fig. 5). Data from swimming sirenid salamanders show that segments along the tail typically reach maximum lateral velocity at 0.20–0.27 cycles, a range which encompasses 0.25, the time at which the axis of forward progression is crossed (Fig. 5). But more specifically, there is a longitudi-
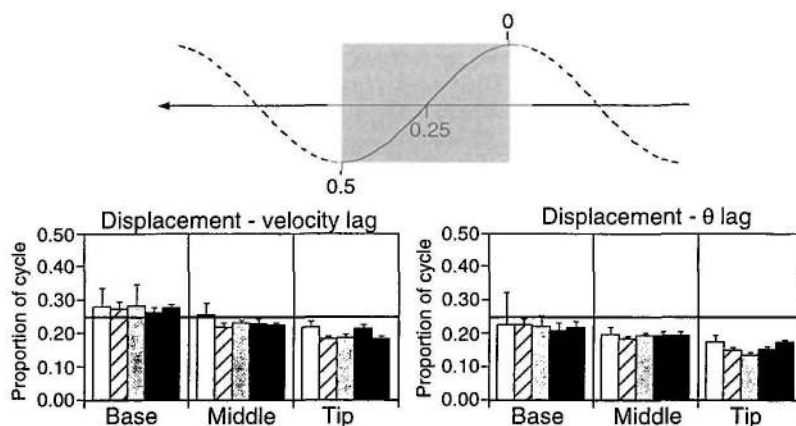

FIG. 5. As any segment of an undulating body moves through one half of an undulatory cycle, at some point it must reach its maximum lateral velocity, as well as its maximum orientation (θ) relative to the axis of forward movement. The phase lag (as a proportion of a tailbeat cycle) between when a segment becomes maximally displaced to either side and when it subsequently reaches its maximum velocity is shown on the left. The dark horizontal line at 0.25 represents the point of the undulatory cycle at which the segment is crossing the axis of forward movement. Values less than 0.25 indicate that the segment reaches maximum lateral velocity prior to crossing this axis, whereas values greater than 0.25 represent maximum velocity being reached after crossing the axis. The lag between when a segment becomes maximally laterally displaced and when it reaches its maximum orientation relative to the axis of forward movement is shown on the right. Data are from sirenid salamanders swimming at 5 speeds, and are plotted for three tail segments (2.3–2.7 cm long) one at the base of the tail, one in the middle of the tail, and one at the tip of the tail. Bars from left to right indicate increasing swimming speeds: White = 0.3 Lsec⁻¹, cross-hatched = 0.45 Lsec⁻¹, light gray = 0.6 Lsec⁻¹, dark gray = 0.9 Lsec⁻¹, black = 1.5 Lsec⁻¹.

nal trend such that more anterior segments tend to reach maximum velocity slightly after crossing the axis of forward progression (0.27 cycles) while more posterior segments reach their highest velocity before crossing this axis (0.20 cycles). Interestingly, in multiple studies of undulatory swimmers, in which the lateral velocity at the tip of the tail has been determined throughout a tailbeat cycle, it has been found to be highest prior to reaching the axis of forward progression (in goldfish [Bainbridge, 1963], cod [Videler, 1981], leopard sharks [Ferry and Lauder, personal communication] and sirenid salamanders [Gillis, unpublished data]). Hence, Gray's generalization regarding the maximum lateral velocity of body segments does not hold near the tip of the tail for a variety of undulatory swimmers.

Orientation of tail segments

Gray (1933) was also interested in the orientation (θ) of body segments during an undulatory cycle (Fig. 4B). Gray concluded that the angle (θ) between any given body segment and the axis of forward movement, will be greatest as that segment crosses this axis (*i.e.*, when it is at its highest lateral velocity). Gray actually measured the orientation of a body segment (θ_M *sensu* Gray, 1933) as the angle between the body segment and its transverse axis of movement, despite an error in his legend to Figure 13 indicating that the angle was measured relative to the axis of forward movement. Regardless, Gray concluded that segment orientation changed consistently during an undulatory cycle, and that any segment would be oriented such that it subtended its largest angle with the axis of forward movement as it crossed that axis (Fig. 4B).

My work on anguilliform swimming in sirenid salamanders suggests that tail segments do not necessarily subtend their largest angles relative to the axis of forward motion as they cross this axis, nor do segments subtend their maximum angles as they are moving at their highest lateral velocity. Figure 5 shows that in sirenid salamanders, tail segments reach their maximum θ between 0.15–0.22 cycles after maximum lateral displacement. As was the case with maximum lateral velocity, these

data vary longitudinally such that more anterior tail segments reach maximum θ relatively later (0.22 cycles) than do more posterior segments (0.15 cycles). Additionally, recall that maximum lateral velocity is reached between 0.20–0.27 cycles after maximum lateral displacement, so it is clear that maximum θ tends to be reached before maximum lateral velocity (they do not coincide in time as Gray had suggested) and also before crossing the axis of forward movement. Data from subcarangiform swimmers such as cod (Videler, 1981) and bass (Jayne and Lauder, 1995*b*) also suggest that tail segments tend to reach their maximum orientation (θ) prior to crossing the axis of forward movement.

The angle of attack of tail segments

Perhaps the most significant point that Gray made in his 1933 paper was that there would be an angle, which he designated α (angle of attack), between any body segment along a fish and that segment's path of travel (Fig. 6). In addition to reactive forces it is the lift and drag forces which act upon body segments as a result of their being oriented at an angle to their paths of travel which propel the animal during swimming.

Interestingly, empirical studies of tail kinematics in anguilliform and subcarangiform taxa have shown that during some portions of an undulatory cycle (typically when the path angle approaches 0 degrees, *i.e.*, when tail segments are near their maximum lateral displacement), tail segments can actually be oriented at a greater angle to the axis of forward motion than is the path of travel. An orientation such as this is considered a negative angle of attack, and while Gray did not mention it as a possibility, the consequence of a negative α is a 180 degree shift in the angle of the lift force acting on the segment (Fig. 6). As shown in Figure 6, when a segment has a negative angle of attack, the resultant force vector acting on the segment no longer has a component oriented in the direction of forward travel. In an anguilliform swimming sirenid salamander, during approximately 10–25% of an undulatory cycle tail segments will be oriented with a negative angle of attack
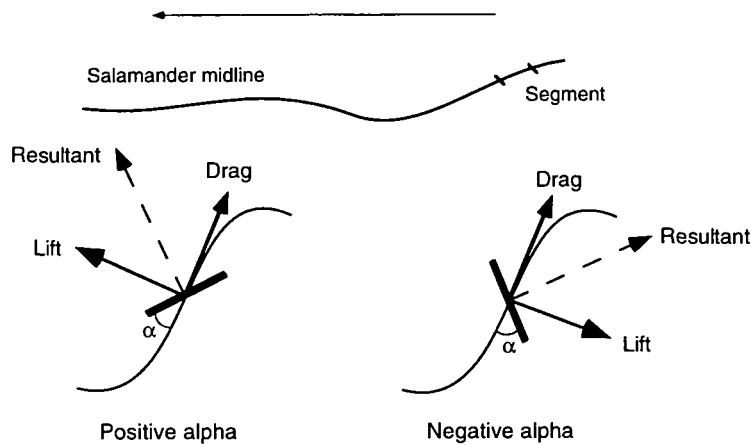
Fig. 6. As a tail segment sweeps from right to left through a tailbeat (as seen in this dorsal view of the midline of an elongate undulatory swimmer), that segment typically subtends an angle, α, to its path of travel. Depending upon whether this angle is positive (segment subtends a smaller angle to the axis of forward motion than does its path), as on the left, or negative (segment subtends a greater angle relative to the path of travel), as on the right, resultant forces acting on that segment can change dramatically.

(Fig. 7). It is unclear how common negative angles of attack are during anguilliform locomotion in other taxa, as they have not been previously described. Perhaps increased tail stiffness plays a role in maintaining continuously positive angles of attack during swimming in animals such as tuna and dolphins (Jayne and Lauder, 1995b). If there is a causal relationship between stiffness in caudal structures and the maintenance of positive angles of attack in the caudal region, then it is likely that negative angles of attack will be common in the tail segments of anguilliform taxa which are typically quite flexible.

An examination of the magnitude of positive angles of attack subtended by the tail of an anguilliform swimmer also leads to an interesting insight concerning the efficiency of anguilliform locomotion at low swimming speeds. Sirenid salamander tail segments subtend very high (often greater than 20 degrees near the tip of the tail) positive angles of attack at slow swimming speeds. High angles of attack [(above α_{crit}, which is 20 degrees for the hydrofoil discussed in Webb, 1975)] cause the coefficient of drag to increase dramatically relative to the coefficient of lift as a result of boundary layer separation from the tail segments (although see Dickinson, 1996). The efficiency (as estimated by the ratio U/V) of a salamander swimming at slow speeds is relatively low (Fig. 3). This may be due, in part, to these large positive angles of attack of tail segments at these speeds. Without more detailed kinematic data from anguilliform swimmers, it will be unclear how the angle of attack at different longitudinal locations varies throughout an undulatory cycle for animals which use this mode of locomotion or to what extent swimming efficiency is correlated with these angles.
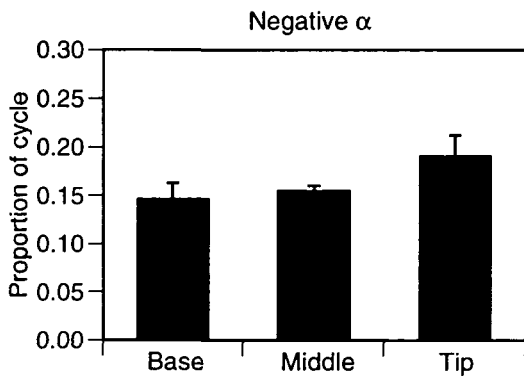

Fig. 7. The average proportion of a tailbeat cycle during which the angle of attack of three tail segments is negative. Data are from sirenid salamanders and have been averaged across all swimming speeds.

CONCLUSIONS

It would be difficult to overestimate the importance of Gray's original work on undulatory swimming in elongate fish to our current understanding of aquatic undulatory locomotion, and to our methodologies used for continued analyses of this problem. His use of cinematographic records to better visualize and analyze the fast, repetitive undulatory movements utilized by swimming fish provided the foundation for the numerous kinematic analyses of swimming we see today. In addition, his general conclusions regarding kinematic aspects describing the waveform and lateral movements of body segments during swimming, and, perhaps most importantly, his recognition that such body segments subtend an angle, α (angle of attack), relative to their path of motion, provided the basis for our understanding of how movements of an undulating body propel a swimming animal forward.

Fortunately, technical advances since the 1930s, such as high-speed video and computer-based analysis systems, allow us now to be much more quantitative and detailed in our kinematic analyses of swimming animals. Such detailed studies across a broad range of elongate vertebrates provide the opportunity to test the generality of Gray's conclusions regarding the patterns of movement used during anguilliform locomotion.

First, as Gray suggested, the amplitude of undulatory waves passed posteriorly along the body of an elongate swimmer typically increases from anterior to posterior. However, it is important to recognize that the absolute extent and longitudinal pattern of increase can vary depending upon taxon and swimming speed. Second, as Gray and others previous to him had described, the velocity of these traveling waves is faster than the velocity of the swimming animal. Again, however, the relative velocity of these waves depends greatly upon swimming speed and taxon. Third, in contrast to Gray's suggestion that body segments reach their maximal lateral velocity and orientation at the same time, as they are crossing the axis of forward movement, tail segments in a swimming elongate salamander

tend to reach maximum lateral velocity prior to maximal orientation, and in addition, variability in the timing of such events exists longitudinally along the body. Finally, angles of attack of body segments, as Gray suggested, depend upon the longitudinal position as well as the swimming speed, and vary continuously throughout an undulatory cycle. In addition, angles of attack can also be negative for a consistent period of time during each tailbeat cycle, a possibility which went unmentioned by Gray in his original paper.

In summary, the study of axial-based undulatory aquatic locomotion in general owes much to the original analyses of swimming fish performed by James Gray in the 1930s. Technical advances since that time have allowed workers interested in axial-based aquatic locomotion to exploit areas far beyond the scope of Gray's kinematic analyses [see for example, Long et al., (1994) and McHenry et al., (1995) for recent biomechanical analyses, Jayne and Lauder (1995a) for interesting approaches to understanding muscle activity patterns during swimming, Altringham et al., (1993) and Rome et al., (1993), for work on axial muscle physiology and function, and Carling et al., (1994), Fauci (1996) and Jordan (1996) for mathematical and computer modeling]. Yet, kinematic analyses of undulatory swimming are still of great importance as only they can tell us specifically about patterns of movement used by animals during swimming. A brief review of several kinematic analyses of anguilliform swimming across a variety of elongate vertebrates suggests that substantial variability exists across these taxa. Such variability is likely to be due to morphological differences as well as to potential differences in the neuromuscular control of swimming across these taxa. I would suggest that the kinematic parameters which characterize the anguilliform mode of locomotion in vertebrates are more diverse and complicated than Gray, or any of us might have expected until recently. And only with further kinematic analyses of swimming behavior in concert with studies of morphology, biomechanics, electromyography, and muscle physiology, as well as mechanical

and mathematical modeling, will we better understand the causal bases for such locomotor complexity and diversity.

REFERENCES

Altringham, J. D., C. S. Wardle, and C. I. Smith. 1993. Myotomal muscle function at different locations in the body of a swimming fish. J. Exp. Biol. 182: 191–206.

Bainbridge, R. 1963. Caudal fin and body movement in the propulsion of some fish J. Exp. Biol. 40: 23–56.

Blake, R. W. 1983. *Fish locomotion.* Cambridge University Press, Cambridge.

Breder, C. M. 1926. The locomotion of fishes. Zoologica 4:159–297.

Carling, J. C., G. Bowtell, and T. L. Williams. 1994. Swimming in the lamprey: Modeling the neural pattern generation, the body dynamics and the fluid mechanics. *In* L. Maddock, Q. Bone, and J. M. V. Rayner (eds.), *Mechanics and physiology of animal swimming,* pp. 119–132. Cambridge University Press, Cambridge.

Dickinson, M. H. 1996. Unsteady mechanisms of force generation in aquatic locomotion. Am. Zool. 36:537–554.

Fauci, L. J. 1996. Computational modeling of the fluid dynamics of locomotion. Am. Zool. 36:599–607.

Gans, C. 1975. Tetrapod limblessness: Evolution and functional corollaries. Amer. Zool. 15:455–467.

Graham, J. B., W. R. Lowell, I. Rubinoff, and J. Motta. 1987. Surface and subsurface swimming of the sea snake *Pelamis platurus.* J. Exp. Biol. 127:27–44.

Gray, J. 1933. Studies in animal locomotion I. The movement of fish with special reference to the eel. J. Exp. Biol. 10:88–104.

Gray, J. 1968. *Animal locomotion.* W. W. Norton and Co. Inc., New York.

Grillner, S. and S. Kashin. 1976. On the generation and performance of swimming in fish. *In* R. M. Herman, S. Grillner, P. S. Stein, and D. G. Stuart (eds.), *Neural control of locomotion,* pp. 181–201. Plenum Press, New York.

Hertel 1966. *Structure form and movement.* Rheinold, New York.

Jayne, B. C. 1985. Swimming in constricting (*Elaphe g. guttata*) and nonconstricting (*Nerodia fasciata pictiventris*) Colubrid snakes. Copeia 1985(1): 195–208.

Jayne, B. C. 1988. Muscular mechanisms of snake locomotion: An electromyographic study of lateral undulation of the Florida banded water snake (*Nerodia fasciata*) and the yellow rat snake (*Elaphe obsoleta*). J. Morph. 197:159–181.

Jayne, B. C. and G. V. Lauder. 1995a. Are muscle fibers within fish myotomes activated synchronously? Patterns of recruitment within deep myomeric musculature during swimming in largemouth bass. J. Exp. Biol. 198:805–815.

Jayne, B. C. and G. V. Lauder. 1995b. Speed effects on midline kinematics during steady undulatory swimming of largemouth bass, (*Micropterus salmoides*). J. Exp. Biol. 198:585–602.

Jordan, C. E. 1996. Coupling internal and external mechanics to predict swimming behavior: A general approach? Amer. Zool. 36:710–722.

Lighthill, J. 1975. *Mathematical biofluiddynamics.* J. W. Arrowsmith Ltd, Bristol.

Lindsey, C. C. 1978. Form, function, and the locomotory habits in fish. *In* W. S. Hoar and D. J. Randall (eds.), *Fish physiology,* pp. 1–100. Academic Press, New York.

Long, J. H., M. J. McHenry, and N. C. Boetticher. 1994. Undulatory swimming: How traveling waves are produced and modulated in sunfish (*Lepomis gibbosus*). J. Exp. Biol. 192:129–145.

McHenry, M. J., C. A. Pell, and J. H. Long. 1995. Mechanical control of swimming speed: Stiffness and axial wave form in undulating fish models. J. Exp. Biol. 198:2293–2305.

Rome, L. C., D. Swank, and D. Corda. 1993. How fish power swimming. Science 261:340–343.

Videler, J. J. 1981. Swimming movements, body structure and propulsion in cod *Gadus morhua.* Symp. Zool. Soc. Lond. 48:1–27.

Videler, J. J. 1993. *Fish swimming.* Chapman & Hall, London.

Webb, P. W. 1975. Hydrodynamics and energetics of fish propulsion. Bull. Fish. Res. Bd. Can. 190:1–158.

Webb, P. W. and R. W. Blake. 1985. Swimming. *In* M. Hildebrand, D. M. Bramble, K. F. Liem and D. B. Wake, (eds.), *Functional vertebrate morphology,* pp. 110–128. Belknap Press, Cambridge.