

## SURFACE AND SUBSURFACE SWIMMING OF THE SEA SNAKE *PELAMIS PLATURUS*

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### SUMMARY

During anguilliform swimming at the surface, four half waves are present along the body of the yellow-bellied sea snake *Pelamis platurus* (Hydrophiidae). As in other anguilliform swimmers, wave amplitude increases towards the tail; however, the relative caudal amplitude of *P. platurus* is less than that of the aquatic snakes *Natrix* and *Nerodia* and the eel *Anguilla*. Kinematic analyses of near-surface swimming at 15 and 32 cm s<sup>-1</sup> were made from high-speed ciné films, and Lighthill's bulk momentum hydromechanical model was used to calculate swimming thrust power at these two velocities. The total thrust power generated by a 51 cm snake is 3.641 × 10<sup>-4</sup> J s<sup>-1</sup> at 15 cm s<sup>-1</sup> and 29.877 × 10<sup>-4</sup> J s<sup>-1</sup> at 32 cm s<sup>-1</sup>, with respective Froude efficiencies of 79% and 81%. Subsurface swimming velocities are low (2–4 cm s<sup>-1</sup>), and snakes usually assume a posture in which the tail is elevated and the posterior part of the body assumes a nearly vertical orientation. Undulatory movements by snakes swimming in this posture involve torsional and rolling motions of the body which, through changes in the camber of the keel and body, may contribute to thrust.

### INTRODUCTION

This paper reports several aspects of the swimming movements of the yellow-bellied sea snake *Pelamis platurus* Linnaeus. *P. platurus* is a totally aquatic pelagic species that commonly occurs in oceanic drift line communities. This snake is known to dive as deep as 50 m and spends about 87% of its time submerged (Rubinoff, Graham & Motta, 1986a,b). Adaptations for locomotion include a paddle-shaped tail and a ventral body keel that extends from just behind the jaw to the vent (Fig. 1; Pickwell, 1972). The long lung of this snake reduces swimming costs by providing positive buoyancy at the surface. Recent work has demonstrated that *P. platurus* regulates lung volume prior to diving (Graham, Gee & Robison,

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1975), dives with a specific lung volume that enables it to achieve near-neutral buoyancy at depth (Graham, Gee, Motta & Rubinoff, 1986), and is able to prolong its dives by using its skin for aquatic respiration (Graham, 1974). Most observations of movements by this species have been made on individuals at the water surface (Pickwell, 1972; Kropach, 1973, 1975). There have been no kinematic analyses or extended observations of subsurface swimming movements.

The first objective of this paper is to describe and compare the surface and subsurface swimming movements of *P. platurus*, one of few anguilliform swimmers that routinely swims both at the surface and at depth. Surface swimming imposes greater energetic costs to an organism because of the drag associated with surface wave formation (Hertel, 1966). Very little is known about how an organism's

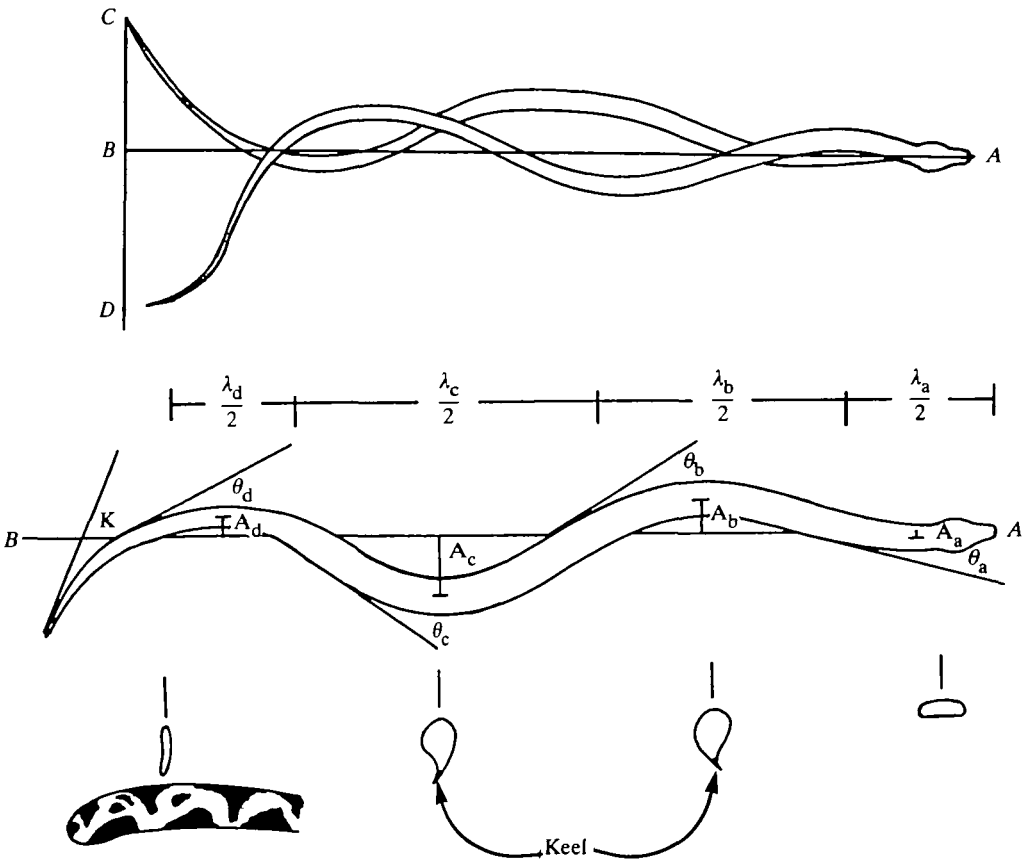


Fig. 1. Top: two superimposed traces of a swimming *Pelamis platurus* defining the axis of progression ( $AB$ ) and maximum tail deflection ( $CD$ ). Middle: trace of a swimming snake illustrating the one-half wavelength ( $\lambda/2$ ) and amplitude ( $A$ ) of each body segment ( $a-d$ ), the angle ( $\theta$ ) between the trailing edge of each segment and axis of progression, and the angle ( $K$ ) of tail sweep (see text). Bottom: cross-section profiles of the body at positions indicated showing the foil shape caused by the ventral body keel, with a side view of the tail.

style of anguilliform swimming may change at depth. We have determined this for *P. platurus* by contrasting the slow, horizontal swimming movements typical of snakes at or just below the surface with those of snakes swimming at 7–10 m depth in the Hydraulics Laboratory tank at Scripps Institution of Oceanography (SIO). Seymour, Spragg & Hartman (1981) showed that inclination of *P. platurus* resulted in the displacement of lung gas towards the highest point in the body. Although hydrostatic pressure would compress lung volume at depth, we tested the hypothesis that the lung volume of subsurface-swimming snakes remained sufficient, if displaced to either end of the body, to bring about changes in the body posture and profile and in regional body lift. Another objective is to compare the near-surface, steady anguilliform swimming of *P. platurus* with that of other aquatic snakes (*Natrix*, *Nerodia*) and the eel (*Anguilla*). Comparisons of this nature may reveal how the morphological specializations for aquatic life noted for sea snakes have influenced the locomotory mechanisms of this family relative to other phylogenetically distant anguilliform swimmers.

#### MATERIALS AND METHODS

Specimens of *Pelamis platurus* (45–70 cm total length, L) were captured by dip net in the Gulf of Panama, transported by air to the Physiological Research Laboratory at SIO and maintained in seawater aquaria (25–27°C) for up to 3 months on a diet of frozen and live fish.

#### *Morphology*

Measurements of the body shape and dimensions of *P. platurus* were made to evaluate specializations for anguilliform locomotion and to aid in hydrodynamic analyses. The following morphological measurements were made using both frozen and fresh snakes: total length (L), wet body mass, surface areas of the head, ventral keel (Fig. 1), paddle tail and of the total body, and vertical body thicknesses at five locations; the head, the 25, 50 and 75 % points of the body length ( $B_{25}$ ,  $B_{50}$ ,  $B_{75}$ ) and the mid-point of the tail ( $T_{50}$ ). Dunson & Robinson (1976) previously estimated the skin surface area of *P. platurus*. In the present study, surface areas were estimated gravimetrically by tightly applying aluminium foil, with a known area:weight ratio, to body surfaces. The foil was smoothed, fitted to the body and then trimmed to obtain a fully-contoured fit. The ventral keel originates behind the jaw and extends to the vent. Its base is formed by ventral fusion of the ribs, and its boundary with the body is usually demarcated by the transition from a convex to concave vertical profile (Fig. 1). Prior to wrapping the body and keel areas, the lung of each snake was filled to the known mean volume for surface-floating snakes (i.e. 8.8 % of body weight, Graham *et al.* 1975) and then sealed by ligation. It was easier to fit the foil if the body was first suspended vertically and frozen. Foil from different sections of the roll was weighed to verify a similar area:weight ratio. As a control for the foil method, replicate surface area measurements on the same snake were performed and these

revealed an estimation precision of within 10%. The total body surface area estimates obtained for these snakes were found to agree with area data presented by Dunson & Robinson (1976, fig. 3), who skinned and traced their study specimens.

To examine the effect of submergence on lung volume and gas displacement, a 60 cm snake was anaesthetized with Halothane and its lung was inflated with 20 ml of air *via* the trachea, which was then ligated. Aluminium foil bands were then placed around its body at several positions to measure circumference at surface pressure. The snake was then loosely suspended and tethered inside an open-ended, 75 cm long  $\times$  8 cm diameter, clear Lucite tube which was then submerged to a position in front of the deep tank observation window (8.5 m). By tilting the tube from the horizontal towards the vertical, the snake could be orientated 'head up' or 'tail up' so that changes in the relative swelling and flotation of the caudal and throat regions could be noted.

### *Swimming studies*

#### *Surface and near-surface observations*

A Locam high-speed camera equipped with a 120 mm Schneider lens was used to make 16 mm overhead films of snakes swimming at velocities of 15 and 32 cm s<sup>-1</sup> and at 1–5 cm depths in a 75 cm long  $\times$  29 cm wide working section of a controlled-speed water tunnel. All filming was carried out at water temperatures from 23 to 25°C. The camera was positioned 1.5 m above the working section of the tunnel. Two 650-W tungsten floodlights were used and camera shutter speed was 1/300 s with an f setting of 2.8. The water tunnel design is similar to that described by Prange (1976). Its total volume is approximately 400 l and a variable-speed, 12-V trolling motor was used to circulate water. Water velocities were measured with a General Oceanics (Model 2035) flow meter. Because the working section surface was open to the air, small standing surface waves were created by the flow. These were smaller at 15 than at 32 cm s<sup>-1</sup>. Ektachrome video news film was used and all films were shot at either 50, 100 or 150 frames s<sup>-1</sup>. Calibration of camera film speed by time dots revealed a framing rate error of less than 1%.

Overhead films of four *P. platurus* that swam for 20–30 min at each velocity were examined using a Lafayette 16 mm motion analyser. Sequences with a 51 cm snake were chosen for complete analysis because these showed the snake swimming in a straight line at constant velocity and at sufficient distances from both sides of the 29 cm wide channel to minimize interference with swimming motions. Depending upon framing rate and the degree of desired analytical resolution, each successive, alternate, or every tenth frame was projected onto paper and the outline of the snake traced. Fig. 1 shows two superimposed tracings of this snake near the opposite extremes of a swimming cycle. For kinematic analyses the axis of progression, *AB*, was drawn to bisect the angle (*CAD*) between the head and maximum tail deflections, and all parameters were measured relative to this line using the method of Jayne (1985). Propulsive waves propagated down the snake's body (Fig. 1) increase in both amplitude and wavelength. We measured the height and length of

each half wave (i.e.  $\lambda_a/2$ ,  $\lambda_b/2$ , etc., Fig. 1) present along the body to determine segment wavelength ( $\lambda_s$ ) and amplitude ( $A_s$ ). Also estimated was the transverse velocity ( $W_s$ ) of each segment

$$W_s = \frac{\pi A_s f}{\sqrt{2}}, \quad (1)$$

where  $A_s$  is mean segment amplitude and  $f$  is wave frequency (Webb, 1975). The posteriorly propagated propulsive wave velocity through each segment ( $c_s$ ) was also calculated from

$$c_s = \lambda_s f. \quad (2)$$

The mean angle ( $\theta$ ) between the axis of progression and the posterior edge of the body segment of each half wave and the mean angle ( $K$ ) described by a line tangential to the tail of the body (Fig. 1) were also determined.

Kinematic data for *P. platurus* swimming at 15 and 32  $\text{cm s}^{-1}$  were used to estimate total power generated, kinetic energy lost to the wake and thrust power, according to Lighthill's (1969, 1970) bulk momentum model. The long, slender body of *P. platurus* is laterally compressed, lacks substantial posterior tapering and terminates in a broad, flat tail and is thus highly amenable to this analysis. Power estimates from the Lighthill model were compared to theoretical drag values estimated from hydrodynamic equations.

### *Subsurface swimming observations*

Video tapes of the subsurface swimming movements of *P. platurus* were made through the underwater window (0.51 × 0.46 m) located at a depth of 8.5 m in the 10 m SIO tank. The tank has a diameter of 3.1 m. Snakes released into it could be easily observed from the window, and previous studies showed that after 24 h most snakes behaved normally and had dive durations similar to those of individuals tracked at sea (Rubinoff *et al.* 1986a). A 2 × 2 m plastic frame containing a rope grid with approximately 10 × 10 cm squares was submerged in the tank and placed opposite the window to allow estimation of subsurface swimming speeds and ascent or descent angles and rates. During video sequences individual snakes were followed for as long as possible. Tank water temperature ranged from 26°C at the surface to 21°C at 10 m. Water was filtered and 10 1000-W metal halide lights set 3.5 m over the tank simulated mid-day light levels over the entire depth range. Subsurface video recordings were analysed with a stop action recorder and colour monitor.

## RESULTS

### *Morphology*

Body measurements were made on seven *P. platurus* (Table 1) ranging in total length from 49.6 to 70.0 cm (weight range 36.4–106.5 g). Tail length of these snakes ranged from 10 to 12 % (mean  $\pm$  s.d. = 11.2  $\pm$  0.7 %) of total length, which is similar to values reported by Kropach (1973). Mean ( $\pm$  s.d.) percentages for the separate body areas of the seven snakes are: head 4.6  $\pm$  0.5 %, body 73.2  $\pm$  2.2 %, keel

Table 1. *Morphological data for seven Pelamis platurus*

L (cm)	SV (cm)	Mass (g)	Tail length		Surface area (cm <sup>2</sup> )				Vertical body depth (cm)				Projected dorsal head surface area (cm <sup>2</sup> )						
			(cm)	(%L)	Tail (%)	Head (%)	Body (%)	Keel (%)	Total (%)	Head	B <sub>25</sub>	B <sub>50</sub>		B <sub>75</sub>	T <sub>50</sub>				
49.6	44.0	36.4	5.60	11.3	14.46	7.0	8.94	4.3	150.46	72.9	32.40	15.7	206.26	1.0	1.3	1.5	1.4	0.9	1.9
58.3	51.3	60.4	7.00	12.0	14.75	4.9	13.92	4.6	220.68	73.3	33.08	11.0	301.08	1.1	1.9	2.2	1.9	1.1	3.3
62.8	55.9	68.2	6.95	11.1	17.69	5.6	13.65	4.3	225.31	71.2	59.65	18.9	316.30	1.4	2.0	2.1	1.9	1.3	4.5
63.3	55.9	86.5	7.40	11.7	22.45	6.4	14.88	4.3	268.29	77.0	42.75	12.3	348.37	1.8	2.0	2.1	1.9	1.9	3.4
66.0	58.5	76.9	7.55	11.4	17.65	5.1	16.22	4.7	249.52	71.6	64.86	18.6	348.25	1.9	1.6	2.1	1.8	1.4	5.6
69.5	62.0	106.5	7.50	10.8	21.46	6.6	18.68	5.7	229.51	70.6	55.31	17.0	324.96	1.7	2.2	2.3	2.0	1.6	7.3
70.0	63.0	86.0	7.00	10.0	16.52	4.8	15.28	4.4	258.08	74.8	55.17	16.0	345.05	1.4	1.9	1.9	1.8	1.1	4.4
					$\bar{x}$	5.8		4.6		73.1		15.6							
					S.D.	0.9		0.5		2.2		3.0							

SV, snout vent length; L, body length.

$15.6 \pm 3.0\%$  and tail  $5.8 \pm 0.9\%$ . The total body surface area estimates for these snakes generally increase with body size, ranging from 206 to 348 cm<sup>2</sup>, and are similar to values given by Dunson & Robinson (1976, fig. 3). The thickness data show that the body of *P. platurus* does not taper posteriorly.

#### *Surface and near-surface swimming observations*

Observations and video recordings were made of snakes swimming at the still surface of the SIO deep tank, where some snakes floated motionless while others routinely swam as fast as 20 cm s<sup>-1</sup>. Snakes swimming on the surface held their heads at or just below the surface and, owing to the long and buoyant lung, their bodies were slightly out of the water while the tail was just below the surface. Even though the body emerged slightly, surface waves were not formed and the body was stable. There were no obvious differences in the anguilliform swimming motions of snakes on the surface of the deep tank and those swimming just under the surface in the water tunnel.

Snakes forced to swim in the water tunnel always swam within 5 cm of the surface with their bodies horizontal and their heads and tails completely submerged (Fig. 2). Whenever a snake raised its head to breathe, it was swept back in the flow, but once its head was resubmerged it would recover its position. Films showed that the snake's ventral keel shifts laterally with each undulation and tends to flare outwards (giving the snake a concave vertical surface on the outer edge, Fig. 1) at maximum  $A_8$ . The flat paddle tail occasionally rolled slightly to the side during a full sweep; however, the stabilizing effect of the ventral keel prevented snakes from rolling or twisting.

The pattern of four propulsive half waves along the body (Fig. 2) was observed at both 15 and 32 cm s<sup>-1</sup>. Inspection of kinematic data for each segment of the 51 cm

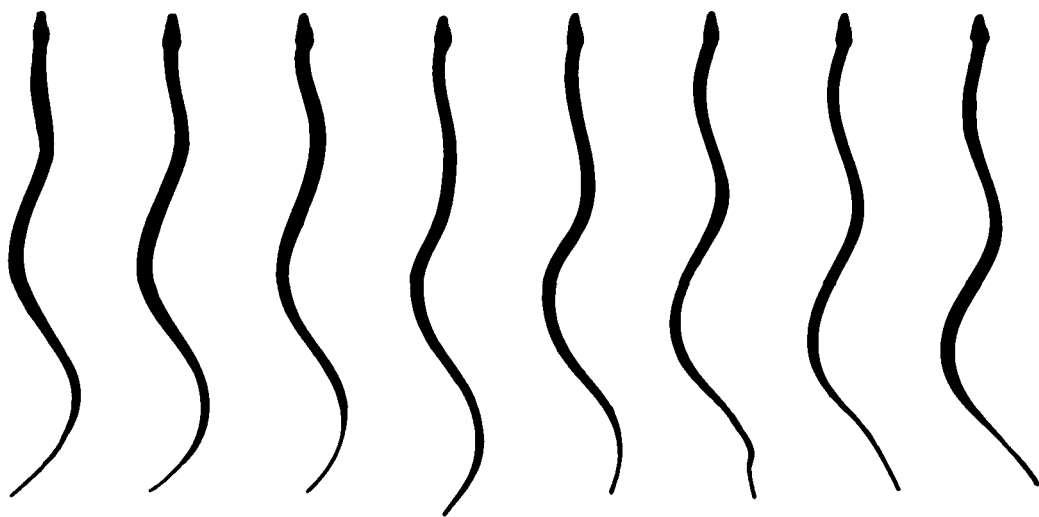


Fig. 2. Tracings of body movements of a 51 cm *Pelamis platurus* swimming at 32 cm s<sup>-1</sup>. Interval between frames is 0.04 s, total sequence time is 0.28 s.

Table 2. *Kinematic data for a 51 cm Pelamis platurus swimming at 15 and 32 cm s<sup>-1</sup>*

Segment	$\lambda_s$ (cm)	$A_s$ (cm)	$W_s$ (cm s <sup>-1</sup> )	$c_s$ (cm s <sup>-1</sup> )	$\theta$ (degrees)
U = 15 cm s <sup>-1</sup> , f = 0.83 s <sup>-1</sup>					
1	10.2 ± 4.2 (8)	0.4 ± 0.2 (7)	0.74	8.5	14.2 ± 2.6 (6)
2	20.4 ± 6.8 (22)	2.4 ± 1.2 (22)	4.44	16.9	23.7 ± 3.0 (7)
3	24.6 ± 3.0 (22)	3.8 ± 1.2 (22)	7.03	20.4	33.4 ± 5.1 (7)
4	25.8 ± 6.0 (22)	5.4 ± 1.8 (22)	9.99	21.4	50.5 ± 3.3 (6)
Tail	—	6.6 ± 2.2 (22)	—	—	—
U = 32 cm s <sup>-1</sup> , f = 1.70 s <sup>-1</sup>					
1	10.4 ± 4.2 (19)	0.8 ± 0.4 (19)	3.03	17.7	7.6 ± 5.6 (10)
2	19.4 ± 6.4 (20)	2.0 ± 1.2 (20)	7.58	33.0	23.4 ± 5.1 (10)
3	26.6 ± 3.4 (21)	4.8 ± 1.0 (21)	18.19	45.2	35.8 ± 3.8 (10)
4	27.2 ± 1.6 (14)	6.4 ± 1.0 (14)	24.26	46.2	44.7 ± 5.4 (10)
Tail	—	6.2 ± 2.3 (21)	—	—	—

Data for measured variables are mean ± S.E. (*N*).

U, swimming speed;  $\lambda_s$ , wavelength of segment;  $A_s$ , amplitude of segment;  $c_s$ , propulsive wave velocity;  $\theta$ , angle between axis of progression and posterior edge of segment; f, wave frequency.

snake (Table 2) reveals that all variables were increased in posterior segments. While  $\lambda_s$ ,  $A_s$  and  $\theta$  remained nearly the same at both velocities, values of  $W_s$  and  $c_s$  were nearly doubled and tail amplitude declined at 32 cm s<sup>-1</sup>. Estimated from Lighthill's model, the total power generated by a 51 cm *P. platurus* is 3.641 × 10<sup>-4</sup> J s<sup>-1</sup> at 15 cm s<sup>-1</sup> and 29.877 × 10<sup>-4</sup> J s<sup>-1</sup> at 32 cm s<sup>-1</sup> (Table 3). After correction for kinetic energy losses at each speed, the Froude efficiencies are 79% at 15 cm s<sup>-1</sup> and 81% at 32 cm s<sup>-1</sup>. As expected, theoretical drag estimates for this snake at the two speeds and under both laminar and turbulent surface boundary conditions (Table 4) are less than the thrust power estimates made from Lighthill's bulk momentum model.

#### *Subsurface swimming*

In contrast to the largely two-dimensional nature of body motions during surface swimming, snakes swimming below the surface typically, but not always, adopted a dorsal-ventral body curvature, usually with the anterior body level or slightly sagging and the tail somewhat elevated relative to the head (Fig. 3). Depending upon velocity, subsurface swimmers commonly had their tails up and the axis of their bodies tilted from 10 to 50° relative to their horizontal plane of progression. The average (±S.D.) velocity of snakes swimming level but in the 'tail-up' mode at depth was 2.0 ± 0.7 cm s<sup>-1</sup> (range 1.0–3.0, *N* = 27). This is significantly slower (one-tailed *t*-test) than the velocity of snakes swimming level but without their tails elevated (4.3 ± 2.0 cm s<sup>-1</sup>, range 1.0–8.0, *N* = 26).

Tail elevation by *P. platurus* during submerged swimming results from this snake's vertebral flexibility and the ascent of gas into the elevated end of its long lung. Observations with the anaesthetized snake suspended at 8.5 m showed that when the tail was elevated the underlying lung expanded, and the caudal region



Table 3. Kinematic parameters and estimates of the swimming power of a 51 cm *Pelamis platurus* swimming at 15 and 32 cm s<sup>-1</sup> using the bulk momentum model of Lighthill (1969, 1970)

U (cm s <sup>-1</sup> )	c (cm s <sup>-1</sup> )	f (s <sup>-1</sup> )	A <sub>t</sub> (cm)	W (cm s <sup>-1</sup> )	w (cm s <sup>-1</sup> )	d (cm)	m <sub>T</sub> (g cm <sup>-1</sup> )	K (degrees)	T (×10 <sup>-4</sup> J s <sup>-1</sup> )	T <sub>k</sub> (×10 <sup>-4</sup> J s <sup>-1</sup> )	T <sub>p</sub> (×10 <sup>-4</sup> J s <sup>-1</sup> )	η (%)
15	21.4	0.83	6.6	24.34	7.28	1.3	1.37	43.4	3.641	0.752	2.889	79
32	46.2	1.70	6.2	47.00	14.50	1.3	1.37	34.0	29.877	5.577	24.300	81

Equations and symbols are given in the text or below (see also Webb, 1978).

A<sub>t</sub>, tail amplitude.

W, lateral velocity of tail =  $\frac{\pi(2A_t)f}{\sqrt{2}}$ , note the doubling of mean tail amplitude.

w, acceleration of water at the tail = W[(c-U)/c].

d, mean tail thickness, Table 1.

m<sub>T</sub>, tail virtual mass =  $\frac{k\pi\rho d^2}{4}$ , where k is a body cross-sectional shape constant and ρ is the sea water density = 1.03.

T, total swimming power = m<sub>T</sub>wUW.

T<sub>k</sub>, kinetic energy lost to wake displacement = 0.5(m<sub>T</sub>w<sup>2</sup>U)  $\frac{1}{\cos K}$ .

T<sub>p</sub>, swimming thrust power = T - T<sub>k</sub>.

η, Froude efficiency = T<sub>p</sub>/T.

Table 4. *Estimates of theoretical frictional drag power for a 51 cm Pelamis platurus at velocities of 15 and 32 cm s<sup>-1</sup> and compared under assumed conditions of laminar and turbulent boundary flow*

U (cm s <sup>-1</sup> )	Re	S (cm <sup>2</sup> )	C <sub>f</sub> laminar	C <sub>f</sub> turbulent	P <sub>lam</sub> <sup>•†</sup> (×10 <sup>-4</sup> J s <sup>-1</sup> )	P <sub>turb</sub> <sup>†‡</sup> (×10 <sup>-4</sup> J s <sup>-1</sup> )
15	76 500	206	0·0048	0·0076	1·719	2·721
32	163 200	206	0·0033	0·0065	11·472	22·596

Equations and symbols given in the text or below (see also Webb, 1975).

Re, Reynolds number =  $UL/\nu$ , where  $\nu$  is the kinetic viscosity of water = 0·0095 at 23°C.

S, surface area = 206 cm for a 50 cm snake (Table 1).

C<sub>f</sub> laminar, coefficient of friction for laminar flow =  $1·33Re^{-0·5}$ .

C<sub>f</sub> turbulent, coefficient of friction for turbulent flow =  $0·072Re^{-0·2}$ .

\* Thrust power needed to balance laminar frictional drag is  $P_{lam} = D_f U$ , where  $D_f = 0·5\rho S U^2 C_f$  laminar.

† Note that since  $D_f$  contains  $U^2$ , the power needed to overcome friction becomes proportional to  $U^{2·5}$  for laminar and  $U^{2·8}$  for boundary turbulent conditions.

‡ Thrust power needed to balance turbulent frictional drag.

became positively buoyant. Conversely, lowering the tail to a point below the head resulted in caudal flattening and sinking. Deep tank video recordings additionally showed that snakes swimming in the 'tail-up' mode, but in a more or less horizontal plane, had a large gas swelling just anterior to the vent where the tip of the lung is located (Fig. 3). Video recordings also showed that the swelling would disappear and reappear as snakes made the transition from 'tail-up' to 'tail-down' and then back to 'tail-up' swimming, which occurred routinely in the course of slight (1–3 m) depth changes as snakes swam around the tank.

The keel of a diving *P. platurus* becomes accentuated by the combined effects of tail elevation, the bending of the body and hydrostatic pressure (i.e. lung compression and concomitant skin stretching), resulting in a largely foil-shaped trunk. Depending upon the degree of tail-up swimming being used by a snake, a section of the ventral keel actually becomes vertical and positioned at the trailing edge of the body (Figs 3, 4). As a result of this, torsional and twisting body motions are incorporated into the basic undulatory movement pattern, and the vertical body and tail appear to act together as an extended caudal fin or wing (Fig. 4). These, along with the horizontal trunk segment, generate swimming thrust. Comparison of the frames in Fig. 3 shows that relative to the mid-body region, the anterior trunk and head both remain level and exhibit low yaw. Also, and unlike the pattern observed in horizontal swimming, the amplitudes of the tail and vertical body segment are low relative to the mid-body region.

## DISCUSSION

### *Comparative aspects of anguilliform swimming*

How does the horizontal locomotion of *P. platurus* compare to that of other slender anguilliform swimmers? Analyses of anguilliform swimming have been made for the

eel, *Anguilla*, by Gray (1933) and for the water snakes *Natrix* (Taylor, 1952; Hertel, 1966) and *Nerodia* (Jayne, 1985). For *Anguilla*, which seldom leaves water, and *P. platurus*, which has a completely aquatic existence, natural selection has refined

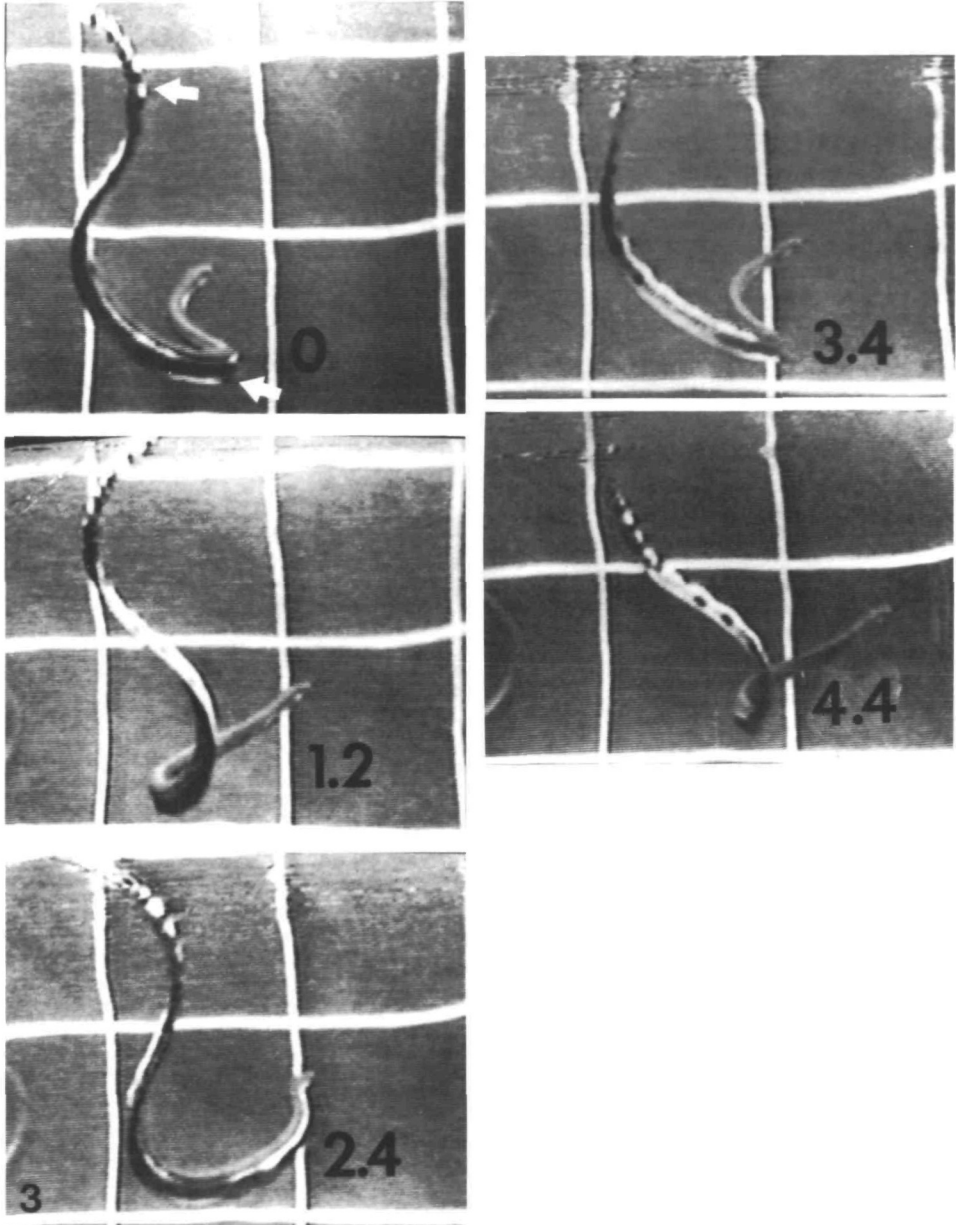


Fig. 3. Photographic prints from a video recording showing the body movements of a *Pelamis platurus* over a period of 4.4 s while it swam in the 'tail-up' mode towards the background grid and away from the observation window. Arrows in frame 0 show bulged section of the saccular lung (this is also seen in frames 1.2 and 3.4) and the outward curvature of the ventral keel (see also frame 3.4).

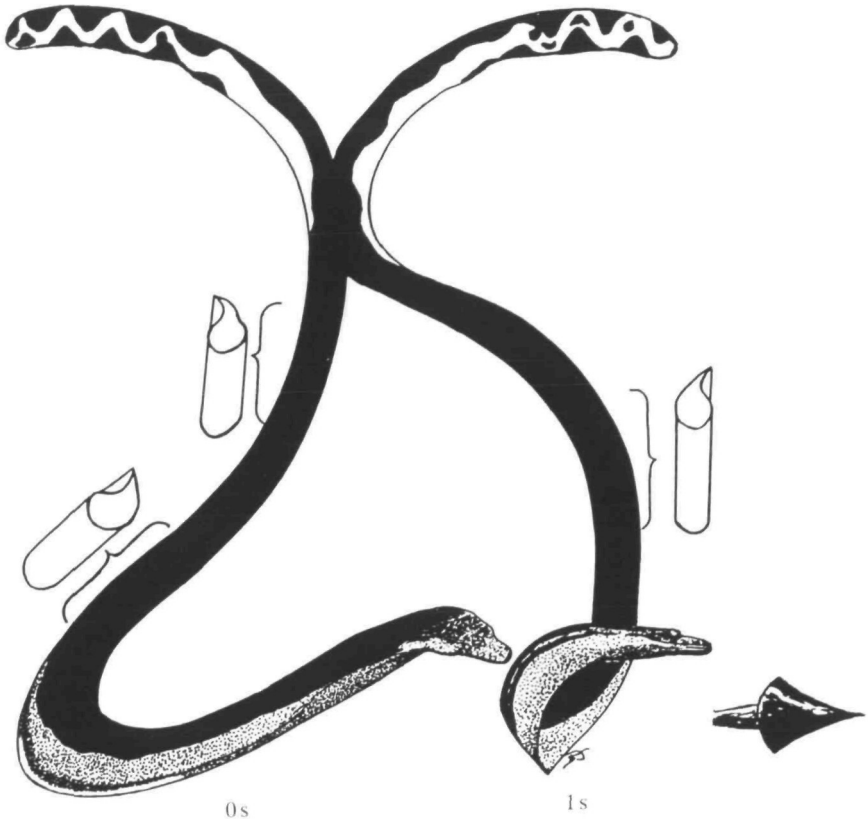


Fig. 4. Diagram showing changes in the body positions of a swimming *Pelamis platurus* over 1 s and illustrating how maximum left and right lateral body undulations in the 'tail-up' mode result in cyclic and sequential changes in the angle of attack and camber (as a result of keel bending) of body segments. Arrow shows direction of motion.

both the nature and degree of development of specializations for aquatic locomotion. *P. platurus*, for example, cannot propel itself on land; females are ovoviviparous and young are born at sea. By contrast, the occurrence in water of snakes such as *Natrix* and *Nerodia* is the result of selection for a behavioural plasticity that includes the capacity to be amphibious. These snakes remain specialized for terrestrial locomotion and, depending upon ecological circumstances, may or may not enter water. In water, *Natrix* frequents shallow areas where it both swims and crawls, but, unlike *P. platurus* it seldom enters deep, open-water bodies except to cross them, and it rarely floats motionless at the water surface. *Natrix* will, however, enter water and dive to escape predators (Schmidt & Inger, 1962).

Fig. 5 compares the body undulation patterns made by these anguilliform swimmers, and reference to Fig. 2 shows that *P. platurus* has more and smaller segment oscillations along its body. A similar pattern has been shown for another sea snake, *Enhydrina*, by Aleyev (1977, fig. 25). The relative caudal amplitudes (expressed as %L) estimated for animals in Fig. 5 are: *Natrix* (L = 24 cm) 43 %L, (105 cm) 41 %L; *Nerodia* 41 %L; *Anguilla* 39 %L. These are all greater than that

of the 51 cm *P. platurus* (26 and 19%L at 15 and 32 cm s<sup>-1</sup>, respectively). Smaller amplitude segment and tail oscillations reflect the greater posterior body and tail thicknesses of *P. platurus* which, together with a ventral keel, provide more stability during swimming. The caudal tapering of *Natrix* and *Nerodia* markedly reduces their posterior virtual mass, and this results in a high caudal amplitude and probably energy loss (Webb, 1978), as well as a twisting of the body (Jayne, 1985) to obtain thrust. Photographs and side-view diagrams of swimming *Natrix* and *Nerodia* show that they often swim at the water surface with their heads above water and their trunks and tails submerged. Common features of this swimming mode are the production of a large surface wake and, depending upon velocity, high amplitude body and caudal oscillations and the tendency for the body to roll (Hertel, 1966, figs 232, 246; Jayne, 1985, fig. 3). This contrasts with the flat, slightly buoyant swimming posture of *P. platurus*. The tendency for the trunk and tail of both

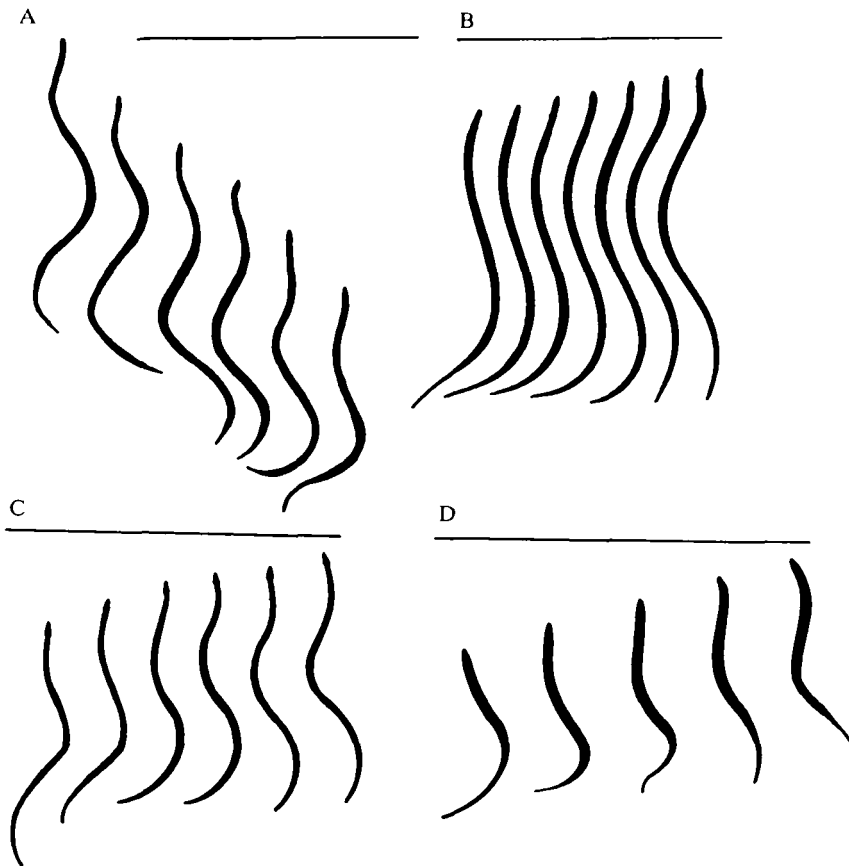


Fig. 5. Comparison of anguilliform swimming patterns. (A) *Natrix natrix* (Taylor, 1952, fig. 5)  $L = 24$  cm,  $U = 32$  cm s<sup>-1</sup>, sequence length 0.32 s. (B) *N. natrix* (Hertel, 1966, fig. 235)  $L = 105$  cm,  $U = 52$  cm s<sup>-1</sup>, sequence 0.7 s. (C) *Nerodia fasciata* (Jayne, 1985, fig. 5)  $L = 24$  cm,  $U = 60$  cm s<sup>-1</sup>, sequence 0.2 s. (D) *Anguilla* (Gray, 1933, fig. 2)  $L = 7$  cm,  $U = 4$  cm s<sup>-1</sup>, sequence 1 s.

*Nerodia* and *Natrix* to sink below the surface is due to their relatively short lungs (about 55 %L vs 90 %L in *P. platurus*, Jayne, 1985; Graham *et al.* 1975).

#### *Energetic and thrust estimates*

Using kinematic data we calculated (Table 5) the total power, kinetic energy loss, and net swimming thrust power of a 24 cm *Nerodia* swimming at 12.4, 24.6 and 35.9 cm s<sup>-1</sup> (Jayne, 1985) and a 7 cm *Anguilla* swimming at 4 cm s<sup>-1</sup> (Gray, 1933; Webb, 1975). Data for *Nerodia* were obtained during steady swimming (Jayne, 1985), and the selected range of velocities permits relevant comparisons to data for *P. platurus*. (Snake morphological data needed for these calculations [e.g. values for *k* and *d*, see Table 3] were obtained from preserved specimens in the herpetological collection at San Diego State University.)

Power production by *Anguilla* and *P. platurus* are first compared with reference to the U<sup>2.8</sup> power scaling ratio predicted from theory for turbulent flow (Table 4). The swimming eel has a total power of 0.055 × 10<sup>-4</sup> J s<sup>-1</sup> at a velocity of 4 cm s<sup>-1</sup> (Table 5). That of *P. platurus* at 15 cm s<sup>-1</sup> is 3.641 × 10<sup>-4</sup> J s<sup>-1</sup> (Table 3), and at 4 cm s<sup>-1</sup> it would be 0.09 × 10<sup>-4</sup> J s<sup>-1</sup> (i.e. 3.641/[15<sup>2.8</sup>/4<sup>2.8</sup>]), which is 36 % higher than the estimated power of *Anguilla* at this velocity. Even without correcting for the body size differences (*P. platurus* weighs about 45 g, *Anguilla* about 5 g) and Froude efficiencies, this calculation shows that the thrust powers of *Anguilla* and *P. platurus* are somewhat similar at 4 cm s<sup>-1</sup>, and thus supports Seymour's (1982) conclusion that the metabolic cost of swimming for a sea snake is similar to that of an eel. We have no means of knowing whether the magnitude of the difference between these two power estimates would be biologically significant.

Table 5 shows that the total swimming thrust power of the 24 cm *Nerodia* at 12.4, 24.6 and 35.9 cm s<sup>-1</sup> is much less than that of the 51 cm *P. platurus* swimming at 15 and 32 cm s<sup>-1</sup> (Table 3). (These comparisons also ignore size differences; a 24 cm *Nerodia* weighs 5.1 g.) However, *Nerodia* has proportionately higher kinetic energy losses at all speeds and correspondingly lower Froude efficiencies. The reduced surface area of the posterior body sections of *Nerodia* relative to *P. platurus* must account for its greater caudal amplitude and its higher propagated wave velocity and both of these factors lower Froude efficiency (Webb, 1978). In view of the larger amplitude motions of the body and tail of *Nerodia*, it is not surprising that its estimated wake energy loss is proportionately greater than that of *P. platurus*. However, these estimated losses may still be low because, when swimming at the water surface, it would encounter a three- to five-fold increase in drag due to surface wave formation (Hertel, 1966), which would further affect its thrust requirement and locomotor efficiency. Finally, the body of this snake is nearly round and, as described above, its tail tapers steadily; virtual mass at the trailing edge of its body becomes quite small compared to that of *P. platurus*. Webb (1978) pointed out that estimates of both total swimming power (*T*) and kinetic energy lost to wake displacement (*T<sub>k</sub>*) for tapered-body forms are usually conservative.

Additional insight into the relative efficiencies of the swimming patterns and body designs of *Nerodia* and *P. platurus* can be gained through a comparison of swimming

Table 5. Kinematic parameters for a 24 cm *Nerodia* (Jayne, 1985) swimming at three velocities and *Anguilla* (Gray, 1933; Webb, 1975) with estimates of swimming power based on Lighthill's (1969) reactive model

L (cm)	U (cm s <sup>-1</sup> )	c (cm s <sup>-1</sup> )	f (s <sup>-1</sup> )	A <sub>t</sub> * (cm)	W (cm s <sup>-1</sup> )	w (cm s <sup>-1</sup> )	d† (cm)	m <sub>r</sub> (g cm <sup>-1</sup> )	K‡ (degrees)	T (×10 <sup>-4</sup> J s <sup>-1</sup> )	T <sub>k</sub> (×10 <sup>-4</sup> J s <sup>-1</sup> )	T <sub>p</sub> (×10 <sup>-4</sup> J s <sup>-1</sup> )	η (%)
<i>Anguilla</i>													
7	4	6	1.6	2.4	8.5	3.0	0.9	0.53	40.6	0.055	0.013	0.042	76
<i>Nerodia</i>													
24	12.4	29.6	1.1	6.8	16.7	9.7	0.4	0.13	34	0.261	0.092	0.169	65
	24.6	49.4	2.0	6.9	30.7	15.4	0.4	0.13	35	1.512	0.463	1.049	69
	35.9	75.0	3.2	8.0	57.0	29.7	0.4	0.13	45	7.901	2.902	4.999	63

Terms and notations as defined below, in the text, or in Table 3.

\* A<sub>t</sub> values for *Nerodia* at each velocity estimated from Jayne (1985, table 2).

† Value of d for *Nerodia* determined from a preserved snake.

‡ Values for *Nerodia* assumed based on tail amplitude estimates.

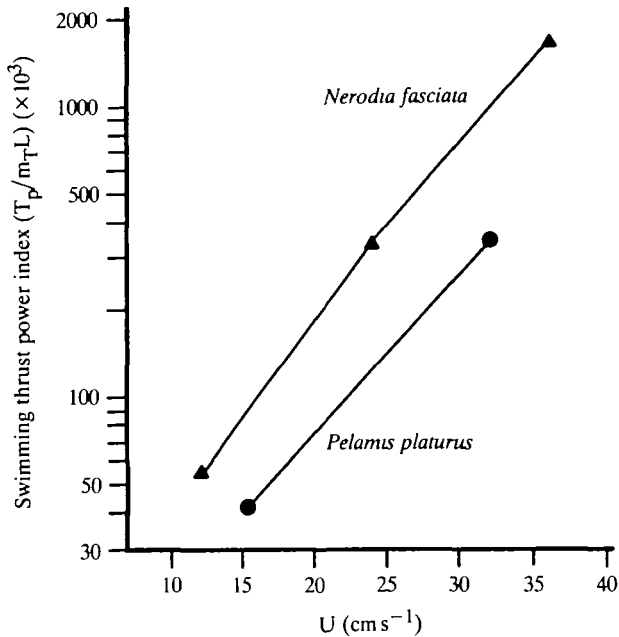


Fig. 6. Relationships between the swimming thrust power indices ( $T_p/m_T L$ ) and swimming speed ( $U$ ) for *Nerodia fasciata* (▲) and *Pelamis platurus* (●).

thrust values that have been in some way normalized for the length and mass differences between these two snakes. Because of their size difference the Reynolds numbers ( $Re$ ) of these snakes hardly overlap and meaningful comparison of size-corrected thrust coefficients or other kinematic properties as a function of  $Re$ , as was done by Yates (1983), is not possible. Rather we compare *Nerodia* and *Pelamis* by dividing swimming thrust power ( $T_p$ ) values for each snake at each speed by the product of segment virtual mass ( $m_T$ ) and body length ( $L$ ) (data provided in Tables 3 and 5). The resulting size-adjusted swimming thrust indices range from 42 to 1602, and when these are compared relative to swimming speed (Fig. 6) it is apparent that, relative to *P. platurus*, *Nerodia* is a less efficient swimmer that requires both a greater swimming thrust and a larger increase in thrust with velocity. It is recognized that Lighthill's bulk momentum model does not adequately describe all active hydromechanical elements of anguilliform swimming (Lighthill, 1983). Future development of a resistive-reactive theory for anguilliform swimming will increase our abilities to compare the hydromechanical forces in these phylogenetically distant yet convergent swimmers.

#### *Subsurface swimming by Pelamis platurus*

Our observations of the subsurface swimming motions of *P. platurus* indicate that proximity to the surface severely limits the scope of swimming motions available to this species. When away from the confining surface, this snake can, by shifting its



body attitude, displace the bulk of its pulmonary gas volume from one end of the lung to the other. Assuming that this action is not solely an artefact of confinement in the SIO tank (i.e. diver verification of this swimming mode for snakes in their natural environment is needed), *P. platurus* appears to use this mechanism to achieve nearly effortless and rapid changes in regional static lift, and thus exercise subtle control of the direction of its swimming thrust.

The ability to shift lung gas has significance for the energetics of subsurface swimming, including angles and rates of depth change, as well as for buoyancy control and pulmonary oxygen storage at depth. Deep tank video recordings and direct observation revealed that the switch from 'head-up' to 'tail-up' swimming always coincided with slight depth changes as snakes circuted the tank. It is important to emphasize that even if a snake swimming below the surface was neutrally buoyant, it could, by inclining its body, concentrate a sufficient amount of gas in its posterior (saccular) or anterior (tracheal) lung area to establish a positive static lift at one end of its body. Thus when a snake elevates its head and swims upwards, lung gas shifts anteriorly, the saccular lung deflates and the tail sinks. Similarly, when the snake levels off at its new depth and then slightly dips its head, the saccular lung will again fill and the tail will rise. Logically, a swimming snake's head should always initiate an upward or downward course change, with the body following. However, the shifts in regional lift accompanying this action in subsurface swimming *P. platurus* can be attributed to specialized structural features of its lung, including its length, the compliance of the posterior sections and a capacious terminal segment.

Subsurface swimming with a vertical tail and posterior body section and the accentuation of the ventral keel by body curvature appear to impart vertical and horizontal stability to the snake in a manner analogous to the median and paired fins of a fish. Depending upon the buoyancy state of a snake, its tail may tend to raise it towards the surface, and this is countered by both forward swimming thrust and the flat surface of the head which acts as a stabilizing plane. Although in the opposite direction, this is analogous to the manner in which the combined functions of swimming and pectoral lift counter the tendency of negatively buoyant sharks and scombrids to sink.

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