

Diving of the sea snake *Pelamis platurus* in the Gulf of Panamá

II. Horizontal movement patterns

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Abstract

The horizontal movement patterns of eleven yellow-bellied sea snakes [*Pelamis platurus* (Linnaeus)] were determined incidentally to acoustic tracking studies of their diving behavior in the Gulf of Panamá during 1983–1985. The average speed of the snakes was 1.9 km h⁻¹ (range 0.3 to 7.1 km). Movement direction is influenced by phasic north-south tidal currents and secondarily affected by combinations of factors that affect local current velocity. The velocity of diving snakes did not always agree with that observed for the surface current. Drift rate was not correlated with average or maximum dive depth, however, snakes that surfaced to breathe one or more times during a period had greater average drift rates than those that did not surface. The role of such factors as feeding, predator avoidance, thermoregulation, orientation, and the avoidance of surface turbulence are considered in a discussion of the adaptive significance of diving for *P. platurus*. Diving in this species may enable it to avoid surface disturbance, facilitate relative position changes within the surface drift, and contribute to various aspects of its feeding behavior.

Introduction

The purpose of this paper is to report on the factors that affect horizontal movement of the yellow-bellied sea snake *Pelamis platurus* (Linnaeus) Hydrophiidae in the Gulf of Panamá and to discuss the possible role of diving in horizontal movement and other aspects of the life history of this species. *P. platurus* is broadly distributed across the Pacific and Indian Oceans from the coasts of Central America and Mexico to the east coast and southern tip of Africa (Graham et al. 1971). It is specialized for a totally pelagic existence, being ovoviviparous (Kropach 1973), having a paddle-shaped tail and ventral body keel for efficient anguilliform swimming (Graham et al. 1987), and,

for hydromineral regulation, possessing a selectively ion- and water-permeable skin as well as salt-secreting glands (Heatwole 1978, Dunson and Stokes 1983).

Although *Pelamis platurus* is regarded as a surface dweller, its ability to dive has been noted (Pickwell 1972, Kropach 1973) and, using telemetry studies in the Gulf of Panamá, Rubinoff et al. (1986) provided the first quantitative information on its diving capacity. These workers found that this snake dove to as deep as 50 m, remained submerged for as long as 213 min, and spent an average of 87% of the track time diving. It was also found that snakes avoided turbulent water-surface conditions and would not dive into water cooler than 19°C.

The broad geographic distribution of *Pelamis platurus* is a consequence of its transport in oceanic surface currents (Graham et al. 1971, Pickwell and Culotta 1980). Yet nothing is presently known about its rate of progression in the surface drift or about the ability of this snake, through activities such as swimming and diving, to affect its drift velocity. Tracking data for *P. platurus* in the Gulf of Panamá permit preliminary examination of the effects of current and snake depth on their rate of horizontal movement. Water flow in the Gulf is dominated by the nearly north-south motions of strong, semi-diurnal tidal currents and the counterclockwise coastal circulation of the Colombia Current (Fleming 1938, Bennett 1965). Also, during the dry season (December–March) northerly trade winds often transport surface water south out of the Gulf and cause upwelling (Smayda 1966). In the present study we relate the movement patterns of tracked snakes to tidal and other current flow and describe instances when snake motion differed from that expected on the basis of local current conditions.

Materials and methods

Dive data and tracking methodologies reported for *Pelamis platurus* by Rubinoff et al. (1986) served as the basis for

analysis of horizontal movement patterns. Tracking was done with ultrasonic pressure transmitters that had an effective range of about 1 km. The signal was monitored with a directional hydrophone and receiver unit coupled to a microprocessor decoder display aboard the Smithsonian Tropical Research Institute's R.V. "Benjamin" [a 63 foot (19.2 m) vessel] or, in the earlier work, a 14 foot (4.3 m) outboard-powered Zodiac. The hydrophone was suspended below the hull of the tracking vessel and linked via a shaft to a steering control that permitted rotation through nearly 360°.

Snakes (90 to 195 g) were collected by dipnet from drift lines in the Gulf of Panamá during 1983–1985. Transmitters incorporated into neutrally-buoyant foam harnesses, were secured to the ventral side of the body (at about one-third of the total length behind the head) of cold-anesthetized snakes. Each snake was allowed to recover for 10 to 12 h in an ambient (25° to 30°C) seawater tank before release. Tracking required a hydrophone operator who continually monitored the signal and adjusted the hydrophone position in order to maintain a constant pulse strength, a helmsman who positioned the vessel optimally to maintain about the same distance between the snake and boat, and a data recorder.

Data on snake position were obtained by compass triangulation from the tracking vessel (which was always near the snake) to fixed points on the islands, at from 0.5 to 3 h periods during daylight. Tracks occurred over depths ranging from 2.7 to 78.7 m. The course of each tracked snake was plotted and the distance and direction of movement within each period determined. The record was examined for correlations with factors such as average depth of the snake, the amount of time it spent at the surface and its number of trips to the surface to breathe, changes in the tide, and surface currents. To determine how snake movement related to surface currents, anchored buoys and surface-drifters were deployed along the track of one snake. A 20-liter bottle filled with sufficient seawater to prevent emergence above the water surface was used as a surface-drifter. This was released from beside the buoy and its velocity recorded. Drift distance was estimated by transit time for the Zodiac from the buoy to the drifter. For speed calibration prior to each set of observations, we measured the time required for a Zodiac to traverse the length of the R.V. "Benjamin" at constant speed.

Depth and current charts of the Pearl Islands aided track analyses, and tide tables for Balboa, Panamá, with appropriate time and elevation corrections applied for the Pearl Islands (Fleming 1938), were used.

Results and discussion

The mean horizontal speed of eleven tracked individuals of *Pelamis platurus* (Table 1) was 1.9 km h⁻¹ (range 0.3 to 7.1 km). This agrees with tidal current speeds shown on hydrographic charts for areas around the Pearl Islands (1 to 2 km h⁻¹) and those indicated for the adjacent areas of the

Gulf of Panamá where tracking took place (1.2 km h⁻¹; Bennett 1965). No correlation was found between snake speed and the time of day or mean snake depth. The selected track records in Figs. 1–4 show overall movement patterns of five snakes. The tracks of Snakes J and K (Fig. 2)

Table 1. *Pelamis platurus*. Speeds of eleven tracked sea snakes. For size data of each snake and other track information see Rubinoff et al. (1986, their Table 1)

Snake	Hours of daylight tracking	No. of observation periods	Speed (km h ⁻¹)		
			\bar{x}	min.	max.
A	7.2	6	3.2	0.9	7.1
B	3.3	4	2.4	0.6	3.7
E	2.5	2	1.5	0.9	2.2
F	4.5	2	1.9	0.8	3.0
I	7.7	8	0.7	0.3	1.2
J	11.8	10	1.5	0.7	2.1
K	12.6	7	1.1	0.5	2.5
L	11.3	7	2.7	1.2	4.5
M	4.9	3	2.1	1.3	3.3
N	6.3	4	2.0	0.9	4.6
O	19.4	17	2.0	1.0	3.9
Overall \bar{x} (\pm SD)			1.9 (0.7)	0.8 (0.3)	3.5 (1.6)

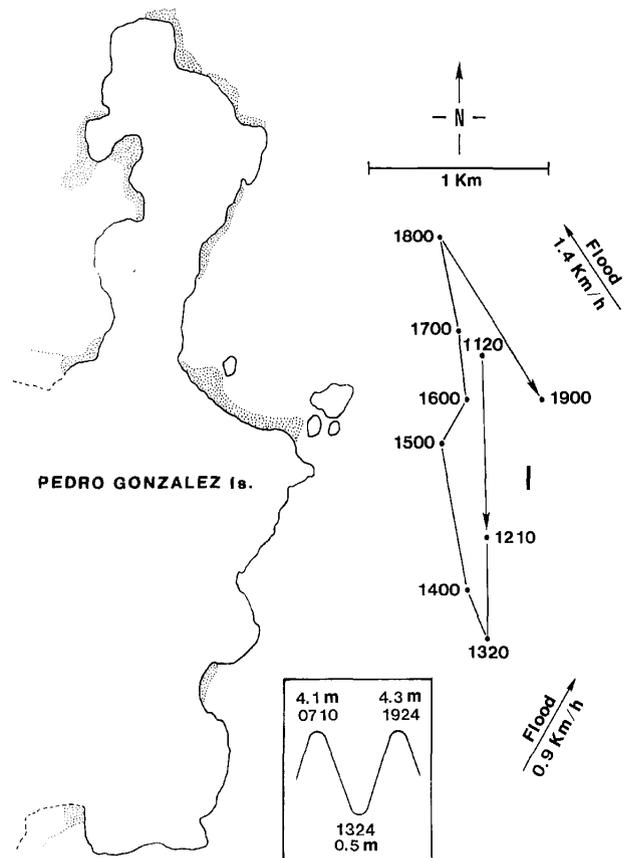


Fig. 1. *Pelamis platurus*. Track line and position of Sea Snake I near Pedro Gonzalez Island, Gulf of Panamá. Arrows indicate direction of movement. Also shown are time of day (hrs), compass direction, distance scale, and flood-tide current-velocity. Inset: tide elevation at 07.10 and 19.24 hrs. For data on snake size and date and duration of track see Rubinoff et al. (1986, their Table 1)

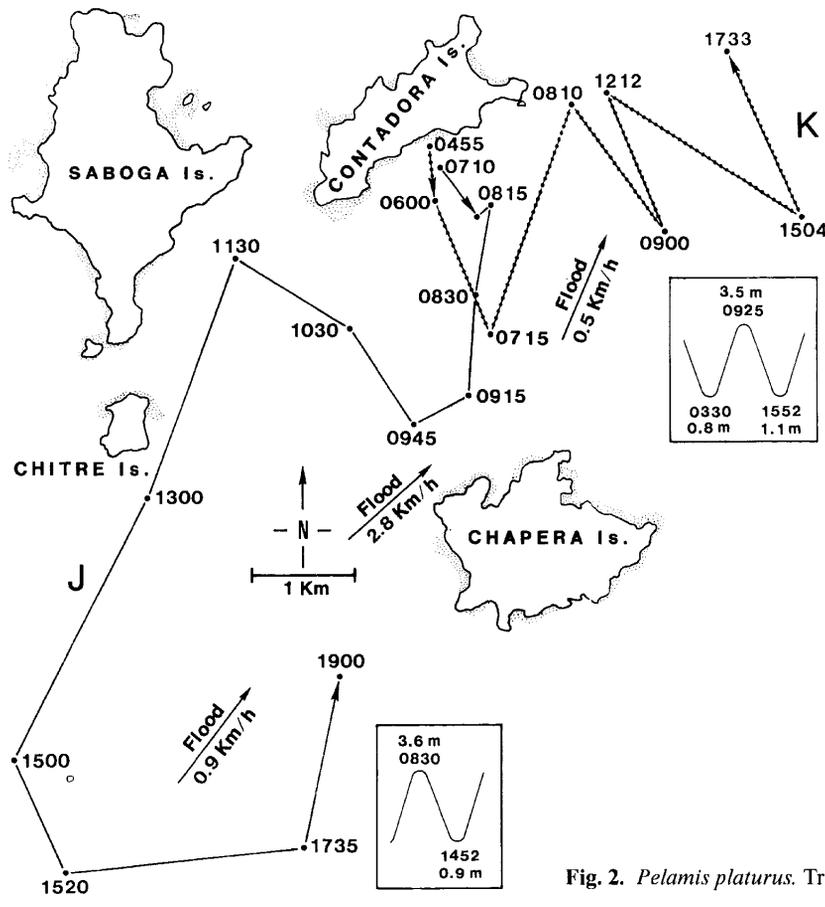


Fig. 2. *Pelamis platurus*. Track lines of Snakes J and K. Further details as in Fig. 1

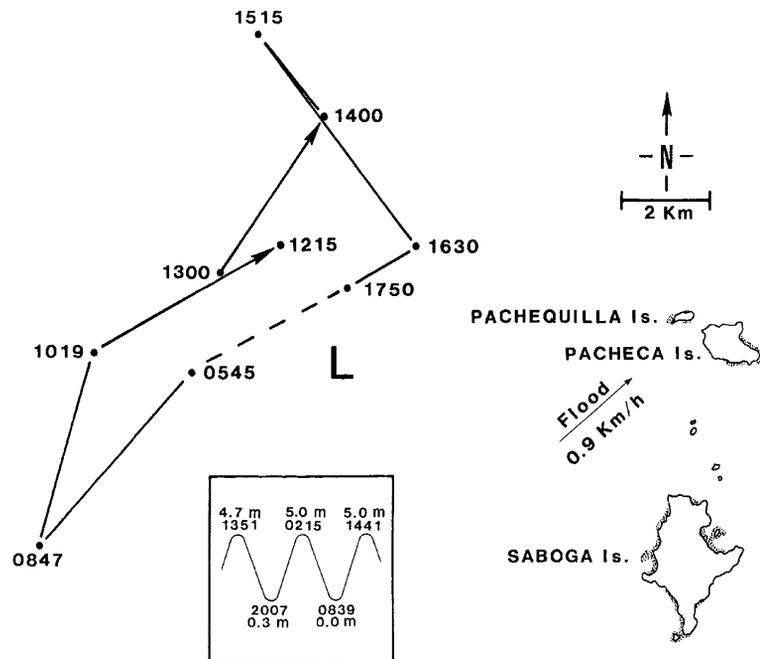


Fig. 3. *Pelamis platurus*. Track line of Snake L; dashed line indicates that no position data were taken at night. Further details as in Fig. 1

were begun in shallow water where both dove to the bottom on several occasions.

Estimates of velocity for *Pelamis platurus* depended upon accurate determination of position. Frequent observations were made, widely separated landmarks were used, and all sightings, except those on Snake 0, were made

by the same observer. Confidence in the accuracy of the horizontal track records comes from the good level of agreement seen for both the mean and range of speeds estimated for each snake and from the observation that predicted tidal current directions were generally correlated with snake-movement direction. The relatively rapid drift

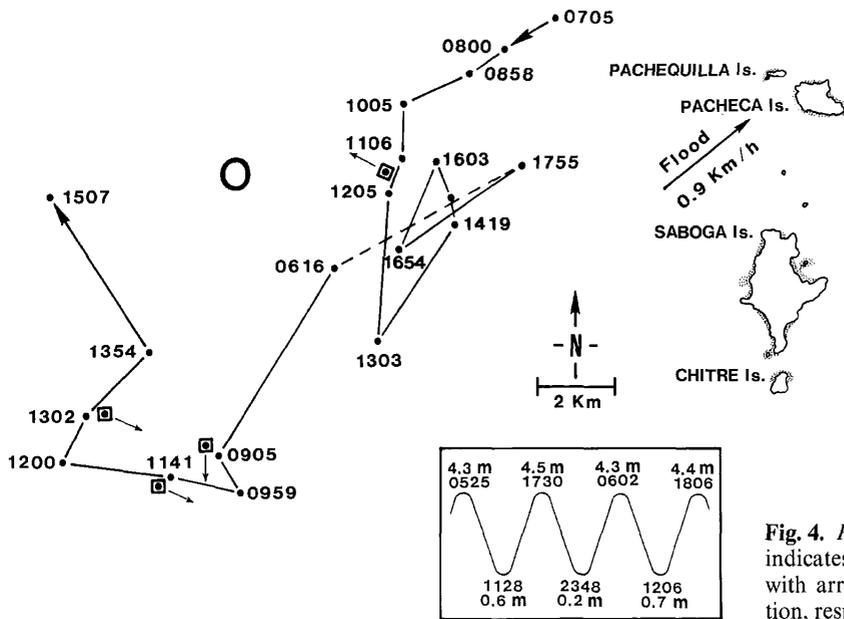


Fig. 4. *Pelamis platurus*. Track line of Snake O; dashed line indicates that no position data were taken at night. Squares with arrows show buoy positions and surface-current direction, respectively

rates measured in some periods probably reflect errors in position determination. However, few high rates were estimated; only 12 of the 71 values were above 3 km h^{-1} .

Effect of tidal current

Tracked snake velocity was dominated by tidal currents. These currents shift direction phasically and exert an influence on flow throughout the water column, although these may vary depending upon tidal range, water depth, the proximity of land, and bottom topography (Fleming 1938, Bennett 1965). Maximum tidal currents in the Gulf of Panamá occur at the half-tides and have a principle compass direction of 330° for flood and 150° for ebb tides (Fleming 1938, Bennett 1965). All snake tracks were of sufficient duration to overlap at least one change in tide phase, and inspection of tide-cycle data for each track (Figs. 1–4) reveals several instances when shifts in snake direction correlated with changes in tide phase (e.g. at 13.20 hrs for Snake I). Good agreement was found between the compass headings for all snake tracks at the times of flood and ebb tides, the half-tides, and the expected tidal-current vectors (Fig. 5). For example, three hours after low tide, when the expected tidal current is 330° , the range of the 12 observed snake vectors was from 150° to 340° (median 35°). Three hours after low tide, with expected tidal flow along 150° , the range of 5 observed vectors was from 115° to 250° (median 210°). Snake vectors at the times of high and low tides, when tidal current flow is slack (Fleming 1938, Bennett 1965), were more variable (Fig. 5). Although snake-movement vectors reflect tide phase, fastest drift rates did not occur exclusively on the half-tides.

Factors such as surface conditions, currents and snake behavior all act in combination with the tides and the Colombia Current to propel snakes in the Gulf of Panamá. In addition to showing a tidal-current influence, the movements of Snakes I, J and K may have also been affected by wind-driven surface flow. These snakes were tracked dur-

ing the dry season (March) of 1984, when strong northerly trade winds and surface chop restricted most of our work to the leeward side of the Pearl Islands. After release, Snake I (Fig. 1) drifted south on the falling tide and then north with the rising tide. Between 13.20 and 18.00 hrs it went north (0.5 km h^{-1}) at a mean depth of 5 m and surfaced to breathe eight times. By 18.00 hrs it had moved beyond the wind shadow of Pedro Gonzalez Island and, over the next hour, while at an average depth of 3 m and surfacing to breathe six times, it was swept 1.1 m to the south. During this period, trade-wind-driven upwellings were experienced and since *Pelamis platurus* does not dive as deeply in cool water (Rubinoff et al. 1986), large numbers of snakes may be transported out of the Gulf during this time.

The tracks of Snakes J and K (Fig. 2) illustrate how random combinations of snake location and tidal current can influence displacement to different locations. These snakes were released on subsequent days from about the same position south of Contadora Island. Two hours after release both had moved south to the Chapara Channel. Snake J entered the channel on a falling tide and was carried to the southwest, then northwest toward Saboga Island, and then south. After about three hours it was beyond the lee of Saboga and Chitre Islands and its velocity increased in the wind drift. By 15.00 hrs, when the tide was again rising, this snake's southerly progression stopped and, by 19.00 hrs, near the time of maximum expected (half-tide) current, it was moving north toward Contadora. Snake K on the other hand entered the Chapara Channel two hours before high tide and was swept to the northeast in the flood current. Within an hour this snake moved beyond the lee of Contadora and, between 08.10 and 09.00 hrs, while at an average depth of 6.5 m, it moved at 1.8 km h^{-1} to the southeast, presumably with the wind drift.

In more open waters, oscillating tidal flow would not lead independently to large changes in net snake position,

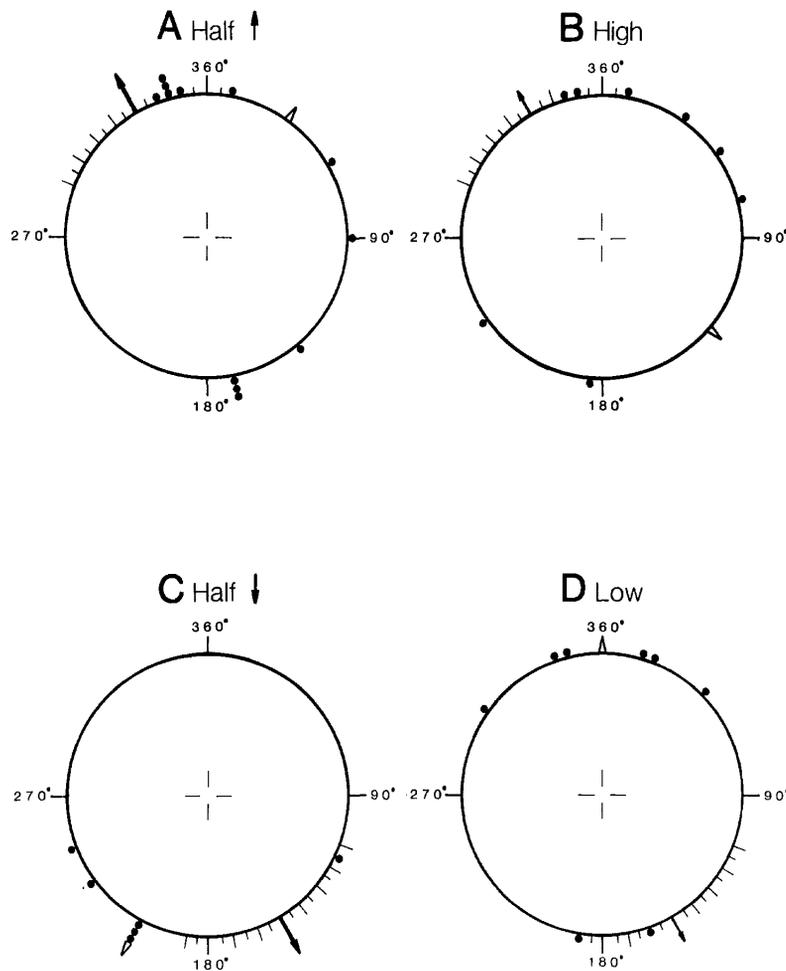


Fig. 5. *Pelamis platurus*. Compass vectors for movement direction of tracked sea snakes during periods coinciding with the four phases of the tidal cycle: (A) half-high tide; (B) high tide; (C) half-low tide; (D) low tide. Arrows indicate expected tidal vector, and length of arrows its relative strength (i.e., strongest on half-tides). Open arrowhead indicates median value of all snake vectors

as was seen for Snakes L and O (Figs. 3 and 4). The tracks of these snakes lasted longer than 24 h, and both exhibited a component of circular oscillation that resembles the long-term loop patterns calculated by Bennett (1965, his Fig. 4) for the end points of the tidal current vectors in the Gulf of Panamá. As a result of tidal oscillation, Snake L had a very small net movement in 24 h, and Snake O moved about 13 km to the west in 32 h.

Movement in relation to surface current and depth

Surface-floating snakes were observed to move with the surface drift. For example, between 05.45 and 08.47 hrs on Day 2, Snake L spent 66% of this time on the surface while it drifted south at 1.2 km h^{-1} (Fig. 3). It floated at the surface during the entire period (08.47 to 10.19 hrs) and drifted north at 2.5 km h^{-1} . Calm surface conditions prevailed during both these periods, and the tidal currents, although opposite, should have had about the same relative speed.

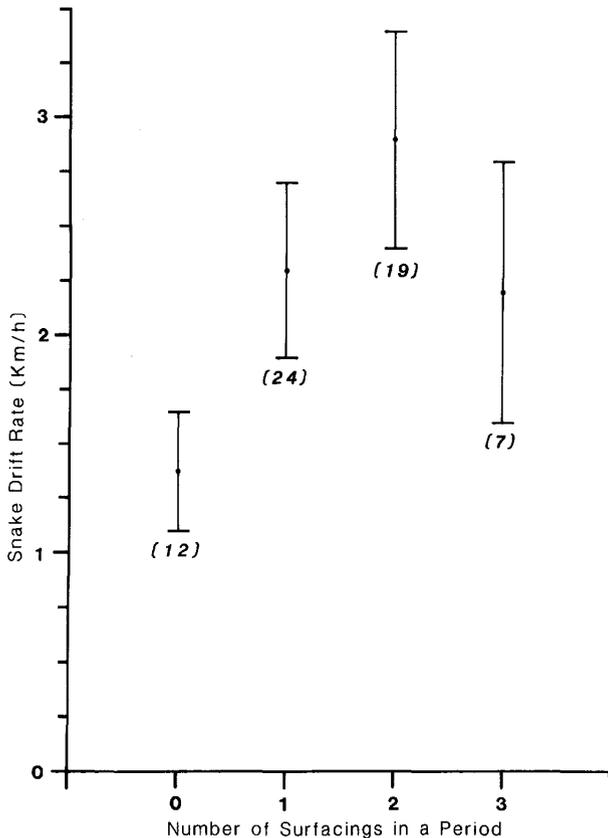
No other tracked snakes spent long periods at the water surface. Because we lacked information about the behavior and swimming velocity, our assessment of snake movement was limited to: (1) considerations of velocity relative to a fixed point, and (2) the effect on velocity of the number of surfacings to breathe that the snake made during a track period. We attempted to correlate velocity and diving

depth, but the combined data for all snakes are highly variable and no correlation was found between speed during a period and either mean or maximum dive depth. However, snakes had regularly to swim to the surface in order to breathe and this was always recorded. Although there was considerable variability in these data, a significant correlation ($r = 0.63$) was found between mean snake speed and the number of surfacings made in a track period (Fig. 6).

Studies with surface drifters, done during the track of Snake O (Fig. 4), show that discrepancies between the velocity of a surface current and a diving snake do occur. Table 2 shows surface current and velocity of Snake O, during our tracking periods. In three cases, snake velocity during the period was different from that of the surface current (Fig. 4). Moreover, it was specifically noted during the 11.06 to 12.05 hrs observations that the snake remained very near the fixed buoy for nearly the entire hour. Between 13.00 and 13.30 hrs, the snake moved 1 km north of the buoy, in almost the exactly opposite direction to the 0.9 km h^{-1} surface current. Snake O was deep during all these studies, but did surface to breathe once (between 11.00 and 12.00 hrs on Day 2), when its fastest rate of movement was also measured. At this time, the snake's velocity was 3.0 km h^{-1} to the west, while surface flow was 1.1 km to the southeast.

Table 2. *Pelamis platurus*. Comparison of surface-current velocity and velocity of Snake O during dives

Observation No.	Date (1985)	Time of day (hrs)	Surface-current velocity		Snake velocity		Dive depth (m)		No. of surfacings during observation period
			Direction	Speed (km h ⁻¹)	Direction	Speed (km h ⁻¹)	Mean	Range	
1	22 May	11.06–12.05	WNW	2.2	S	1.0	29.6	21–36	0
2	23 May	08.30–09.59	SE	2.1	SE	2.0	26.0	6–29	0
3	23 May	11.00–12.00	SE	1.1	W	3.0	25.0	0–38	1
4	23 May	13.00–13.30	SE	0.9	NE	1.5	28.6	27–30	0

**Fig. 6.** *Pelamis platurus*. Relationship between mean number of surfacings for breathing and mean snake speed during each period of tracking for eleven sea snakes. (Numbers of observations in parentheses)

The drifter studies show that diving snakes can move at a different velocity than surface-water flow. This may be explained by the decreases in current speed and changes in direction that commonly occur at depth (Winant and Olson 1976, Winant 1979, Ross 1982). Also, other factors (tides, surface conditions) will probably affect surface currents in the Gulf (Bennett 1965, Smayda 1966). Surface currents such as those indicated in Fig. 4 might increase a snake's speed as it ascends to breathe.

Role of diving in biology of *Pelamis platurus*

Rubinoff et al. (1986) determined that *Pelamis platurus* normally spends about 87% of its time diving. Because this

species has been generally regarded as primarily a surface dweller, the biological significance of its repetitive diving behavior merits discussion.

The surface-floating behavior long thought typical for this snake has two advantages: continuous access to air for respiration and, through positive buoyancy, a reduced energy expenditure (Graham et al. 1975). Surface floating is also an integral part of the stereotyped feeding behavior of *Pelamis platurus* (Hunter and Mitchell 1967, Graham 1974a, Graham et al. 1975). Stomach-content analyses indicate it feeds principally on juvenile, surface-orientating fishes (Kropach 1975, Voris and Voris 1983). Our laboratory observations suggests diving is not related to feeding, because snakes in a 10 m-deep tank readily devoured live fish (*Gillichthys mirabilis* and *Carassius auratus*) offered at 7 to 9 m. It has also been suggested that diving may attract prey; i.e., subsurface-dwelling prey animals may orientate to a diving snake and follow it to the surface where predation can result. We observed a tracked sea snake that returned to the surface with a small carangid swimming along side. Because forage organisms that aggregated under floating snakes may also be vulnerable to other surface predators, snakes may dive after feeding to disperse uneaten prey, thus reducing their availability to competitors.

Two unlikely reasons suggested for the diving of *Pelamis platurus* are predator avoidance and thermoregulation. Heatwole et al. (1974) reported that Australian sea snakes (*Lapemis hardwicki*, *Aipysurus laevis*) were eaten by sharks and Pickwell et al. (1983) reported that a *P. platurus* was regurgitated by a pufferfish (*Sphoeroides annulatus*). But, predatory pressure on *P. platurus* is apparently not large, because Rubinoff and Kropach (1970) were unable to identify any eastern Pacific predatory fishes that were willing to attack this snake. Moreover, the behavior of this aposematically colored snake suggests it does not have many natural enemies. Diving is not a reflexive response to disturbance and snakes in drift lines often did not dive after being prodded with a dipnet. In any case, diving is not likely to protect this snake from most aquatic marine predators, which can swim faster than and go as deep as *P. platurus*. Sea birds are thought to be snake predators (Wetmore 1965), but there have been few observations of this and Caldwell and Rubinoff (1983) reported avoidance of *P. platurus* by naive herons and egrets.

The suggestion that *Pelamis platurus* dives to shed solar heat gained during surface floating (Dunson and Ehlert 1971) does not account for the length or depth of its dives or for dives at night and on cloudy days (Graham 1974b). The finding that snakes spent more time diving when the holding tank surface was turbulent (Rubinoff et al. 1986) does suggest a reason for diving. But this again would not explain deep and frequent dives.

Our findings that the horizontal velocity of a diving snake can be both slower and in a different direction from the surface flow suggests that diving and subsurface swimming may enable *Pelamis platurus* to reposition itself relative to the surface drift. If, for example, a snake became located in an area of water devoid of prey or other snakes, it could simply dive, allowing faster moving surface water to pass over it for a while, and then resurface at a new relative position. If, by contrast, a snake elected to change its relative position by swimming at the surface, it would either have to swim against the surface current or along with it, although faster. In either case, expenditure of energy would be required and the snake's movement relative to the location in the water in which it started would be small. On the other hand, subsurface swimming requires less energy (Seymour 1982, Graham et al. 1987), and a snake could achieve greater relative movement away from the water parcel where it was by submerging to depths of slower flow and later surfacing.

Our hypothesis that diving may enable *Pelamis platurus* to shift its position relative to the surface water is similar to that first suggested by Hardy (1953) to explain the adaptive significance of diurnal vertical migration by zooplankton, and it may function for the similar purpose of renewing foraging resources. Moreover, from a submerged vantage point a snake may be able to observe a large area of the surface and possibly discern drift material, other snakes, or even prey.

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