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I. Dive depth and duration

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Abstract

Fifteen yellow-bellied sea snakes, *Pelamis platurus,* fitted with pressure-sensitive ultrasonic transmitters, were tracked in the Gulf of Panamá during 1983–1985. Snakes spent up to 99.9% ($\bar{x}=87\%$) of the tracking time under water and dived to 50 m. The maximum voluntary submergence time observed was 213 min, and of 202 complete dives logged, 19 exceeded 90 min. Dive durations of tracked snakes were typically longer than expected, based upon their estimated body-oxygen stores, and some were even longer than the reported survival times of forceably submerged snakes. Snakes, however, dived repeatedly and did not spend long periods at the surface between dives, suggesting that they did not develop an oxygen deficit during diving. Diving snakes may be able to avoid anaerobiosis by having a reduced metabolic rate, an enhanced rate of cutaneous oxygen uptake, or both. Surface conditions and subsurface temperatures influence the diving behavior of *P. platurus.* Laboratory experiments in Panamá indicated that a larger number of snakes were submerged when surface water was turbulent. During February and March, the period of dry season upwelling in the Gulf of Panamá, sea snakes were found to avoid cooler, subsurface water and to make significantly shallower dives: mean maximum depth 6.8 m ($n=76$) in contrast to a mean maximum depth of 15.1 m ($n=147$) during the wet season. The dives during the dry season tended to be of shorter duration, with 44% lasting less than 15 min, compared to only 19% of the dives recorded during the wet season being completed in less than 15 min. General avoidance of subsurface temperatures cooler than 19 °C was confirmed by laboratory experiments in the 10 m-deep tank at Scripps Institution of Oceanography.

Introduction

The purpose of this paper is to describe and quantify the diving capabilities of *Pelamis platurus,* to evaluate factors that control its vertical distribution in the water column, and to assess the role of diving in the natural history of this species. Diving is one of the adaptations to aquatic life exhibited by all marine snakes. Heatwole (1978) examined the specific adaptations of marine snakes to the aquatic environment, and more recently Seymour (1982) reviewed the literature on the aquatic adaptations of reptiles in general. The diving capabilities of a wider spectrum of vertebrates have been reviewed by Scholander (1962) and Andersen (1966).

With the exception of the yellow-bellied sea snake *Pelamis platurus,* the non-amphibious species of sea snakes that have been observed spend most of their time submerged, surfacing only for breathing. Observations of *P. platurus* in drift lines in the Gulf of Panamá indicated that this species appeared to spend considerable time at the surface. Laboratory observations and stomach-content analysis (Kropach, 1973; Voris and Voris, 1983; Rubinoff, Graham and Motta, personal observations) also indicated that this species feeds exclusively at or near the surface. It also appears that *P. platurus* is generally free of predators (Rubinoff and Kropach, 1970), and therefore diving may not be important as an escape behavior for this species. Nevertheless, diving by this snake has been observed by several investigators (Dunson and Ehlert, 1971; Pickwell, 1972; Kropach, 1975).

A study of the diving behavior of *P. platurus* in the Gulf of Panamá was conducted by tracking snakes fitted with ultrasonic, depth (pressure)-sensitive transmitters. Our objective was to determine the depth and duration of its dives, to evaluate the effects of water temperature on diving depth, and to determine the relative amounts of time spent by these snakes at and below the water surface.

Materials and methods

To increase our understanding of diving in *Pelamis platurus,* field and laboratory observations of snakes were conducted in the Gulf of Panamá, in the Marine Laboratory at the Smithsonian Tropical Research Institute (STRI) in Panamá and in the 10 m deep tank at the Hydraulics Laboratory of Scripps Institution of Oceanography (SIO), in La Jolla, California, USA. The SIO deep tank has view ports through which subsurface behavior and swimming patterns can be observed directly.

Field studies

Ultrasonic pressure transmitters were used in all field diving studies. These were two sizes: a commercially available (V3-PM) transmitter (60 mm length × 16 mm diam), and a specially constructed smaller unit (V5P-2; 52 mm length × 12 mm diam); both were manufactured by Vemco, Ltd., of Halifax, Nova Scotia, Canada. All transmitters used were rated for 100 to 300 psi and calibrated for pulse-interval and pressure relationships. Some transmitters were field-tested to verify the linearity of the signal with depth. The transmitters (frequency ranges 65 to 78 kHz) emitted pulses with a 15 ms width and an effective range of about 1 km. Transmitter pulse-rate was monitored with a directional hydrophone (V-10) and receiver unit (CR-40) connected to a (CI-40) microprocessor decoder display unit (Communication Associates, Inc., New York). On the basis of the pre-determined linear pressure and pulse-rate relationship for each transmitter, this decoder translated the signal to a digital display (± 1 m). Both the STRI "R. V. Benjamin" [a 63-foot (19.2 m) vessel] and a 14-foot (4.3 m) Zodiac were used for tracking. The hydrophone was positioned below the hull of the tracking vessel and linked via a shaft to a steering control that permitted rotation through nearly 360°. Another control allowed the hydrophone to be tilted up or down through approximately 100° in order to direct it at the surface or the bottom.

A hand-held hydrophone (DH1) and receiver (USR-4), manufactured by Sonatronics, Tucson, Arizona, were used occasionally from a second boat to triangulate the position of the snake. This provided information about the distance from the boat to the individual being tracked and aided in its recapture.

Sea snakes were collected by dipnet from drift lines near the Pearl Islands in the Gulf of Panamá (Fig. 1). We attempted to track twenty snakes, ranging from 80 to 195 g in weight, and from 50 to 74 cm total length. In most cases, we used snakes that had recently (1 to 48 h) been collected; however, snakes that had been in captivity for up to two weeks were also tracked. Each snake was anesthetized in cold water (5° to 10 °C for not longer than 20 min), weighed and measured. The transmitter, which had been activated several hours previously and incorporated into a flotation-foam harness that made it neutrally buoyant, was then attached to the snake. The harness was fitted to the ventral side of the snake at about one-third of the total length behind the head. The "V" shape of the harness conformed to the snake's ventral body shape and allowed a snug fit (Fig. 2) when secured by four stitches of

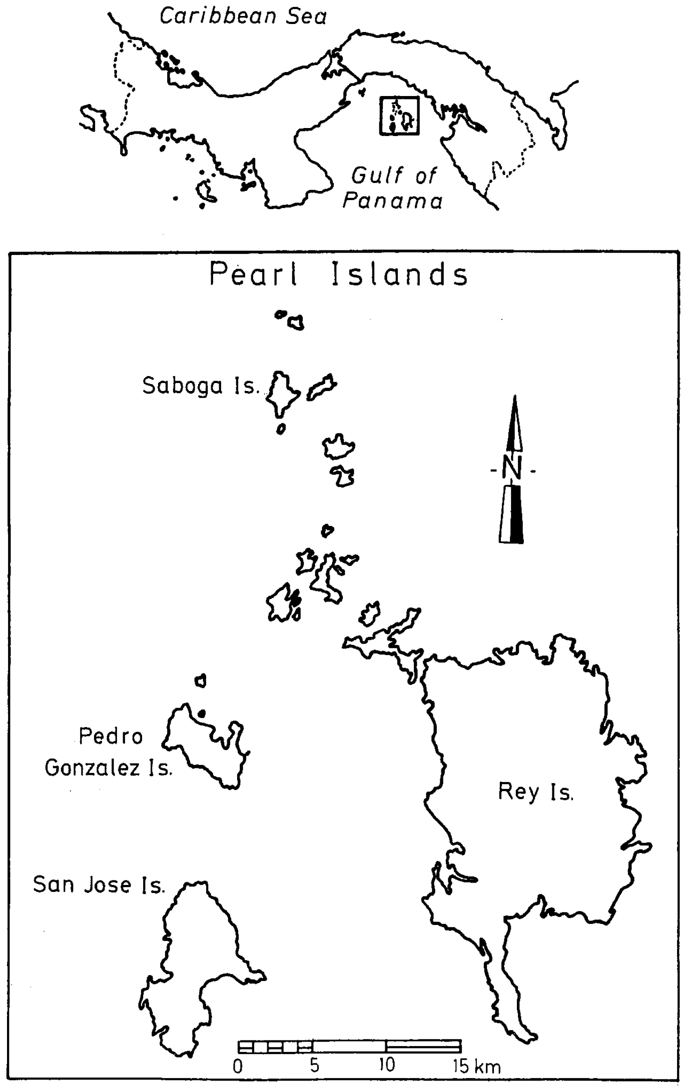

Fig. 1. Location of Pearl Islands and snake-tracking area in Gulf of Panamá

surgical silk. Laboratory observations confirmed that the snake could swim normally, both at the surface and at depth with the transmitter pack, and that the latter would remain attached to the snake for at least 4 to 5 d, which exceeded both transmitter battery life and the endurance of the tracking team.

After attachment of the package, the snake was allowed to recover in ambient (25° to 30 °C) seawater tanks. This recovery prior to the initiation of tracking allowed us to determine that the snake was able to carry the package and that the transmitter was functioning properly. Most snakes were held for 10 to 12 h prior to release.

Tracking involved a team of three persons: a hydrophone operator, helmsman, and data recorder. The hydrophone operator continually monitored the receiver for pulse strength and moved the hydrophone in an effort to maintain a nearly constant signal, while the helmsman maneuvered the boat to the optimal tracking position given the prevailing swell, wind, and surface current direc-

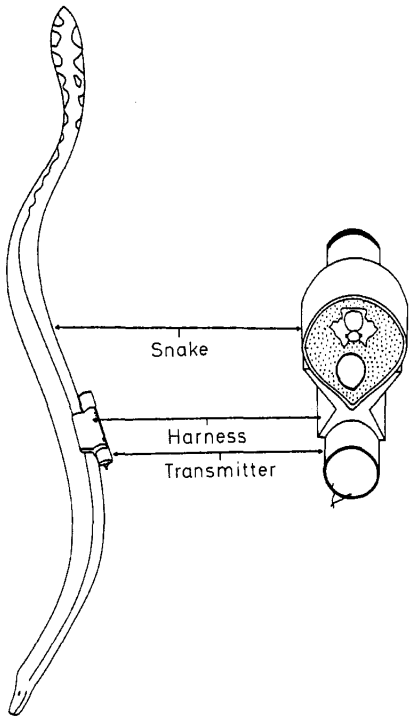

Fig. 2. Relative size and approximate position of transmitter pack fitted on *Pelamis platurus*. Transmitter harness was fashioned from flotation foam in order to make the pack neutrally buoyant. For scale reference, transmitter is about 5 cm long

tions. Snake depth was monitored at 2 min intervals or whenever it changed. Also, rapid depth changes during ascent and descent were recorded to the nearest second. Most tracking was done in the vicinity of the Pearl Islands (Fig. 1) in the area west of Saboga Island where sea snakes commonly occur in drift lines. One snake (Snake F: Table 1) was tracked outside the ship anchorage of the Panamá Canal. Whenever possible, snakes were released in or near drift lines. Each snake to be released was first transferred from a holding tank to a floating net-enclosure (1 m diam × 1 m depth) that was set adrift. After a final calibration of the tracking instrumentation, the snake was gently lifted from the enclosure and released. During the course of the track, compass sightings of distant landmarks were made every 1 to 3 h in order to determine position and thus snake movement. A Yellow Springs Instruments Co. submersible probe and meter was used to determine temperature and oxygen profiles in the vicinity of the tracking operation.

Laboratory studies

Captive populations of sea snakes were maintained in large laboratory tanks (up to 280 000 liters, 2.1 m deep) at STRI and in the 10 m deep tank at SIO. The captive snakes were used to observe the effects of the transmitter package upon snake swimming behavior and to determine the effectiveness of various sites of transmitter attachment. These captive populations were used to experimentally examine: (1) the effects of surface turbulence on the occurrence of snakes on the surface (STRI); (2) the effects of thermal stratification on diving behavior (SIO); (3) the relative number of snakes in an undisturbed group that were on the surface as opposed to diving (STRI and SIO); (4) the dive duration and percentage of time spent submerged by free-swimming snakes that were continuously observed in the shallow (STRI) and deep (SIO) tanks.

To examine the effect of waves and turbulence on sea-snake submergence, three tipping buckets and a surface discharge pump were used in a large rectangular tank (8.7 m long × 6.6 m wide × 2.1 m deep) containing thirty recently caught specimens. Using a two-factor randomized-block experiment (Hicks, 1982), we compared the number of snakes at the surface on alternating turbulent and calm days (Factor 1), as a function of time of day (Factor 2), for each two day (block) interval of snake captivity. The block design was used because the condition of snakes was expected to degrade with time. The experiment ran for 14 d (seven blocks). The order of conditions (24 h of turbulence vs 24 h of calm) in each block was determined by a coin flip. Daily counts of the number of snakes on the surface were made at 09.00, 13.00, 15.00, and 19.00 hrs.

From 15–17 August 1984, we used the deep tank at SIO to examine the effect of thermal stratification on diving behavior. We first determined the depth distribution of eleven snakes, in particular noting the mean number of snakes occurring between 7.25 and 10 m depth when water temperature there ranged from 19.5° to 22.8 °C (control). A cool (16.0° to 20.2 °C) layer was then established in this region and mean snake density was again estimated. Following this, the control thermal regime was re-established and mean snake abundance again determined.

From 13 October 1983 to 16 June 1984, regular observations on a captive snake population were made in the 2.1 m tank at STRI in order to determine how the percentage of snakes at the surface varied with time. At different times each day, the number of individuals at the surface vs the number diving was recorded every 5 min for 1 h. The study population ranged from 10 to 62 snakes, which were fed approximately once per week. The individuals comprising this population changed with time as some were used in other experiments or died, or as newly captured snakes were added.

Continuous observations of four snakes were made for a period of from 62 to 129 min in the STRI tank to determine the number of dives and the total time spent diving of each individual. To compare the effects of water depth on these variables, four additional snakes were observed for approximately 500 min in the SIO tank.

Results

Time and depth relationships

Time-depth diving records obtained for fifteen tracked *Pelamis platurus* during four cruises (October, 1983; March, 1984; October, 1984; May, 1985) are shown in

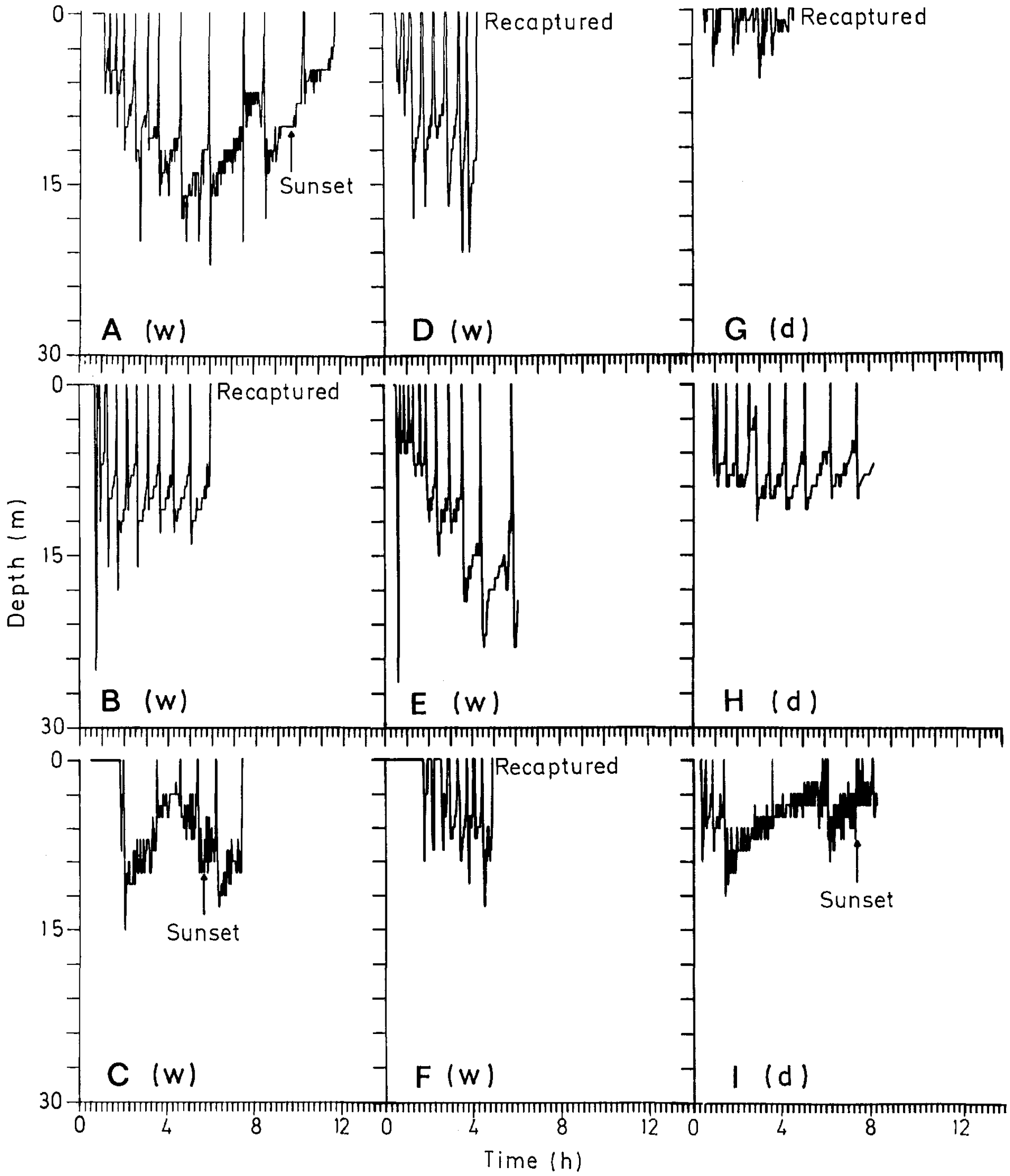

Fig. 3. *Pelamis platurus.* Time-depth profiles for sea snakes (A–O), ten tracked during the wet (w) season (October 1983, A–F; October 1984 and May 1985, L–O) and five during the dry (d) season (March 1984, G–K). Exact times for the hours of each track are given in Table 1. Information about sunrise and sunset, whether or not a snake was recaptured, and parts of the record where the signal was lost are indicated where appropriate

Fig. 3, and the dives of each snake are summarized in Table 1. We were able to track snakes in a variety of sea states during day and night and could generally maintain the tracking vessel within 25 to 100 m of the snake. It was frequently possible to see the snake when it surfaced. Our ability to stay close to snakes allowed us to recapture them on six occasions at the end of the tracking period. Snake recaptures are indicated in Fig. 3.

Track records for the snakes range from 3.8 to 31.2 h; a total of 163.6 h of tracking data were obtained. We gathered data on a total of 223 dives which, for purposes of analysis, were designated as either complete or incomplete. Dives were defined as complete if the snake dived to 3 m or deeper, if we had a continuous time and depth record of the dive, and if we knew both the exact (within a few seconds) submergence and surfacing times. We excluded shallow dives (less than 3 m) because it was sometimes difficult to be certain that the snakes did not ascend for a breath and quickly submerge. This was particularly true in rough water where ocean swell contributed to fluctuations in the readings so that discrimination between 0 and 1 m became difficult to achieve reliably. (Also our track data suggested that in rough water snakes make very fast surfacings and then dive immediately.) We tabulated 202 complete dives plus 13 that were less than 3 m, and 8 more that were incomplete (one in which the signal was lost during the dive and seven where we terminated our tracking before the dive in progress was completed). The record for Snake K (Fig. 3) shows an incomplete dive lasting from Hours 5 to 10. We lost the signal from this snake for 23 min during

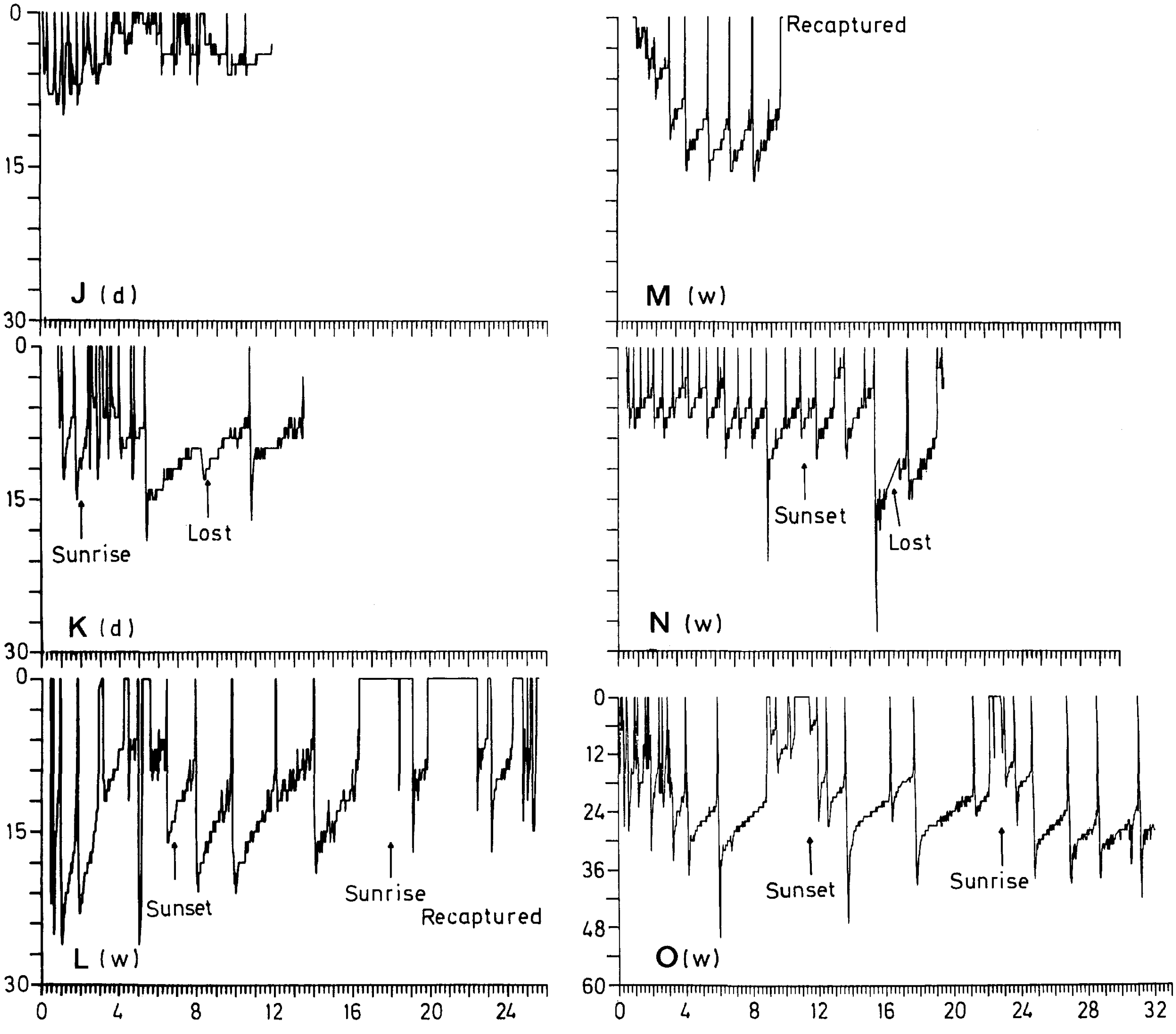

Fig. 3 (continued)

this time, and, judging from its ascent rate and depth after tracking resumed, and its apparent submergence time of 5 h, we conclude that this snake probably surfaced while we had lost contact. On the other hand, the twenty-fourth dive of Snake N (Fig. 3) contains a 30 min gap, but it seems unlikely, using the same criteria, that the snake surfaced; and this dive is included in our calculations.

Recently-surfaced snakes were observed to raise their heads out of the water and take at least one breath before diving again. Inter-dive surface times ranged from 1 s to 153.7 min (Snake L) and were not related to previous submergence time.

General dive-characteristics

Table 1 shows the mean of the maximum diving depths of all dives and mean of the submergence times of all complete dives. The deepest dive was to 50 m (Snake O, 01.43 hrs). The longest recorded complete dive was 213 min (Snake O, 00.49–04.23 hrs). Upon release, some snakes spent periods of time at the surface (e.g. 103 min for Snake F) before beginning to dive, while others began to dive immediately (Table 1). To correct for this variable in our estimates of relative time spent at the surface and diving by each snake, we computed these times commencing with the first dive. Table 1 shows diving times to range from 51 to 99.9% of the total track duration ($\bar{x} = 87\%$).

Fig. 4 shows the frequency distribution of the 202 complete dives grouped in 15 min-duration intervals. Most dives lasted less than 30 min and only 19 exceeded 90 min. Except for more 16 to 30 min dives in the wet season, the distribution of the 61 complete dives recorded in the dry season (black histogram in Fig. 4) is similar to that of all dives.

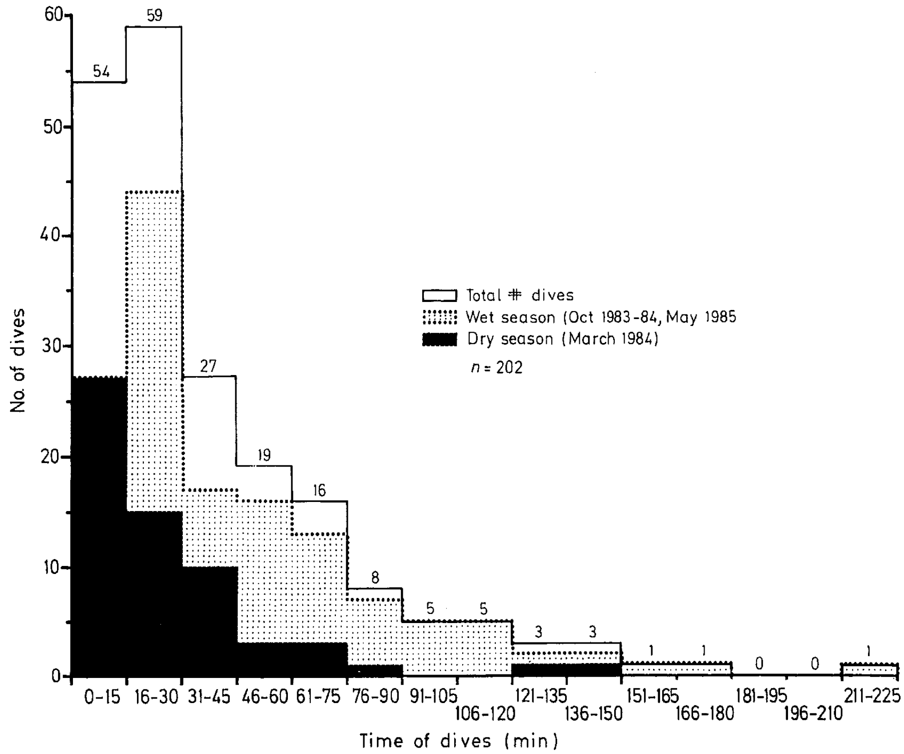

Fig. 4. *Pelamis platurus.* Frequency distribution of duration of the 202 complete dives in the dry and wet seasons. Numbers over each column indicate total dives in each time group

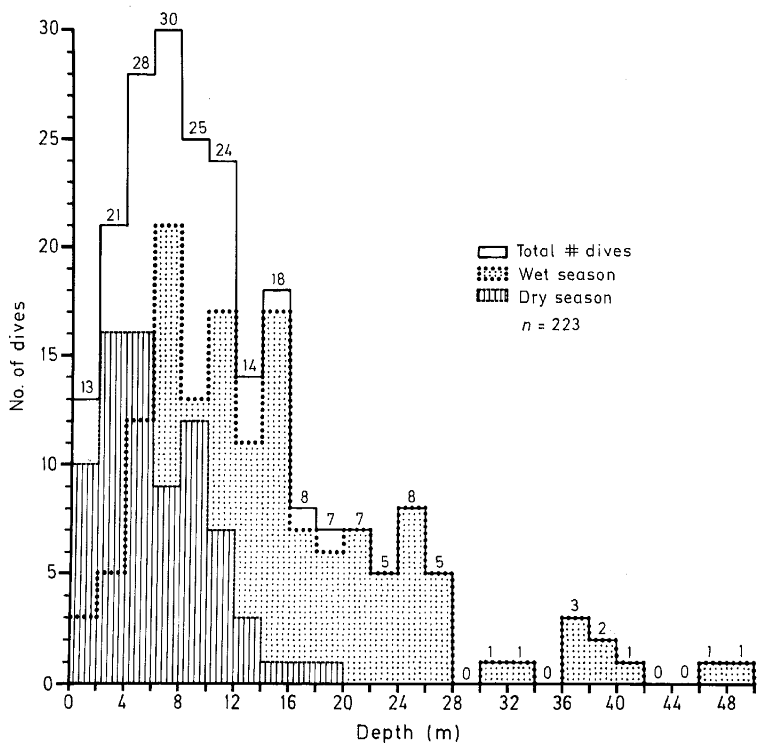

Fig. 5. *Pelamis platurus.* Frequency distribution of maximum depth of all 223 dives and comparison of dive-depth distributions recorded in wet and dry seasons. Numbers over each column indicate total dives in each depth group

Fig. 5 shows the maximum depth-frequency distribution of all 223 dives (grouped in 2 m intervals) and compares the distribution of 76 dives in the dry season (March, 1984) with 147 recorded in the wet season (October, 1983, 1984 and May 1985). Snakes tracked during the dry season had a significant ($p<0.005$, Student's t-test) reduction in mean ($\bar{x}\pm SD$) maximum dive depth ($\bar{x}=6.8\pm3.8$ m, $n=76$) compared to the wet season ($\bar{x}=15.1\pm9.4$ m, $n=147$). Between December and April, seasonal upwelling of variable annual intensity occurs in the Gulf of Panamá (Smayda, 1966; Glynn, 1972). Fig. 6 compares wet- and dry-season water-temperature profiles recorded near the tracked snakes and reveals that snakes which in the dry season dived to a mean maximum depth of 6.8 m and to a maximum depth of 19 m typically entered 22 °C water, but seldom penetrated water cooler than 19 °C (dashed line in Fig. 6).

Table 1. *Pelamis platurus.* Body size, tracking time, dive frequency, duration and depth, and percentage of time spent submerged by each snake. L: length; Dur.: duration of tracking; Surf. time: time snake spent on surface before beginning first dive; Dive time: total time spent diving; Dive dur.: mean dive duration

Snake	L (cm)	Wt (g)	Date	Start time (hrs)	Dur. (min)	Surf. time (min)	Dive time (min)	% Time submerged	No. complete dives	Dive dur. (min)	Shortest dive (min)	Longest dive (min)	Deepest dive (m)
A	74	118	8. X. 1983	09.34	668.0	31	633.2	94.8	12	52.8	16.0	106.8	22
B	70	147	9. X. 1983	12.05	352.2	36	312.5	88.7	10	28.4	7.6	55.6	25
C	72	160	11. X. 1983	14.31	415.8	78	335.6	80.7	6	48.0	10.7	90.5	15
D	66	161	10. X. 1983	13.32	224.6	< 1	199.5	88.8	8	24.9	15.7	32.3	21
E	66	161	11. X. 1983	06.28	324.8	5	317.8	97.8	11	28.9	10.8	86.1	26
F	60	101	19. X. 1983	10.01	292.3	103	147.9	50.6	8	18.5	7.2	27.2	13
G	65	120	6. III. 1984	13.29	234.7	< 1	145.3	61.9	7	11.2	6.5	14.0	6
H	60	90	7. III. 1984	08.53	393.7	< 1	393.5	99.9	9	43.7	10.5	72.0	12
I	60	110	8. III. 1984	11.20	469.6	< 1	466.9	99.4	11	42.4	4.4	137.4	12
J	70	150	10. III. 1984	07.10	620.9	< 1	526.1	84.7	21	21.0	6.3	68.2	10
K	72	195	11. III. 1984	04.55	265.8	< 1	251.7	94.7	13	19.4	4.8	43.7	19
L	71	130	22. X. 1984	12.26	1 502.6	< 1	1 090.5	72.6	20	54.5	4.8	139.3	26
M	71	128	24. X. 1984	09.47	458.7	9	447.4	97.5	6	74.6	49.1	102.5	16
N	74	150	25. X. 1984	09.25	985.8	< 1	981.2	99.5	25	37.7	7.0	103.0	28
O	65	140	22. V. 1985	07.01	1 871.4	< 1	1 760.1	94.1	35	50.3	0.5	213.0	50
$\bar{x}$ =	67.7	137.4						87.1		37.1	10.8	86.1	20.1
(SD) =	(5.0)	(27.4)						(14.9)		(17.3)	(11.4)	(51.7)	(10.6)

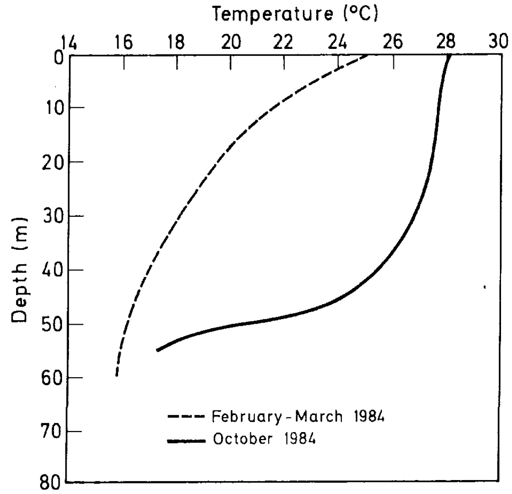

Fig. 6. Gulf of Panamá. Depth-temperature profiles taken in vicinity of tracked sea snakes during dry season (March, 1984) and wet season (October, 1984)

Table 2. *Pelamis platurus.* Total number of snakes observed on water surface at four times each day on successive days, when the surface was turbulent or calm. Numbers are sums for seven total observation days of each condition for 30 snakes

Time of day (hrs)	Turbulent	Calm
09.00	49	79
13.00	48	76
15.00	56	83
21.00	35	86
	188	324

Two-factor randomized block results:

waves $p < 0.01$ waves × time $p > 0.05$
time $p > 0.05$ blocks $p < 0.001$

Laboratory observations

Aspects of our laboratory studies corroborate the tracking observations and give us confidence that we have accurately described the depth, duration, and percent-time characteristics of the dives of *Pelamis platurus.*

Surface turbulence resulted in a significant ($p < 0.001$) decrease in the number of snakes occurring at the water surface (Table 2). The number of snakes diving, however, was not significantly influenced by time of day, nor was there any interaction between time of day and turbulence.

A study of the effect of thermal stratification on snake distribution indicated that the mean number of snakes occurring deeper than 7.25 m in the SIO deep tank was significantly ($p < 0.05$) reduced during the period that a cool thermocline was established there (Table 3). Rewarming of the bottom layer resulted in the return of the snakes to this depth and a mean snake density similar to that of the control period (Table 3). The control and cool-layer tests were both done on 15 August, and the lower level of the tank was not rewarmed until 17 August. On 16 August, 5.5 h of

Table 3. *Pelamis platurus.* Effect of temperature on mean number of sea snakes present in 7.25 to 10 m depth range of SIO deep-tank. Total of eleven snakes were in tank; n is total number of 5-min observations used to estimate mean number. Statistical comparison was by Student's t test, with multiple-test corrections: $A = C + B$, $p < 0.025$

Condition	Date (1984)	Time (hrs)	Temp. range (°C)	Snakes present, [$\bar{x} \pm SE$ (n)]
Control (A)	15 Aug.	09.00–12.00 14.00–15.10	19.5–22.8	4.94±0.15 (47)
Cool (B)	15 Aug.	16.40–19.35	16.0–20.2	2.03±0.18 (36)
Warm (C)	17 Aug.	13.15–14.10	20.0–21.6	4.08±0.31 (12)

Table 4. *Pelamis platurus.* Relative depth distribution of eleven sea snakes in SIO deep tank from 08.35 to 12.00 hrs and 13.15 to 14.20 hrs on 17 August 1984; n is total number of observations made at 5-min intervals that were used to estimate the mean

Depth range (m)	Temp. range (°C)	Snakes present	
		$\bar{x} \pm SE$ (n)	%
0 – 0.3	26.7	0.93±0.11 (57)	8.5
0.3 – 4.0	26.7–26.1	2.73±0.18 (56)	24.8
4.0 – 7.25	26.1–22.6	3.77[a] (–)	34.2[a]
7.25–10.0	22.6–21.4	3.57±0.19 (53)	32.5

[a] Calculated by difference, since this depth range could not be accurately surveyed

continuous observations were made on snake distribution in and above the 7.25 to 10 m cool layer in order to detect fine-scale temperature avoidance by *Pelamis platurus.* Using the YSI temperature probe, four depth-temperature strata within the cool layer were delineated – 7.25 m, 20.6 °C; 8.15 m, 19.4 °C; 9.05 m, 16.6 °C; 10 m, 16.3 °C – and the number of snakes present in each of these strata was recorded at 5 min intervals. Snakes were almost always present (49 of 66 observation periods recorded one or more snakes) in the 20.6 °C water. Snakes were also common in the 19.4 °C water (37 of 66 periods showed one or more snakes). In contrast, a snake was recorded in the 16.3 °C water during only one observation period. This same snake was also recorded once at 16.6 °C, but no other snakes entered these cool temperatures. Thus, while snakes will enter 19 °C water, they will generally avoid cooler water.

Regular observations in the 2.1 m-deep tanks (26° to 27 °C) indicated that an average 66.4±4.0% (±SD, for a total of 40 dates of observation with several determinations on each day) of the snake population were likely to be at or within 0.3 m of the water surface at any given time. Similar observations made on eleven snakes over a 6 h period in the SIO deep tank indicated that an average of only 8.5% of the population was at the surface at any time, and most snakes (67%) were deeper than 4 m (Table 4). Snakes in the SIO tank spent more of their time diving than snakes in shallower tanks in Panamá (Table 5). The maximum dive time observed for the SIO snakes was 141 min; a period exceeded in the field by only four dives of tracked Snake "O".

Discussion

Diving and the behavior of *Pelamis platurus*

Although *Pelamis platurus* is regarded to be a primarily surface-dwelling snake, we have determined that this species spends from 51 to 99.9% ($\bar{x} = 87\%$) of its time diving (Table 1). Unless its depth penetration is restricted by subsurface temperatures cooler than 19 °C, this snake dives to an average maximum depth of 15 m. The deepest dive measured was 50 m and, of the 223 total dives recorded, 35 went to depths greater than 21 m (Fig. 5). Nine of the snakes tracked had dives in excess of 2 h, and 43 of the 202 complete dives were longer than 1 h (Fig. 4). The track periods were not long enough to allow conclusions about diel differences in diving. Some observations, however, did suggest that depth may be influenced by a sudden change in ambient light level. Snake N, for example, was tracked for most of the day under cloudy skies and rain, but some sunlight appeared in the late afternoon (Track Hours 7 to 9), during which time a deep dive was made. The longest surface times observed for any snake, once diving had begun, were seen in Snake L. These occurred early in the morning and while the snake was in a calm drift-line that contained other snakes. During the previous night, there had been a rain storm with very rough surface conditions, and Snake L had made a series of long (110 min) dives.

The tracking data enable us to reject the idea that the deepest dives were solely the result of an immediate escape response by the snake following handling or an attempt by the snake to shed the transmitter pack. Although two snakes (Snakes B, E) did make their deepest dives just after release, some did not dive immediately (Fig. 3), and the deepest dives of the other twelve snakes occurred at various points in the course of the track (Fig. 3). Even though the transmitter pack was neutrally buoyant, its buoyancy probably decreased with depth (due to compression of the flotation foam), and the pack also added drag to the swimming snake. We do not know how transmitter-drag affected snake behavior or endurance. Snake L (Fig. 3), which we tracked for about 25 h, was the only snake to spend long periods on the surface once diving was begun; this may have been due to fatigue.

Factors affecting diving depth and duration

Our finding that *Pelamis platurus* did not dive into water cooler than 19 °C is consistent with the established cool temperature limit of its latitudinal distribution (about 18 °C, Graham *et al.,* 1971; also see Dunson and Ehlert,

Table 5. *Pelamis platurus.* Comparison of time spent submerged by four snakes in STRI and SIO tanks

Snake No.	Time observed (min)	Total dives	Dives/h	Mean duration (min)	Range (min)	% time diving
STRI tank (2.1 m deep)						
1	129	12	5.6	8.0	0.8–22	84
2	127	10	4.7	11.0	0.5–25	80
3	62	9	9.0	3.0	1.0–20	49
4	69	3	3.0	8.0	6.5–20	38
$\bar{x}$			5.6	7.5		63
SIO deep-tank (10 m deep)						
1	491	24	2.9	11.0	0.5– 38	54
2	489	27	3.0	17.0	0.5–141	95
3	494	17	2.0	17.0	1.5– 97	92
4	508	17	2.0	28.0	3 – 55	95
$\bar{x}$			2.5	18.3		84

1971). The proximity of 19 °C water to the surface during the dry season (Fig. 6) significantly reduced the mean dive depth of *P. platurus* and also resulted in fewer long dives. Fig. 4 shows that 69% of the dry-season dives were 30 min or less (44% were 15 min or less), whereas only 50% of the wet season dives were 30 min or less. Moreover, it was during the dry season that most (77%) of the incomplete shallow (< 3 m) dives occurred. While temperature no doubt restricted the depth of most dry-season dives, their relative brevity was probably linked to factors stemming from the buoyancy problems encountered by a snake on shallow dives. Due to its large lung, *P. platurus* is positively buoyant at the surface, and Graham *et al.* (1975) observed that a diving snake must swim against this buoyant force until it reaches a depth of at least 3 m where hydrostatic pressure would compress the lung sufficiently to achieve neutral buoyancy. [Recall that observations in the SIO deep tank (Table 3) showed that most snakes were always deeper than 4 m.] If a snake did not dive to, or deeper than such a depth or if it descended more gradually in cool water, it would need to swim continuously to stay down. Thus, depth and buoyancy state, and a likely increase in aerobic swimming-power requirement on shallow dives all may have affected dive duration.

Comparison of the time-depth data with the estimated oxygen stores available to a diving snake permits further insight into the combined demands imposed by both hydrostatic pressure and dive duration on the respiratory function of diving *Pelamis platurus.* First, the total oxygen stores available during a dive can be estimated. Graham *et al.* (1975) established that *P. platurus* makes shallow (2.2 m) dives with a lung volume equal to 8.8% of its wet weight and that the lung of a diving snake initially contains about 12% oxygen. A 137 g snake (mean weight of the tracked snakes) would thus have a 12.23 ml lung volume containing 1.47 ml of oxygen. The blood volume of *P. platurus* is equivalent to 6.95±0.44% ($\bar{x}\pm$SD, $n=4$, Graham, 1973) of its body weight. Combining this with Pough and Lillywhite's (1984) estimate for blood oxygen capacity (10.2±1.4 ml O_2 100 ml^{-1} blood), we calculate that a diving snake would initially have 0.99 ml O_2 in nearly air-saturated blood. *P. platurus* has low amounts of myoglobin (Graham, personal observation), thus, the total oxygen reserve available would be 2.46 ml (1.47±0.99) on a shallow dive.

How does this reserve compare with the oxygen requirement of a diving snake? The mean oxygen uptake of *Pelamis platurus* at 30 °C is 0.083 ml $O_2 g^{-1}$, h^{-1} (Graham, 1974). Assuming a Q_{10} of 2.0, correction of this rate to a subsurface temperature of 25 °C yields 0.062 ml $O_2 g^{-1}$, h^{-1} which is a total rate of 8.49 ml $O_2 h^{-1}$ for a 137 g snake. If the snake can use nearly all of its available oxygen stores, it could sustain aerobic metabolism for 17 min, clearly less than the times observed for tracked snakes. The mean submergence time of all dives is 37.9 min, and Fig. 4 shows that 43 of the 202 complete dives lasted 60 min or longer, with 9 of these longer than 120 min. By contrast, Graham (1974) found that two snakes forceably submerged in small containers (30 °C) only survived 86 and 108 min. Finally, it was common for a snake, after surfacing from a long dive, to quickly dive again. All this suggests that long submergence does not result in an oxygen debt which would have to be repaid by a period of aerial surface respiration. This was also Seymour's (1982) conclusion for other sea-snake species.

In order to remain submerged for longer than 30 min, without incurring an oxygen deficit, *Pelamis platurus* must be able to increase its lung-oxygen stores, dramatically reduce its metabolic rate, or significantly increase its rate of cutaneous oxygen-uptake (which is only 33% of total uptake in a surface-floating snake at 30 °C – Graham, 1974), or all of these. Prior to diving, tracked snakes were often observed to raise their heads and breathe two or three times in succession, as if they were hyperventilating their lung. Also, observations in the deep tank suggest that snakes, when diving deeper, may take in a larger lung volume than was measured for snakes that could only dive to 2.2 m (Graham *et al.,* 1975), and this is currently under study. We have no data on diving metabolism; however, Seymour (1982) pointed out that subsurface swimming is more efficient. There are several ways that cutaneous respiration might be enhanced. Diving snakes use cardiac and pulmonary shunts to conserve lung oxygen while cutaneously removing nitrogen, and carbon-dioxide (Seymour, 1974, 1982). Continuous motion by the submerged snake would reduce boundary-layer thickness along the body while maintaining the oxygen diffusion gradient at a maximum. Finally, our observations in the deep tank suggest that lung compression tends to stretch the skin, which may lessen diffusion distance from water to capillaries.

The gradual ascent typical of most dives (Fig. 3) may be related to oxygen economy during diving. If the initial rapid diving descent had the effect, via pulmonary vascular shunting (Seymour, 1982), of sealing off the lung, then an untapped and ever-expanding volume of lung oxygen would be available as the snake slowly ascended. Modulation of both body position and cardiac output to the lung might allow the snake to utilize this resource (Seymour, 1982; Graham *et al.,* unpublished observations).

Comparative and ecological aspects of sea-snake diving

Recent reviews (Heatwole and Seymour, 1975; Heatwole, 1978; Seymour, 1982) indicate 100 m to be the maximum diving depth expected for any species of sea snake. This is deeper than the depth at which human divers normally make observations and is somewhat deeper than areas along the coast of northern Australia where most snake depth-distribution data have been obtained. Some depth records were for sea snakes taken at the surface "over" deeper water and may have involved individuals moving between reefs or into shallower depths. Diver confirmation of any species of sea snake at depths greater than 40 m is rare. McCosker (1975) observed several species of Indo-Pacific hydrophiids foraging and feeding at depths less than 10 m. He also recorded *Acalyptophis peronii* and *Hydrophis melanocephalus* at depths of 40 to 50 m off Ashmore Reef, northern Australia. Similar shallow-water feeding observations have been made by Heatwole *et al.* (1978). Sea-snake foraging and other subsurface behaviors, as well as study of their maximum diving limits may be amenable to investigation with research submarines.

Since *Pelamis platurus* inhabits waters off the continental shelf, its depth limitation cannot be inferred from water depth. Heatwole and Seymour (1975) reported an unverified sighting of this species at 37 m in Australian waters. In the Gulf of Panamá, Kropach (1975) followed diving *P. platurus* to 20 m and reported that they continued downward until out of sight. Snakes observed by divers in our study were followed to 25 m and were seen to continue deeper.

The maximum submergence time found for tracked and laboratory *Pelamis platurus* (213 min) is longer than times found by Heatwole (1975) and summarized by Seymour (1982). Heatwole (1975) reported maximum voluntary submergence times of 70 min for *Aipysurus laevis,* 83.4 min for *Emydocephalus annulatus,* and 116.9 min for *Acrochordus granulatus,* and mean dive depth for these snakes was about 15 min (23° to 28 °C). We observed good agreement between captive (SIO tests) and tracked snakes in the percentage of time they spent submerged (84 vs 87%). However, laboratory snakes typically made many more short-duration dives as opposed to the fewer but longer dives of snakes tracked at sea. The diving behavior of captive snakes was affected by wall contact. This would first cause a snake to stop swimming which, depending upon depth and buoyancy, might cause it to sink or rise; then the snake would resume swimming, usually parallel to the wall. The longer mean dive durations of the SIO snakes as compared to those at STRI (18.3 vs 7.5 min) seems attributable to the deeper container at the former institution.

Our findings that *Pelamis platurus* spends most of its time (87.3%) below the surface, and that 90% of the population studied in the SIO deep tank was always below the surface at any one time, have implications for field estimates of the abundance of this species. Tu (1976) reported collecting *P. platurus* at the calm surface of Bahía de las Culebras, Costa Rica, at rates of up to 185 snakes h^{-1}. This is similar to the highest snake density encountered in this study (165 h^{-1}, 10 July, 1984). However, if only a small percentage of the snake population is at the surface, then the actual biomass of snakes in those areas would have been much larger. *P. platurus* is patchily distributed, abundant and easy to find in some drift lines, but even in areas where it occurs commonly there are still occasions when a day's search will yield no specimens. Dunson and Ehlert (1971) reported releasing 23 snakes in a slick in Bahía Manzanillo, Mexico, and finding only one specimen when they retraced the same area an hour later. Snakes of course become even harder to find in rough water, and our studies suggest that fewer may actually be at the surface then.

The disturbance produced in the laboratory experiment was considerably less than these animals would experience during periods of high winds and in storms. The diving capability of *Pelamis platurus* may have, in a large measure, evolved as an adaptation to avoid being beaten about by rough surface conditions. Our work also shows that conclusions about the vertical distribution and relative abundance of *P. platurus* must take subsurface temperatures into account. In areas like the Gulf of Panamá that are subject to seasonal upwelling, a restricted diving depth range would tend to concentrate a larger percentage of the snake population nearer the surface.

Although we do not yet have an adequate understanding of the purpose of its dives, our study has described the diving of *Pelamis platurus* in terms of depth and duration and the effects of surface and subsurface conditions on this behavior. It has further determined that, in contrast to the general impression that exists for this species, *P. platurus* spends most of its time submerged. Further studies that examine its subsurface swimming activity and behavior and determine how diving affects individual movement pattern are needed to fully appreciate the adaptive significance of this species' diving behavior.

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