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UNDERWATER OBSERVATIONS ON SEA SNAKE BEHAVIOUR

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SUMMARY

Sea snakes forage on the bottom but often bring prey to the surface to swallow. Surface activity not exclusively associated with feeding or breathing, sometimes occurs, especially at night. The skin is usually shed entire; it is loosened by rubbing against coral, curling and knotting or expanding the body. Courtship consists of the male swimming above the female and slightly behind her and then later pressing his body against hers while she rests on the sea bottom. Other topics are briefly discussed.

INTRODUCTION

The book, *The Biology of Sea Snakes* (ed. W.A. Dunson, 1975), has summarized the literature on sea snakes and presented much new information; it has also served to indicate some of the gaps in current knowledge about this group of reptiles. One of the most conspicuous areas in which almost no data are available is the behaviour of the animals in their natural habitat. Few herpetologists are divers, and vice versa; only recently have undersea observations been made and information is still mostly fragmentary and opportunistic. The data we have collectively accumulated contribute to little-known areas of sea snake biology and we present them here. Underwater observations were made either by snorkeling or diving with SCUBA; timing was done with a Nivada-Grenchen underwater chronograph.

FEEDING

Except for the pelagic, surface-feeding *Pelamis platurus,* and perhaps *Lapemis hardwickii* which is reported to take prey at various levels of the water column (McCosker 1975), the food of most sea snakes would indicate that they capture prey on the bottom. Many, for example, eat burrowing eels, crevice-inhabiting fish, or species that are restricted to the bottom (McCosker 1975).

Records of The Australian Museum, 1978, **Vol. 31 No. 18,** 000-000, Figures 1-12

Observation confirms the bottom-feeding habit for many species. Most snakes observed underwater were either (1) inactive and resting on the bottom or coiled among corals or rocks, or (2) engaged in what we interpret as foraging on the bottom. Most of our observations have been on coral reefs so our results apply primarily to that habitat. Foraging behaviour in *Aipysurus laevis, Aipysurus duboisii* and *Astrotia stokesii* has been observed many times and is practically identical. The snakes differ primarily in the places they forage (Heatwole 1975a, McCosker 1975) rather than in their manner of foraging.

These snakes swim leisurely among the coral, nearly continuously investigating crevices in the coral or algae by protruding their snouts into them (Fig.1). In some cases, the snake will enter crevices with most or all of the body. Often a snake systematically searches a complete clump of coral before moving on to the next one. When an area of sand or other flat substrate is reached the snake swims rather rapidly and in a generally straight line to the next area of coral. The directness of such swimming contrasts markedly with the sinuous path followed while foraging. Individual snakes have been followed and observed to forage continuously for over half an hour. However, we have actually witnessed the capture of a fish by a sea snake in the wild only once.

The above species usually ignore free-swimming fish even when they swim close to the snake's head, and it is probable that they are unable to catch fish unless they corner them in crevices. Excerpts from field notes illustrate this point:

Cato Lagoon, Coral Sea, 2 May 1968, 1645 hrs, notes by H.H. "An *A. duboisii* in 2-15 cm of water on reef flat; slowly swimming or crawling depending on depth; poked head into small crevices in dead coral rubble; ignored small fish (2-4 cm long) that came within about 5 cm of head; on some occasions small fish left crevices when the snake investigated them and darted away; snake seemed to pursue them for about 15 cm but then returned to foraging."

Swain Reefs, Coral Sea, 29 June 1971, 1415 hrs, H.H. "An *A. laevis* foraging in 10 m water; . . . it foraged over a semicircle of about 50 m during 21 min.; a number of small fish of various species came within 2-5 cm of its snout; it didn't react overtly to them; approached by a large fish, seemingly by chance; the fish swam away; touched a sea turtle while foraging; no overt reaction by either animal."

Saumarez Reef, Coral Sea, 1 July 1971, daytime, H.H. "An *A. duboisii* loosely coiled in a cavity in a piece of dead coral in 4 m of water; it did not change position or location for 1 hr 20 min (when observations were terminated); during that time four species of small fish swam in and out of the cavity, even among the coils of the snake; no overt response by the snake."

Ashmore Reef, 3 Jan 1973, S.A.M. "In an area of coral with water 1-2 m deep, watched an *Emydocephalus annulatus* for about 15 min as it swam just above the bottom investigating crevices and holes in the coral and sand. During this time it surfaced once for breath and immediately submerged. It passed within a few cm of an *Aipysurus foliosquama* lying on the bottom. It was more or less oblivious to contact with various reef fish and they ignored it." Also at the same place H.H. saw several small fish enter a loose clump of coral in which a resting *A. dubosii* was coiled; the snake did not overtly respond to the fish. See also notes of 30 June 1971, 1324 hrs, quoted below.

Swallowing sometimes occurs at the surface, even if fish are caught on the bottom. On 1 July 1971 at Saumarez Reef, Coral Sea, an *A. duboisii* was first observed (H.H.) leaving the bottom in about 10 m of water. It was heading for the surface with a still struggling (presumably just caught) fish about 3 cm long in its mouth. In an attempt to observe swallowing, the investigator approached closely and the snake released the fish

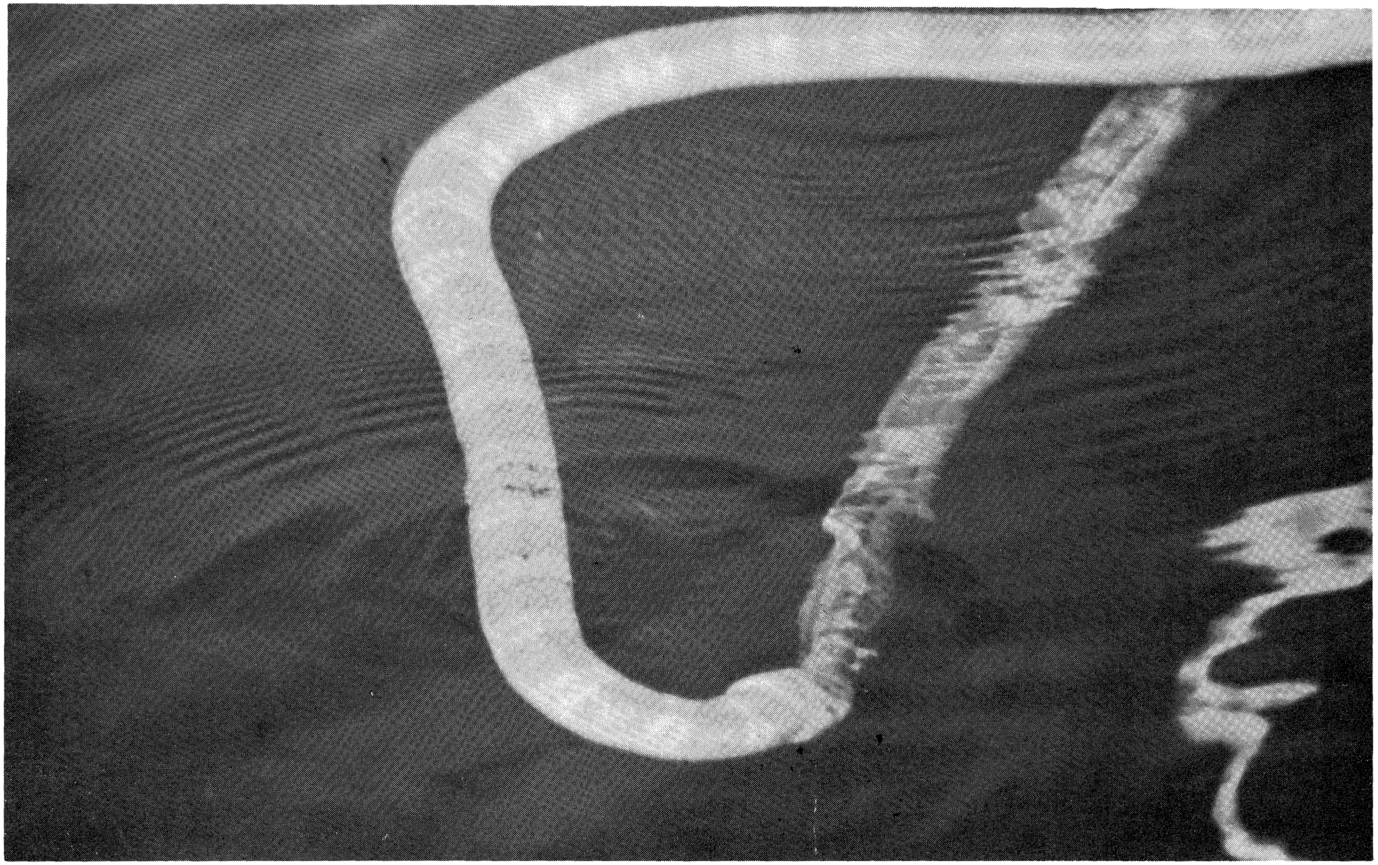

Fig. 1. *Disteira major* subduing and swallowing an eel in the sea. Photograph by Ron and Valerie Taylor.

and returned to the bottom. The fish floated at the surface for a few seconds, flapping feebly, and then recovered and swam away; it was not identified. Similarly, an *Astrotia stokesii* was observed on the surface in about 10 m of water at Ashmore Reef, Timor Sea. It had a fish, which appeared to be a scorpaenid (a bottom dwelling group) transversly in its mouth; the snake's neck was curved and it was holding the fish against its body, apparently attempting to turn the fish around to swallow it headfirst. It released the fish when an attempt was made to catch the snake; the fish swam away.

A nearly complete feeding sequence was observed near Magnetic Island, Australia (notes by V.T.). "Ron thought he could see a sea snake doing something strange on the surface. It was a large pale sea snake about 2 m long and it was fighting with an eel about 1½ m long. The snake was obviously winning althought the eel had drawn blood in many places. Ron filmed from the surface in 35 mm movie as the two animals writhed around on the surface . . . The sea snake finally got the eel by the tail and began to swallow him. We all got into our diving gear but . . . by the time we entered the water only the head of the eel stuck out the snake's mouth. When the snake saw us coming he made a last giant swallow and the head disappeared. The snake lay upsidedown in a sort of stupor. The eel could be seen slowly moving down inside the snake's body which was stretched to bursting . When the head of the eel was about 15 cm down his throat the snake came to life and snatched a breath of air . . . It took the snake about 6 minutes to swallow the eel. The water was about 20 m deep." The sea snake was subsequently identified as *Disterira major* from the photographs (see Fig. 1). These observations are important as they indicate that some sea snakes can actively subdue large prey, even rivalling land snakes in terms of the size of prey taken.

Swallowing at the surface is not obligatory, however. *A. laevis* swallows its prey on the bottom. At Swain Reefs in November 1976, five different individuals of this species were fed fish at night. The technique was to place the recently killed fish in the path of a foraging snake. When it bumped the fish with its snout it protruded its tongue against it several times and then rapidly bit the fish 1-3 times. A small fish would be then immediately swallowed. When dealing with larger fish, the snake would work its head completely around the periphery of the fish, finally returning to the original site. This procedure probably enables the snake to assess the fish's size and aids in determining whether it is small enough to swallow. If the fish were very large the snake would leave it and swim away, but if it were of moderate size, the snake would find the head and swallow the fish head-first. The swallowing process was very similar to that in a terrestrial snake. Prey wider than the diameter of the snake's head or body could be swallowed. Usually the snake surfaced and breathed immediately after the meal. Several swallowing sequences have been recorded on film by Ben Cropp Productions. On 8th January 1973, at Scotts Reef, Timor Sea, in about 4 m of water, a large *A. laevis* was observed in a clump of coral with its tail and part of the posterior body protruding. It was grasped by the body and pulled from the coral, at which time it was noted to have a scorpaenid fish in its mouth. Even after capture the snake continued trying to swallow the fish but eventually it dropped it; the fish swam away.

The fact that in all these cases, captured fish were still alive and capable of swimming away when released suggests that the venom of sea snakes may not not be as lethal to fish as is generally believed.

It is not necessary for the prey to be alive to be taken by *A. laevis*. On two occasions in Cato Lagoon, Coral Sea, large individuals were observed to approach and attempt to eat the dead, but fresh, heads and offal of fish which had been thrown overboard. In one case, the snake bit into the head despite the fact it was much too large to be swallowed by the snake (also see feeding experiments mentioned above).

Other fish-eating species probably actively forage much in the manner described above. Some are known to investigate holes in the bottom (Fig. 2).

Some species eat only fish eggs (Voris 1966, McCosker 1975) and would perhaps be expected to use somewhat different foraging patterns.

Emydocephalus annulatus and *Hydrophis gracilis*[1] are two such species. Although inhabiting coral reefs, they do not investigate crevices in coral. Rather they poke their snouts into the sand. The former species has a sharp spine on the snout which may aid in penetrating the sand (Fig. 3) although since the spine is more pronounced in males it may have other functions. *H. gracilis* has been observed with its head down in the sand feeding on fish eggs:

Saumarez Reef, Coral Sea, 3 July 1971, 1400 hrs, H.H. "An *H. gracilis* in 5 m of water on bare sand; head and part of neck down a hole just large enough to receive it; posterior part of body floating upward and waving back and forth in the current; caught after 35 min." (See also photo in Macleish 1972).

E. annulatus ingests large quantities of sand while eating eggs buried in sand. Of 15 specimens of this species from the Coral Sea that were opened and the gut examined, 14 (93%) had the stomach and /or intestine packed with sand (Heatwole 1975a). Such a large amount of ballast undoubtedly influences the buoyancy of this species. A number of sea snakes swallow fish with heavy spines. As fish are swallowed, their spines may sometimes penetrate the body of the snake. M. A. Smith (1926) states, "According to Annandale, when fishes with strong spines are devoured, the spines can be eliminated from the snake's body by passing out through the wall of the alimentary canal and the body-wall to the exterior. He states that he has frequently found sea snakes with the fish spines actually protruding from the integument without apparently causing any inflammation or inconvenience." We have observed this in three specimens of *Hydrophis ornatus* collected in the Visayan Sea. In two cases a fish spine had penetrated the body wall at about the level of the stomach, in a third it had penetrated the tissues of the head (Fig. 4). One of these snakes died the day following capture; however, death could not be confidently attributed to the injury. *H. ornatus* in Philippine waters seems to feed almost exclusively on catfish of the genus *Plotosus* that are equipped with strong, serrate venomous spines, and such injuries must be relatively frequent in the snake population. However, in at least 13 additional instances snakes had fed on these catfish without sustaining any obvious injuries.

DAILY ACTIVITY

Heatwole and Seymour (1975a, b, 1976) indicated a diel rhythm in metabolic rate of sea snakes (6 species) such that values were higher during the day than at night; this suggests a diurnal activity pattern. Certainly, in all the species of sea snakes we have observed underwater, some individuals foraged by day; others, however, were observed to be inactive, either lying on the bottom or coiled in crevices (Fig. 5). We have observed *A. laevis* underwater probably more than any other species. It is sometimes active by day as described above but is also active at night. More than 7 hours were spent at night observing snakes at Swain Reefs in November 1976 (H.H.). Many were actively foraging and readily accepted fish when fed by hand. Others, however, were inactive, coiled motionless among the corals. The following excerpts from field notes illustrate these two activity categories:

1. This species was identified in the field as *Hydrophis gracilis*. A single live specimen was retained for postive identification; however, it died and disintegrated in transit and its identification must remain tentative until further specimens are obtained. These remarks apply wherever the name *H. gracilis* appears throughout the paper.

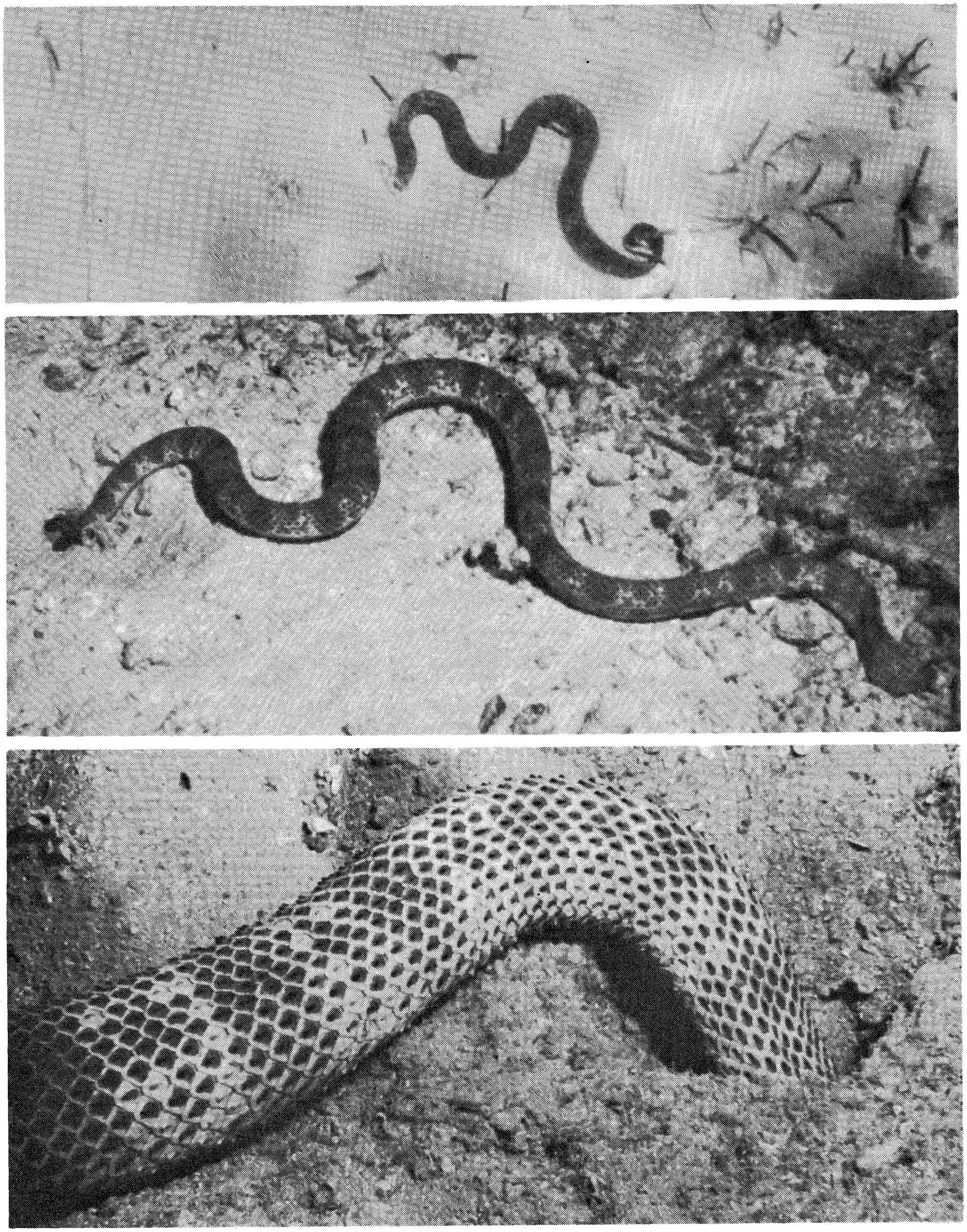

Fig. 2. Sea snakes foraging in holes in the bottom. Upper: *Aipysurus apraefrontalis*. Photograph by Sherman Minton. Centre and Lower: *Acalyptophis peronii*. Photographs by Ron and Valerie Taylor.

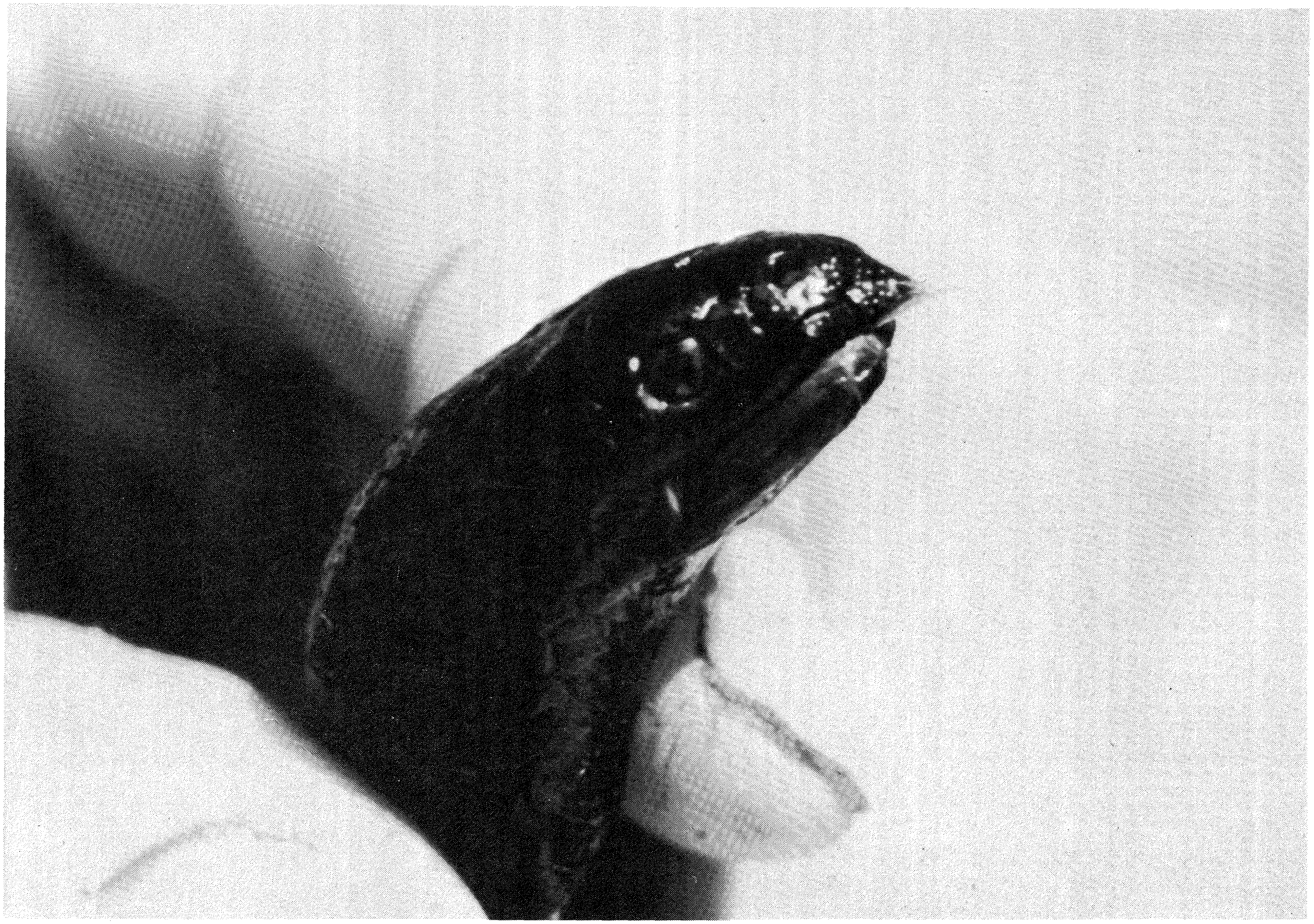

Fig. 3. Head of a male *Emydocephalus annulatus*. Note sharp spine on snout. Photograph by Ben Cropp.

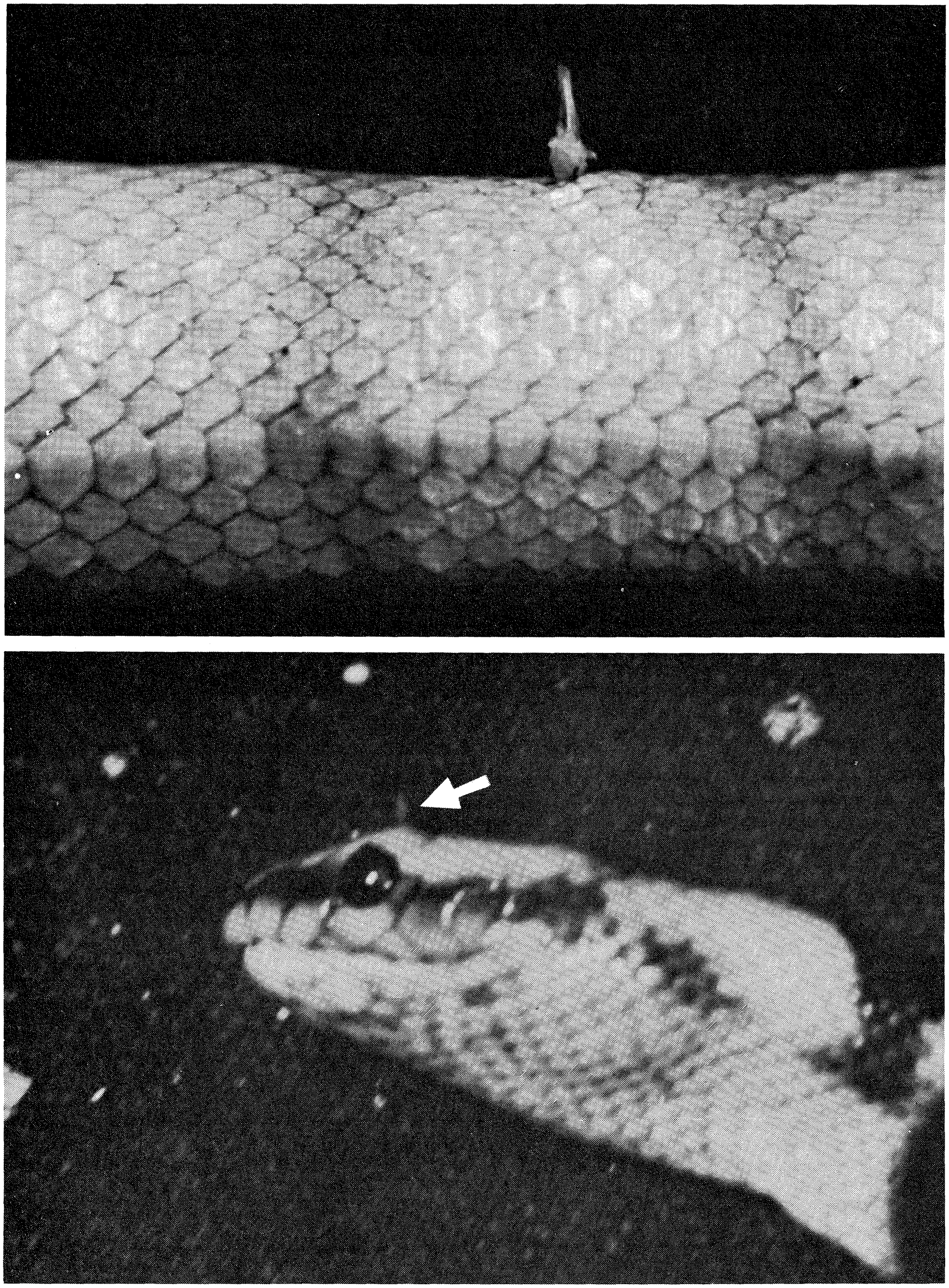

Fig. 4. Spines of a fish protruding through the body wall (upper) and through the head (lower, at point of arrow) of *Hydrophis ornatus*. Photographs by Sherman Minton.

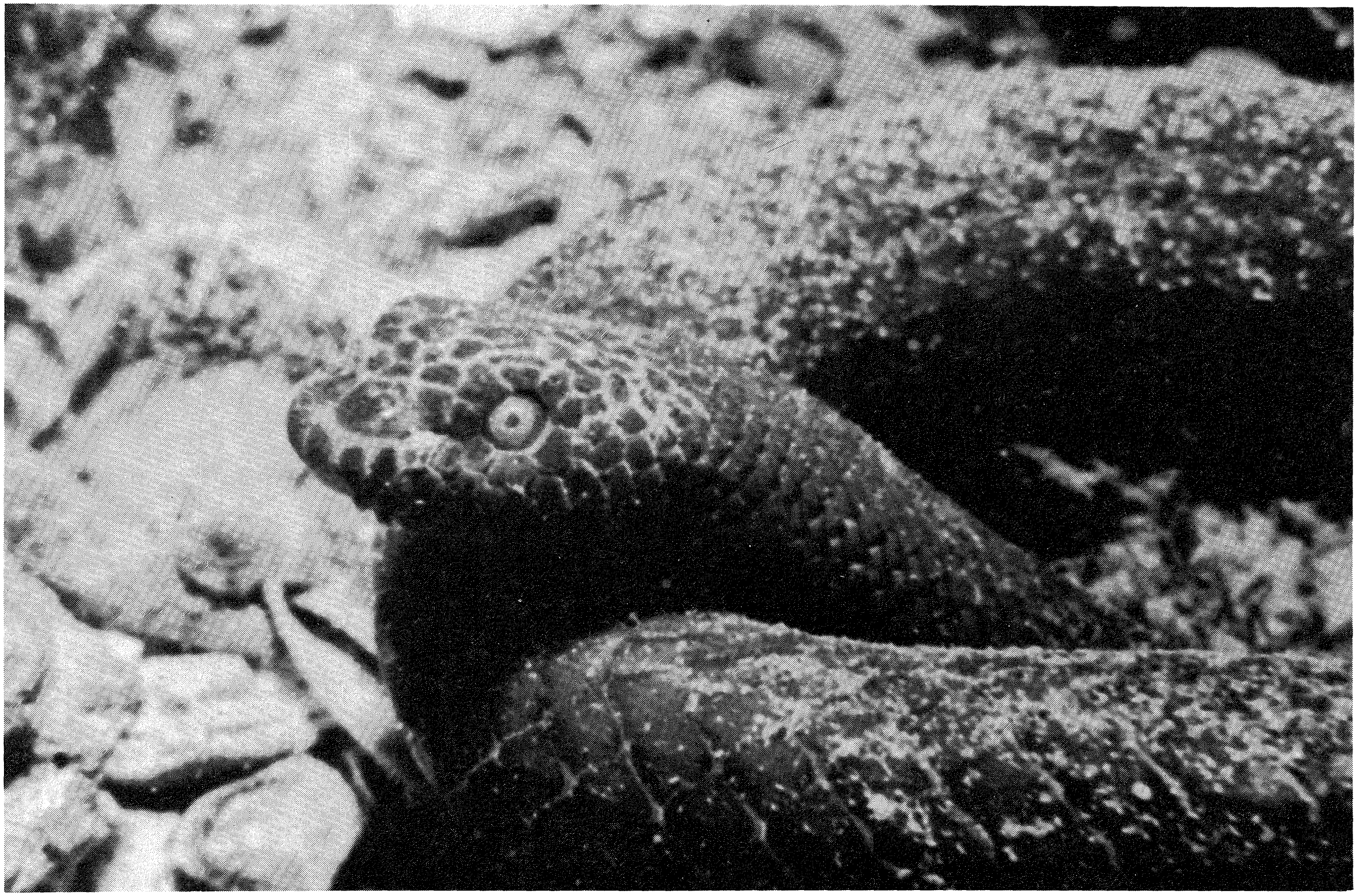

Fig. 5. An inactive *Aipysurus duboisii* coiled on the bottom. Photograph by Ron and Valerie Taylor.

Active:

Swain Reefs, Coral Sea, 29 June 1971, 1455 hrs, H.H. "*A. laevis* found foraging around edge of large coral head in 10 m water. It poked snout under edge of coral where it abutted on sand; crossed sand-patch rapidly and repeated same process at next coral head; after 9 min came up for 1 breath, then came over to me; I nudged it gently with the snake tongs and it went to bottom and continued foraging for 10 min. 2 sec. more, then surfaced for 1 breath and dived again and continued foraging; observations discontinued 2 min later."

Swain Reefs, Coral Sea, 30 June 1971, 1324 hrs, H.H. "*A. laevis* found foraging on bottom; investigated all species and morphological types of corals including soft corals, shelf corals, brain corals, etc.; didn't forage on extensive patches of dead coral rubble or sand; crossed those rapidly, or turned back to live coral; all foraging was at base of coral except for investigation of one crevice 1 m up side of a coral head; surfaced for a breath after 16 min, then continued foraging 26 min more; ignored all free-swimming fish 2 cm to 15 cm long even when they came within several cm of the snake; once several swam out from under a coral head when the snake stuck its head under; the snake ignored them and they returned to the crevice as soon as it left; observations terminated." See also notes of 2 May 1968 and 29 June 1971 previously quoted.

Inactive:

Ashmore Reef, Timor Sea, Jan 1973, 1512 hrs, H.H. "An adult *A. duboisii* coiled motionless under a clump of staghorn coral in 2 m water; after 9 min 20 sec moved head out of coral and 30 sec later gradually rose toward surface and when free of coral went straight up; took one breath and then went straight to bottom, then along bottom for 3 m and entered a different clump of staghorn coral; became motionless; 32 min 40 sec later moved head out and then surfaced; it swam horizontally on surface for 3-4 m with head out (breathed?) then dived vertically, investigated an overhanging coral ledge for about 5 sec, then moved into a staghorn clump 4-5 m from its previous resting site; entered clump and became motionless." See also notes for 1 July 1971 quoted above.

Foraging and resting are often closely interspersed throughout the day as indicated by the following excerpts from field notes:

Cato Lagoon, Coral Sea, 2 May 1968, 1445 hrs, H.H. "*A. duboisii* under *Porites* coral in 1.5 m water; came up for one breath, then swam slowly, investigating crevices in coral; after 5 min 40 sec coiled up under dead staghorn coral; total distance travelled about 24 m; 16 min 43 sec later came up and breathed once, then swam slowly away into deeper water and was lost."

Table 1 summarizes all the data recorded of the activity of snakes at the time they were first sighted while making underwater observations. Even allowing for the fact that inactive snakes are more difficult to see than foraging ones, a high degree of diurnal activity is indicated.

The factors determining whether a given snake will be active or inactive are not known. Although nutritional state may be involved, it is not always the decisive factor as some foraging snakes have food in the stomach (one *A. duboisii* had a conspicuously large food bulge) and inactive ones may be post-absorptive; no quantitative assessment of such observations was made, however.

Table 1. Activity of sea snakes for which activity was recorded when first observed underwater. The category "other" includes swimming on surface, surfacing to breathe, and courting.

SPECIES	NO. OF SNAKES (% OF TOTAL) FORAGING	INACTIVE	OTHER	TOTAL
Aipysurus laevis	28(74)	8(21)	2(5)	38
Aipysurus duboisii	10(46)	11(50)	1(5)	22
Aipysurus apraefrontalis	1	0	0	1
Aipysurus foliosquama	0	1	0	1
Aipysurus fuscus	1	0	0	1
Emydocephalus annulatus	19(63)	6(20)	5(17)	30
Astrotia stokesii	4	2	1	7
Hydrophis gracilis	1	2	0	3
Total	64(62)	30(29)	9(9)	103

Snakes secreted in crevices of coral are difficult to dislodge and their use of such places may be a protection against predation. On one occasion an attempt to pull an *Astrotia stokesii* from among coral resulted in the coral breaking off and coming with the snake. In some cases when snakes entered crevices in large coral heads, they retreated so deeply that they could not be seen, or reached by snake tongs, a distance of a metre or more.

Some species are frequently observed swimming on the surface at night, as well as by day. Diurnal surface activity seems to be more common when the surface of the sea is glassy smooth; no quantitative data are available however. At Ashmore Reef, many snakes were captured at night from the deck of the *Alpha Helix*. Most of the surface activity of *Hydrophis melanocephalus* occurred after dark. Of the 115 specimens of this species taken, nearly all were secured by nocturnal dip-netting from the ship. *Acalyptophis peronii* also usually surfaced at night but sometimes did so in the late afternoon. Diurnal captures of *Astrotia stokesii* on the surface were about as frequent as nocturnal ones. *A. laevis* was predominantly diurnal and occasionally swam at the surface in the daytime; a few were captured at the surface at night. *A. duboisii* was collected at night on one occasion. Although active by day, it was not often identified on the surface. No nocturnal observations at Ashmore Reef were made in the shallow water zone favoured by *Aipysurus fuscus, Aippsurus foliosquama, Aipysurus apraefrontalis,* and *Emydocephalus annulatus* and no specimens of these species were secured by nocturnal dip-netting. Diurnal observations indicated these species spend little time at the surface even by day.

Nocturnal surface activity of snakes could not be correlated with either time or meteorological conditions. Some nights many snakes appeared, other nights few or none. On the night of January 4-5, 1973, snakes appeared in great numbers between 2200 and 0200 hrs and about 40 were captured. On January 13, 1973, about the same number were captured between 0100 and dawn.

Sea snakes were also observed on the surface at night in the Visayan Sea (Philippines) during the *Alpha Helix* cruise in 1975. The largest single night's catch was 22 snakes taken September 10-11, the majority being *Laticauda laticaudata, L. colubrina,* and *Hydrophis cyanocinctus.* Two of the most common sea snakes of the area, *Laticauda semifasciata* and *Hydrophis ornatus,* were rarely observed from the *Alpha Helix* at night. Many were brought to the ship by local fishermen. However, precise collecting data were not available. Among the other relatively common species, *Hydrophis belcheri* appeared to be predominantly nocturnal and *H. inornatus* almost exclusively diurnal. In comparison with species observed at Ashmore Reef, Philippine sea snakes remained on the surface for shorter periods and dived with much less provocation. This may reflect species differences or adaptation to a longer and more frequent contact with man.

The function(s) of prolonged surface activity by sea snakes, either diurnally or nocturnally, remains a mystery. Sea snakes seldom if ever, build up extensive oxygen debts when diving (Seymour and Webster 1975, Heatwole and Seymour 1975b, 1976) and hence a prolonged stay at the surface is not required for respiratory reasons. Thermoregulation remains a possibility as vertical thermal gradients occur in the water column; this would not explain the highly sporadic nature of the occurrence of nocturnal surface activity, however. It has been suggested that diurnal surface activity in sea snakes is thermoregulatory basking (Cowles 1962). However, snakes in water elevate their body temperature only slightly above water temperature by absorbing solar radiation (Dunson and Ehlert 1971, Graham *et al.* 1971, Graham 1974) and it is doubtful whether surface activity in sea snakes is really related to basking.

It would seem that diurnal surface activity may in fact be disadvantageous in areas where sea eagles are common as these birds prey on sea snakes (Heatwole 1975c).

To date, no explanation of surface activity in sea snakes (except for the surface-feeding *P. platurus)* is completely convincing and this is an aspect of sea snake biology which should be studied further.

LOCAL MOVEMENTS

At least some species of sea snakes undergo seasonal inshore-offshore movements (Shuntov 1971). However, their local movements when in a given locality are poorly known.

The only information currently available consists of observations by two of us (R.T., V.T.) on the reefs just north of Lizard Island, Queensland. There was an old steel drum submerged on the bottom in about 25 m of water which served as a shelter for a number of marine organisms and was consequently visited frequently over a 3-week period for filming purposes. Three snakes were associated with this drum throughout this period, 2 *Aipysurus laevis* and 1 *Astrotia stokesii*. They were usually curled up next to it or foraging nearby. If they were not there when the divers arrived they usually appeared shortly thereafter.

This suggests that these two species have a home range and remain associated with a given area for extended periods.

There is also evidence that fidelity to a given site by *A. laevis* may last for long periods. A large number of this species was noosed for filming purposes and sustained injury to the skin of the neck as a result. A visit to the same locality a year later revealed the presence of many snakes with scars around the neck.

Within their home range, snakes do not always return to exactly the same spot for their inactive periods, however, as indicated by the following field notes:

Scotts Reef, Timor Sea, 8 Jan 1973, daytime, H. H. "*A. duboisii* found coiled on sand by dead coral in 3.5 m of water; motionless for 16 min 35 sec, then started to gradually move head and body slowly; ascended to surface for one breath, dived straight to a flat brain coral about 2 m from previous location; coiled in crevice at base." Similar observations of change in shelter site have been noted above (see notes of 2 May 1968, Jan 1973).

The distance covered while foraging between breaths undoubtedly varies with species and with condition of the habitat. The values obtained in the present study ranged up to about 500 m during a given submergence; many smaller values, of only 10-15 m were also recorded. A map of the movements of an *Aipysurus laevis* which was continuously followed for 26 minutes is presented in Figure 6.

The senior author is now engaged in a mark-recapture study with the objective of studying movements of snakes on coral reefs.

DIVING AND SURFACING BEHAVIOUR

As indicated by various of the excerpts from field notes quoted above and by numerous other observations, sea snakes in the sea commonly ascend to the surface to breathe (Fig. 7) take one breath and then immediately return to the bottom. This is by far the most common behaviour pattern during the day; rarely, more than one breath is taken before returning to the bottom. On some occasions the momentum of ascent carries the snake's head and part of the neck well above the surface of the water. Breaths are often audible to a person above the surface. Occasionally, exhalation begins a short distance below the surface and bubbles can be seen streaming from the snake's nostrils just before it breaks the surface. Generally surface time is very brief, only a few seconds.

Ascent and descent are usually nearly vertical and the journey to the surface or bottom made without interruptions. Several exceptions were noted, however. On 5 Janurary, 1973, an *Acalyptophis peronii*, attached to an XBT lead (for recording heart rate at depth), remained on the surface for 12 minutes, then gradually descended at an oblique angle toward the bottom to a depth of about 12 m, then levelled off at an even more oblique angle toward the bottom; after 5 min of swimming it was lost to sight at a depth of about 37 m. On another occasion (6 Jan, 1973) a snake on an XBT lead leisurely swam at an angle toward the bottom. After 4 min and reaching a depth of 17 m it returned to the surface and shortly dived again, whereupon it went nearly to the bottom (30 m) where it was captured and retrieved. It is probable that both the angle and rate of diving was influenced by the fact that the animal was tethered, even though the XBT wire was extremely fine.

The rate of ascent or descent of 5 individuals was measured (Table 2). In most cases the rate was 0.30-0.36 m/sec. One individual ascended much faster (0.60 m/sec) and one dived much more rapidly (0.90 m/sec). Most snakes which were observed, but which were not specifically timed seemed to dive and surface at about the same speed as the three slower animals in Table 2. Hence 0.30-0.40 m/sec seems a good general estimate of diving and surfacing speed of sea snakes, with the qualification that they are capable of and sometimes employ speeds double or triple that rate. Most snakes seemed to dive at the same speed at which they surfaced.

Surface-active snakes vary in their behaviour, depending on how long they have been on the surface. At first they are reluctant to dive when approached and are more easily captured than when they have been on the surface for some time. Nocturnally surface-active *Hydrophis melanocephalus* and *Acalyptophis peronii* tended to remain on the surface for 10 to 20 minutes.

In the sea, it was difficult to tell when surface-active snakes breathed. However, in the laboratory snakes on the surface undergo prolonged periods of apnea, comparable to the submergence times of snakes that return to the bottom between breaths (Heatwole and Seymour 1975a); it is likely that surface-active snakes in the sea are also apneic most of the time.

Table 2. Rates of ascent and descent of individual sea snakes in their natural habitat.

SPECIES	WATER DEPTH (M)	TIME TO ASCEND OR DESCEND	M/sec
ASCEND			
Aipysurus duboisii	**3**	**5**	**0.60**
Aipysurus fuscus	**6**	**20**	**0.30**
DESCEND			
Emydocephalus annulatus	**6**	**18**	**0.33**
(two individuals)	**4**	**11**	**0.36**
Aipysurus laevis	**9**	**10**	**0.90**

The mode of locomotion is usually typically sinuous and serpentine. One unusual aspect it that some sea snakes (and also the file snake, *Acrochordus granulatus)* can swim backward as well as forward by reversing the direction of the lateral undulations of the body. This behaviour seems especially well developed in *Pelamis platurus*. In a laboratory tank one sometimes has to look carefully in order to ascertain which is the head end of a swimming snake.

On one occasion an *Aipysurus duboisii* which had surfaced remained vertically in the water, with the head and about 5 cm of the neck protruding above the water, and using a sculling movement propelled itself backward in the water, all the time facing the observer.

SHEDDING

There are reports in the literature that sea snakes do not shed the skin whole as do land snakes but rather lose it piece by piece (e.g. Loveridge 1946). Other reports indicate that the whole skin is shed. We have had many snakes of a number of species shed their skin in the laboratory and always the skin was shed whole; in the field we have seen snakes with torn skins but never any that shed piece-meal. We have kept no data on the frequency of shedding. On 1 July 1971, 2 of the 20 *A. laevis* seen on a dive on Saumarez Reef, Coral Sea, were shedding or had the eyes cloudy (an indication that shedding is imminent, see Figure 8) an incidence of 10%. At Swain Reefs in November 1976, 85 snakes were captured over a two-week period; 4 (5%) were shedding. We have never observed snakes with cloudy eyes foraging. They usually lie quietly on the bottom, moving only to surface for air; some were heavily covered with algae.

We have observed snakes shedding in the sea; the following excerpts from field notes describe the process:

Saumarez Reef, Coral Sea, 2 July 1971, 1345 hrs, H. H. "*A. laevis* observed on bottom on patch of dead coral rubble in 10 m water. Its behaviour appeared unusual so it was not immediately caught. It rubbed its head against the dead coral and loosened the skin around the mouth; it continued to rub the sides of the head and the chin on the rubble as it slowly swam along; during rubbing it turned sideways and bent its neck as it scraped the side of the head against the substrate; after head skin was peeled back, it continued rubbing venter and sides of the neck and body against bottom until its skin peeled (entire) back from the anterior ¼ of its body. This took about 5 min. Animal then captured."

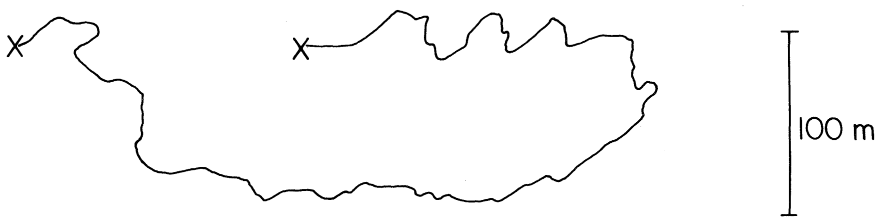

Fig. 6. Map of the path followed by a foraging *Aipysurus laevis* in the Swains Reefs, Coral Sea.

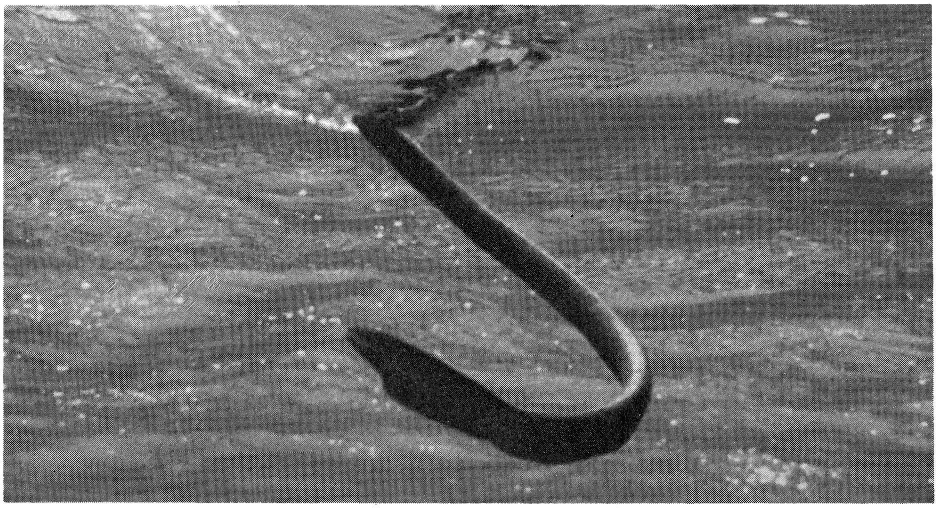

Fig. 7. An underwater view of *Aipysurus laevis* at the surface with its head out breathing. Photograph by Harold Heatwole.

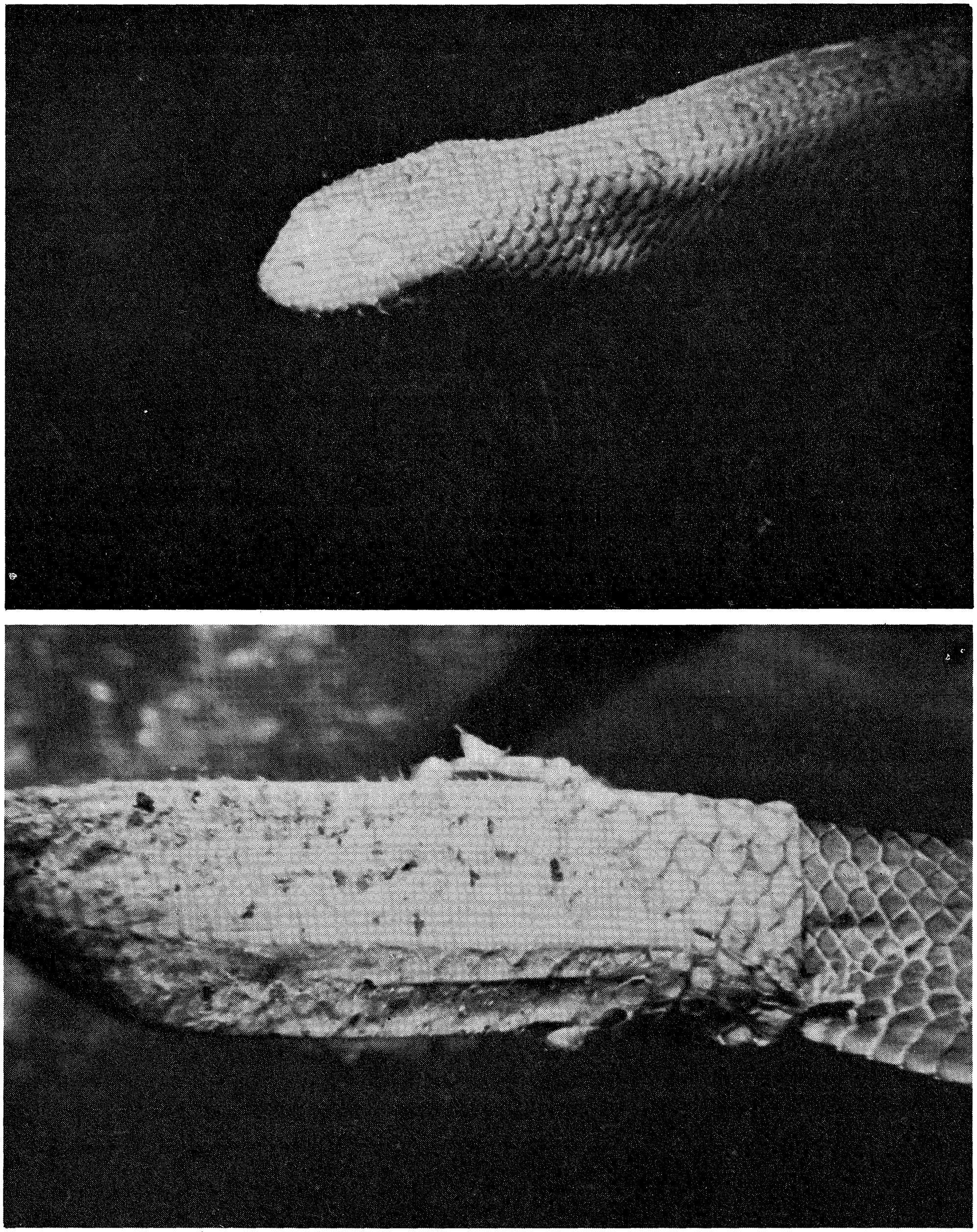

Fig. 8. Shedding in *Aipysurus laevis*. Upper: A snake with cloudy eyes about ready to shed. Lower: Skin (torn) everted over tail of shedding snake. Photographs by Ron and Valerie Taylor.

On 4 July 1971 at the same locality, another *A. laevis* was similarly observed. It was captured when the skin of the anterior half of the body had been turned inside out and extended back over the posterior half. See also Figure 8.

The shedding of *Pelamis platurus* has been described by Pickwell (1971). He indicated that knotting and coiling by *P. platurus* aids in freeing the skin (intact) and must be an advantage to a surface-dwelling animal where solid objects for scraping against would not be abundant (and would give when pushed against). We have observed knotting and coiling during shedding of *P. platurus* in a large laboratory tank and in addition have observed a previously unreported mode of loosening the skin. The following notes illustrate the procedure:

"Snake first observed with anterior ¼ of skin free; it frequently swam backward, then forward; the drag of the water on the loose skin seemed to aid in loosening the skin from the body; the snake also knotted, rubbed against other snakes, the side of the tank and the outlet tubes; at frequent intervals the girth of the body was momentarily locally expanded at the boundary between loose and adhering skin. The expanded area was only about 2 cm long and resembled a large food bolus; expansion repeatedly occurred always at the place where the skin was being loosened. Consequently the site at which the bulge would appear shifted posteriorly during shedding. After 5½ min the skin was ½ off and turned inside out over the posterior part of the body; the snake then became inactive; later, the completely shed skin was recovered from the tank; it was all in one piece, turned inside out except for the posterior part of the tail."

The mechanism whereby the local bulge was produced was not ascertained but its function was clearly aiding loosening of the skin.

May and Nickerson (1968) noted that the sea krait *Laticauda semifasciata* in captivity shed the skin entire and that ecdysis was accompanied by knotting and coiling; immediatley before and during shedding the animals individually floated at the surface in a "tight ball." They also mention that shedding was facilitated by expanding the body by increased air intake although they do not specify that the expansion was localized in their species. Brief field notes on this species are also available.

Gigantes Island, Philippines, 12 Sept 1975, S.A.M. "Area of very beautiful and diverse coral growth; maximum depth about 15 m. Caught 2 *Laticauda semifasciata* each about 1 m long curled around coral clumps. One was shedding its skin . . . most of the skin came off as it was caught and brought to the surface."

One function of shedding may be to remove sessile organisms that attach to sea snakes, such as algae, foraminiferans, hydrozoans, perpulid polychaetes, some bivalve molluscs, bryozoans, barnacles and ticks which sometimes are found on sea snakes (Zann *et al.* 1975). Most sea snakes are relatively free of such fouling organisms although occasional individuals are found with heavy infestations (Fig. 9), and one species of barnacle is restricted to sea snakes (Zann 1975). An individual of *Aipysurus laevis,* taken at Heron Island on a fishing line had a goose barnacle on each eye, rendering it completely blind (Cogger, personal communication). Of 85 *A. laevis* caught on Swain Reefs in November 1976, only 3 had heavy algae infestations.

SOCIAL INTERACTIONS

There is both interspecific and intraspecific variation in aggressiveness of sea snakes toward humans (Heatwole 1975b) and it would be surprising if interaction among snakes themselves did not show similar variability. However, in most cases sea snakes seem to pay little attention to each other. In the field sea snakes usually are solitary. Where they

Fig. 9. An *Aipysurus laevis* with a heavy covering of algae. Photograph by Ron and Valerie Taylor.

come into close proximity with each other, presumably by chance, they usually do not respond overtly to each other. On a number of occasions, we have seen foraging snakes pass close to a resting one without either showing any signs of response. The following field notes illustrate this point:

Ashmore Reef, 4 Jan 1973, S.A.M. "While watching an *Aipysurus laevis* swimming along a coral trench at 4-5 m, saw it encounter an *A. duboisii* of about the same size. Neither snake responded to the other."

An exception occurs in the mating season. Notes by S.A.M. indicate that on 3 Jan 1973 a (uniformly dark) snake was seen moving along the bottom at a depth of 6 m. It located a second (variegated) snake under a coral ledge and began rubbing its head over the head and neck of the other. The pair swam slowly together around a small coral clump for about 10 min, one individual (presumed male) swimming above and slightly behind the other (presumed female) (see also Fig. 2 in Heatwole 1975b). Later in the day similar behaviour was observd in another pair of snakes at a depth of about 4 m. Again the presumed male located the presumed female under a clump of coral, rubbed her head and neck with his head, and followed her closely until she surfaced to breathe. He did not follow her but resumed contact with her after she returned to the coral. Soon afterwards he broke off contact and swam away. On 11 and 12 of January 1973, several other courting pairs were observed and sex of some was verified by capture and examination. In one instance the male voluntarily followed the captured female almost to the surface. In one case the male rubbed the neck and back of the female with his nose and may have bitten at her as they were lying on the bottom in water about 7 m deep. He lay with his body closely pressed against her back and attempted to work his tail under hers (Fig. 10). All courtship behaviour observed took place near the bottom. Although two divers (S.A.M., H.H.) frequently observed courtship in *E. annulatus* at Ashmore Reef, in no case was a complete copulation seen.

Courtship was very similar in *Aipysurus laevis* (Fig. 10; also see photo in MacLeish 1972). Pairs swimming together much as described above for *E. annulatus* were observed from time to time in the Coral Sea. Courtship could be induced in the mating season by towing dead snakes through the water. A hole was pierced through the upper and lower jaws near the midline of a dead *A. laevis* and a transparent, nylon fishing line passed through the hole and tied fast; the line extended about 40 cm below the snake and had a sinker attached to keep the snake near the bottom. The other end of the line was extended to the surface where a snorkeler slowly swam, towing the snake along. The forward motion, in conjunction with the sinker dragging on the bottom, resulted in a life-like sinuous swimming movement by the dead snake. Excerpts from field notes during such experiments are instructive:

Saumarez Reef, Coral Sea, 3 July 1971, 1100 hrs. H.H. "An adult *A. laevis* sighted swimming about 25 cm off bottom over sand and dead coral in 10-12 m of water. I towed a dead *A. laevis* about ½ m above the bottom on an intercepting course with it. It swerved to it and bumped its nose along the side (smelling with tongue?) and followed it moving along the side and swimming above it in close proximity until its snout was just behind the head of the dead snake. It moved up and back, at times swimming with its snout at the tip of the dead snake's tail and at other times with its head at more anterior locations, up to the base of the dead snake's head. It followed the snake for about 75 m. When I stopped towing the dead snake, the live one would stop also and eventually turn away. When I resumed towing the snake, the live one returned and followed it again. The snake surfaced to breathe, noticed me, came over and had to be repeatedly repulsed; it thereafter refused to follow the dead snake." Similar behaviour toward towed dead

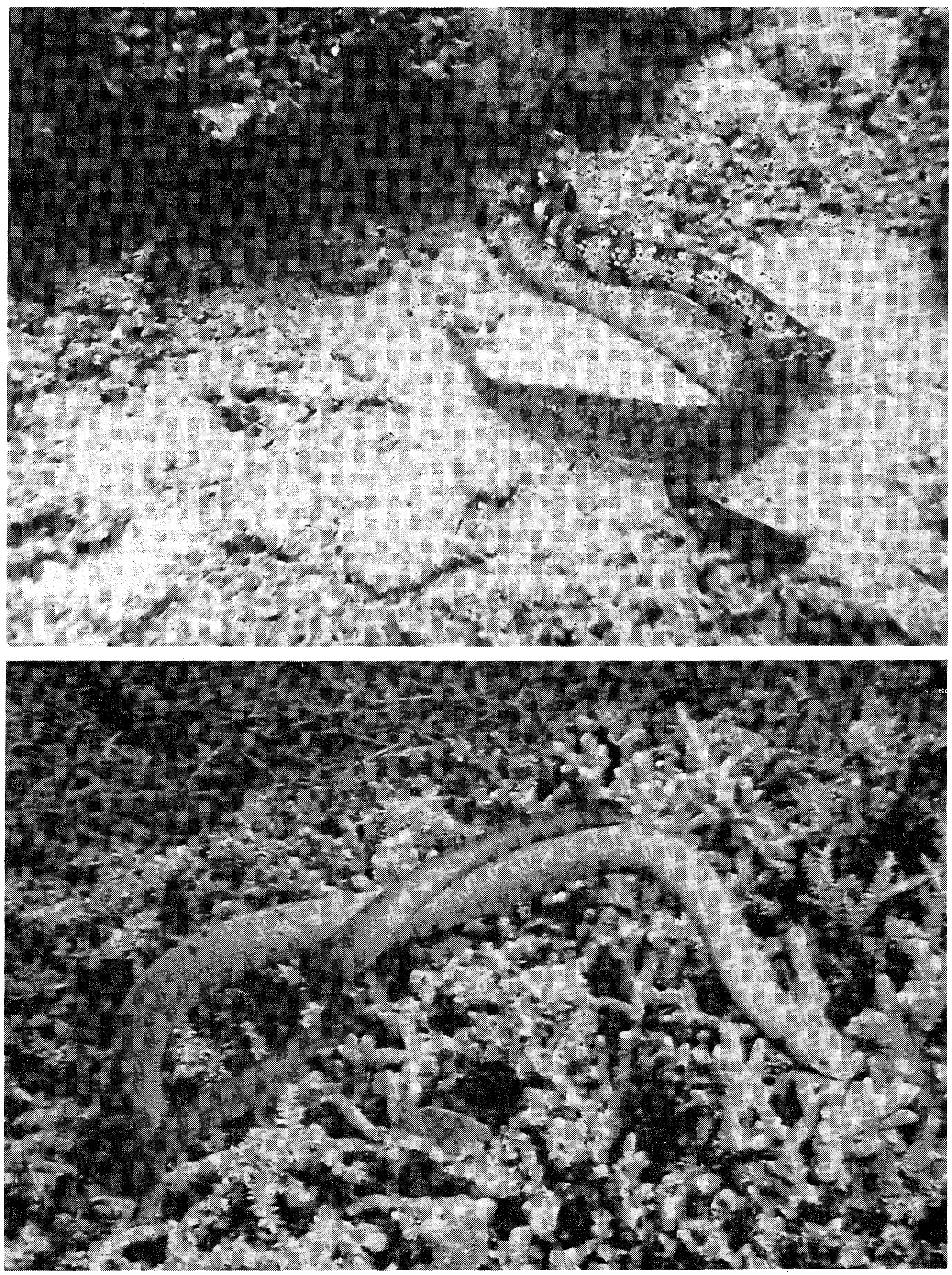

Fig. 10. Pair of sea snakes courting. Upper: *Emydocephalus annulatus* at Ashmore Reef. Photograph by Sherman Minton. Lower: *Aipysurus laevis*. Photograph by Ron and Valerie Taylor.

snakes was observed on a number of other occasions on several expeditions during the mating season of *A. laevis*. *Emydocephalus annulatus* showed no overt response to a towed *A. laevis*.

No complete copulations were ever observed. On several occasions a pair was interrupted in what was probably copulation. However, during courting and mating *A. laevis* tends to be aggressive toward humans (Heatwole 1975b) and behaviour was altered by the approach of an observer. Mating by a pair of *Aipysurus laevis* on the bottom was observed. When the pair was approached, they attempted to separate, both swimming away, the female dragging the male which still had the hemipenis inserted (Fig. 11).

REACTIONS TO OTHER SPECIES

Small fish sometimes associate with sea snakes as indicated by figure 12 and the following notes:

Ashmore Reef, 3 Jan 1973, S.A.M. "At about 7 m depth saw an adult *Astrotia* cruising along just above the bottom. Around its head was a group of about 8 tiny black and gold fish. After I captured the snake, they remained around me swimming usually just in front of my mask for about 15 min." C. J. Limpus (personal communication) indicated that the fish in the photograph "appeared to be identical to the juvenile golden trevalley *Caranx speciosus* (Forskal) which I am observing with my sea turtles and others are seeing with sharks, etc."

One diver on the Ashmore Reef expedition reported cleaner fish attending sea snakes the way they do large fish.

Although sea snakes are preyed upon by a few species of sharks, especially the tiger shark, *Galeocerda cuvieri* (Heatwole *et al.* 1974, Heatwole 1975c) most sharks pay little attention to sea snakes and R.T. and V.T. have observed *Aipysurus laevis* swimming among packs of feeding sharks without the snakes being molested.

Response to humans varies interspecifically and according to season, reproductive condition of the snakes, and the behaviour of the person (Heatwole 1975b). Some species never attempt to bite even when maltreated although most will bite defensively; a large number of fatalities from sea snake bite occur each year in southeast Asia (Reid 1975, Vick *et al.* 1975). A few species will attack a person if sufficiently provoked and occasional unprovoked attacks by *Aipysurus laevis* have been recorded. This species, however, often either ignores humans in the water or swims away when molested. If undisturbed, these snakes will often approach a diver and investigate him. They seem to be attracted by divers' activities and frequently associate themselves with persons underwater, sometimes following them around. In November 1976, metal tags were affixed to the tails of 85 sea snakes on Swain Reefs; only 3 of these attacked divers and two of these did so only after they had been released after having had their tails pierced by the tags. On some occasions when we have stirred up the bottom they appeared to be feeding on small items dislodged from cover. One of us (V.T.) has fed *A. laevis* by hand on small chunks of fish during the day and another (H.H.) has fed this species at night (see section on feeding). In the former case, when the morsel was held out, the snake approached, and after touching the cut piece of fish with its tongue several times, ate it from the diver's fingers.

On one occasion a snake surfacing, presumably to breathe, saw a diver and when about 3 m below the surface changed its course and approached the diver and followed her to the bottom and remained with her for a further 15 min. without resuming its trip to the surface.

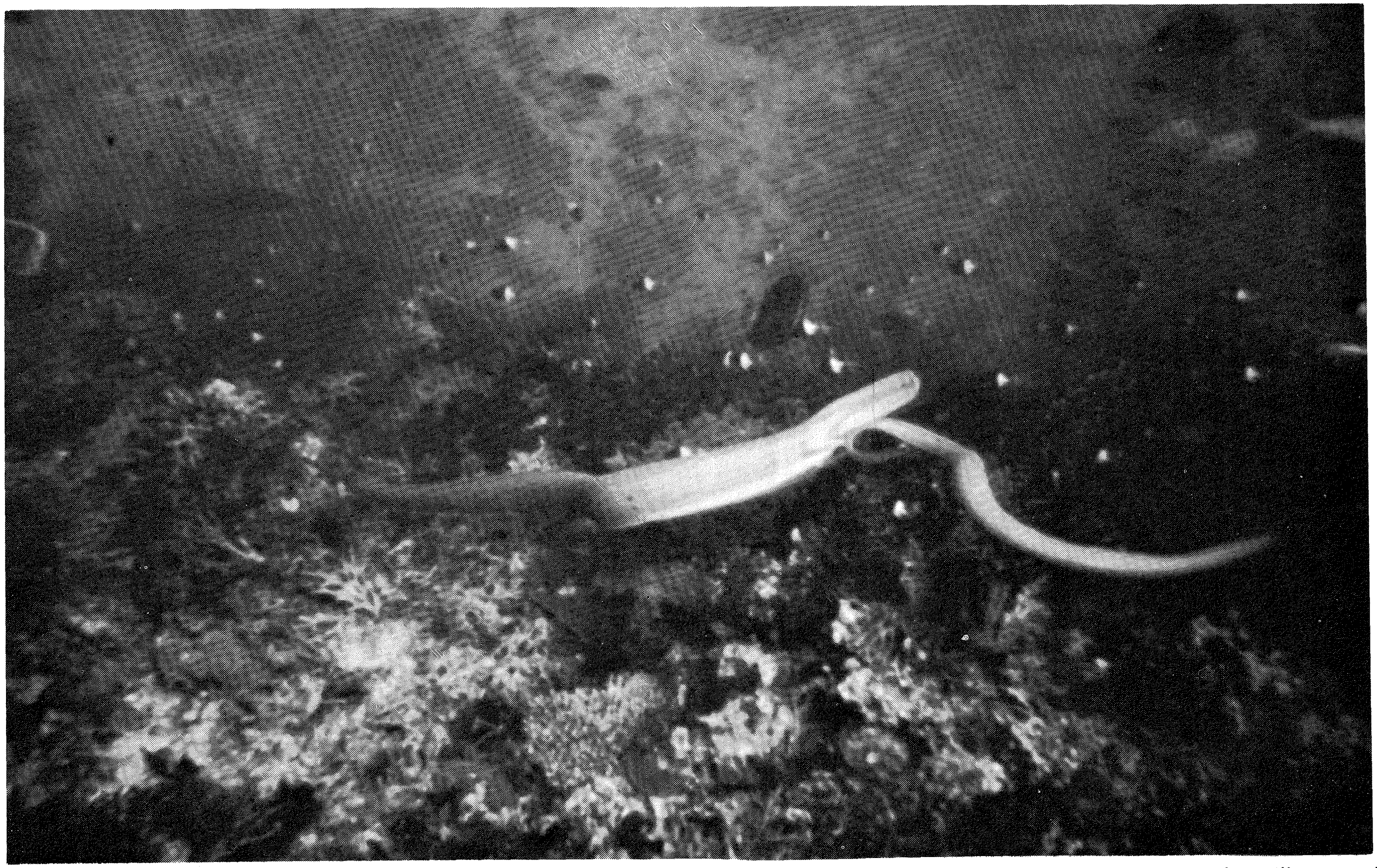

Fig. 11. A pair of *Aipysurus laevis* interrupted during copulation. The female is towing the male through the water by the still-inserted hemipenis. Photograph by Ron and Valerie Taylor.

Fig. 12. An *Astrotia stokesii with a group of juvenile Caranx speciosus* swimming above the neck region. Photograph by Sherman Minton.

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