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THE RÔLE OF SEA SNAKES (HYDROPHIIDAE) IN THE TROPHIC STRUCTURE OF COASTAL OCEAN COMMUNITIES*

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ABSTRACT

The Hydrophiidae is a family of poisonous marine snakes consisting of 51 species placed in 16 genera. The center of the geographic range for the family is the Straits of Malacca where 27 species coexist. Because essentially all species are associated with coastlines, the range is more or less linear. As their range extends from the Straits of Malacca along the east and west coast of India to the Persian Gulf, the number of species present steadily decreases from 27 to 11. The coastal waters of southern India harbour 20 species, representing 8 genera.

Although the taxonomy of this group is comparatively well understood, our knowledge of its ecology is sorely lacking. In this study, the feeding habits of sea snakes are examined. Data on 13 genera and 39 species were obtained from the stomach contents of 95 sea snakes collected during the International Indian Ocean Expedition and from specimens borrowed from over 19 museums. Also data from 84 additional snakes were extracted from the literature. Prey have been identified and then classified according to body form and ecology. Body forms fall into four general categories: (1) eels (*e.g.* Apodes) and eel-like fish (*e.g. Synodus*); (2) bullet-shaped fish (*e.g.* mullet); (3) vertically or laterally oversized fish (*e.g*, puffers and flatfish); (4) other than fish (*e.g.* birds' eggs, fish eggs and prawns). Five general categories were constructed to describe prey ecology: (1) inshore, on or near bottom; (2) rock dweller; (3) reef dweller; (4) pelagic inshore; (5) pelagic offshore. The fact that sea snakes utilize such a wide range of food types demonstrates their niche diversity.

Correlation studies on the relationships of prey class, prey ecology, snake dentition and snake girth reveal the extent of feeding specialization. Generally, species in which the adult males have an average neck circumference of more than 30 mm, the average fang length is greater than 1.7 mm. These species are taxonomically diverse and include most of the monotypic genera and numerous *Hydrophis* species. Their feeding habits are diverse and include every class of food. The *Aipysurus* and *Emydocephalus* whose average neck circumference is greater than 30 mm, have average fang lengths of only 1.4 mm and 0.8 mm respectively. These forms feed on eels and demersal fish eggs. The microcephalic species have neck circumferences of less than 30 mm and fang lengths of less than 1.7 mm. These forms belong to three genera, *Microcephalophis*, *Kerlia* and *Hydrophis* which feed almost exclusively on bottom dwelling Apodes eels. From such data and that in the literature, a preliminary qualitative picture of the rôle of sea snakes in ocean communities can be constructed.

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Introduction

The Hydrophiidae is a family of poisonous marine snakes consisting of 51 species representing 16 genera. The center of the geographic range for the family is the Straits of Malacca where 27 species have been reported. In general, the number of species present decreases as the distance from the Straits increases. For example, where their range extends along the coastal waters (the habitat of most species) from the Straits of Malacca to the Persian Gulf, the number of species present decreases from 27 to 11.

The taxonomic relationships of sea snakes have been studied and reported on extensively by Smith in 1926 and by Voris in 1969. Although the taxonomy of the group is comparatively well understood, knowledge of its ecology is sorely lacking. The purpose of this paper is to suggest the possible rôle of sea snakes in marine coastal food chains. This problem has been approached from two directions: one, data on what sea snakes eat and where they feed have been obtained by an analysis of their stomach contents, and two, this information has been related to certain morphological features which are of special importance in feeding.

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Materials and Methods

A total of 632 sea snakes have been examined for stomach contents. Some of these specimens were collected during the International Indian Ocean Expedition, while others were borrowed from 19 museums. Stomach contents were removed from 95 snakes representing 13 genera and 39 species. Data on an additional 84 stomach contents were accumulated from the literature (Table 1).

Each prey item was identified as completely as possible and then classified according to body form and general habitat. Body forms were found to fall into four general categories: 1. Eels and eel-like fish: A. Apodes eels (scales minute or lacking), *e.g.*, *Congrellus*, and B. Operculoid eels, eel-shaped fish, *e.g.*, *Synodus*;

TABLE 1. *Summary of sea snake stomach contents*

Species	Museum Number or Literature Source[1]	No. of Stomach Contents	Locality	Snake S-V Length (mm)	Prey Forms[2]	Prey Habitat[3]	Prey Item
Laticauda colubrina	FMNH 97963	1	New Hebrides	325	1-A	1a, b	Moringuidae
	FMNH 4047	1	E. Indies	710	1-A	1a, b	Muraenidae, *Gymnothorax*
	FMNH 86148	1	Palau Is.	800	1-B	1a, b	Synodontidae, *Synodus*
	Wall, 1921	1	..	..	3	1a, b	Pomacenteridae, *Glyphidon* sp. (*Glyphisodon* sp.)
L. laticaudata	AMNH 66580	1	Okinawa	830	..	..	..
L. schistorhynchus	AMNH 44962	1	Savage Is.	370	2	1a, b	Eleotridae, *Eviota*
	USNM 61907	1	Savage Is.	670	2, 3	..	..
	USNM, 61909	1	Savage Is.	620	2, 3	..	..
Aipysurus apraefrontalis	BM 1926, 5.28.22	1	Ashmore Reef	380	1-A	1a, c	..
	AMNH 43355	1	Ashmore Reef	670	..	..	..
	Smith, 1926	1	Ashmore Reef	..	1-A	1c	Eel
A. dubosii	AMNH 43354	1	Ashmore Reef	630	2	..	..
A. eydouxi	JRH 6470	1	S.E. Asia	570	..	..	..
	AMNH 14169	1	Gulf of Siam	445	4	1a	Fish eggs
	FMNH 11572	1	Gulf of Siam	480	4	1a	Fish eggs
A. foliosquama	BM 1926, 5.28.24	1	Ashmore Reef	355	2	1c	Clinidae, *Tripterygion*
	BM 1926, 11.1.24	1	Ashmore Reef	390	..	..	..
	MCZ 23482	1	Ashmore Reef	400	2	1c	Eleotridae
	USNM 71050	1	Ashmore Reef	510	2	1c	Eleotridae
	BM 1926, 5.28.23	1	Ashmore Reef	565	..	..	..
	MCZ 23496	1	Ashmore Reef	515	..	..	..
	MCZ 23495	1	Ashmore Reef	480	1-A	1c	..
	Smith, 1926	3	Ashmore Reef	..	2	1c	Labridae, *Halichoeres trimaculatus*

[1] For the complete names of the museums abbreviated in this column, see the acknowledgments.

[2] Key to prey forms. (1) Eels and eel-like fish: A. Apodes eels (scales minute or lacking), *e.g.*, *Congrellus*; B. Operculoid eels and eel-like fish, *e.g.*, *Synodus*; (2) Bullet-shaped fish, *e.g.*, Mullidae; (3) Vertically or laterally oversized fish, *e.g.*, Scorpaenidae or Ariidae; (4) Forms other than fish, *e.g.*, birds' eggs, fish eggs, and prawns.

[3] Key to prey habitats. (1) Neritic zone: a. on or near bottom; b. rock dweller; c. reef dweller; d. pelagic; (2) Oceanic zone a. pelagic.

TABLE 1. (*Contd.*)

Species	Museum Number or Literature Source[1]	No. of Stomach Contents	Locality	Snake S-V Length (mm)	Prey Forms[2]	Prey Habitat[3]	Prey Items
A. fuscus	BM 1926, 11.1.20	1	Ashmore Reef	360	4	1a, b, c	Fish eggs, and unidentified vertebrate
	BM 1926, 11.1.21	1	Ashmore Reef	550	2	1a	Gobiidae
	UMNZ 64466	1	Ashmore Reef	565	..	..	..
A. laevis	AMNH 86178	1	E. Australia	935	2, 3	..	..
Emydocephalus ijimae	FMNH 120875	1	Orchid Is.	370	4	1a, b, c	Fish eggs in mouth
	FMNH 120878	1	Orchid Is.	365	4	1a, b, c	Stomach full of eggs, rectum full of sand & fine debris—egg sacks
	FMNH 120880	1	Orchid Is.	665	..	..	Rectum with sand
E. annulatus	AMNH 4998	1	..	856	4	1a, c	Rectum with egg cases
	MCZ 23536	1	Ashmore Reef	310	..	..	Rectum with sand
	MCZ 23537	1	Ashmore Reef	265	4	1a, c	Fish eggs
	MCZ 23538	1	Ashmore Reef	305	4	..	Rectum with sand
	MCZ 23539	1	Ashmore Reef	320	4	1a, c	Fish eggs
Kerilia jerdoni	FMNH 11570	1	Gulf of Siam	620	1-A	1a, b	Ophichthidae
	FMNH 11569	1	Gulf of Siam	750	1-A	1a, b	Ophichthidae
Thalassophina viperina	JRH 5037	1	Gulf of Siam	303	2	1a	Callionymidae
	FMNH 11567	1	Indochina	335	1-A	..	..
	MCZ 23818	1	Gulf of Siam	585	2	1a	Callionymidae
	MCZ 23817	1	Gulf of Siam	590	..	..	..
	Volsøe, 1939	1	Persian Gulf	..	2	1a, b	Callionymidae, *Callionymus* sp.
Enhydrina schistosa	FMNH 152557	1	W. India	795	2	1d	Sciaenidae
	FMNH 152564	1	Straits of Malacca	355	2	..	..
	FMNH 79989	1	W. India	950	..	..	..
	FMNH 152562	1	Straits of Malacca	850	..	..	..
	FMNH 142662	1	Straits of Malacca	995	..	..	..
	Minton, 1966	5	W. Pakistan	..	4	..	Prawns, *Tetrodon*, *Coilia*, *Harpodon*
Acalyptophis peronii	BM 1935, 4.7.2	1	W. Pacific Is.	425	1-B	1a, b	Gobiidae, *Oxyurichythys*
Thalassophis anomalus	MCZ 23812	1	Sarawak, Borneo	530	1-A	1a, b	Congridae, *Congrellus*
Kolpophis annandalei	BM 1926, 11.1.1	1	Indochina	580	3	2a	Clupeidae
Pelamis platurus	Klawe, 1964	15	Coast of Ecuador	..	2	1d	Polynemidae, *Polynemus approximans*

	Klawe, 1964	14	Coast of Ecuador	..	2	1d	Mullidae, *Pseudupeneu grandisquamis*
	Klawe, 1964	5	Coast of Ecuador	..	2	1d	Mugilidae
	Klawe, 1964	1	Coast of Ecuador	..	3	1d, 2a	Carangidae, *Selar crumenophthalmus*
	Klawe, 1964	1	Coast of Ecuador	..	3	1d, 2a	Carangidae. *Caranx hippos*
	Klawe, 1964	1	Coast of Ecuador	..	1-B	1d, 2a	Fistulariidae, *Fistularia cornuta*
	Visser, 1967	1	S.E. Africa	..	2	2a	Nomeidae, *Psenes whiteleggi*
	Visser, 1967	1	S.E. Africa	..	3	1d, 2a	Carangidae, *Decapterus lajang*
Lapemis hardwickii	FMNH 141144	1	N. Borneo	530	3	1a, b	Scorpaenidae
	FMNH 133063	1	N. Borneo	610	3	1d	Ariidae, *Arius*
	FMNH 141152	1	N. Borneo	590	2	..	..
	FMNH 131255	1	N. Borneo	650	3	1d, 2e	Carangidae (*Caranx* ?)
	FMNH 63558	1	N. Borneo	660	4	..	Amphipod
	FMNH 131256	1	N. Borneo	610	2	..	..
	FMNH 133086	1	N. Borneo	580	3	1d	Carangidae ? (*Alectis*?)
	FMNH 133074	1	N. Borneo	435	3	1a	Soleidae, (*Cynoglossus*?)
	FMNH 141148	1	N. Borneo	540	..	..	..
	FMNH 141153	1	N. Borneo	625	2, 3	..	..
	FMNH 141147	1	N. Borneo	570	3	1d, 2a	Carangidae, *Caranx*
	Smith, 1935	1	Manila Harbor	..	1-B	1a, b, d	Fistulariidae, *Fistularia*
	Smith, 1935	1	Manila Harbor	..	1-B	1a	Callionymidae
L. curtus	Volsøe, 1939	1	Persian Gulf	..	2	1a, b	Gobiidae, *Gobius* sp.
	Volsøe, 1939	1	Persian Gulf	..	2	1d	Dussumieridae, *Stolephorus* sp.
	Volsøe, 1939	1	Persian Gulf	..	3	1d, 2a	Sparidae, *Sparus spinifer*
Astrotia stokesii	MCZ 23499	1	Indian Ocean	1190	2, 3	..	..
Microcephalophis gracilis	JRH 6178	1	Straits of Malacca	879	1-A	1a, b	Ophichthidae, *Ophichthys*
	Wall, 1921	1	..	..	1-A	1a, b	Ophichthidae, *Ophichthys boro*, or *O. orientalis*
	Volsøe, 1939	1	Persian Gulf	..	1-A	1a, b	Xenocongridae, *Muraenichthyes schultzei*
Hydrophis belcheri	FMNH 14270	1	Lembeth Straits	515	1-A	..	..
	FMNH 14268	1	Lembeth Straits	880	2	..	..
	JRH 6493	1	S.E. Asia	740	1-A	1a, b	Moringuidae

TABLE 1. (*Contd.*)

Species	Museum Number or Literature Source[1]	No. of Stomach Contents	Locality	Snake S-V Length (mm)	Prey Forms[2]	Prey Habitat[3]	Prey Items
H. cyanocinctus	JRH 6150	1	Straits of Malacca	950	1-A	1a, b	..
	JRH 6171	1	Kuala Kuran	890	1-B	1a, b	Gobioididae
	Volsøe, 1939	1	Iranian Gulf	..	2	1a	Gobiidae, *Boleophthalmus tenuis*
	Smith, 1935	1	Formosa	..	1-A	1a, b	Conger eels
H. spiralis	Wall, 1921	1	..	..	1-A	1a, b	Ophichthidae, *Ophichthys boro*, or *O. orientalis*
	Volsøe, 1939	1	Persian Gulf	..	1-A	1a, b	Ophichthidae, *Pisodonophis hoeveni*
H. melanocephalus	USNM 33959	1	Riukiu Is.	1000	1-A	1a, b	Congridae
	AMNH 67178	1	Okinawa	855	1-A	1a, b	Ophichthidae, *Myrichthys*
H. melanosoma	JRH 6272	1	Krian	..	1-A	1a, b	Muraenidae, *Gymnothorax schismatorhynchus* ?
	JRH 6174	1	..	715	1-A	1a, b	..
H. fasciatus	UMMZ 64503	1	Gulf of Siam	675	1-A	1a, b	Moringuidae
	JRH 6257	1	Straits of Malacca	660	1-A	1a, b	Moringuidae
	JRH 6211	1	Gulf of Siam	790	1-A	1a, b	Moringuidae
	FMNH 142455	1	India	1100	1-A	1a, b	Muraenidae
	JRH 6570	1	Malaya	990	1-A	..	..
H. f. atriceps	Denburgh and Thompson, 1908	1	..	..	1-A	1a, b	Xenocongridae, *Muraenichthyes thompsoni*
H. lapemoides	FMNH 82577	1	Persian Gulf	605	1-A	1a, b	..
	Volsøe, 1939	1	Persian Gulf	..	1-A	1a, b	Ophichthidae, *Pisodonophis hoeveni*
	Volsøe, 1939	1	Persian Gulf	..	2	1a, b	Gobiidae, *Gobius* or *Eleotris*
H. torquatus	JRH 6572	1	Malaya	450	2	1a, b	Gobioididae
H. obscurus	Wall, 1921	1	..	..	3	1b, 2a	Triacanthidae, *Triacanthus brevirostris*
H. nigrocinctus	BM 64.4.7.6	1	Malay Arch.	560	1-A	1a, b	Congridae

H. ornatus	FMNH 11568	1	Cochin China	620	..	..	..
H. inornatus	USNM 39947	1	Riukiu Is.	610	2	1d	Atherinidae, *Atherina* sp.
	USNM 38657	1	Luzon	400	1-B	1a, b	Gobioididae
H. kingi	MCZ 23649	1	E. Australia	1300	1-A	1a, b	..
H. major	MCZ 23664	1	Holothuria Bank	850	1-B	1a, b	Carapidae, *Carapus*
H. brookii	UMMZ E74341	1	S.E. Asia	845	1-A	1a, b	Moringuidae
	JRH 6486	1	S.E. Asia	727	1-A	1a, b	..
	JRH 6476	1	S.E. Asia	710	1-A	1a, b	..
	JRH 6475	1	S.E. Asia	810	1-A	1a, b	..
	JRH 6478	1	S.E. Asia	770	1-A	1a, b	Moringuidae
	JRH 6481	1	S.E. Asia	740	1-A	1a, b	..
	JRH 6589	1	S.E. Asia	700	1-A	1a, b	..
	JRH 6488	1	S.E. Asia	780	1-A	1a, b	Moringuidae
	JRH 6491	1	S.E. Asia	720	..	..	..
	JRH 6477	1	S.E. Asia	535	1-A	1a, b	Moringuidae
H. caerulescens	FMNH 141149	1	N. Borneo	670	2	1a, b	Gobioididae
	JRH 6561	1	Straits of Malacca	675	1-B	1a, b	Trypauchenidae
	JRH 6558	1	Straits of Malacca	545	1-B	1a, b	Gobioididae

[7]

2. Bullet-shaped fish, *e.g.*, Mullidae; 3. Vertically or laterally oversized fish, *e.g.*, Scorpaenidae or Ariidae; 4. Forms other than fish, *e.g.*, birds' eggs, fish eggs, and prawns.

The general habitats of the prey items were determined in order to provide information on where snakes feed. The habitats were classified as follows: 1. Neritic zone[1]: (*a*) on or near bottom; (*b*) rock dweller; (c) reef dweller; (*d*) pelagic; 2. Oceanic zone: (*a*) pelagic. The bulk of the information used in the identification of prey items and the determination of prey habitats was derived from five sources: Berg and Edwards (1947); Böhlke (1956); Greenwood, *et al.* (1966); Inger (1957); and Weber and de Beaufort (1911-62).

In the process of carrying out a taxonomic study on the Hydrophiidae, data on more than 150 characters were collected from 546 preserved snakes and 134 skull preparations (Voris, 1969). Among these characters, several were particularly relevant to feeding habits, namely girth and fang length. Body circumference measurements were made to the nearest millimeter with a flexible metal tape modified into a lasso-like adjustable loop. These measurements were first made on males and females of all sizes. However, the intra-specific range of females exceeded all intra-generic variation of the males because of the gravid females. Also, the inclusion of recently fed snakes and juveniles in the sample increased variation tremendously. In view of these sources of variation, comparisons were limited to adult males shown to have empty stomachs through dissection or X-ray. Even for males however, variation due to preservation and state of nutrition somewhat limited the use of body circumference measurements.

Measurements of fang length were made with an ocular micrometer in arbitrary units and converted to millimeters (one unit equaling 0.084 mm). Here again sample sizes were not large and because the exact size or sex of the snakes from which the skulls were taken could not be known in many cases, it is impossible to eliminate variation due to these factors. However, total skull length measurements from skulls prepared from measured snakes were used to eliminate from considerations those skulls that obviously came from juvenile snakes.

Results

The results of the stomach contents analysis are presented in Table 1. Data from specimens examined and from the literature have been integrated to allow a species by species account.

The data on prey form and habitat which are presented for individual specimens in Table 1 are summarized for each species in Table 2. For purposes of discussion each species was placed in one of several groups on the basis of two aspects of overall body form, namely length and girth. There are relatively short, thick snakes (*e.g.*, *Laticauda colubrina*); relatively long, thin snakes (*e.g.*, *Hydrophis cyanocinctus*): and relatively short, thin-necked and thick-bodied snakes (*e.g.*, *Hydrophis fasciatus*). The latter group are the so-called 'microcephalic' species. Fig. 1 graphically illustrates the relationship of girth and snout-vent length for the

[1] The categories 1b and 1c are indistinguishable in the context of much of the data available here. They have been retained for instances in which real differences can be shown. Where the distinction could not be made, both categories have been designated.

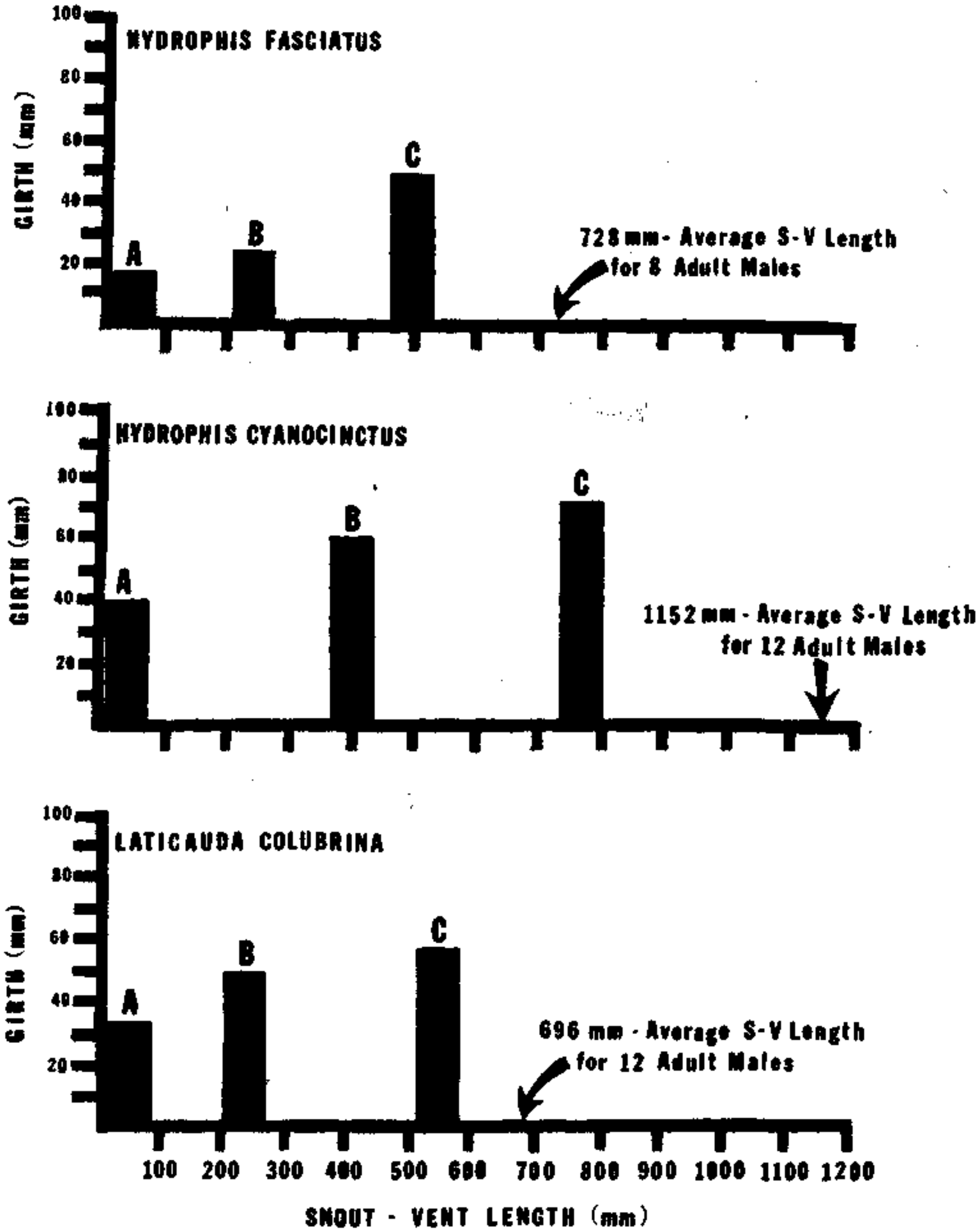

Fig. 1. Graphs showing the relationship of girth and snout-vent length in three species of sea Snakes.

TABLE 2. *Summary of species data on prey characteristics, snake neck girth and snake fang length*

Species	No. of Stomach Contents	Prey Form[1]					Prey Habitat[1]					Mean Neck Girth of Adult Males (mm)		Mean Fang Length (mm)	
		1A	1B	2	3	4	1a	1b	1c	1d	2a	N	$\bar{X}$	N	$\bar{X}$
Laticaudinae with Typical Snake Head, Neck and Body Proportions															
Laticauda															
L. laticaudata	1	..	..	..	..	..	..	..	..	..	..	..	..	3	2.3
L. colubrina	4	2	1	..	1	..	X	X	X	..	..	13	35	5	2.5
L. schistorhynchus	3	..	..	1	2	..	X	X	X	..	..	6	43	1	2.2
Summary[2]		1	1	1	2	0	2	2	2	0	0	19	39	6	2.3
Aipysurus															
A. eydouxi	3	..	..	..	..	2	X	..	X	..	..	3	35	1	1.0
A. fuscus	3	..	..	1	..	1	X	..	X	..	..	4	41	1	1.5
A. laevis	1	..	..	..	1	..	..	..	..	..	..	2	90	..	..
A. duboisii	1	..	..	1	..	..	..	..	..	..	..	4	38	1	1.1
A. foliosquama	10	1	..	6	..	..	..	..	X	..	..	5	35	..	.
A. apraefrontalis	3	2	..	..	..	..	X	..	X	..	..	1	45	..	0.8
Summary		2	0	3	1	2	3	0	4	0	0	19	47	4	1.1
Emydocephalus															
E. annulatus	4	..	..	..	..	4	X	..	X	..	..	2	30	1	0.6
E. ijimae	2	..	..	..	..	2	X	..	X	..	..	1	32	2	0.9
Summary		0	0	0	0	2	2	0	2	0	0	3	31	3	0.75

						Hydrophiinae with Typical Snake Head, Neck and Body Proportions									
Hydrophis															
H. nigrocinctus	1	1	..	..	..	..	X	X	X	..	..	2	34	..	..
H. kingi	1	1	..	..	..	..	X	X	X	..	..	..	..	..	1.7
H. spiralis	2	2	..	..	..	..	X	X	X	..	..	4	37	..	..
H. melanosoma	2	2	..	..	..	..	X	X	X	..	..	4	32	1	2.1
H. belcheri	3	2	..	1	..	..	X	X	X	..	..	1	33	3	2.4
H. cyanocinctus	4	2	1	1	..	..	X	X	X	..	..	12	40	9	2.0
H. obscurus	1	..	..	..	1	..	..	..	..	X	X	..	..	..	..
H. ornatus	1	..	..	..	..	..	X	X	X	..	..	6	40	2	1.8
H. inornatus	2	..	1	1	..	..	X	X	X	X	..	2	37	2	1.9
H. major	1	..	1	..	..	..	X	X	X	..	..	1	52	1	2.5
Summary		6	3	3	1	0	9	9	9	2	1	32	38	19	2.1
Other Hydrophiinae															
T. viperina	5	1	..	3	..	..	X	X	X	..	..	5	32	1	1.9
A. peronii	1	..	1	..	..	..	X	X	X	..	..	3	37	1	1.5
T. anomalus	1	1	..	..	..	..	X	X	X	..	..	5	40	1	2.0
K. annandalei	1	..	..	..	1	..	..	..	..	..	X	2	36	1	2.1
P. platurus	39	..	1	35	3	..	..	..	..	X	X	11	43	12	2.0
A. stokesii	1	..	..	..	1	..	..	..	..	..	..	3	101	2	3.6
E. schistosa	6	..	..	2	..	1	..	..	..	X	..	14	44	9	2.6
L. hardwickii	13	..	3	2	6	..	X	X	X	X	X	13	57	11	2.5
L. curtus	3	..	..	2	1	..	X	X	X	X	X	4	46	1	3.8
Summary		1	3	5	5	1	5	5	5	4	4	60	48	39	2.4
						Hydrophiinae with Small Head and Neck									
Microcephalophis, Kerilia, and *Hydrophis*															
M. gracilis	3	3	..	..	..	..	X	X	X	..	..	7	20	1	1.3
K. jerdoni	2	2	..	..	..	..	X	X	X	..	..	1	28	1	1.3
H. melanocephalus	2	2	..	..	..	..	X	X	X	..	..	2	29	1	1.0
H. torquatus	1	..	..	1	..	..	X	X	X	..	..	8	20	7	1.5
H. lapemoides	3	2	..	1	..	..	X	X	X	..	..	6	29	3	1.7
H. caerulescens	3	..	2	1	..	..	X	X	X	..	..	7	23	5	1.3
H. fasciatus	6	6	..	..	..	..	X	X	X	..	..	5	17	5	1.2
H. brookii	10	9	..	..	..	..	X	X	X	..	..	7	18	5	1.0
Summary		6	1	3	0	0	8	8	8	0	0	43	23	28	1.3

[1] For the key to Prey Form and Prey Habitat categories, see footnotes 2 and 3 of Table 1.
[2] The summary gives the total number of species with each Prey Form and Prey Habitat, the total number of specimens examined, and the averages for neck girth and fang length.

abovementioned species and Plate I shows a typical microcephalic species. A third aspect of general body form, cross-sectional shape (flattened, oval, round), varies considerably among the sea snakes, although all are round at the neck. *Laticauda* are generally round or slightly oval from vent to neck. Other species are more or less oval over the posterior two-thirds of the body although they differ in both the degree and location of the vertical body compression. When considering these aspects of morphology in relation to the feeding habits of snakes, it is likely that the girth at the neck is the most significant measurement to be considered since it is invariably the narrowest region of the sea snake body. For this reason I have included these data in Table 2.

Skull morphology is, of course, another important aspect of morphology related to feeding. In the sea snakes, skull morphology is highly variable, but an almost continuous series of forms exist. At one extreme is the cobra-like skull of *Aipysurus laevis* and all species of *Laticauda* (Plate II A), while at the other exist the consolidated 'fossorial-like' skulls of *Emydocephalus* and *Hydrophis caerulescens* (Plate II B). Because of the high degree of variation and the complex nature of snake skulls, it is impossible to determine the functional significance of the various forms without a detailed study of their mechanics. However, a few features are of obvious importance in feeding, and fang length which has been included in Table 2, is one such feature.

Discussion

Several important points emerge from an analysis of the data presented in Table 2. First, although the *Laticauda* and *Aipysurus* feed on a variety of forms, the habitat of their prey is rather narrowly restricted to bottom dwelling forms associated with rock and coral outcroppings. Additional locality data on these species further support the data given in Table 2 on *Aipysurus*, which indicate it to be a coral reef form (Smith, 1926). Additional data on *Laticauda* confirm that it is associated with coral outcroppings as well as rocky shores (Saint Girons, 1964).

All the Laticaudinae are rather short, stout snakes of similar proportions, although *A. laevis* is distinctive due to its overall larger size. Fang length in the *Laticauda* is long ($\bar{X}$=2.3 mm) compared to that found in the *Aipysurus* ($\bar{X}$=1.1 mm) and *Emydocephalus* ($\bar{X}$=0.75 mm). The dentition of the latter genus is highly specialized in terms of the reduction of both tooth size and number. The diet and to some extent the habitat of *Emydocephalus*, is correspondingly restricted. The data that are available indicate that they are obligate feeders on demersal fish eggs (Voris, 1966) and are a part of the coral reef community. Two species of *Aipysurus* (*A. eydouxi* and *A. fuscus*) also feed on fish eggs and show some of the same adaptations, although they are developed to a lesser degree.

Among the Hydrophiinae with typical-sized head and neck, the *Hydrophis* show a tendency to prey on eels and eel-like forms. *Thalassophina viperina*, *Acalypthophis peronii*, and *Thalassophis anomalous* are very similar to these *Hydrophis* in diet and morphology. The remaining genera within this group of Hydrophiinae, show a much more diverse diet in terms of both prey forms and prey habitat. They eat relatively fewer eels and evidently feed either on or near the surface, as does, for example, *Pelamis platurus*, or throughout the water column as may *Lapemis*. Neck girth and fang length do not vary sharply with this difference in feeding habits in these genera, although the above average girth of *Lapemis* must be important in

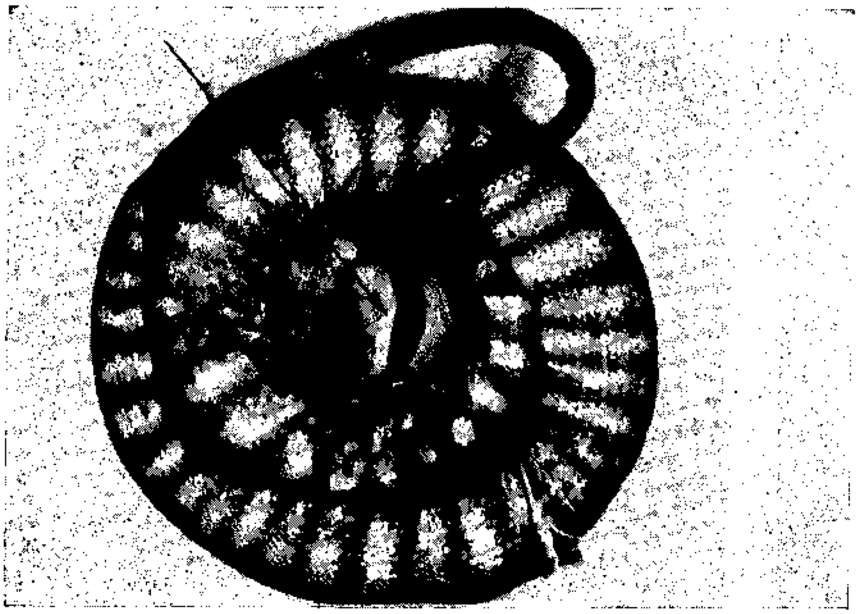

PLATE I. *Hydrophis parviceps* (ZMC R66182) illustrating the typical body form of the microcephalic species. The arrow indicates the head of the specimen.

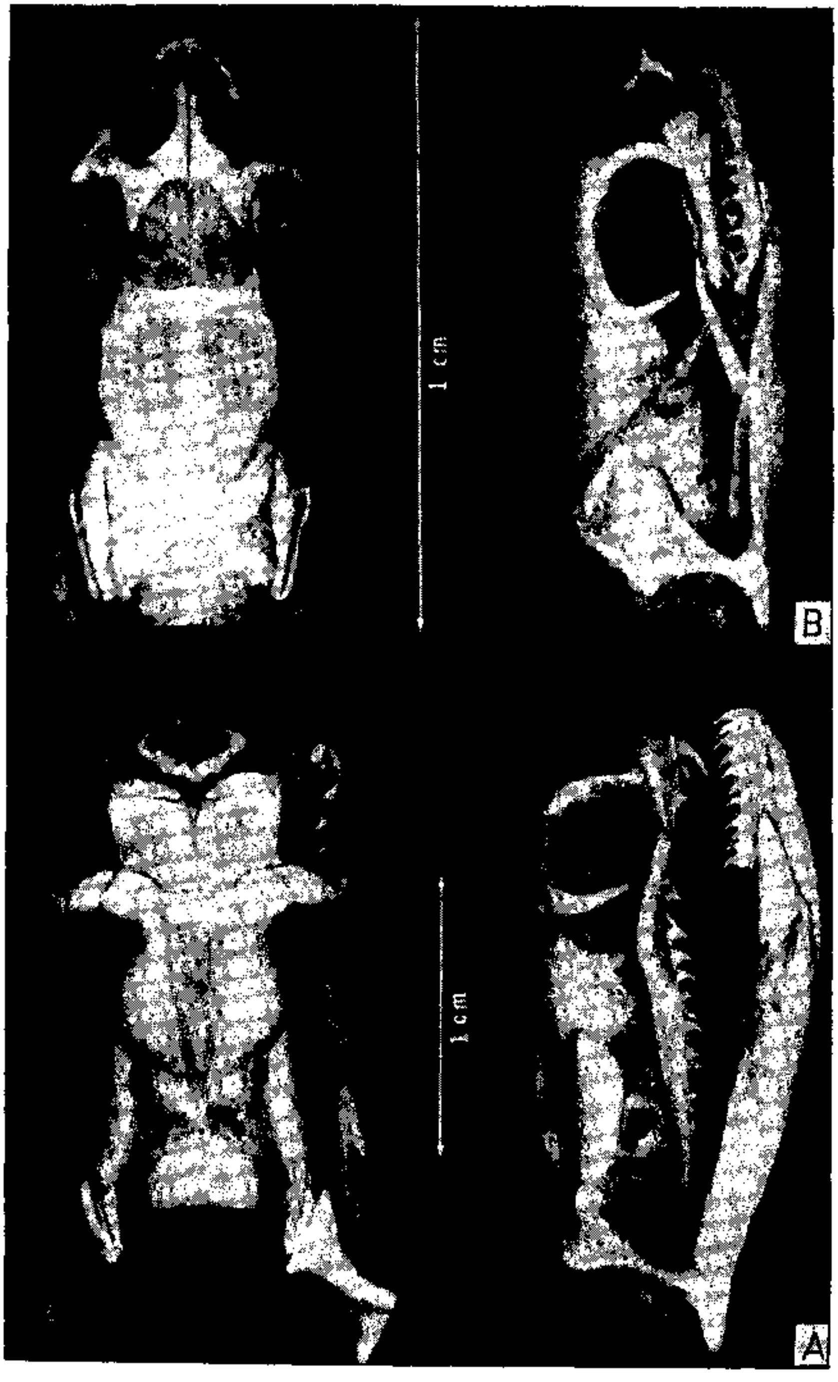

PLATE II. A. Dorsal and lateral views of the skull of *Laticauda laticaudata* (AMNH 66580) and B. Dorsal and lateral views of the skull of *Hydrophis caerulescens* (MCZ 2358).

the consumption of odd, irregularly-shaped food items (*e.g.*, certain Carangidae, see Table 1).

The microcephalic Hydrophiinae show an even stronger tendency to prey upon eels than do their typical-sized head and neck counterparts discussed above. The stomach contents of these snakes consisted almost entirely of eels, and 24 out of 29 of the eels were of the non-operculoid (soft-skinned) type. The strong restriction of the diet to eels and eel-like forms in general is evidently a prerequisite due to the tiny head and neck of these Hydrophiinae (average neck girth less than 30 mm), while their strong preference for the non-operculoid forms is probably related to their relatively short fangs ($\bar{X}$=1.3 mm). This interpretation complements the observations of Mahadevan and Nayar (1965)[1] which strongly suggest that these snakes locate and capture eels by reaching their tiny heads and necks into small nooks and crevices in rock and coral formations.

It is clear at this point that we have only begun to understand sea snake ecology. More data of the type presented here, as well as direct observations of the natural history of sea snakes are necessary to complete the picture. It is hoped that the information discussed in this paper will foster further interest in the rôle of sea snakes in ocean communities and encourage research in this area.

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[1] Although the authors were unable to capture and identify the snakes, their published photograph is of sufficient quality to assign the snake to this group.

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