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Diversity of Marine Snakes on Trawling Grounds in the Straits of Malacca and the South China Sea

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ABSTRACT.– Prior to World War II, traditional hand-operated fishing methods prevailed throughout Southeast Asia. However, by 1950, mechanized diesel-powered trawlers were being introduced and the modern boom-and-bust of fisheries was set into motion. Besides targeted fish, squid, and prawns, otter trawls on the bottom brought up a vast diversity of demersal by-catch including marine snakes. This paper reports on the diversity of the marine snake by-catch obtained from otter trawlers operating at two locations in the Straits of Malacca (Sungai Buloh and Parit Botak) and one location on the eastern coast of the Malay Peninsula (Endau) in the mid-1970s. At Sungai Buloh 11 species of snakes were observed and a single species, *Hydrophis curtus*, strongly dominated the assemblage, comprising 82% of the by-catch. Eleven species were also observed in the by-catch from Parit Botak but there, three species (*Hydrophis fasciatus*, *H. curtus*, and *Aipysurus eydouxii*) shared dominance with each making up more than 22% of the assemblage. At Endau, 13 species appeared in the by-catch and two species (*H. curtus* and *Hydrophis viperinus*) dominated, comprising 33% and 32% of the catch respectively. Besides differences between locations, some small differences in species diversity were detected between collection periods at Sungai Buloh. In addition, a review is undertaken of published trawl surveys of marine snakes in Southeast Asia in the context of the steady depletion of fisheries in the region that took place in the second half of the twentieth century. This review emphasizes that marine snake species diversity needs to be understood on a relatively fine spatial scale and in the context of the health of the fishery as a whole.

KEY WORDS: Elapidae, Hydrophiinae, Acrochordidae, sea snake, otter trawl, demersal by-catch, species richness, species evenness, Southeast Asian commercial fisheries

INTRODUCTION

The first major survey of marine snakes was published by Malcolm Smith in 1920. Smith reported on marine snakes collected from the coastal waters of the Gulf of Thailand and the Malay Peninsula between 1915 and 1918. Most of the sea snakes were obtained from local fishermen using a variety of traditional hand-operated fishing methods including stake nets and baskets placed in river mouths. Some also were obtained by hand nets and trawling along coasts. In all, 17 species were collected. The number of specimens collected per species ranged from two to 98, but the author notes that "A full list of all the specimens examined has not been given in every case," (Smith, 1920, p.4) thus making it impossible to know the relative abundance of species collected.

Two decades later, Bergman (1938, 1943) began to report on another large collection of marine snakes from coastal areas near Sourabaya (Surabaya, Java). Made by local fishermen between 1936 and 1942, this collection consisted of six identified species represented by 984 specimens, and four rare species represented by fewer than four snakes each that were disregarded in his report (Bergman, 1943). Although the purpose of the collection was

descriptive anatomical studies (e.g. Bergman, 1949; 1954; 1956) it represents the first major collection of marine snakes in which all specimens from a single coastal area were collected, identified, and counted, thus providing nearly complete data on species richness and relative abundance. Unfortunately, the methods of collection were not defined but most likely traditional fishing gear accounted for most of the snake catch.

By 1950, fishing methods in Southeast Asia were becoming mechanized and the subsequent systematic depletion of fisheries was underway (Morgan and Staples, 2006). The focus of this paper is on documented collections of marine snakes obtained by diesel-powered trawlers operating in Southeast Asia following World War II. In particular, new results on species richness and relative abundance are presented for two locations in the Straits of Malacca, and one location on the eastern coast of the Malay Peninsula, and then these findings are compared and contrasted to other comparable studies conducted in the region. Finally, all the studies of the by-catch of sea snakes from trawls carried out in Southeast Asia are placed into the context of the simultaneous overexploitation of the fisheries, largely resulting from the expansion of mechanized diesel-powered bottom trawlers.

MATERIALS AND METHODS

Trawlers and trawling grounds.– In November 1971 and between 18 December 1974 and 27 August 1975, 1,575 marine snakes were collected from three sites along the coast of the Malay Peninsula (Fig. 1). Two localities were sampled in the Straits of Malacca (Sungai Buloh, 3°14'45"N, 101°18'10"E; Parit Botak, 1°41'45"N, l03°6'15"E) and one was sampled in the South China Sea (Endau, 1°41'45"N, l03°6'15"E). Sungai Buloh was sampled in November 1971, December 1974, and between January and August 1975. Parit Botak was sampled between January and April 1975, while Endau was sampled only once in April 1975.

Snakes were obtained as by-catch from small diesel-powered otter board trawlers (~12–16m lg) at Sungai Buloh, Parit Botak and Endau (See Appendix). The trawlers normally remained at sea for 12–24 hours and ranged no more than 20–40 km from port. Generally they were limited to 3 to 4 hauls of 2 to 3 hours each before returning to port. Trawlers usually would leave port on high tides in either the early morning or late afternoon. Throughout the year trawling was limited to fair weather, taking special care to avoid high winds and waves. The number of trawlers contracted to save marine snake by-catch on a given day varied from 1 to 6.

Environmental monitoring.– On some days the author accompanied one of the boats to the trawling grounds to collect environmental data. Data were collected at the beginning and end of each haul, and the speeds and depths of trawls were monitored at regular intervals. Salinity was measured using a LaMotte salinity kit (LaMotte Co., Chestertown, MD, USA) based on the titration of silver nitrate (Boyle's method). Turbidity was measured using both a Secchi disk (plain white circular disk 50.8 cm diameter) providing Secchi depths (m) and the Jackson turbidity method (LaMotte turbidity kit, LaMotte Co., Chestertown, MD, USA) providing readings in Jackson Turbidity Units (JTUs). The speed of the trawlers was measured using a mechanical propeller flowmeter with a standard rotor

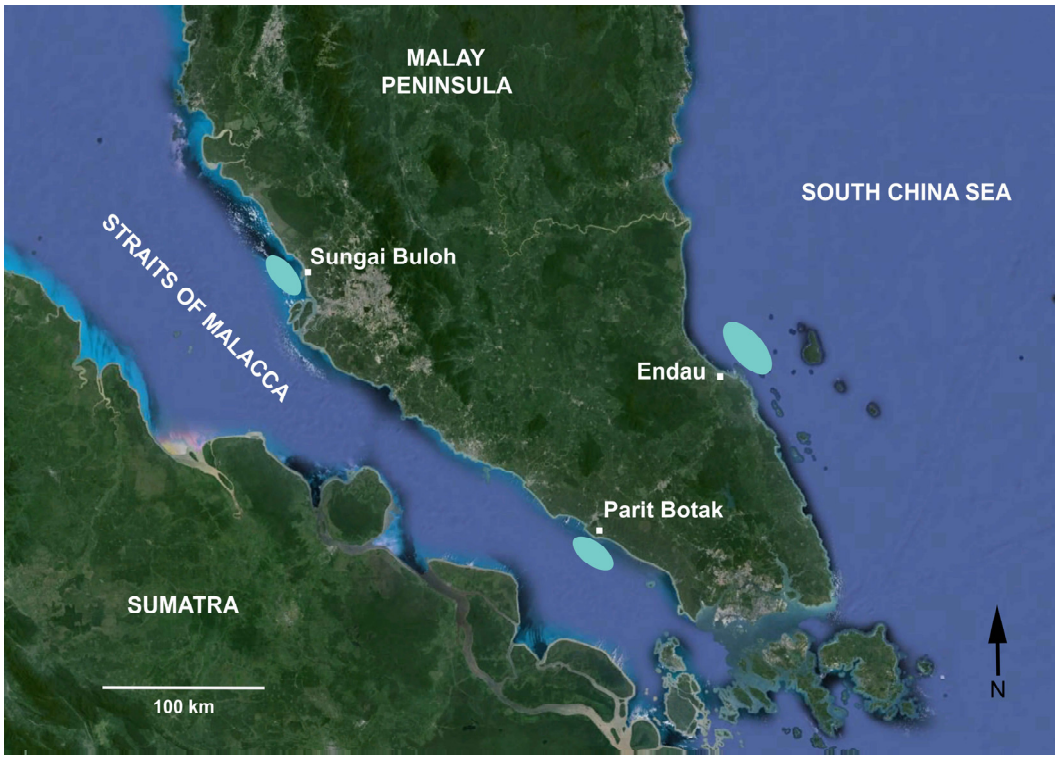

FIGURE 1. Map showing the location of the three trawling grounds at Sungai Buloh, Parit Botak, and Endau

(General Oceanics, Miami, FL, USA; Threshold approx. 10 cm/s: Range 10 cm/s – 790 cm/s). Depth was measured using a portable sonar depth finder, Model LFP-300 (Lowrance Co., USA). Water-temperatures were recorded at a depth of 1 m using a mercury thermometer. Substrate samples were collected using a galvanized steel cylinder (15.2 cm diam, 45.7 cm lg) with the top 30.5 cm perforated by 0.31 cm holes. Retrieved samples were processed in sequence through coarse mesh (~8 squares per 2.54 cm), medium mesh (~18 squares per 2.54 cm), and fine mesh (~40 squares per 2.54 cm) sieves. Extensive hydrographic surveys both in the Straits of Malacca (Hydrographer of the Navy, 1958; Ministry of Agriculture and Fisheries, 1972; Chong, 1974) and along the east coast of the Malay Peninsula (Ministry of Agriculture, 1967) provided a robust context for the measurements associated with the trawl days of this study.

Processing the by-catch and identification of snakes.– After snakes were separated from the haul, living snakes were placed in Styrofoam boxes and kept in the shade while drowned snakes were placed in Styrofoam boxes with crushed ice for the duration of the trip. All snakes were brought back to the laboratory, where living ones were euthanized with an injection of sodium pentobarbital. Prior to preservation each relaxed snake was tagged and measured (snout-vent and tail length, and girth at the neck and mid-body). Stomach contents were removed, preserved in 12% formalin and later transferred to 70% ethanol for

TABLE 1. Numbers of marine snakes collected as by-catch from trawlers operating on three Malaysian trawling grounds in 1971 and 1974-1975. The species names in the first column are the names applied at the time of the field work. The names used throughout this paper appear in column two and largely follow Figueroa et al., 2016.

		Sungai Buloh		Parit Botak		Endau	
Name (1975)	**Name (2016)**	**Number**	**%**	**Number**	**%**	**Number**	**%**
Aipysurus eydouxi	*A. eydouxii**	0	0	120	22.7	16	8.2
Acrochordus granulatus	*A. granulatus**	59	6.9	21	4.0	0	0.0
Hydrophis brookii	*H. brookii*	2	0.2	1	0.2	0	0.0
Hydrophis caerulescens	*H. caerulescens*	48	5.6	51	9.7	0	0.0
Lapemis curtus	*H. curtus*	702	82.4	147	27.8	65	33.3
Hydrophis cyanocinctus	*H. cyanocinctus*	11	1.3	13	2.5	9	4.6
Hydrophis fasciatus	*H. fasciatus*	22	2.6	164	31.1	5	2.6
Microcephalophis gracilis	*H. gracilis*	1	0.1	1	0.2	3	1.5
Hydrophis inornatus	*H. inornatus*	0	0.0	0	0.0	2	1.0
Hydrophis klossi	*H. klossi*	0	0.0	0	0.0	1	0.5
Hydrophis ornatus	*H. ornatus*	3	0.4	1	0.2	11	5.6
Acalyptophis peronii	*H. peronii*	0	0.0	0	0.0	13	6.7
Enhydrina schistosa	*H. schistosus*	2	0.2	7	1.3	5	2.6
Hydrophis spiralis	*H. spiralis*	1	0.1	0	0.0	0	0.0
Hydrophis torquatus	*H. torquatus*	0	0.0	2	0.4	0	0.0
Thalassophina viperina	*H. viperinus*	0	0.0	0	0.0	63	32.3
H. sp.	*H.* sp.	1	0.1	0	0.0	1	0.5
H. sp.	*H.* sp.	0	0.0	0	0.0	1	0.5
	Total	**852**		**528**		**195**	

* The generic names from 1975 remain unchanged.

permanent storage. Other particulars on the data collection can be found in Voris and Glodek (1980), Lemen and Voris (1981) and Voris and Voris (1983).

The species collected represent two families of marine snakes, Acrochordidae (*Acrochordus granulatus*) and Elapidae (Hydrophiinae, true sea snakes). Identifications were based on the key in Smith (1926), data and descriptions in Smith (1920; 1926), and confirmed by comparisons to preserved specimens collected by Malcolm Smith and deposited at the Field Museum of Natural History (FMNH) and the British Museum of Natural History (BMNH). The nomenclature has been updated where appropriate to be largely consistent with Figueroa et al. (2016). Table 1 provides the list of species collected from the three trawling grounds. The first column gives the names applied in 1975 which largely followed Smith (1926) and the second column gives the names used in the present publication that largely follow Figueroa et al. (2016).

Diversity measures and statistics.– Several estimates of species diversity were applied in the analysis of the snake assemblages sampled from the three trawling grounds. All the measures assess information both on numerical species richness and species evenness, and each has been used widely over the past half century. Simpson's index, D (Simpson, 1949; Magurran, 1988) and the

complement of Simpson's D, the probability of interspecific encounter, PIE (Hurlbert, 1971), were used for some comparisons. The Shannon index, H' (Shannon and Weaver, 1963; Magurran, 1988), the Brillouin index, HB (Brillouin, 1960; Lloyd, 1968; Pielou, 1966; Magurran, 1988), and the related evenness index, E (Pielou, 1966; Hurlbert, 1971; Magurran, 1988) were applied in other analyses.

Several of the above measures of diversity have statistics associated with them and those may be found in Magurran (1988) or the other citations provided for the measures. In addition, the non-parametric Chi-square test (Sokal and Rohlf, 1995) was used to compare observed species abundances with those that would be expected on the basis of chance alone.

RESULTS

Environmental conditions.– Trawler captains normally did not attempt to trawl in an exact location. The environmental data within each trawling ground indicate considerable variation in many physical conditions within individual three-hour hauls (continuous trawl pull), between hauls, and between days. For example, during one three-hour haul, a trawler traveled in one general direction for a distance of about 14 km. The course of the track was subjectively determined by the captain and intersected depths ranging from 6 to 18 m. Substrate varied from rather homogeneous fine sand and mud to particulate samples containing 5 to 10 percent broken shells and coarse sand. Generally, measurements of Secchi disk turbidity ranged from 0.8 to 1.6 meters. Salinity (28–31 p.p.t.) and surface water temperature (28–30°C) were fairly constant within a trawling area on a given day. Local weather conditions were usually fair but afternoon squalls were not uncommon. Because of the duration of hauls and the distances covered over three hours, snake by-catch could not be attributed to any specific condition or feature observed within the trawling grounds.

Published data document seasonal shifts in salinity, temperature, precipitation, river discharge, and plankton productivity in the Straits of Malacca. For example, at Sungai Buloh, salinity varied from 29.0 p.p.t. in November to 30.5 p.p.t. in June (Soeriaatmadja, 1956). Sea surface temperature ranged from 29.5°C in September-March to 30.5°C in April-June (Hydrographer of the Navy, 1958). Also, there were seasonal variations in rainfall from about 10 cm of rain in June and July to about 23 cm in November and December (Dale, 1959). The river discharge rates on the Selangor River near Sungai Buloh vary seasonally with lows in June and July of 0.022 $m^3/sec/km^2$ to highs in November of about 0.092 $m^3/sec/km^2$ (taken from five-year averages given by the Ministry of Agriculture and Fisheries, 1972).

Trawling grounds: Size and Patchiness.– Table 1 provides the numbers and relative abundance (%) of marine snakes collected as by-catch from otter trawls operating on the three trawling grounds: Sungai Buloh, Parit Botak, and Endau (Fig. 1). The trawling grounds were large in comparison to the area fished on a given day. For example, the trawling ground at Sungai Buloh was roughly oval in shape and was normally set off from the coast by a 3 km no-trawl zone. The oval extended about 20 km parallel to the coast with a width of about 6 km. Thus, the area was approximately 377 sq km. A single trawler traveling at 3 km/h with a net width at the

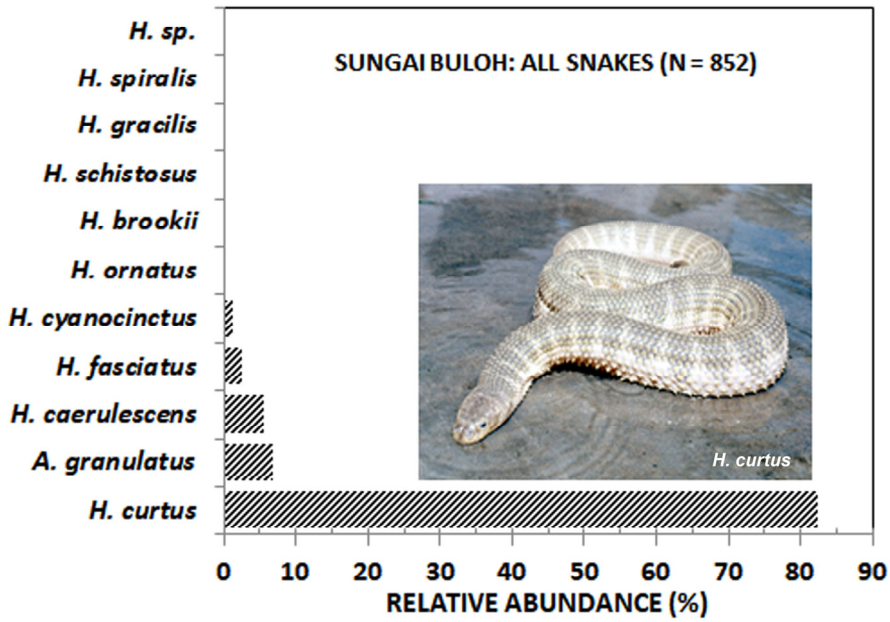

FIGURE 2. Bar graph showing the species composition and relative abundance for 852 marine snakes collected as by-catch from otter trawlers operating on the trawling grounds at Sungai Buloh (See Fig. 1). The snakes were collected in 1971 and 1974-75 and represented 10 species of true sea snake (Elapidae) and one species of file snake (Acrochordidae). The assemblage is strongly dominated by *Hydrophis curtus* (see inset in figure, FMNH 202179) that made up 82% of the snake by-catch. The three most common species, *Hydrophis curtus*, *Acrochordus granulatus*, and *Hydrophis caerulescens,* made up 95% of the sample.

mouth of 18 meters would cover only a tiny proportion of the trawling ground in one pull of 3 hours (roughly only 0.16 sq km). The catch of fish and prawns along with the snake by-catch varied greatly, documenting patchy distributions of fish, prawns, and snakes over the grounds. For example, 18 individual three-hour trawl pulls at Sungai Buloh taken over three months resulted in snake by-catches that ranged between 0 and 27 snakes while both the median and modal number of snakes per trawl pull was just 2 snakes.

Sungai Buloh: Species richness and evenness.– The 852 marine snakes caught as by-catch on the Sungai Buloh trawl ground were distributed among 11 species in two families of snakes, Acrochordidae (*Acrochordus granulatus*), and Elapidae (Hydrophiinae, true sea snakes). This assemblage is strongly dominated by the short sea snake, *Hydrophis curtus* (Fig. 2). The overall diversity of the assemblage as measured by Simpson's index (D), the probability of interspecific encounter (PIE), the Shannon index H', Evenness (E), and the Brillouin index (HB) were as follows: D = 0.688, PIE = 0.313, H' = 0.729, E = 0.304, and HB = 0.976.

Sungai Buloh: Species diversity accumulation curves.– To examine species diversity (species richness and evenness) over time, the Brillouin diversity index (HB) was calculated for all snakes (adults and juveniles) and adult snakes only captured in December 1974 and in 1975 (Fig. 3). The final HB values for all snakes captured (adults and juveniles, n = 768) and adult

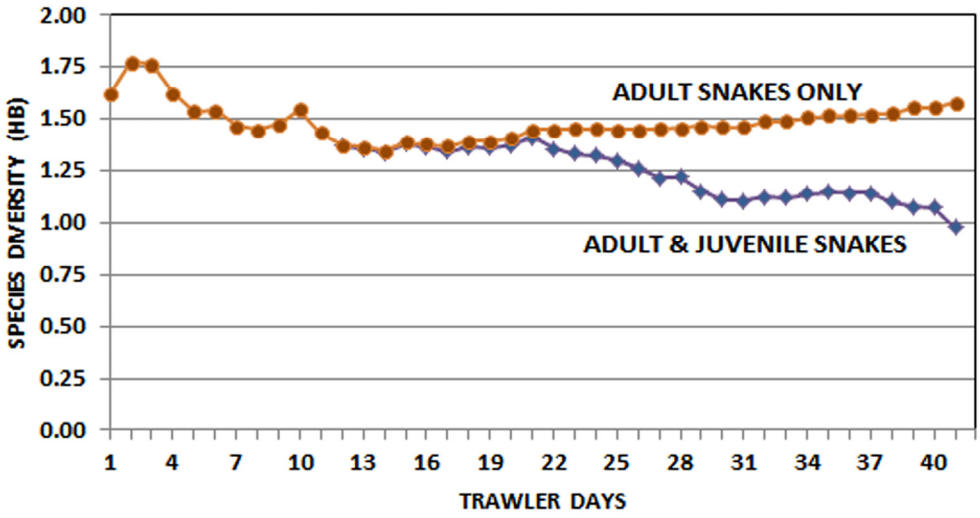

FIGURE 3. A comparison of plots of the values of the Brillouin diversity index (HB) for all snakes (adults and juveniles) and for adult snakes only caught on the Sungai Buloh trawling grounds in 1974-1975. A trawler day is the catch from one boat during a one-day trip from port. The values of the HB diversity at the end of the curves (far right) were 1.579 for adult snakes only and 0.976 for all snakes (adults plus juveniles).

snakes only (n = 363) were 0.976 and 1.579 respectively. The plots in Figure 3 document three phenomena: 1) The diversity values for adult snakes attained the highest levels at the very beginning of the sampling in the first few trawler days; 2) The two curves are identical until trawl day 12 (23 February 1975) when the first neonate appeared in a trawl pull; 3) The curve based on adult snakes only remains remarkably flat through 41 trawler days while the capture of numerous neonate and juvenile snakes (mainly *H. curtus*) in March, April, and August steadily reduced species diversity.

Sungai Buloh: Diversity through time.– Table 2 gives the total number of marine snakes caught and relative abundance for species caught in November 1971, and between December 1974 and August 1975. To determine if the assemblage of snakes in the by-catch varied between time periods, the catches from late December and early January (combined) were compared to catches from February and from March. Collections from April and August were not compared due to the presence of many neonates and juveniles. The single most noticeable difference among the samples is the high proportion (15.9 %) of *A. granulatus* in the trawls made in December and early January. A Chi-square test comparing the distributions of the three sampling periods revealed that the observed distributions differed significantly from the expected ($\chi^2 = 17.57$, df = 8, $p < 0.05$). A pairwise Chi-square test comparing the distributions from December-January with February also proved significantly different ($\chi^2 = 13.99$, df = 4, $p < 0.01$) while the comparisons of December-January with March, and February with March showed no significant differences ($\chi^2 = 4.50$, df = 4, $p > 0.05$; $\chi^2 = 9.10$, df = 4, $p > 0.05$). The PIE value of 0.055 (Table 2) also shows that the

TABLE 2. Number of marine snakes collected and their relative abundance (%) for 11 species collected on the trawling grounds at Sungai Buloh during six fishing periods. Samples from November 1971 and from December 1974 to February 1975 included adults only while samples from March to August 1975 included neonates and juveniles (See Fig. 3). Comparisons of the monthly distributions using Chi-square tests were limited to the five most common species to avoid the numerous zero cells present in the last six rows.

	November 1971		**Dec-Jan 1974-75**		**February 1975**		**March 1975**		**April 1975**		**August 1975**	
	N	**%**	**N**	**%**	**N**	**%**	**N**	**%**	**N**	**%**	**N**	**%**
H. curtus	67	79.8	96	63.6	73	79.3	52	70.3	191	93.6	223	90.3
A. granulatus	1	1.2	24	15.9	8	8.7	4	5.4	5	2.5	17	6.9
H. caerulescens	1	1.2	23	15.2	4	4.3	11	14.9	6	2.9	3	1.2
H. fasciatus	9	10.7	3	2.0	6	6.5	3	4.1	0	0.0	1	0.4
H. cyanocinctus	3	3.6	4	2.6	1	1.1	2	2.7	1	0.5	0	0.0
H. ornatus	3	3.6	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
H. brookii	0	0.0	0	0.0	0	0.0	1	1.4	0	0.0	1	0.4
H. schistosus	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	2	0.8
H. gracilis	0	0.0	0	0.0	0	0.0	1	1.4	0	0.0	0	0.0
H. spiralis	0	0.0	0	0.0	0	0.0	0	0.0	1	0.5	0	0.0
H. sp.	0	0.0	1	0.7	0	0.0	0	0.0	0	0.0	0	0.0
Total	**84**		**151**		**92**		**74**		**204**		**247**	
PIE	**0.354**		**0.550**		**0.361**		**0.485**		**0.123**		**0.181**	
1 STD	**0.064**		**0.039**		**0.061**		**0.065**		**0.031**		**0.032**	

relatively large numbers of *A. granulatus* and *H. caerulescens* in the December – January sample contribute to a significantly more diverse sample.

Parit Botak: Species richness and evenness.– The by-catch of marine snakes from the Parit Botak trawling grounds (Fig. 1) included 528 snakes distributed among 11 species in two families, Acrochordidae (*Acrochordus granulatus*), and Elapidae (Hydrophiinae, true sea snakes). This assemblage was dominated by three species, *H. fasciatus*, *H. curtus, and Aipysurus eydouxii* (Fig. 4). Four other species made up from 2 to 9 percent of the total catch. The overall diversity of the assemblage as measured by Simpson's index (D), the probability of interspecific encounter (PIE), the Shannon index H', Evenness (E), and the Brillouin index (HB) were as follows: D = 0.237, PIE = 0.764, H' = 1.615, E = 0.674, and HB = 2.290.

Parit Botak: Species diversity accumulation curves.– Figure 5 shows two plots of the Brillouin diversity index accumulation over time. The main plot of diversity values for all snakes shows HB increasing sharply at first as species were added to the collection but then the curve levels off after just four or five trawler days. The second graph (inset in Fig. 5) shows two similar curves starting with trawler day 26 on March 9 when neonates first appeared in the catch. The neonates and juveniles (24 *H. curtus* and 1 *H. schistosus*) appeared across the catches in March and April and because of their modest numbers the HB accumulation curves of adults only and all

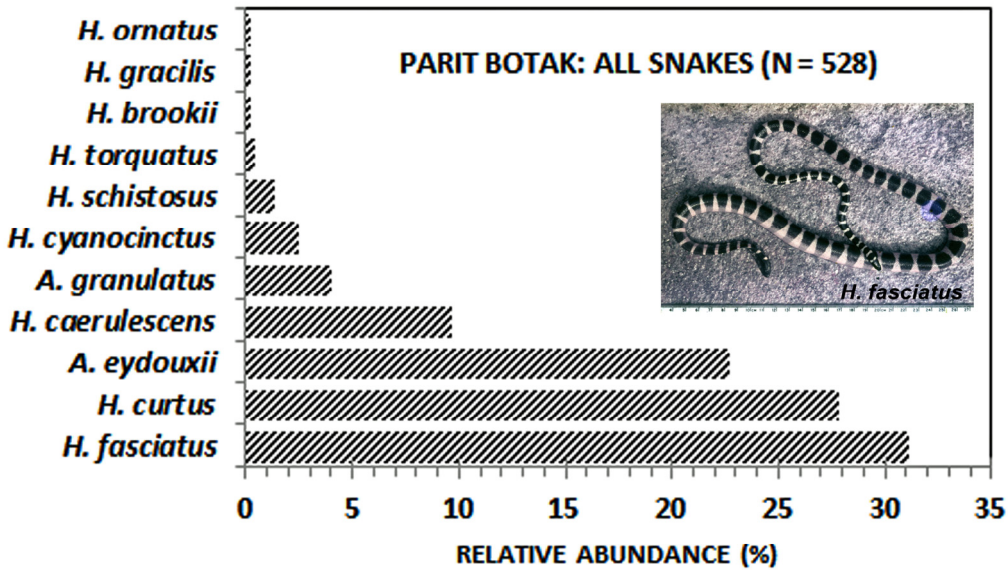

FIGURE 4. Bar graph showing the species composition and relative abundance for 528 marine snakes collected as by-catch from otter trawlers operating on the Parit Botak trawling grounds (See Fig. 1). The snakes were collected in 1975 and represented 10 species of true sea snake (Elapidae) and 1 species of file snake (Acrochordidae). The assemblage is dominated by *Hydrophis fasciatus* (see inset in figure, FMNH 198841), *Hydrophis curtus*, and *Aipysurus eydouxii* that combined made up 81.6% of the snake by-catch. Table 3 provides the monthly results as well as the totals.

snakes remained nearly identical. The final HB values for all snakes captured (adults and juveniles, n = 528) and adult snakes only (n = 503) were 2.280 and 2.290 respectively.

Parit Botak: Diversity through time.– The total number of sea snakes caught and relative abundances for species caught during three periods, January (plus February 1-4), March, and April are given in Table 3. The table shows that the samples from the three periods are remarkably similar in that the same four species are the most common species in each of the periods. The order of relative abundance among the four species is also nearly identical, with *H. fasciatus* most common in January and March, and *H. curtus* most common in April. Pairwise Chi-square tests were used to compare the distributions from the three sampling periods with each other. The comparisons included only the seven most common species in Table 3 to eliminate the numerous zero cells among the four least common species. None of the three tests (Jan. vs. Mar.; Jan. vs. Apr.; Mar. vs. Apr.) showed a significant difference at the $p < 0.05$ level.

Endau: Species richness and evenness.– The 195 marine snakes caught as by-catch on the Endau trawling grounds over just two days were distributed among 13 species of true sea snakes (Elapidae, Hydrophiinae). This assemblage was sharply dominated by two species, *H. curtus* and *H. viperinus* (Fig. 6). The overall diversity of the assemblage as measured by Simpson's

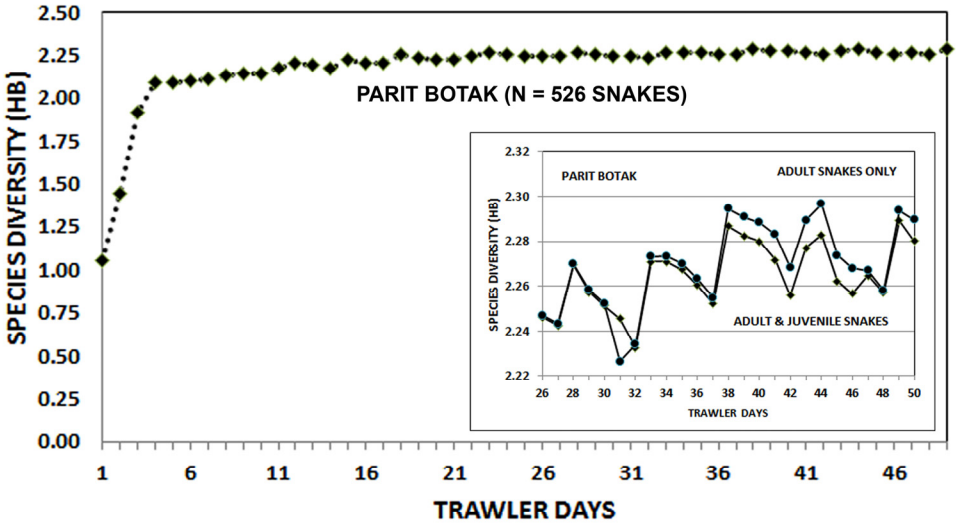

FIGURE 5. Plots of Brillouin diversity index (HB) values for all snakes (adults and juveniles) caught on the Parit Botak trawling grounds in 1975. A trawler day is the catch from one boat during a one-day trip from port. The HB diversity value at the end of the curve (far right) was 2.290 for all 528 snakes (adults plus juveniles). The inset graph shows that the effect of the 25 juveniles (24 *Hydrophis curtus* and 1 *Hydrophis schistosus*) appearing in the samples after day 26 on the species diversity was very small (< 0.01 HB units on any day). This was the case because the young were distributed across the last 25 of the 50 trawler days.

index (D), the probability of interspecific encounter (PIE), the Shannon index H', Evenness (E), and the Brillouin index (HB) were as follows: D = 0.234, PIE = 0.770, H' = 1.801, E = 0.702, and HB = 2.435.

DISCUSSION AND CONCLUSIONS

Comparisons within trawl grounds.– Overall the species composition on trawling grounds remained very similar over the time periods observed. At Sungai Buloh, the three most common species, *H. curtus*, *A. granulatus*, and *H. caerulescens* (Fig. 2), were observed in all six sampling periods (Table 2). At Parit Botak, the seven most common species (Fig. 4, Table 3) were present in all three sampling periods. Thus, the species composition over the sampling periods was remarkably constant within both trawling grounds in the Straits of Malacca.

The relative abundance of species over time at Sungai Buloh did show one significant difference between periods, namely, among adult snakes collected in Dec.-Jan. and February (Table 2). This could be due to any number of factors. For example, trawlers may have fished in unique areas in December and January resulting in their obtaining the larger numbers of *A. granulatus* and *H. caerulescens,* or these species may have moved into the trawling grounds in larger numbers. The relative abundance of species taken during three periods on the Parit Botak trawling grounds (Table 3) did not differ significantly from each other.

TABLE 3. The relative abundances of 11 species of marine snakes collected on the Parit Botak trawling grounds (Fig. 1) during three periods in 1975. Samples from January also included snakes from February 1 through 4, and all were adults. Samples from March and April included some neonates (see Fig. 5, inset). The asterix denotes the full species designations for *Aipysurus eydouxii* and *Acrochordus granulatus*. Pairwise Chi-square tests comparing the distributions of the top seven species over the three months showed no significant differences at $P < 0.05$.

	January		March		April	
	N	**%**	**N**	**%**	**N**	**%**
H. fasciatus	48	28.9	63	35.2	53	29.0
H. curtus	43	25.9	45	25.1	59	32.2
*A. eydouxii**	38	22.9	45	25.1	37	20.2
H. caerulescens	25	15.1	9	5.0	17	9.3
*A. granulatus**	7	4.2	5	2.8	9	4.9
H. cyanocinctus	3	1.8	7	3.9	3	1.6
H. schistosus	1	0.6	3	1.7	3	1.6
H. torquatus	0	0.0	1	0.6	1	0.5
H. brookii	0	0.0	0	0.0	1	0.5
H. gracilis	1	0.6	0	0.0	0	0.0
H. ornatus	0	0.0	1	0.6	0	0.0
Total	**166**		**179**		**183**	
PIE	**0.777**		**0.749**		**0.764**	
1 STD	**0.068**		**0.103**		**0.094**	

Comparisons between trawl grounds: species composition.– The species compositions of Sungai Buloh and Parit Botak with 11 species each and Endau with 13 species showed several major differences (Table 1). Sungai Buloh and Parit Botak shared 9 species with a Sørenson similarity index of 0.82 (Similarity = (2 x number of species in common)/ [(number of species in area A) + (number of species in area B)]. The notable differences were the absence of *A. eydouxii* and the dominance of *H. curtus* at Sungai Buloh. Sungai Buloh shared seven species with Endau with a similarity of 0.58. The main differences in composition were the absence of *A. eydouxii* and *H. viperinus* at Sungai Buloh, and the absence of *A. granulatus* and *H. caerulescens* at Endau. Parit Botak also shared 7 species with Endau with a similarity of 0.58 and the major differences were the same as those between Sungai Buloh and Endau.

The species occurrence data may reflect the geographic location. Sungai Buloh may be most representative of species in the Straits of Malacca while the presence of *A. eydouxii* at Parit Botak may reflect the area's proximity to the South China Sea. Endau reflects the South China Sea fauna but it is in close proximity both to the southern end of the Straits of Malacca and to the Gulf of Thailand to the north.

Comparisons between trawling grounds: relative abundances.– Species diversity and evenness on the three trawling grounds add perspective to the data on species

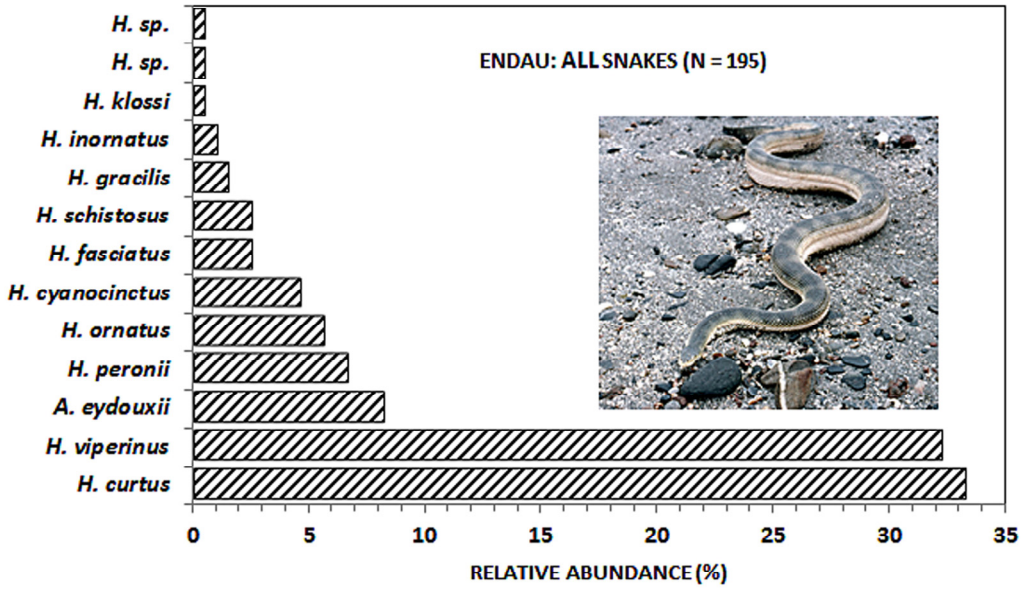

FIGURE 6. Bar graph showing the species composition and relative abundance for 195 marine snakes collected as by-catch from otter trawlers operating on the Endau trawling grounds (See Fig. 1). The snakes were collected in 1975 and represent 13 species of true sea snake (Elapidae). The numbers of individuals of each species are given in Table 1. The assemblage is dominated by *Hydrophis curtus* and *Hydrophis viperinus,* that when combined made up 65.6% of the snake by-catch. The catch was made over just two days. The inset shows *Hydrophis viperinus* (FMNH 202182) from the Endau trawling grounds.

composition. Sungai Buloh's trawl assemblage (Table 1) has low diversity and low evenness (PIE = 0.313, E = 0.304). This is largely due to the strong dominance of *H. curtus* (Fig. 2) which comprises 82% of the assemblage. The trawl samples from both Parit Botak (PIE = 0.764, E = 0.674) and Endau (PIE = 0.770, E = 0.702) have much higher diversity and evenness. This is largely due to the fact that at Parit Botak three species share dominance (Fig. 4), and at Endau two species share dominance (Fig 6). These results support the notion that each assemblage is distinct but our understanding of why they differ is limited. The fact that *A. eydouxii* is found only on the Endau trawling grounds is almost certainly due to the occurrence of patch coral reefs off the coast of Endau. This is a habitat with which *A. eydouxii* is associated in the South China Sea, whereas reefs are absent from the turbid waters found in the Straits of Malacca. On the other hand, why *H. viperinus* is absent from the Straits of Malacca is not understood.

Comparisons between trawling grounds: species diversity accumulation curves.– The Brillouin diversity index (HB) curves (Figs. 3 and 5) show that the early by-catch of marine snakes was highly representative of the catches that were made over the additional months of sampling. These curves document the robustness of the sampling method and suggest that otter trawls taking as few as 4 to 9 hauls of several hours each can provide a reliable

TABLE 4. Comparative data from ten published quantitative studies on the by-catch of marine snakes from trawlers operating in South Asian and Southeast Asian waters. The studies are grouped by general geographic area. The fifth column labeled DOMINANCE gives the relative abundance and name of the most common or dominant species in the sample. PIE is the abreviation for probability of interspecific encounter. For the calculations here on the Tu (1974, Table 2) data unidentified snakes were not included and the number of *H. ornatus* in the 1969 collection was corrected from 73 to 65.

Publication	Southeast Asian Location & Year	Species	Sea Snakes	DOMINANCE	PIE VALUE	1STD
Shuntov, 1966	Gulf of Thailand 1963	7	75	71% *P. platura*	0.4883	0.4219
Tu, 1974	Gulf of Thailand 1969	10	5138	84% *H. curtus*	0.2933	0.5013
Tu, 1974	Gulf of Thailand 1972	11	8304	84% *H. curtus*	0.2908	0.5039
Voris (this paper)	Endau 1975	13	195	33% *H. curtus*	0.7702	0.0188
Voris (this paper)	Sungai Buloh 1974-75	11	852	82% *H. curtus*	0.3127	0.0202
Voris (this paper)	Parit Botak 1975	11	528	31% *H. fasciatus*	0.7641	0.0071
Voris, 1964	E. Sabah 1961	7	62	57% *H. curtus*	0.6415	0.2746
Stuebing & Voris, 1990	W. Sabah 1987	9	2169	77% *H. curtus*	0.3925	0.4745
Wong, 2006	W. Sabah 1999	11	277	44% *H.curtus*	0.7498	0.1684
Padate et al., 2009	Goa India 2006-08	2	43	65% *H. schistosus*	0.4651	0.2129

snapshot of the snake assemblage on the sea floor in a limited area. Of course, snakes that are associated with coral reefs or rock outcrops will always be under-represented in these samples because trawlers try to avoid coral outcrops. When they failed to do so, as they did on one night that I was with them, they lost time, equipment, and their catch.

Comparisons within Southeast Asia.– Studies of sea snake assemblages using trawlers have mainly centered on the coasts of northern Australia and Southeast Asia. Although such studies along the coasts of northern and northeastern Australia are numerous and important (Shuntov, 1971; Dunson, 1975; Redfield et al., 1978; Wassenberg et al., 1994; Ward, 1996a,b; Fry et al., 2001; Milton, 2001; Tonks et al., 2008), detailed comparisons given below focus on studies of South and Southeast Asian waters and its marine snake fauna.

Within Southeast Asia, Lim and Balasingam (1961), Shuntov (1962), and Lim and Sawai (1975) were among the first to report on collections of marine snakes obtained exclusively from trawlers in Southeast Asia. These studies reported on the species richness of marine snakes and overall numbers of marine snakes obtained but did not provide the numbers of each species captured from an area. Studies reporting counts of specimens for each species of marine snake obtained as by-catch from trawlers operating in South and Southeast Asia include Voris (1964), Shuntov (1966), Tu (1974), Stuebing and Voris (1990), Wong (2006), and Padate et al. (2009). The studies carried out in the Gulf of Thailand by Shuntov (1966) and Tu (1974) are closest both in space and time to the samples from coastal Peninsular Malaysia reported in this paper. Three studies (Voris, 1964; Stuebing and Voris, 1990; Wong, 2006) are based on bottom-trawls off the northern and eastern coasts of Borneo, and Padate et al. (2009) reported on collections made on the west coast of India.

The trawl samples collected by Shuntov (1966) and Tu (1974) were obtained by different methods and, to a large extent, from different parts of the Gulf of Thailand. Shuntov's (1966) seven species of snakes were obtained using a research vessel that sampled widely in the Gulf. The dominant species in the collection of 75 specimens was *H. platurus*, comprising 71% of the snakes trawled (Table 4). Many of the trawling stations were in the middle of the Gulf (Shuntov, 1966, Fig. 3) where depths range from 60 to 80 meters and the dominance of *H. platurus* strongly suggests that some or all of the collections were made with a mid-water trawl rather than a bottom trawl. In any case, the diversity of the sample is modest with a PIE value of 0.488.

The huge trawl samples on which Tu (1974) reported were obtained mainly in 1969 and 1972 using commercial mid-water trawlers operating from 16 to 32 km off the Thai coast on the east side of the Gulf between Nakhon Si Thammarat and Songkhla. The area of the trawling ground was approximately 3,200 sq km, and depths in this coastal area range from 15 to 25 meters (NOAA Nautical Chart 93010, Southeast Asia, Gulf of Thailand, 1991). The by-catches from 1969 and 1972 were 5,138 and 8,304 snakes respectively (Table 4). Although the number of species observed for the two years was 10 and 11 respectively, the diversity of the samples as measured by PIE were the lowest recorded for by-catches of marine snakes in Southeast Asian waters. The low diversity for both years is due to the strong dominance of *H. curtus*. All other species combined made up only 15% of each sample (Table 4).

Although *H. curtus*, *H. viperinus,* and *A. eydouxii* are ranked as the first, second, and third most common species in Tu's samples from the Gulf of Thailand, and the Endau samples from just outside the Gulf, there are also many differences between these two areas. In the Gulf samples, *H. curtus* comprised 84% of the by-catch, while at Endau, *H. curtus* made up only 33% of the by-catch (Table 4). In the Gulf samples, *H. viperinus* and *A. eydouxii* each made up just 3% of the snakes captured. At Endau, *H. viperinus* made up 32% of the by-catch and *A. eydouxii* made up 8%. Thus, although the Gulf and Endau samples share eight species, the balance within the communities is very different.

Three factors are likely major contributors to the observed differences in relative abundances of by-catch between the two trawling grounds: distance, habitats, and the presence of a long-term sea surface temperature boundary (SST). The distance between the two trawling grounds is about 550 km. The habitats of the two areas differ in terms of many environmental factors but average turbidity and monsoon exposure are likely two of the biggest differences, with turbidity of the Gulf of Thailand much higher than that of the South China Sea, and with the Endau coast much more exposed to the northeast monsoon winds and rains (Camerlengo and Demmler, 1997). The Gulf of Thailand has been designated as a Large Marine Ecosystem (LME) that is separated from the South China Sea by an oceanic front that includes a SST boundary of 2 to 3 C° (Belkin and Cornillon, 2003) as well as other physical differences (Belkin and Cornillon, 2007; see map of LME 35, p.32). The map of Belkin and Cornillon (2007) shows the front of the Gulf of Thailand approximately halfway between Tu's sites in the trawling grounds of the Gulf of Thailand (Tu, 1974) and those of Endau.

Eight of 11 species present at Parit Botak in the Straits of Malacca were also collected

by Tu in the Gulf of Thailand. However, although the snake fauna of the two areas were very similar, the structure of these assemblages was very different. At Parit Botak, *H. fasciatus*, *H. curtus,* and *A. eydouxii* shared dominance (Fig. 4) with a combined 82% of the by-catch, while *H. curtus* alone made up 81% of the catch in the Gulf of Thailand. These differences result in the very divergent PIE values in Table 4.

Although Sungai Buloh is approximately 1,250 km from the trawling ground that Tu (1974) sampled in the Gulf of Thailand, their assemblages are very similar in that both are dominated by the same species and to the same extent. *Hydrophis curtus* made up 82% of the catch at Sungai Buloh and 84% in the Gulf. Although only 6 of 11 species at Sungai Buloh were present in the Gulf, the diversity as measured by PIE were nearly the same for the two areas (Table 4).

Three bottom trawl by-catch samples from off the coasts of Borneo between 1961 and 1999 were dominated to different extents by *H. curtus* (Table 4). In addition, the second most common species was *H. cyanocinctus* on the east coast of Sabah in 1960, but *A. eydouxii* dominated on the west coast of Sabah in 1987 and 1999. The causes behind the observed differences between these relatively nearby samples are largely unknown, but one factor distinguishing the samples is that the large collections obtained in 1987 were drawn from a much more extensive, undefined area than the other two samples that were more restricted geographically. The range in diversity for these three Bornean samples (PIE values from 0.3925 to 0.7498) is not very different than the values from the three trawling grounds presented in the present study (PIE values from 0.3127 to 0.7641).

The trawled collection made by Padate et al. (2009) off the coast of Goa, India consisted of 43 specimens representing just two species, *H. schistosus* and *H. curtus,* despite considerable effort (Table 4). In general, this low number of species is not unexpected given that the distance is more than 5,000 coastal kilometers from the Straits of Malacca and the center of Southeast Asian marine snake diversity (Voris, 1977, Fig. 7). At the same time, it is noteworthy that *H. schistosus* is also the dominant species in the Straits of Malacca at Muar (Voris, 2015), and *H. curtus* is strongly dominant in the Straits at Sungai Buloh (Table 4).

Historical perspectives: collapsing fisheries.– The history of mechanized fishing practices in Southeast Asia has been thoroughly chronicled in several relatively recent publications (Butcher, 2004; Morgan and Staples, 2006; Bankoff and Boomgaard, 2007). Butcher (2004) described this history as “the great fish race”. As early as the 1890s, sail-powered trawlers began to operate in the Japanese fishery in Manila Bay (Morgan and Staples, 2006). These trawlers were largely ineffective given their dependence on weather, but at about the same time (1894) the first proposal for the use of steam-powered trawling vessels in Southeast Asia was submitted in Penang. This proposal was denied, but by 1907 a trawl survey was initiated in the Java Sea using a refitted steam barge. Other surveys followed on the coast of Burma, in the Philippines, and in the South China Sea but none proved that the wide use of steam-powered commercial trawlers was practical in Southeast Asia. However, by the late 1920s Japanese companies began to operate diesel-powered trawlers in the Philippines and their use spread during the 1930s until

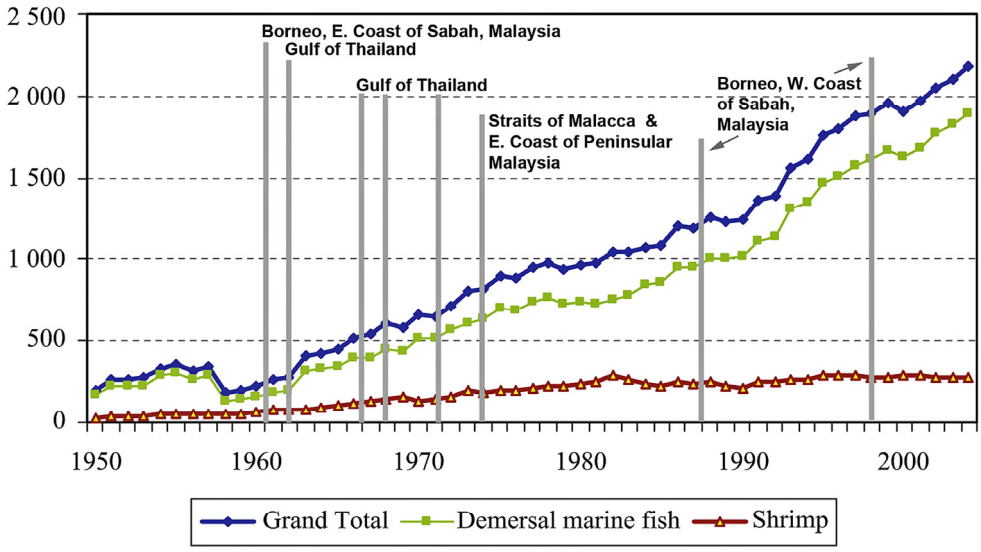

FIGURE 7. Plot of landings (thousands of tonnes) of demersal marine fish and shrimp in Southeast Asian countries between 1950 and 2002 (Morgan and Staples, 2006, p. 8). Added to the original chart are data from six marine snake trawl projects conducted in Southeast Asian waters within the same time period. The geographic location, year(s), sample size, and author(s) of the published projects in chronological order are: Borneo, East Coast of Sabah, Malaysia, 1961-1963, n=62 (Voris, 1964); Gulf of Thailand (South China Sea and East Indian Ocean), 1963-1964, n=175 (Shuntov, 1966); Gulf of Thailand, (near Isthmus of Kra) 1967, 1969, 1972, n=14,282 (Tu, 1974); Straits of Malacca and East Coast of Peninsular Malaysia, 1974-1975, n= 1,575 (see Table 1); Borneo, West Coast of Sabah, Malaysia, 1987-1988, n=2,168 (Stuebing and Voris, 1990); Borneo, West Coast of Sabah, Malaysia, 1998-1999, n=277 (Wong, 2006).

the expansion was halted by World War II (Morgan and Staples, 2006).

Thus, it was not until about 1950 that intensive fishing practices based on small diesel-powered otter board trawlers began to deplete fish stocks in Southeast Asian seas (Fig. 7). As small-scale coastal trawling expanded a pattern emerged. As the number of trawlers expanded rapidly in an area, and harvests of fish and shrimp boomed and then decreased, trawlers shifted to new coastal trawling grounds and eventually to further offshore grounds that required larger vessels and longer cruises. Thus, Figure 7 shows a steady increase in overall harvest in Southeast Asia but the graph masks the depletion of local trawl grounds that was taking place throughout the second half of the century as documented, for example, by Kleinen (2007) in "Stealing from the Gods": Fisheries and Local Use of Natural Resources in Vietnam 1800-2000.

Figure 8 details the changes in two variables that describe this boom-and-bust exploitation that took place in the fishery of the Gulf of Thailand during this time (Boonyubol and Pramokchutima, 1984). In 1960 just 99 trawlers were operating in the Gulf. Over the following 20 years the number increased to nearly 8,000 trawlers. During just the first part of this period (1962 to 1972), the demersal catch per unit of

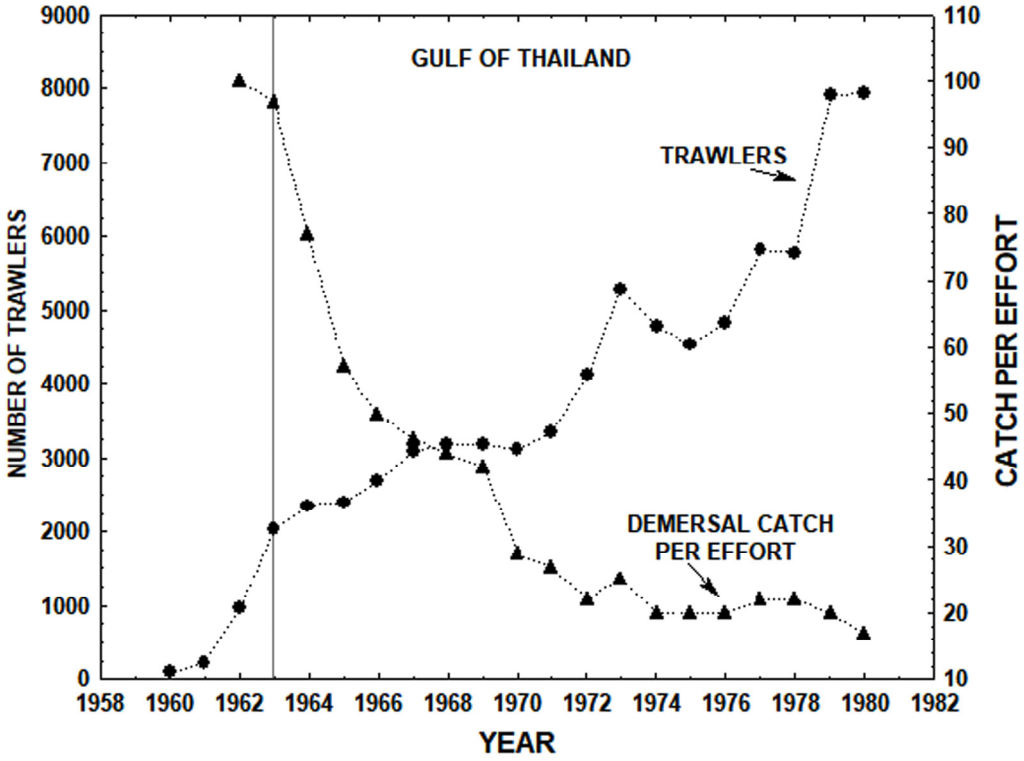

FIGURE 8. The number of commercial trawlers operating in the Gulf of Thailand between 1960 and 1982 is plotted on the y-axis on the left. Plotted on the y-axis on the right is the annual catch-rate from the demersal trawls of two research vessels operating in the Gulf of Thailand during the same time period. The data are drawn from tables 4 and 5 in Boonyubol and Pramokchutima (1984). The vertical line at 1963 designates the first study of marine snake by-catch from trawls conducted in the Gulf of Thailand (Shuntov, 1966).

trawling effort decreased from 100 in 1962, to 22 in 1972. These results along with others lead fisheries experts to assert that the Gulf of Thailand was overfished by the mid-1970s (Boonyubol and Pramokchutima, 1984; Eiamsa-ard and Amornchairojkul, 1997; Pauly and Chuenpagdee, 2003).

With the dramatic increase in the number of bottom trawlers, overfishing was not the only problem. For example, by 1966 the 3,000 bottom trawlers operating in the Gulf of Thailand were capable of making 9,000 pulls of several kilometers each day. The physical destruction that the otter boards and the chains on the bottom of the nets caused to benthic habitats was vastly underappreciated at the time. Studies since then (e.g. Caddy, 1973; Jones, 1992; Thrush and Dayton, 2002) have documented the extent of the damage. How this disruption to the habitat impacted marine snakes is not known, but it is likely that over the decades it has favored dietary generalists like *H. curtus* and stressed specialists like the microcephalic species (e.g., *H. brookii, H. caerulescens, H. fasciatus,* and *H.*

torquatus) that feed on just a few species of eels (Voris and Voris, 1983).

Figures 7 and 8 place marine snake by-catch studies conducted in Southeast Asia in the context of a huge expansion of trawling effort and the subsequent degradation of the habitat and the "rolling" collapse of the fisheries. The surveys of marine snakes in the early 1960s (Voris, 1964; Shuntov, 1966) were conducted just as the expansion of mechanized trawling was getting underway. The large surveys by Tu (1974) in the Gulf of Thailand in 1969 and 1972 took place in the midst of the expansion of fishing effort and the crash of the fishery. The number of trawlers had increased to 3,000 and the catch per effort had dropped below 50 (Fig. 8). The snake surveys at Sungai Buloh, Parit Botak, and Endau took place during the time that inshore trawling grounds also were undergoing intensive overfishing. The degree to which these assemblages of marine snakes were shaped by the boom-and-bust exploitation of fishing grounds that began in the 1950s will likely never be known, but it most certainly must have had a very significant impact. However, although we must view the surveys of the marine snake by-catch in Southeast Asia through the lens of collapsing fisheries, sufficient clues remain within the results to strongly suggest that in the past marine snake assemblages formed a complex tapestry across the Sunda Shelf. Furthermore, the assemblages characterized here support the impressions reported nearly a century ago by Malcolm Smith (1920, p. 2).

> "By systematically collecting at every available spot, it has been possible in course of time to search the whole of the Gulf very thoroughly. The result of this has been to bring out one noteworthy fact, namely, the curiously local distribution of many of the species. Certain forms will be more or less abundant along a small stretch of coast, at one or more river mouths, and almost or entirely absent in other parts of the Gulf. … It is difficult to assign a reason for this phenomenon."

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APPENDIX

Photographs documenting diesel-powered trawlers in 1975 and their catches from otter-trawling. **A-B.** Sungai Buloh port, Malaysia, in 1975. Trawlers, loading docks, coffee shops, and homes are in the background. Photographs were taken at dawn prior to departure at high tide. **C.** Trawler on Sungai Buloh trawling grounds in 1975 with pull in progress. **D.** Trawler on Sungai Buloh trawling grounds in 1975. Net being brought up to boat. **E.** Catch being sorted on trawler operating on the Sungai Buloh trawling grounds in 1975. **F.** Catch being sorted on trawler on the Endau trawling grounds in 1975. Note the *Hydrophis viperinus* (arrow) on the tarp to the left of the fisherman's knee. **G.** Large pile of sea snakes on pier at Songkhla, Thailand in 1996. It was reported that these snakes were collected for the leather trade by trawlers over a two week period in Vietnamese waters.