Tropical Natural History 15(1):1-21, April 2015

Marine Snake Diversity in the Mouth of the Muar River, Malaysia

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Received: 2 March 2015; Accepted: 22 March 2015

Abstract.– Prior to entering the Straits of Malacca the Muar River meanders nearly at sea level for about 20 kilometers. Much of this portion of the river is influenced by semi-diurnal tides that occur in the Straits. In the 1970s and 1980s several stationary stake nets (kelongs) located adjacent to the town of Muar were operated by local fisherman. Besides the sought after catch of shrimp, squid, and fish, the harvest from these nets often included a by-catch of marine snakes. Collections over a period of eight months revealed that eight resident species were present in the mouth of the Muar River and that the beaked sea snake, *Enhydrina schistosa*, strongly dominated the assemblage of snakes. Surprisingly the relative abundance of species differed between several of the nets despite the fact that they were all located in a relatively small area and in one place located within just ~10 m of each other. Some small differences in species diversity between tidal periods were also detected at one of the nets. A review of published marine snake surveys conducted in Southeast Asian and Australian seas revealed that only four provided data on relative abundance of marine snake species in a defined small area on a scale of < 100 km^2 . Although the Muar survey demonstrated the lowest species diversity values of the published studies, it also covered the smallest spatial scale surveyed and yet it still revealed differences within the survey area. This work emphasizes the fact that marine snake species diversity needs to be understood on a fine spatial scale before surveys done by trawling, which cover thousands of km^2, can be interpreted in ecological terms.

KEY WORDS: **Elapidae, Hydrophiini, Acrochordidae, sea snake, ecology, estuary, fine spatial scale**

INTRODUCTION

In 1920 the results of the first major survey of marine snakes were published by Malcolm Smith. The survey covered the coastal areas of the Gulf of Thailand and the Malay Peninsula between 1915 and 1918 and yielded a collection of 548 sea snakes representing 17 species (Smith, 1920). These snakes were obtained as by-catch from local coastal fisherman using a variety of fishing techniques. About 20 years later Bergman (1938, 1943) began to report on another large collection of marine snakes from coastal areas near Sourabaya (Surabaya, Java). Made by local fisherman between 1936 and 1942, this collection consisted of 984 specimens representing 6 species (3 or more additional species were "disregarded" due to rarity). This collection may represent the first major collection of marine snakes in which all specimens from a single coastal area were caught, retained and identified, thus providing both the species richness and some data on relative abundance.

Shortly after World War II the use of mechanized diesel-powered bottom trawlers expanded in Southeast Asia (Morgan and Staples, 2006) and as the demersal fish harvest increased, so must have the marine snake by-catch. This technology allowed for numerous sea snake surveys that covered very large geographic areas (80,000 to >120,000 km^2) such as Tonking Bay (Shuntov, 1962), the South China Sea (Shuntov, 1966), the Sahul Shelf (Shuntov, 1971), the Gulf of Carpentaria and northern coast of Australia (Redfield et al., 1978; Wassenberg et al., 1994; Ward, 1996a; Ward, 1996b; Fry et al., 2001), the Gulf of Thailand (Tu, 1974), and coastal areas of Borneo (Voris, 1964; Stuebing and Voris, 1990). Although many of these surveys resulted in both a species count and the relative abundance of each species, they lacked value at the level of ecological communities because the areas sampled were vast and often ill defined. The two partial exceptions to these cases are the surveys by Redfield et al. (1978) and Wong (2006) that were limited to trawlers fishing in relatively small (~1,000 to 5,000 km^2) defined areas in the Gulf of Carpentaria, Australia and southeast of Kota Kinabalu, Malaysia.

The present study is the first of its kind in that it reports on an extensive collection of marine snakes obtained from a few stationary stake nets in one locally defined area of about two km^2. Each captured snake was identified to species and tallied over a period of nine months to allow for overall estimates of species diversity as well as comparisons of diversity between collections from different stake nets within the area, and between collections made during different tidal cycles. This survey of marine snakes in the mouth of the Muar River had two goals. First, it aimed to determine the overall marine snake diversity in the river mouth. Second, it sought to determine if there might be differences in species diversity on a small spatial scale within the mouth of the river.

MATERIALS AND METHODS

Fishing grounds and methods.– Between January and September 1975, marine snakes were collected from the mouth of the Muar River (2°3'20"N, 102°34'20"E) on the Straits of Malacca (Fig. 1). Nearly all the collections were obtained as by-catch from four of seven stationary stake nets (locally called kelongs or puket togok) that were managed by local fisherman to catch fish and prawns. The nets operate by filtering the river discharge on the outgoing tide. Figure 2 shows the mouth of the Muar River and the location of the seven stake nets that were operated in the 1970s and 1980s.

At the mouth of the Muar River tides are semi-diurnal. Fishermen operated the stake nets on both of the daily ebbing tides during the two monthly spring tides, about 7 days around the astronomical full moon and new moon. Thus, during each lunar synodic period (approx. 29.5 d) the nets could be operated for a total of roughly 14 days or 28 ebb tides. Due to weather, river conditions, and equipment maintenance the nets were not operated at their full potential.

The greatest amount of the marine snake by-catch from the Muar River mouth was collected from the two up-stream (east) nets (Fig. 2, nets 1 and 2) and the two nets closest to the Straits (Fig. 2, nets 6 and 7). These four nets were also operated on the most regular basis. Nets 1 and 2 were 2.5 km from nets 6 and 7. Figure 3 provides top and side views and the dimensions of one of the two most up-stream stake nets. The dimensions of the stake portion of the nets at Muar varied greatly with nets 6 and 7 (Fig. 2) five to eight times longer than the staked distance of nets 1 and 2. The net portions of the stake nets were similar in size and design (see Fig. 3).

Environmental measures.– The maximum tidal range at Muar was about 3 m during spring tides. Melaka has the closest tide station to the Muar River mouth (35 km northwest) and it has a maximum tidal range of 2.44 m. Kuala Batu Pahat is the next

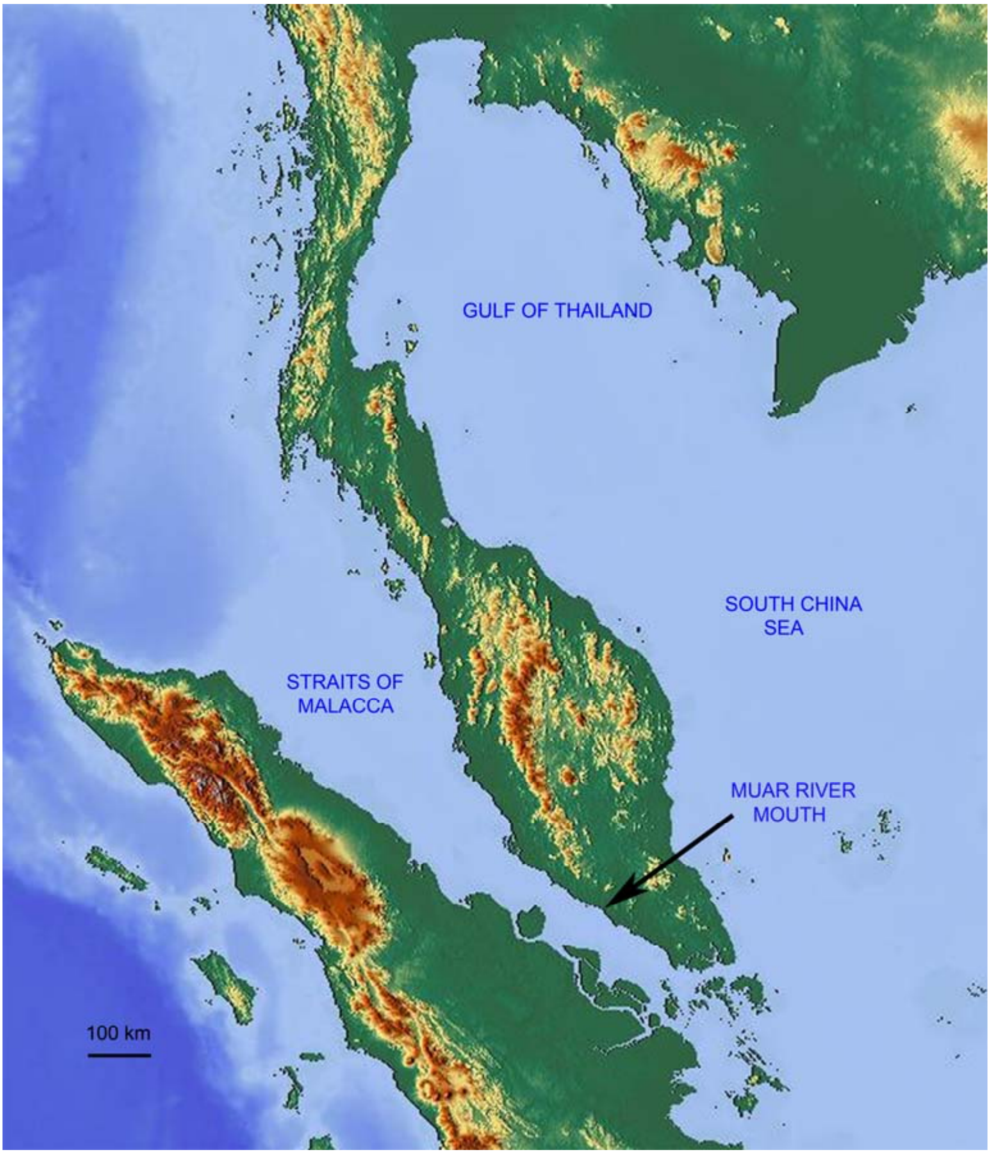

FIGURE 1. Map showing the location of the mouth of the Muar River adjacent to the town of Muar (Bandar Maharani) in the state of Johore, Malaysia where stake nets (also known as puket togok or kelong) were operated to collect fish and prawns. Marine snakes were obtained as by-catch from these nets.

closest tide station to Muar (50 km southeast) and it has a maximum tidal range of 3.21 m (Hydrographic Department, 1975). Stake nets were normally deployed as soon as the tide began to ebb and operated until the water level had fallen at least 2 m.

Measurements of depth and samples of the bottom substrate were taken on transects A through F to characterize the snakes' habitat (Fig. 2). Measurements of depth

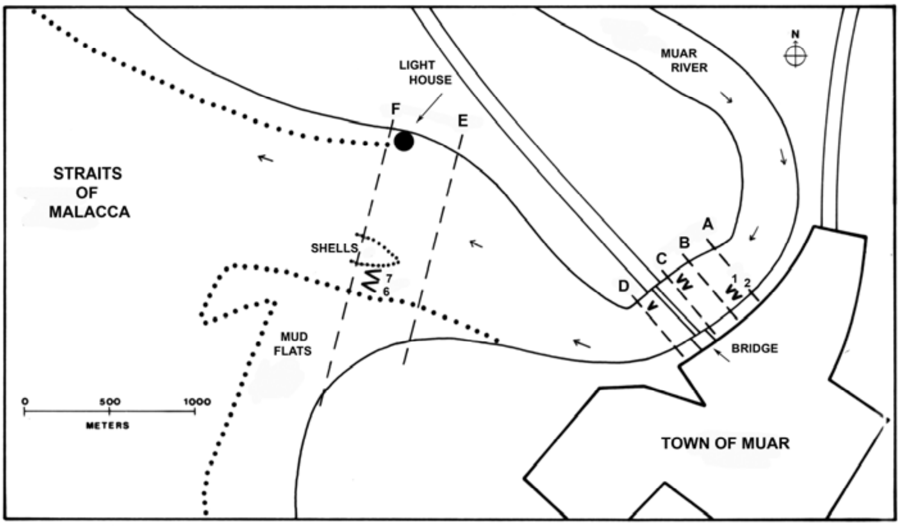

FIGURE 2. Map of the mouth of the Muar River showing the location of seven stake nets that were operated in the 1970s and 1980s. Four nets east of the bridge, one nearly below the bridge on the west side, and two nets further west opposite the light house on the north side of the river are shown. Several other stake nets were operated two to three km off the coast of Muar. The majority of the marine snake by-catch reported on in this study were collected from the two up-stream (east) nets (numbers 1 and 2) and the two most down-stream (west) nets (numbers 6 and 7) that were operated on the most regular basis. Measurements of depth and samples of the substrate were taken on transects A through F to characterize the snake's habitat. The extensive mud flats adjacent to the south side of the Muar River mouth (delineated by dotted lines) were inhabited by homalopsid snakes (e.g. *Cerberus schneiderii* and *Bitia hydroides*) that rarely appeared in the stake net by-catch (Jayne et al., 1995; 1998).

were made during ebbing neap tides to minimize the tidal effect on depth, starting about 5 m from the shore. Also shown in Figure 2 is a scoured channel of coarse shells adjacent to net 7, closest to the Straits. The extensive mud flats adjacent to the south side of the Muar River mouth (delineated by dotted lines in Fig. 2) were inhabited by homalopsid snakes (e.g. *Cerberus schneiderii* and *Bitia hydroides*) that rarely appeared in the stake net by-catch (Jayne et al., 1988; 1995).

In addition to the depth and the bottom substrate transects noted above, salinity, turbidity, current speed, and water temperature were frequently measured while the nets were deployed during the ebbing tide. These data document the dynamic nature of the snakes' habitat. Salinity was measured using a LaMotte salinity kit (LaMotte Co., Chestertown, MD, USA) based on the silver nitrate titration method (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 water during the ebb tide was measured from a boat to the side of the net platform using a mechanical propeller flowmeter with a standard rotor (General Oceanics, Miami, FL, USA, threshold approx. 10 cm/s: range 10 cm/s – 790 cm/s). The depth of the water was measured using

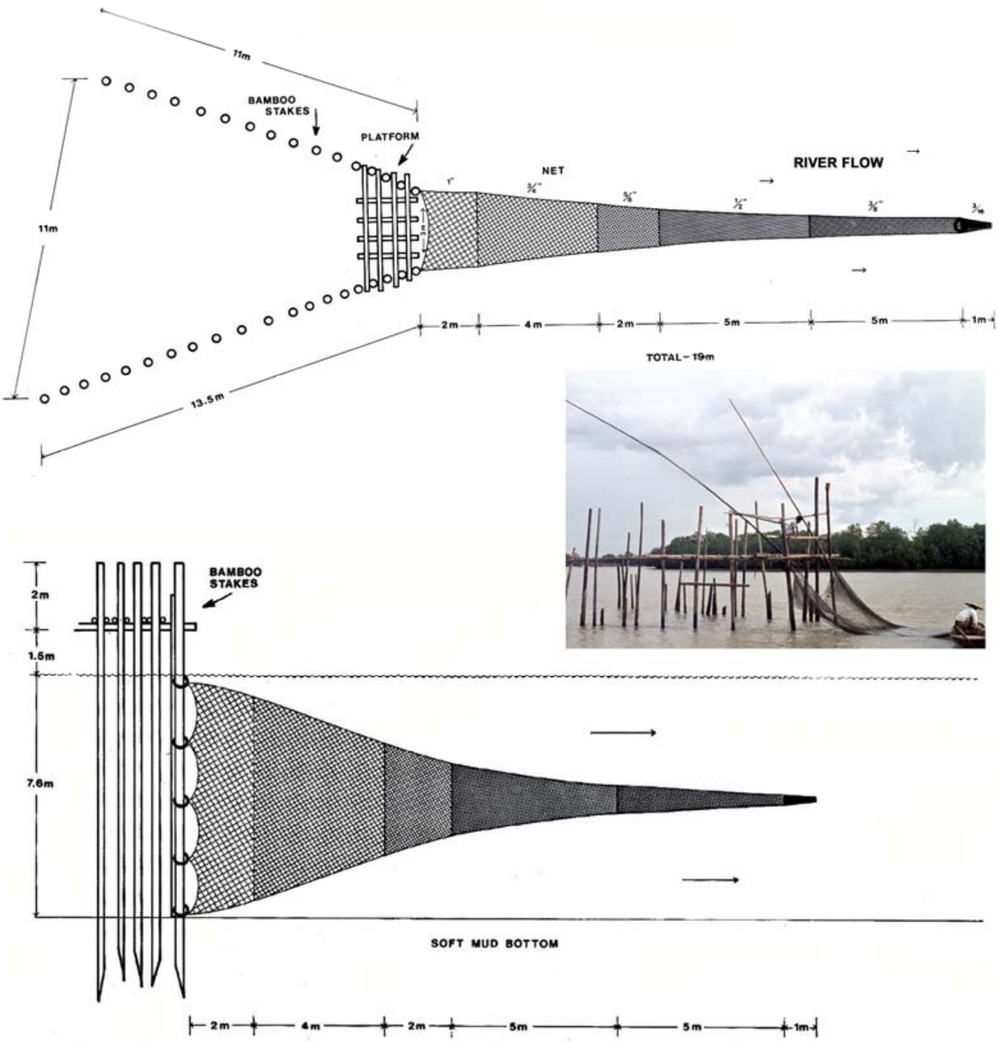

FIGURE 3. Illustrations showing top and side views of stake net 1 located in the mouth of the Muar River and used to harvest fish and prawns. The nets were operated on the out-going semi-diurnal spring tides of each lunar cycle and marine snakes were a frequent by-catch. The overall dimensions of the stake nets varied. Nets 1 and 2 (see Fig. 2) were similar in size as were nets 6 and 7. However, the dimensions of the staked portion of nets 6 and 7 were five to eight times longer than the staked distance of nets 1 and 2. The net portion of the stake nets were similar in size and design with mesh size (see top view) decreasing from the mouth (2.54 cm mesh) to the net bag (0.48 cm). The inset shows stake net 1 near low tide.

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. Samples of the substrate were collected using a galvanized steel cylinder (15.2 cm diameter, 45.7 cm lg) with the top 30.5 cm perforated with 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) metal sieves.

Published data also document seasonal shifts in salinity, temperature, precipitation, river discharges, and plankton productivity in the Straits of Malacca. For example, in the Straits of Malacca salinity varies spatially and in response to the monsoons in November from 28.0 p.p.t. to 32.0 p.p.t. (Soeriaatmadja, 1956). Sea surface temperatures range from 29.5°C in September-March to 30.5°C in April-June (Hydrographer of the Navy, Malacca Strait Pilot, 1958). There are also seasonal variations in average monthly rainfall at Muar ranging from 15 to 25 cm in June and July to 5 to 15 cm in January and February (Dale, 1974) that result in fluctuations in the river's discharge. For example, the discharge rates on the Selangor River (north of the Muar River) 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 (Ministry of Agriculture and Fisheries, 1972).

Processing the by-catch and the identification of snakes.– After snakes were caught the date, time, and net number were recorded. The snakes were kept in plastic bags inside Styrofoam coolers until the end of the fishing session and then brought to the informal local laboratory where they were euthanized with an injection of sodium pentobarbital. Prior to preservation each relaxed snake was tagged and measured (snout-vent length, 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 permanent storage.

Beginning on 26 February 1975 neonate snakes began to appear in the nets and they were common in the catch from March to June. A total of 898 neonates appeared in the nets between February 26 and the end of the field work in September. In the majority of the analysis presented I have elected to exclude neonates and include adults only because of the drastically different average clutch sizes between *E. schistosa* ($\bar{x}$ = 18.3 oviducal eggs) and the 5 other species ($\bar{x}$ = 3.3 – 6.0) reported on by Lemen and Voris (1981).

The snake species collected represent three families: Acrochordidae (*Acrochordus granulatus*), Homalopsidae (*Cerberus schneiderii*), and Elapidae (Hydrophiini, 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. The nomenclature has been updated where appropriate to be consistent with Elfes et al. (2013).

Measures of diversity.– Several estimates of species diversity were applied in the analysis of the snake assemblage sampled at the mouth of the Muar River. All the measures assess information both on numerical species richness and on 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) are 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, E (Pielou, 1966; Hurlbert, 1971; Magurran, 1988) are applied in other analyses.

Statistics.– Several of the above diversity measures 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

Dynamic environment.– The marine snakes that inhabit the mouth of the Muar River have adapted to a very dynamic environment. Twice each day during spring tides the water at the stake nets changed from relatively clear sea water to slightly cooler turbid river water, and four times each day the river flow stopped completely for an hour or so. When the current stopped at the two high tides the water at the nets was largely sea water from the Straits and when it stopped at low tide the water was largely river water. As current speed rose and then decreased during the ebb tide, turbidity steadily increased (Fig. 4). Likewise, as the water level dropped at the nets the turbidity rose and the salinity fell (Fig. 5). The particulars of salinity, turbidity, and water levels at the nets varied each day depending on tidal range of the particular day of the lunar cycle, as well as other local environmental conditions such as the intensity and direction of the wind and the local patterns of rainfall impacting the volume of the river's discharge. In addition, the southwest monsoon (May to September) and the northeast monsoon (December to March) seasons have major impacts on rainfall and wind at Muar and over the Muar River catchment.

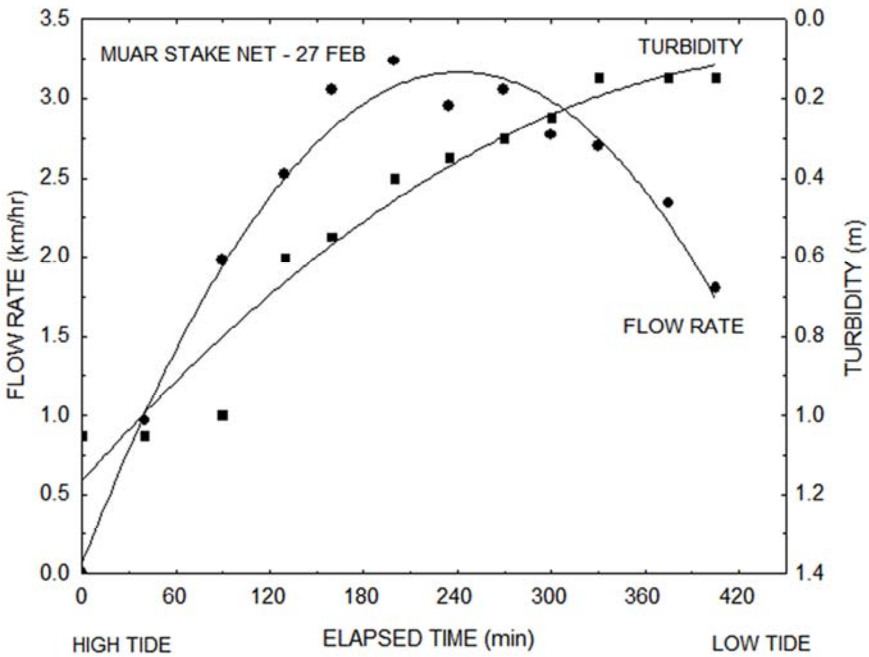

FIGURE 4. A plot of the flow rate (km/hr) and the turbidity (m) of the Muar River versus the elapsed time (min) during the ebb tide at net 1 on 27 February 1975. The river's current increases steadily for the first three hours, holds steady for about an hour and then begins to decrease in speed. Initially at high tide, sea water from the Straits has pushed up-river and the turbidity is relatively low while as the tide falls fresh water from upstream increases the turbidity at the nets.

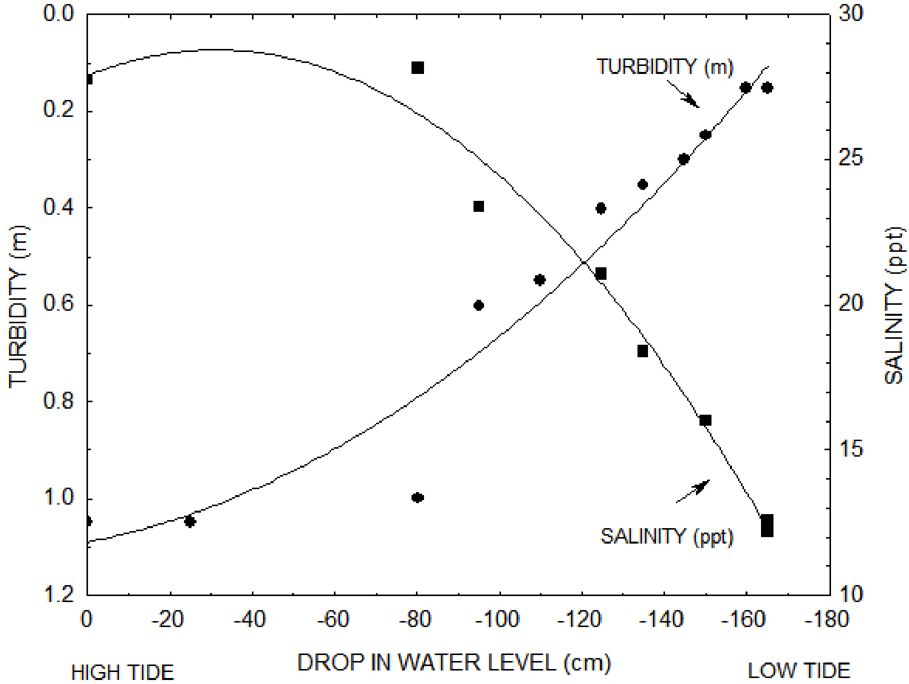

FIGURE 5. A plot of turbidity (m) and salinity (ppt) versus the water level (cm) at net 1. As the tide ebbs and sea water flows into the Straits, turbidity steadily increases in response to muddy freshwater from upstream.

Depth and substrate.– Measurements of depth and samples of the substrate were taken on six transects (A – F, Fig. 2) to characterize the profile and the bottom of the river in the vicinity of the stake nets. Table 1 provides depths along the six transects measured on 7 March 1975. The distances on the transect between measurements were roughly equal. The greatest depth detected (10.4 m) was on transect A northwest of net 1 (Table 1). The depths on transect A immediately above the mouths of both nets 1 and 2 were between 9 m and 7 m. Likewise the depths on transect B on the southeast side of the river just below nets 1 and 2 were in the range of 7.5 m to 8.5 m. These data confirm that nets 1 and 2 on the outside bend in the river were located in the main channel. The readings of depth on transects C and D confirm that the main channel in the vicinity of the bridge is on the west side of the river with maximum depths of 7.6 m and 8.2 m (Table 1). Both transects E and F had a maximum depth of 4.6 m. Although the deepest parts of both transects E and F were just above and below the stake nets 6 and 7, the channel in this section of the river appears wider and only about 1 m deeper than much of the northern portion of these transects. Thus, the measurements of depth along the transect show that nets 1, 2, 6, and 7 are all in a channel within the river bed but that the channel in the vicinity of nets 1 and 2 is more than twice as deep as it is in the vicinity of nets 6 and 7.

Two bottom samples were taken on transect A (A8 and A11, Table 1) upstream from nets 1 and 2. Both of these samples consisted of fine compact mud. More than 98% of the samples passed through all three sieves (coarse, medium, and small mesh).

TABLE 1. Depths (m) measured on 7 March 1975 along transects A - F in the mouth of the Muar River (see Fig. 2). The lengths of transects A - F were as follows: A and B, 0.30 km; C and D, 0.35 km; E, 0.91 km; and F, 1.10 km. The nine depths underlined and in bold (transect and station, A8, A11, D7, E4, E9, E11, F2, F8, and F15) indicate stations where bottom samples were also taken. Depths were taken from north to south beginning about 5 m from shore on an ebbing neap tide.

	TRANSECT					
STATION	**A**	**B**	**C**	**D**	**E**	**F**
1	2.4	2.4	3.7	0.6	1.8	2.4
2	3.0	2.7	4.0	3.7	2.4	**2.4**
3	3.7	6.1	4.9	4.3	3.0	2.4
4	4.0	6.7	6.1	4.6	**3.7**	3.0
5	5.5	7.6	6.7	6.4	4.0	3.0
6	7.0	8.2	8.2	7.3	3.0	3.7
7	7.6	8.5	7.6	**7.6**	2.4	4.6
8	**9.1**	7.9	5.5	7.0	4.3	**4.6**
9	10.4	4.6	7.0	4.6	**4.6**	4.6
10	9.8				4.0	4.3
11	**9.1**				**4.6**	4.6
12	7.6				3.7	4.6
13	7.3				4.6	4.3
14	3.0				3.7	4.0
15					1.8	**3.0**
16						2.4
17						1.8
18						0.6
19						1.2
Minimum	**2.4**	**2.4**	**3.7**	**0.6**	**1.8**	**0.6**
Maximum	**10.4**	**8.5**	**8.2**	**7.6**	**4.6**	**4.6**

One sample was taken on transect D in the vicinity of the bridge (D7, Table 1) and also consisted mostly (> 98%) of fine compact mud but with more vegetable matter retained in the medium-mesh sieve.

Three bottom samples were taken on transect E just upstream of nets 6 and 7. The sample taken on the northern side of the transect (station E4, Table 1) appeared identical to the samples from transects A and D and consisted entirely of fine compact mud. However, the sample (station E9) taken upstream and slightly north of net 7 was very heterogeneous. The coarse sieve retained 90% of the sample and contained whole bivalves and relatively large fragments of shells. About 8% of the sample was retained in the medium sieve and contained smaller shell fragments while the fine sieve retained the rest of the small shell fragments (Fig. 2, see area marked "shells"). The sample taken just slightly further south on transect E (E11, Table 1) consisted of fine compact mud similar to the samples associated with transect A. On transect F below nets 6 and 7 the samples taken at stations F1, F8, F15, and F19 consisted primarily of fine compact mud that passed through all three sieves. However, the sample taken northwest of net 7 (F8) included 5 fragments of shells that were retained in the coarse sieve. Multiple additional bottom samples taken north of net 7 confirmed a scoured channel consisting of some live bivalves and fragments of bivalve shells (Fig. 2).

Thus, our samples suggest that the substrate at the mouth of the Muar River consists mostly of fine compact mud but at least one portion of the channel near net 7 has become scoured and consists primarily of bivalve shells.

Species richness and evenness.– The 968 adult marine snakes collected at the stake nets at Muar belonged to 11 species in three snake families: Acrochordidae (*Acrochordus granulatus*), Homalopsidae (*Cerberus schneiderii*), and Elapidae (Hydrophiini, true sea snakes). This assemblage is strongly dominated by the beaked sea snake, *Enhydrina schistosa* (Fig. 6). Furthermore, *E. schistosa* and three species of *Hydrophis* (*H. melanosoma*, *H. brookii*, and *H. torquatus*) make up 98% of the snakes

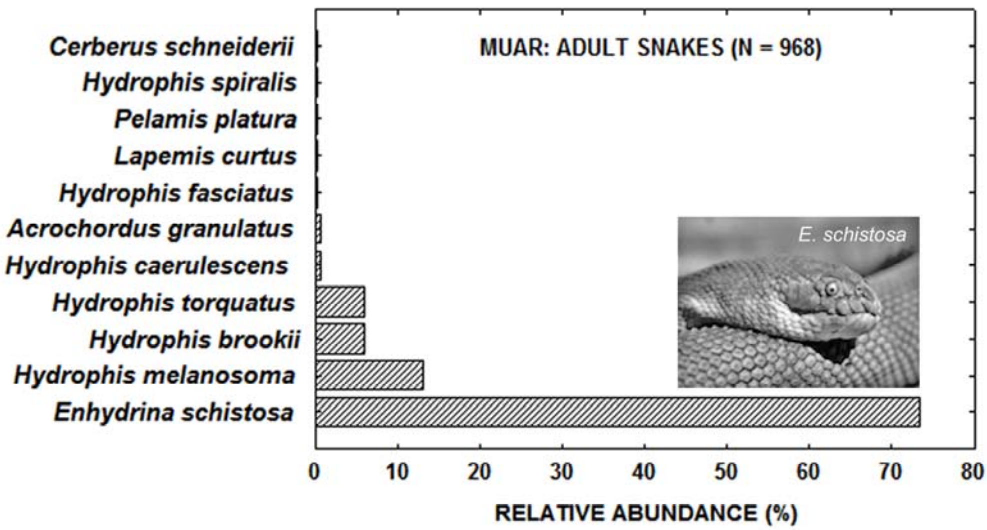

FIGURE 6. Bar graph showing the species composition and relative abundances of 968 adult marine snakes obtained as by-catch at nets 1, 2, 6, and 7. The dominant species, *Enhydrina schistosa*, is pictured. The four most abundant species make up 98% of the snakes collected. The nomenclature follows Elfes et al., 2013 and Murphy and Voris, 2014.

sampled (Fig. 6). The numbers of adult individuals collected of each of the 11 species were as follows: *E. schistosa* (710), *H. melanosoma* (126), *H. brookii* (57), *H. torquatus* (56), *H. caerulescens* (6), *A. granulatus* (6), *H. fasciatus* (2), *Lapemis curtus* (2), *Pelamis platura* (1), *H. spiralis* (1), *and C. schneiderii* (1). The latter three species represented by a single specimen each were considered waifs and excluded from most analyses.

For the sample of 965 adult snakes the overall diversity 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 = 0.565, PIE = 0.435, H' = 0.913, E = 0.439, and HB = 1.314.

Species diversity accumulation curves.– To examine species diversity (species richness and evenness) over time, the Brillouin diversity index (HB) was calculated for the samples from all nets (1, 2, 6, and 7; plus 30 snakes from net 3 and 5 by bridge) collected through a total of 167 net deployments on 54 tidal cycles on 44 days (Fig. 7). The final HB values for all snakes captured (adults and juveniles, n = 1,866) and adult snakes only (n = 968) were 1.124 and 1.314 respectively. The plots in Figure 7 demonstrate two points. First, both curves show diversity initially increasing sharply and reaching the range of their total accumulated diversity in the first five net deployments. Second, the curve based only on adult snakes remains remarkably flat after about 35 accumulated deployments while the curve based on all snakes drifts lower as neonate *E. schistosa* became more common among the samples beginning in late February.

Diversity between nets.– Plots of Brillouin diversity index (HB) values for successive net deployments over time for nets 1, 2, 6, and 7 are shown in Figure 8. All four curves stabilized and became relatively flat after 12

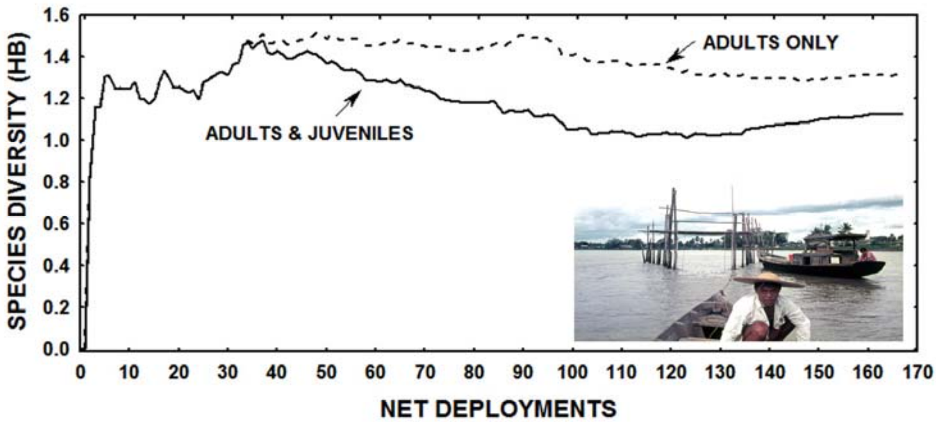

FIGURE 7. A plot of Brillouin diversity index (HB) values over 167 deployments of nets for all snakes captured (adults and juveniles) and for adult snakes only. The final HB values at the end of the curves (far right) for all snakes captured (adults and juveniles) and adult snakes only were 1.124 and 1.314 respectively. The inset image shows Chua Song Chen checking the deployed net at stake net 1.

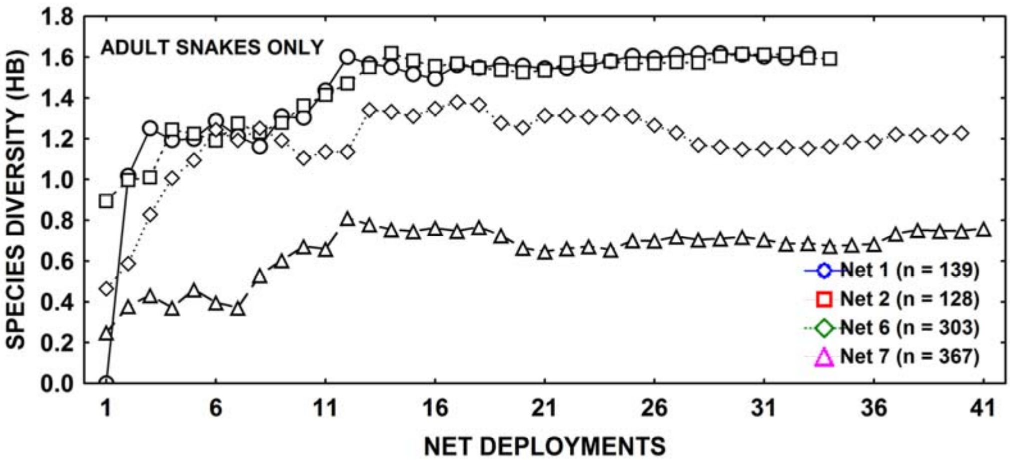

FIGURE 8. A comparison of plots of Brillouin diversity index (HB) values for adult snakes captured at nets 1, 2, 6, and 7 over net deployments of 33, 34, 40, and 41 respectively. The HB diversity values at the end of the curves (far right) for nets 1, 2, 6, and 7 were 1.617, 1.592, 1.227, and 0.759 respectively. The total number of adult snakes captured (n) in each net is given in the legend. The total number of snakes for the four nets (n = 937) is less than the total in figure 7 (n = 968) because snakes from nets 3 and 5 and snakes from two instances when catches from nets 6 and 7 were accidently combined, were not included in this comparison of four nets.

to 15 net deployments. The curves for nets 1 and 2 show the highest diversity values and are nearly identical to each other following 15 net deployments. The captures from net 6 resulted in lower values of diversity than either nets 1 and 2 starting from deployment 10 while the curve for net 7 showed substantially lower diversity throughout all deployments. The final HB values (Fig. 8, far right) for adult snakes only from the four nets were as follows: net 1, 1.617; net 2, 1.592; net 6, 1.227; net 7, 0.759.

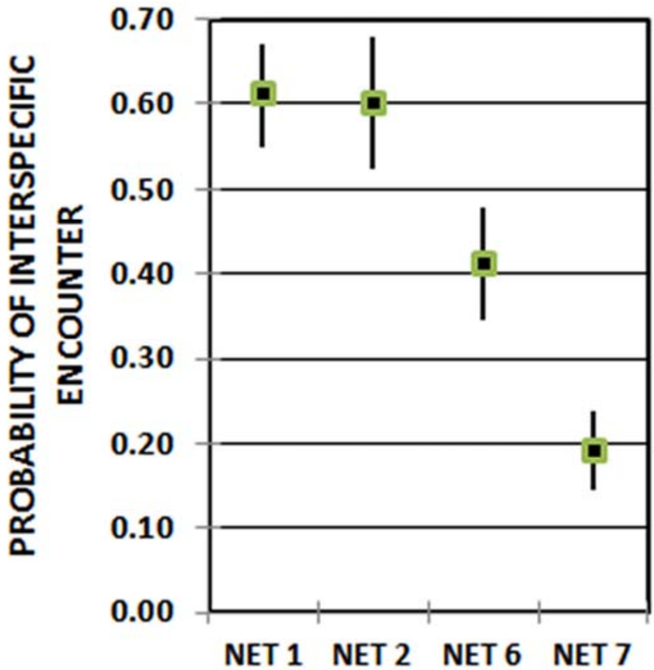

FIGURE 9. A plot of the probabilities of interspecific encounters (PIE) or the complement of Simpson's D, for nets 1, 2, 6, and 7 is presented. The whiskers provide 2SD for the PIE values. The PIE values from nets 1 and 2 do not differ from each other statistically while all other pairwise comparisons are significantly different (see text for details).

Shannon (H') diversity values for the four nets were compared using pairwise t-tests (see Magurran, 1988). The H' values for nets 1 (H' = 1.199) and 2 (H' = 1.178) were found to not differ statistically ($t = 0.178$, $df = 267$, $p > 0.05$). However, the H' values for nets 6 (H' = 0.874) and 7 (H' = 0.457) were found to be statistically different from each other ($t = 5.241$, $df = 302$, $p \leq 0.01$). In addition, net 6 H' values differed from values at nets 1 ($t = 3.128$, $df = 305$, $p \leq 0.01$) and 2 ($t = 2.941$, $df = 285$, $p \leq 0.01$) and the net 7 H' values also differed from values at nets1 ($t = 9.522$, $df = 241$, $p \leq 0.01$) and 2 ($t = 7.624$, $df = 224$, $p \leq 0.01$).

A plot of the probability of interspecific encounter (PIE) for nets 1, 2, 6, and 7 further demonstrates the differences in snake diversities observed at the nets (Fig. 9). Simpson's D values for nets 1 (D = 0.391) and 2 (D = 0.407) were found to not differ statistically ($t = 0.331$, $df = 13$, $p > 0.05$. All other comparisons of D values between nets proved to be significantly different from each other: net 1 compared with net 6 (D = 0.589), $t = 4.490$, $df = 14$, $p < 0.001$; net 1 compared with net 7 (D = .808), $t = 11.093$, $df = 11$, $p < 0.001$; net 2 compared with net 6, $t = 3.566$, $df = 13$, $p < 0.001$; net 2 compared with net 7, $t = 8.802$, $df = 10$, $p < 0.001$; net 6 compared with net 7, $t = 5.290$, $df = 11$, $p < 0.001$.

In addition, the distributions of catches from the four nets were compared using Chi-square (χ^2) tests (Table 2). To reduce the number of empty cells for Chi-square tests a subset of the 6 most common species

TABLE 2. A comparison of the collections of adult snakes from four stake nets in the mouth of the Muar River. To reduce the number of empty cells for a Chi-square test two *Lapemis curtus* (nets 1 and 2), one *Pelamis platura* (net 6), one *Hydrophis fasciatus* (net 6), and one *Cerberus schneiderii* (net 1) were not included in the table. The total number of snakes for the four nets (n = 931) is less than the snake total in figure 7 (n = 968) because snakes from nets 3 and 5 and snakes from two instances when catches from nets 6 and 7 were accidently combined were not included in this comparison. A Chi-square test demonstrated a highly significant difference between the observed distribution of snakes across the four nets and the expected numbers ($\chi^2 = 122.95$, df = 15, $p < 0.001$).

	E. schistosa	*H. melanosoma*	*H. torquatus*	*H. brookii*	*H. caerulescens*	*A. granulatus*	N
NET 1	73	46	7	6	1	4	137
NET 2	75	28	13	9	1	1	127
NET 6	228	31	17	22	1	1	300
NET 7	319	14	16	16	2	0	367
Totals	**695**	**119**	**53**	**53**	**5**	**6**	**931**

TABLE 3. Numbers of adult snakes collected at stake net 7 during five tidal periods. The tidal periods are designated by the date of the full moon or new moon for that period. A Chi-square test revealed that the observed abundances for the 5 periods differed significantly from the expected abundances ($\chi^2 = 29.34$, df = 16, $p < 0.05$).

TIDAL PERIOD	*E. schistosa*	*H. melanosoma*	*H. torquatus*	*H. brookii*	*H. caerulescens*	N
Jan. 27	38	0	2	2	0	42
Feb. 25	81	3	7	6	0	97
Mar. 26	145	4	5	7	1	162
May. 10	34	2	0	0	0	36
Sept. 5	21	5	2	1	1	30
Totals	**319**	**14**	**16**	**16**	**2**	**367**

was tested (Table 2). Two *Lapemis curtus* (from nets 1 and 2), 1 *Pelamis platura* (net 6), 1 *Hydrophis fasciatus* (net 6), and 1 *Cerberus schneiderii* (net 1) were not included in the test. The Chi-square test comparing the distribution of adult snakes from the four nets found a significant difference between the observed and expected distributions ($\chi^2 = 122.95$, df = 15, $p \leq 0.001$). A comparison between the distribution of snakes from nets 1 and 2 resulted in no significant difference ($\chi^2 = 8.24$, df = 5, $p > .05$) while the other five pairwise comparisons of nets 1, and 2, with nets 6, and 7, and between nets 6 and 7 resulted in significant differences at $p \leq .01$.

Table 2 reveals some of the noteworthy differences between the collections made at the four nets. For example, *H. melanosoma* is the second most common snake at nets 1, 2, and 6 while at net 7 it is the fourth most common snake representing just 3.8 percent of the snakes captured. Also, *H. torquatus* was roughly twice as common at net 2 (10 percent) as at net 1 (5 percent).

Diversity through time.– Because collections differed significantly among nets, comparisons between tidal periods must be

TABLE 4. Numbers of adult snakes collected at stake net 6 during five tidal periods. The tidal periods are designated by the date of the full moon or new moon for that period. Snakes from two instances when catches from nets 6 and 7 were accidentally combined were not included. A Chi-square test based on the first four species (those without zero cells) revealed that the observed abundances for the five periods did not differ significantly from the expected abundances ($\chi^2 = 17.46$, df = 12, $p > 0.05$).

Period	*E. schistosa*	*H. melanosoma*	*H. torquatus*	*H. brookii*	*H. caerulescens*	*H. fasciatus*	*A. granulatus*	*P. platura*	N
Jan. 27	15	1	2	4	0	0	0	0	22
Feb. 25	34	9	3	4	0	0	0	1	51
Mar. 26	128	14	4	9	0	2	1	0	158
May. 10	24	2	3	3	0	0	0	0	32
Sept. 5	27	5	5	3	1	0	0	0	41
Totals	228	31	17	23	1	2	1	1	304

made within net collections. The total numbers of snakes captured at nets 1, 2, 6, and 7 were 137, 127, 300, and 367 respectively (Table 2). Distributing snake abundances over five tidal periods within the four nets further partitioned the samples and resulted in many empty cells. Although the small samples at nets 1 and 2 precluded meaningful comparisons, nets 6 and 7 were compared. Table 3 provides the abundances for all adult snakes of six species collected at net 7 during five tidal periods. A Chi-square test revealed that the observed abundances for the 5 periods differed significantly from the expected abundances ($\chi^2 = 29.34$, df = 16, $p < 0.05$). However, a Chi-square test on the observed distribution of snakes of the four most common species over the five tidal periods at net 6 (Table 4) detected no significant differences from the expected values ($\chi^2 = 17.46$, df = 12, $p > 0.05$).

DISCUSSION AND CONCLUSIONS

The marine snakes that inhabit the mouth of the Muar River have adapted to a very dynamic tidal environment that is relatively small in area and spatially restricted by shorelines on two sides. In addition to the hourly changes in salinity, turbidity, speed of the current and direction of flow, the river also varies in depth. The stake nets 1, 2, 6, and 7 are also in, or adjacent to a channel within the river bed.

Extensive sampling over many months at Muar revealed an assemblage of marine snakes that included one very common species, three common species, four rare species, and three very rare species that likely represent waifs. These collections strongly support the view that the numerical marine snake species richness for the mouth of the Muar River is eight species.

Diversity among nets.– Species-diversity-accumulation curves using Brillouin's index (HB) for nets 1, 2, 6, and 7 are shown in Figure 8. Comparisons of the diversity of the catches from the four nets using the Brillouin index, the Shannon index, the Simpson index and Chi-square tests all demonstrate that the collections of snakes from nets 1 and 2 were essentially the same while the collections from those two nets differed from collections from nets 6 and 7, and collections from nets 6 and 7 differed from each other. Table 2 shows that the especially strong dominance of *E. schistosa* and the relatively low numbers of *H.*

melanosoma at net 7 contribute strongly to the observed differences among nets.

The significant differences between collections made at the stake nets, especially between nets 6 and 7, were unexpected given their close proximity to each other. The causes underlying the observed differences are not known but they may be due to differences in depths, substrate, or location relative to the shore and/or the Straits. The results of a mark-and-recapture study (Voris et al., 1983; Voris, 1985) at the mouth of the Muar River demonstrated that *E. schistosa* maintains very local populations despite the extremely dynamic nature of the river mouth. Thus, the available evidence strongly suggests that marine snakes living in dynamic estuarial settings can maintain very local populations that can differ on a scale of just tens of meters.

These fine-scale differences observed at Muar are strongly corroborated by population studies of sea kraits (e.g. Lading et al., 1991; Shetty and Shine, 2002; Brischoux et al., 2009; Tandavanitj et al., 2013), Australian sea snakes living on the Great Barrier Reef (Burns and Heatwole, 1998; Lukoschek et al., 2007; Lukoschek and Shine, 2012), and possibly the pelagic sea snakes resident in the Gulf of Dulce, Costa Rica (Bessesen, 2012).

Diversity among tidal periods.– The observed distributions of snakes over the 5 tidal periods at nets 6 and 7 (Tables 3 and 4) strongly suggests that *E. schistosa* is the dominant species throughout the year and that *H. brookii*, *H. melanosoma*, and *H. torquatus* are a persistent part of the marine snake assemblage during most tidal cycles. Results from net 7 suggest that there may be subtle seasonal differences in the marine snake assemblage at the mouth of the Muar River but overall this study found very little evidence of significant fluctuations in species composition or relative abundances through time.

Sex ratios over time.– In general, the sex ratio of adult *E. schistosa* collected at the nets was 1:1. A notable exception was between March 18 and April 21 at net 7 where 53 males and only 28 female adult *E. schistosa* were observed. These observed numbers deviate significantly from the expected 1:1 ratio ($\chi^2 = 7.72$, df = 1, $p < 0.01$). Although the cause of this “shortage” of adult females at net 7 during this period is unknown it may be related to the fact that this was the same time that neonates first appeared in the nets. Thus, adult females may have relocated or changed behavior around the time of giving birth. Males also outnumbered females during this time at nets 1, 2, and 6, but the differences were not significantly different from 1:1.

Diversity between years.– On three days in October and November of 1971 the author collected marine snakes from nets 1 and 2 in the Muar River. The location and operation of the nets was the same as described here. The catch from nets 1 and 2 were pooled and consisted of 28 *E. schistosa*, 3 *H. melanosoma*, 5 *H. brookii*, 2 *H. torquatus*, and *1 A. granulatus*. The catches of 1971 were compared to the combined ones of 1975 from nets 1 and 2 (Table 2) and found to not differ significantly ($\chi^2 = 10.26$, df = 6, $p > 0.05$).

Between 27 May and 26 July 1983 collections were again made at Muar. During this period many neonate and juvenile snakes were captured and released. The 1983 collections from adjacent nets 1 and 2 and 6 and 7 were combined, identified, counted, and released near their point of capture. The combined catches of adult snakes from nets 1 and 2 consisted of 59 *E. schistosa*, 34 *H. melanosoma*, 7 *H. brookii*, 13 *H. torquatus*, and *3 A.*

granulatus. These numbers were compared to the combined values from nets 1 and 2 in 1975 (Table 2) using a Chi-square test and the observed distribution was found to not differ significantly from the expected distribution ($\chi^2 = 2.75$, df = 5, $p > 0.05$).

In 1983, the combined catches of adults from nets 6 and 7 consisted of 66 *E. schistosa*, 18 *H. melanosoma*, 7 *H. brookii*, 5 *H. torquatus*, and 1 *A. granulatus*. These numbers were compared to the combined values in 1975 from nets 6 and 7 (Table 2) in a Chi-square test and the observed distribution was found to differ significantly from the expected ($\chi^2 = 506.78$, df = 5, $p < 0.01$). Contributing to this finding were two notable differences. *Enhydrina schistosa* made up 82 percent of the collection from nets 6 and 7 in 1975 but only 68 percent in 1983. Meanwhile, the percentages increased for *H. melanosoma* from 7 to 19 percent and for *H. brookii* from 6 to 7 percent. The cause of these differences in relative abundance of species between 1973 and 1983 is unknown. It is possible that the observed change at net 7 might be rooted in the removal of many adult and juvenile snakes from the populations in 1975. Although this is only one possible explanation it should be taken seriously. Studies that removed specimens from populations have provided much needed natural history information on reproductive biology (e.g. Lemen and Voris, 1981; Voris and Jayne, 1979), diet (Voris and Glodek, 1980; Voris and Moffett, 1981; Glodek and Voris, 1982), behavior (Voris et al., 1978), and epibionts (Jeffries and Voris, 1979) but these benefits must always be balanced against possible disruption of the populations under study.

Comparisons between Southeast Asian localities.– Historically the vast majority of collections of marine snakes come from trawlers operating over large undefined areas. A few studies have focused on small defined areas such as particular reefs or island/reef complexes and identified and recorded each snake observed, thus providing relative abundance data. The latter studies provide valuable results for comparisons to our findings at Muar. The two most comparable studies are those of Dunson and Minton (1978) and Takahashi (1984) because they were also conducted in Southeast Asian waters.

Dunson and Minton (1978: Table 2) reported on a collection of marine snakes that were obtained by night-lighting and by daytime free diving and Hookah diving over 6 days in Sept. 1975. The collection was made on the shoals east and southeast of the Gigante Islands, Carles, Western Visayas, Philippines. The shoals cover an area of roughly 20 km^2 (estimate by the present author) with depths between 2 and 10 m. A total of 421 marine snakes representing12 species were observed on the shoals. The most common species, *Hydrophis ornatus*, made up 62% of the total while the four most common species made up 90% of the sample. Simpson’s D value for this collection is 0.410, STD 0.338 (Table 5).

Takahashi (1984) reported on snorkel surveys made at nine locations in the Ryukyu Islands, Japan between 1975 and 1981. Most locations were visited only once but one location, Hatoma Island, was surveyed four times. The area surveyed covered about 12.6 km^2. It should be noted that in this study snakes were not collected or tagged so it is possible individuals were observed more than once. Eighty-two snakes were observed belonging to two species of true sea snake and three species of sea krait. The most common species, *Hydrophis melanocephalus*, was observed 38 times and made up 46% of the

TABLE 5. Comparison of marine snake diversity at several locations. The geographic locations in the top row refer to the following publications: Muar River Mouth (this study), Gigantes Isl. Shoals (Dunson and Minton, 1978, table 2), Hatoma Isl. (Takahashi, 1984, table 2), Chesterfield Reefs (Minton and Dunson, 1985), Ashmore Reef 2005 (Guinea and Whiting, 2005, table 2) and Ashmore Reef 2013 (Lukoschek et. al., 2013, table 4). PIE in column 1 refers to the probability of interspecific encounter (Hurlbert, 1971). The duration and area data are estimates and do not imply exact comparability between studies.

	Muar River Mouth	**Gigantes Isl. Shoals**	**Hatoma Isl.**	**Chesterfield Reefs**	**Ashmore Reef 2005**	**Ashmore Reef 2013**
Number of Species	8	12	5	6	8	5
Snakes Observed	965	421	82	74	80	212
Simpson's D	0.565	0.410	0.332	0.351	0.204	0.369
PIE	0.435	0.591	0.668	0.649	0.796	0.631
Duration	49 d	5 d	157 hr	7 d	7 d	10 d
Area (sq km)	1.25	20	12.6	105	0.38	-
Community	Estuarial	Coral	Coral	Coral	Coral	Coral

observations. Simpson's D for this collection is 0.332, STD 0.142 (Table 5).

It is worth noting that at the Gigante Island shoals, Hatoma Island, and Muar the dominant species made up 62, 46, and 74 percent of the snakes observed at the respective locations. This is reflected in Figure 10 where the Gigante Island shoals, Hatoma Island, and Muar are compared in terms of the probability of interspecific encounter (PIE) values. The Muar collection in which *E. schistosa* made up nearly three-quarters of the snakes collected is the collection in which the PIE is the lowest (Table 5).

Although the studies of Dunson and Minton (1978) and Takahashi (1984) do provide data on relative abundance and are the most similar published studies to the Muar study in area surveyed and in fauna, many important differences set them apart. For example, the differences in diversity values are likely confounded by the fact that the samples from the Gigante Island shoals were obtained over the largest area in the shortest time period while the Hatoma Island sample was obtained over a much greater length of time from a much smaller area than the latter. In addition, the shallow water adjacent to both Gigante Island shoals and Hatoma Island are dominated by corals while the mouth of the Muar River supports no corals.

Comparisons to Australian localities.– In Australian waters three studies providing relative abundance data from discreet areas are comparable to the Muar study: Minton and Dunson, 1985; Guinea and Whiting, 2005; and Lukoschek et al., 2013 (Table 5). The early surveys of Ashmore Reef reported by Guinea and Whiting (2005) document the highest marine snake diversity reported for a single contiguous habitat. In fact, in the 1990s a total of 17 species of marine snake were reported from the 583 km^2 Ashmore reef complex. The loss of species on the Ashmore Reef since the 1990s is documented by Lukoschek et al., 2013 and is reflected in the survey reported on in Table 5. The seven-day survey on Chesterfield Reefs reported on by Minton and Dunson, 1985 produced six species and a PIE value of 0.649 (Table 5), very similar to the five species and PIE of 0.631

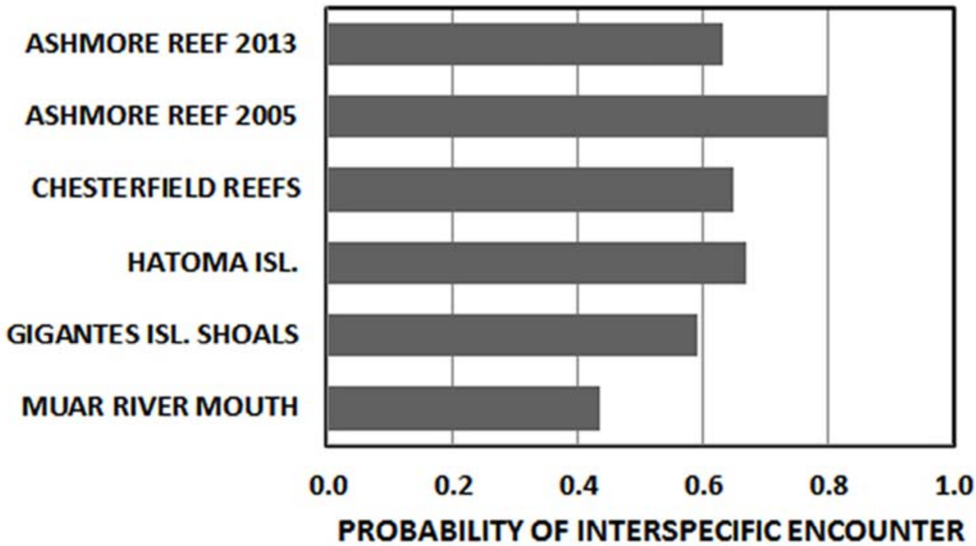

FIGURE 10. A comparison of six marine snake surveys using the probability of interspecific encounter (PIE) or the complement of Simpson's D. Differences in species, habitats, and methods among the surveys preclude definitive explanations for the variation in PIE values (see text and Table 5) and demonstrate the need for further studies.

resulting from the more recent surveys of Lukoschek et al., 2013 on Ashmore Reef. Again, the single most significant difference lies in the fact that the most common species at Muar made up 74 percent of the adult snakes collected while the comparable percentages were only 54, 35, and 33 percent for the Chesterfield Reefs, Ashmore Reef (2005) and Ashmore Reef (2013) respectively.

Although the sample from the mouth of the Muar River represents an assemblage from only one river mouth, the eight species observed (numerical species abundance or richness) at Muar falls in the middle of the range of 5 to 12 species recorded in the other surveys (Table 5). Yet, when it comes to relative abundance (proportional abundances of species) the strong dominance of *E. schistosa* in the mouth of the Muar River makes the Muar assemblage the least diverse of all comparable surveys. These comparisons highlight the unique nature of the marine snake survey at the mouth of the Muar River. Muar is apparently the only discreet estuarial location in the world that has been surveyed for relative abundances of marine snakes.

ACKNOWLEDGEMENTS

I am deeply grateful to my wife, Helen Hahn Voris, for her extensive contributions to the field and laboratory work conducted in Malaysia, as well as assistance with the analysis back in Chicago. I thank Chua Song Chen, Ab Rahman, Lim Ching Chiz, Kiew Bong Heang, William B. Jeffries, Chang Man Yang, Yeo Keng Loo, and Kelvin Lim Kok Peng for essential assistance with all aspects of the field work in Malaysia and Singapore between 1971 and 1985.

Field work was supported by the Ray A. Kroc Environmental Education Fund and the Philip K. Wrigley Fund for Marine Biological Research. Both field and laboratory aspects of this research were supported by gifts from the Allen-Heath Memorial Foundation in 1975 and 1976. The field work in Malaysia was conducted under the sponsorship of the Institute of Medical Research (IMR), Kuala Lumpur with the close cooperation of Mr. Lim Boo Liat of the Medical Ecology Division of IMR.

At the Field Museum of Natural History Marilyn Belka, Raymond Bernard, Carolyn Donovan, Jayne Freshour, Bruce Jayne, Molly Ozaki, Sarah Derr, and Alan Resetar contributed many hours to various facets of the project. Special thanks are also due to the members of the "Sea Snake Sweatshop" crew Phyllis Bieri, Paul Gritis, Cliff Lemen, and Peter Tortorice for long hours of work on preserved specimens. I thank Robert Inger, John Murphy, and Alan Resetar for comments on early drafts of this manuscript. The map of the Muar River mouth (Fig. 2) and the illustration of the stake nets (Fig. 3) were drawn by Zbigniew T. Jastrzebski.

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