Diversity, distribution, and natural history of the marine snakes of Sri Lanka

Article *in* Marine Biodiversity · April 2022

DOI: 10.1007/s12526-022-01259-3

4 authors:

Kanishka Ukuwela
Rajarata University of Sri Lanka
53 PUBLICATIONS 264 CITATIONS

Anslem De Silva
Amphibia and Reptile Research Organization of Sri Lanka
133 PUBLICATIONS 2,313 CITATIONS

Abyerami Sivaruban
University of Jaffna
19 PUBLICATIONS 29 CITATIONS

Kate Laura Sanders
University of Adelaide
106 PUBLICATIONS 3,628 CITATIONS

Marine Biodiversity _####################_
https://doi.org/10.1007/s12526-022-01259-3

SENCKENBERG

ORIGINAL PAPER

Diversity, distribution, and natural history of the marine snakes of Sri Lanka

K. D. B. Ukuwela[1,2] · A. de Silva[3] · A. Sivaruban[4] · K. L. Sanders[1]

Received: 25 June 2021 / Revised: 15 December 2021 / Accepted: 14 January 2022

Abstract

Marine snakes comprise 90% of all marine reptiles, yet they are the least known of all marine reptiles. Among the marine snakes, very little is known about the marine snakes of the Indian Ocean (IO) compared to the marine snake fauna of the Indo-West Pacific (IWP). Hence, there is a dearth of information about the diversity, systematics, distribution, abundance, natural history, and conservation of IO marine snakes. Therefore, to gain insights to the IO marine snake fauna, we conducted a systematic survey on the marine snakes in the island of Sri Lanka, a central tropical location in the IO. Eight sites around the island were sampled for fisheries by-catch from 2010 to the end of 2012. The study documented 14 species (Acrochordidae 1, Homalopsidae 2, Elapidae (Hydrophiinae) 11) of marine snakes from Sri Lankan waters. Our by-catch data indicates that *Acrochordus granulatus*, *Hydrophis curtus*, *Hydrophis cyanocinctus*, *Hydrophis schistosus*, *Hydrophis spiralis*, and *Hydrophis viperinus* are highly abundant (n>20). Further, data demonstrates that the most widely distributed species in Sri Lankan waters are *H. spiralis* and *H. curtus*. However, high volumes of marine snakes in fisheries by-catch indicate that fishing-related mortality is a major threat to marine snakes of Sri Lanka. Given the distinct evolutionary history of these snakes in the IO and the unique conservation value, the IO marine snake fauna (inclusive of Sri Lankan marine snakes) should be considered a separate conservation management unit.

Keywords By-catch · Evolutionary significant units · Conservation management unit · Indian Ocean

Introduction

Marine snakes comprise 90% of all marine reptiles, yet they are poorly known compared to marine turtles (Rasmussen et al. 2011). Snakes with marine habits are present in the snake families Acrochordidae, Colubridae (subfamily Natricinae), Homalopsidae, and Elapidae (subfamily Hydrophiinae) (Heatwole 1999). Of these, homalopsids, natricines, and acrochordids with marine habits are predominantly brackish water inhabitants. However, the viviparous (i.e., ovo-viviparous) marine snakes inthe family Elapidae are truly marine (i.e., live and give birth to live young at sea) and hence called "true sea snakes." Marine snakes are distributed in tropical and subtropical coastal waters throughout the Indo-Pacific region. However, the majority of studies on marine snakes have been centered on the Southeast Asian and Australian marine snake fauna (Voris 1972; Dunson, 1975; Voris et al. 1978). Therefore, very little is known about the Indian Ocean marine snakes (Ganesh et al. 2019).

An estimated 36 species of marine snakes inhabit the coastal waters of the Indian Ocean (IUCN, 2010). However, there is a dearth of information about the systematics, distribution, abundance, biology, threats, and conservation of these species. To gain insights in to the Indian Ocean marine snake fauna, we conducted a systematic survey on the marine snakes in the island of Sri Lanka, a central location in the IO. Sri Lanka is a continental tropical island situated at the southern tip of India. Eighteen species of marine snakes have been

Communicated by R. Thiel

✉ K. D. B. Ukuwela
kanishkauku@gmail.com

1 School of Biological Sciences, The University of Adelaide, Adelaide, SA 5005, Australia

2 Department of Biological Sciences, Faculty of Applied Sciences, Rajarata University of Sri Lanka, Mihintale 50300, Sri Lanka

3 Amphibia & Reptile Research Organization of Sri Lanka, 15/1 Dolosbage Road, Gampola, Sri Lanka

4 Department of Zoology, Faculty of Science, The University of Jaffna, Thirunavely, Jaffna 40000, Sri Lanka

reported from Sri Lanka (Wickramasinghe 2012), including four South Asian endemics that are listed as Data Deficient on the IUCN Red List (IUCN 2010). Twelve of the 18 species reported from Sri Lanka have ranges that extend either along the IO coasts of the Arabian Gulf, Pakistan, India, Bangladesh, Myanmar, and Thailand, or occur throughout the Southeast Asian region (Rezaie-Atagholipour et al. 2016; Razzaque Sarker et al. 2017). Many species have disjunct ranges and show geographical variation in morphology, thus may contain currently unrecognized species. Hence, the actual marine snake diversity could be higher than the currently known diversity in the IO as well as Sri Lanka (Ukuwela et al. 2014; Ukuwela et al. 2016). Yet, there has never been any formal systematic study conducted on the marine snake fauna of Sri Lanka or not even on the marine snakes that are also found in the South Asian region of the IO. As a result, there are major gaps in the knowledge on the marine snakes of Sri Lanka, including (1) the actual species diversity and distribution in Sri Lanka, (2) the phylogenetic relationships to their relatives in other geographic areas, (3) population connectivity in Sri Lanka and elsewhere, (4) biology, and (5) threats. To address these issues, a survey was conducted covering almost all the coasts of Sri Lanka from 2010 to 2013. The results of this study relating to reproductive biology (preliminary findings) (de Silva et al. 2011a), population genetic structure (Ukuwela et al. 2014) and phylogenetic relationships (Ukuwela et al. 2013; Ukuwela et al. 2017b) and biogoegraphic origins (Ukuwela et al. 2016) have already been published elsewhere. Here, we report the diversity and distribution of the Sri Lankan marine snakes with brief notes on their natural history from the above survey and summarize and compare findings from our previously published work and published work from other resources.

Materials and methods

Study region and sampling sites

Sri Lanka lies between latitudes 5° 55′ – 9° 51′ N and longitudes 79° 41′ – 81° 54′ E. With a coastline of 1562 km in length, the island has a shallow continental shelf that has an average width of 22 km from the coast. The coastline of Sri Lanka consists of lagoons, bays, headlands, peninsulas, sand bars, and islets. Sri Lanka encompasses a diverse array of tropical coastal habitats including lagoons and estuaries (42,000 ha), mangroves (6,000–10,000 ha), sea grass beds, salt marshes, and coral reefs (about 50 linear km in length) (Anonymous 1997).

Eight main sampling sites were selected during an island-wide pilot study conducted in early 2010. The main sampling sites selected were (1) Mannar Island, (2) Vankale-Mannar, (3) Puttalam lagoon, (4) Negambo, (5) Kirinda, (6) Uppaveli-Nilaveli coast, (7) Pulmude, and (8) northern coastline of Jaffna Peninsula. Additional samples were opportunistically collected from (9) Jaffna lagoon, (10) Hikkaduwa, (11) Kumana, (12) Thampattai (near Ampara), and (13) Pottuvil areas (Fig. 1). The following is a brief description of these sampling sites.

Mannar Island is a small island off the northwestern coast of Sri Lanka in the Gulf of Mannar. The area surrounding the island constitutes shallow coastal seas (depth 1–11 m), coral reefs, and mangrove habitats. Vankale-Mannar is a coastal fish-landing site in the northwestern coast of northern Sri Lanka facing the Gulf of Mannar. The marine habitats in the area consist of shallow coastal seas (depth 1–11 m) with coral reefs, sea grass beds, and an estuary with extensive mangrove habitats. Negambo is a major fishing port in the western coast of Sri Lanka. This area comprises a lagoon and estuarine mangroves as well as shallow coastal seas (depth 1–30 m). The Puttalam Lagoon is the second largest lagoon (327 km^2) in Sri Lanka, situated in northwestern Sri Lanka. The lagoon's water is brackish to saline and has extensive mangroves, sea grass beds, mud flats, and salt marshes (depth 1–75 m). Kirinda, a fishing port in the southern coast of Sri Lanka, consists of shallow coastal seas (depth 1–100 m) and scattered coral reefs. Uppaveli-Nilaveli is a 12-km coastal stretch, which consists of several small fishing villages in the northeastern coast of northern Sri Lanka. The area comprises of shallow coastal seas (depth 1–200 m), scattered coral reefs, and a river mouth with mangroves. Pulmude is a small fishing village in the northeastern coast of northern Sri Lanka, which consists of shallow coastal seas (depth 1–50 m) and a bay. On the northern coast of Jaffna, small fish landing sites along a 6-km stretch from Valvettithurai to Inparsiddy (i.e., Valvettiturai, Polikandy, Thikkam, Erincha amman kovilddy, and Inparsiddy) were selected for sampling. This stretch consists of shallow coastal seas (depth 1–20 m) with small scattered coral reefs.

Sampling

Marine snakes were collected with permits from the Department of Wildlife Conservation, Sri Lanka, by liaising with local fishermen to obtain their marine snake by-catch from 2010 to the end of 2012. Information including the GPS location, distance (km) from the landing site, and collection time were recorded when available. Tissue samples (liver or muscle tissue preserved in 70% Isopropyl alcohol) were collected for DNA analysis in the laboratory from dead marine snake specimens. The specimens were identified following descriptions and diagnoses of Rasmussen (2001) and Smith (1926). A total of 189 voucher specimens were collected while another 157 specimens were identified in the field but were not vouchered. The voucher specimens were fixed in 10% formalin solution, washed thoroughly in running water,

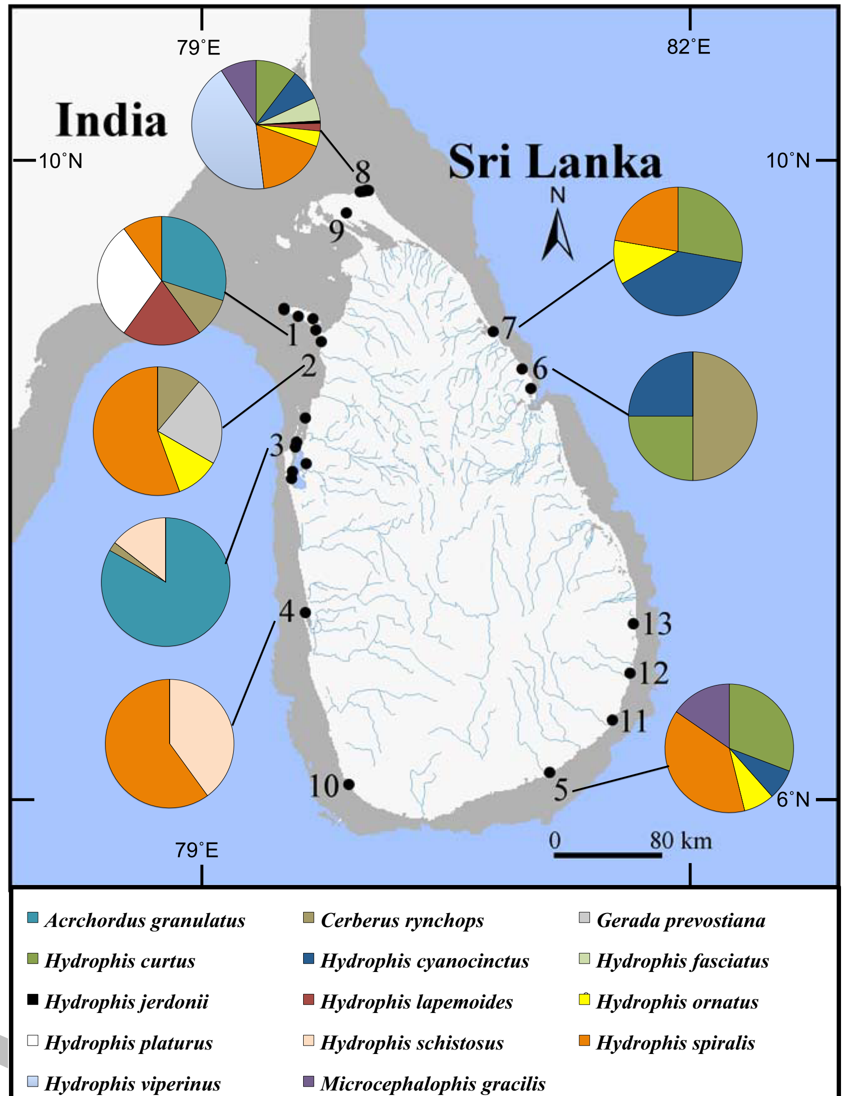


Fig. 1 Sampling locations of the study and the observed distribution patterns of the marine snakes. The numbers denote the sampling sites, Mannar Island (1), Vankale-Mannar (2), Puttalam lagoon (3), Negambo (4), Kirinda (5), Uppaveli-Nilaveli coast (6), Pulmude (7), northern coastline of Jaffna (8), Jaffna lagoon (9), Hikkaduwa (10), Kumana (11), Thampattai (12), and Pottuvil (13). The pie charts represent the proportional percentages of marine snakes observed in each site. The gray area denotes the 120-m isobath drawn from bathymetric data obtained from the General Bathymetric chart of the Oceans (http://www.gebco.net/.)

and later transferred to 70% Isopropyl alcohol. The voucher specimens are accessioned in the Zoology Division in the National Museum of Sri Lanka in Colombo (NMSL) and the Zoology Museum at Girithale National Wildlife Research and Training Center (NWRTC) of the Department of Wildlife Conservation of Sri Lanka (Supplementary Material).

Voucher specimens were dissected to examine reproductive condition and the gut contents. The gut contents were identified to the family level when possible. Reproductive condition was examined only in females by examining for the presence of vitellogenic follicles, oviducal eggs and embryos (also see de Silva et al. 2011b). Standard measurements, snout to vent length (SVL) measured from the tip of the snout to posterior end of the anal plate, and tail length (TAL) from posterior margin of anal plate to tip of tail, were taken from the preserved specimens up to the nearest mm. The sum of SVL and TAL was used to obtain total length of the specimens in mm. When sample size was greater than 5, the total length was averaged in females in reproductive condition to determine the mean size at sexual maturity in each species. Studies on the molecular systematics of the Sri Lankan snakes and IO marine snakes have already been published elsewhere. (See Ukuwela et al. 2013; Ukuwela et al. 2014; Ukuwela et al. 2016; Ukuwela et al. 2017a; Ukuwela et al. 2017b for further details on the methods and outcomes of the individual studies.) Comments on the systematics of the marine snakes of Sri Lanka summarized here have been derived from findings of the above studies.

Results

Diversity and distribution of marine snakes

The study documented 346 specimens of marine snakes belonging to 14 species (file snakes (Acrochordidae) 1, mud snakes (Homalopsidae) 2, viviparous sea snakes (Elapidae) 11) from Sri Lankan waters (Table 1). *Acrochordus granulatus*, *Hydrophis curtus*, *Hydrophis cyanocinctus*, *Hydrophis schistosus*, *Hydrophis spiralis*, and *Hydrophis viperinus* were observed in relatively high abundance (n>20). In comparison, *Gerarda prevostiana* (n=2), *Hydrophis platurus* (n=4), and *Hydrophis jerdonii* (n=1) were recorded in very small numbers. Of the eight main sites sampled, the northern coast of Jaffna had the highest species diversity with 9 species (Fig. 1). Mannar Island and Kirinda had the next highest species diversity with five species each, followed by Vankale and Pulmude, both of which yielded four species (Fig. 1). Based on by-catch data, the most widely distributed species were *H. spiralis* and *H. curtus*, which were collected from six and five sampling sites respectively covering western, southern, northern, and eastern coasts of Sri Lanka (Fig. 1). *Gerarda prevostiana*, *Hydrophis fasciatus*, *H. jerdonii*, and *H. viperinus* were only recorded from a single site/region (Fig. 1). Below we provide accounts for each species with notes on their distribution, habitat, abundance, and natural history and highlight the taxonomic issues based on our previous molecular phylogenetic analyses (Ukuwela et al. 2013; Ukuwela et al. 2014; Ukuwela et al. 2016; Ukuwela et al. 2017a).

Analysis of gut contents

Of the 174 specimens examined for gut contents, 85 (48.85%) specimens had stomach contents. Of these, only in 50 (58.82%) specimens were the contents identifiable while in the rest (35), the contents were unidentifiable due to complete digestion. In all the identified stomach contents, a single individual (*Hydrophis curtus*) had an invertebrate (Mollusca, Gastropoda, Babylonidae), while the rest had fish (98%). Fish belonging to 10 families (Callionymidae, Clupeidae, Congridae, Engraulidae, Gobiidae, Ophichthyidae, Plotosidae, Sciaenidae, Siganidae, Synodontidae) were present in the contents (Fig. 2). Snake eels (Ophichthyidae: 20.83%) were the most dominant type of prey observed in the stomach contents followed by gobies (Gobiidae: 16.67%) (Fig. 2).

Species accounts

Acrochordus granulatus

This species (Fig. 3a) was collected from three locations, two of which were brackish water habitats (Fig. 3d) and the other was a shallow coastal location (Northern coast of Jaffna). Total lengths ranged from 707 to 835 mm. Four gravid females were collected, two in May and another two in August that had well-developed embryos (de Silva et al. 2010). The four gravid females ranged between 707 and 731 mm in total length. Two individuals contained partially digested gobies (Gobiidae) in their guts. Based on our by-catch specimens (113 (32%) out of 346), *Acrochordus granulatus* seems to be a very common species that is caught in large numbers in gill nets in the Puttlam lagoon.

Cerberus rynchops

Eight individuals (2.31% out of 346) (Fig. 3b) were collected from brackish water habitats (Fig. 3d) from the northern, western, and eastern coastal regions of Sri Lanka. Total length ranged from 518 to 668 mm. Two females collected in January and June contained vitellogenic follicles and had total lengths of 668 mm and 775 mm. Gut contents of two individuals contained a partially digested fish that could not be identified and another contained a goby (Gobiidae). Our observations indicate that this is an uncommon species in brackish water habitats that is regularly caught in fishing nets.

Gerarda prevostiana

Two juveniles (0.57% of 346) were caught as fisheries bycatch from Vankale area in Mannar (Mannar district, Northern Province) in the open ocean about 1 km off the coast (Fig. 3c). Total lengths ranged between 175 and 196 mm. This is a rare species in Sri Lanka known from only a few previous records from brackish water habitats in western and northwestern coastal locations (see Somaweera et al. 2006, Karunarathna et al. 2018). Based on analyses of the mitochondrial *cytochrome b* gene (*Cyt-b*), the Sri Lankan individuals of *G. prevostiana* form a distinct clade with conspecifics in Singapore with a pairwise divergence of 3.08–3.87% (Ukuwela et al. 2017a).

Hydrophis curtus

This common species (24 (6.93%) out of 346) was frequently collected from fishing nets of the coastal regions of northern, eastern, and southern coasts of Sri Lanka (Fig. 4a). Total lengths ranged between 446 and 911 mm. Females collected in March, April, May, and October contained vitellogenic follicles while two females collected in March and April contained 4–10 eggs (mean number of eggs=8.67) (de Silva et al. 2011b). The total length of females in reproductive condition ranged between 539 and 911 mm (mean=717.00 mm, SD=±114.45 mm) (Fig. 5). Gut contents included various types of fish (Clupeidae, Engraulidae, Synodontidae) and a shelled gastropod (de Silva et al. 2011a). Based on *Cyt-b* analyses, the Sri Lankan population of *H. curtus* forms a monophyletic group with other IO *H. curtus* populations, and this clade differs from a West Pacific (WP) *H. curtus* clade by 9.3–9.5% (Ukuwela et al. 2014).

Table 1 Marine snake species, sampling regions, and numbers

Species	Sampling site											
	Mannar island	Vankale	Negambo	Puttalam Lagoon	Jaffna N.C.	Pulmude	Kirinda	Kumana	Uppaveli-Nilaveli	Pothuvil	Hikkaduwa	Thampattai, Ampara
Family: Acrochordidae												
Acrochordus granulatus	3	-	-	6 (103)	1	-	-	-	-	-	-	-
Family: Homalopsidae												
Cerberus rynchops	1	1	-	3	-	-	-	-	2	-	-	1
Gerarda prevostiana	-	2	-	-	-	-	-	-	-	-	-	-
Family: Elapidae (Hydrophiinae)												
Hydrophis curtus	-	-	-	-	16	5	1	-	1	1	-	-
Hydrophis cyanocinctus	-	-	-	-	12	7	4	1	1	-	-	-
Hydrophis fasciatus	-	-	-	-	9	-	-	-	-	-	-	-
Hydrophis jerdonii	-	-	-	-	1	-	-	-	-	-	-	-
Hydrophis lapemoides	2	-	-	-	3	-	-	-	-	-	-	-
Hydrophis ornatus	-	1	-	-	6	2	1	-	-	-	-	-
Hydrophis platurus	3	-	-	-	-	-	-	-	-	-	1	-
Hydrophis schistosus	-	-	2	19	-	-	-	-	-	-	-	-
Hydrophis spiralis	1	5	3	-	10 (17)	4	5	-	-	-	-	-
Hydrophis viperinus	-	-	-	-	29 (37)	-	-	-	-	-	-	-
Microcephalophis gracilis	-	-	-	-	14	-	2	-	-	-	-	-

*Values in parentheses indicate the number of individuals observed (not collected) while the values outside parentheses indicate the number of voucher specimens collected from each site

Hydrophis cyanocinctus

This common species (25 (7.22%) out of 346) was frequently collected from the fishing nets of northern, eastern, and southern coasts of Sri Lanka. Total lengths ranged from 454 to 1295 mm (Fig. 4b). Females collected in January, February, and October contained vitellogenic follicles while a specimen collected in August contained four eggs and another female collected in May contained five fully developed embryos (de Silva et al. 2011b). Females in reproductive condition ranged between 757 and 1295 mm (mean=1109.91 mm, SD=±167.29 mm) (Fig. 5). Gut contents comprised eel-tail catfishes (Plotosidae), garden eels (Congridae), and gobies (Gobidae). The Sri Lankan population of *Hydrophis cyanocinctus* forms a monophyletic group with other sampled IO *H. cyanocinctus* populations based on *Cyt-b* analyses. This IO lineage is genetically divergent from their conspecifics in Southeast Asia by a distance of 4.01–4.95% in *Cyt-b* gene and does not show a sister species relationship (Sanders et al. 2013; Ukuwela et al. 2016).

Hydrophis fasciatus

This uncommon species (9 (2.6%) out of 346) was recorded only from the northern coastal region of the island (also see Abyerami & Sivashanthini 2008) (Fig. 4c). Total lengths of the sampled specimens ranged from 757 to 993 mm. Females with vitellogenic follicles were recorded from May to August while females with 4–7 eggs were recorded in August (mean number of eggs and embryos =5.67, SD=±1.53). A female with five partially developed embryos and one egg were recorded in January. The females in reproductive condition ranged between 757 and 993 mm in total length (mean=898.50 mm, SD=±94.38 mm) (Fig. 5). Phylogenetic analysis of the *Cyt-b* gene indicates close affinities (mean p-distance: 0.294%) between IO (i.e., Sri Lanka only) and Southeast Asian populations of this species (Ukuwela et al. 2016).

Hydrophis jerdonii

A single specimen (0.28% of 346) with a total length of 902 mm was recorded from the northern coast of Jaffna in January 2013 (Fig. 4d), in close proximity to the most recent previous record of this species (Abyerami & Sivashanthini 2008). The specimen was a gravid female that contained three eggs. The species seems to be rare in Sri Lankan waters.

Hydrophis lapemoides

This uncommon species (5 (1.44%) out of 346) was recorded from two different locations in the northern coastal region of Sri Lanka (Fig. 4e). The total length of the specimens ranged between 674 and 853 mm, and the two females that were in reproductive condition had total lengths of 674 and 763 mm. A female with a total length of 674 mm collected in January was gravid with 3 eggs.

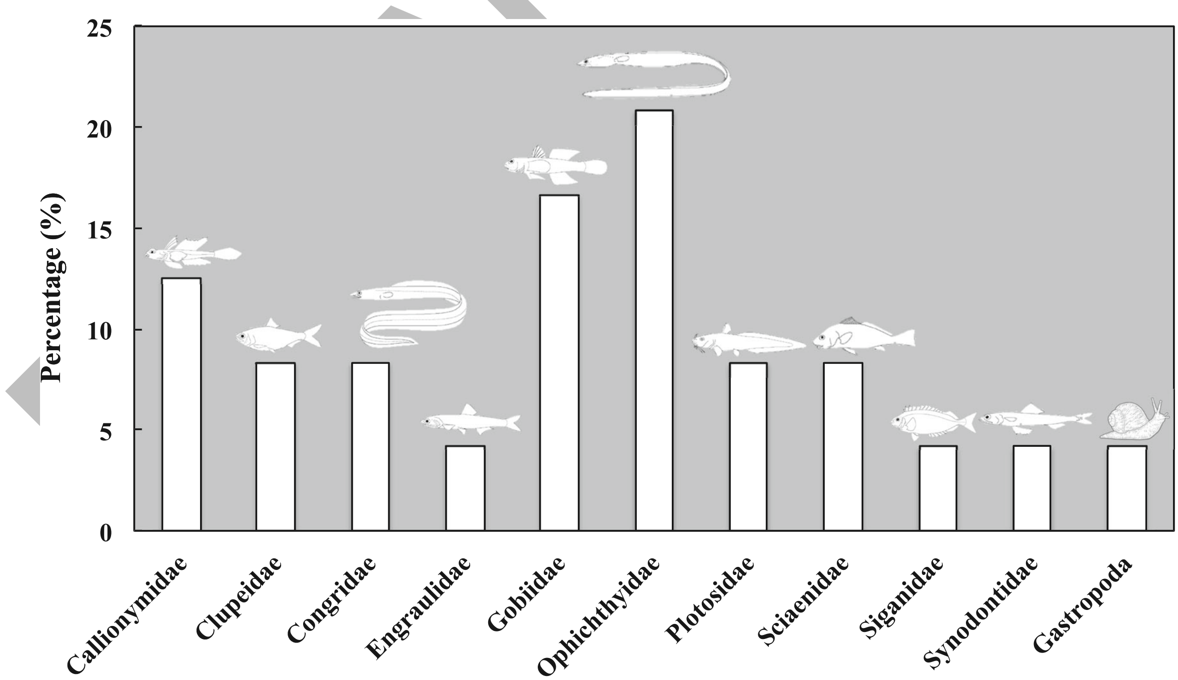


Fig. 2 Diversity of prey types observed in the stomach contents of marine snakes dissected in the study

Fig. 3 Brackish water marine snakes observed during the survey; **a***Acrochordus granulatus*; **b***Cerberus rynchops*; **c***Gerarda prevostiana*; **d** a pristine mangrove, habitat of the brackish water marine snakes (photos; **a**, **b**—K.D.B. Ukuwela; **c**, **d**—A. de Silva)

Hydrophis ornatus

This uncommon species (10(2.89%) out of 346) was collected from the by-catch from northern, eastern, and southern coasts (Fig. 4h). The total length of the specimens ranged between 335 and 925 mm. Females with vitellogenic follicles and gravid females (n=4) with 2–3 eggs were collected in January and had total lengths ranging between 615 and 925 mm (mean= 819.75 mm, SD=±145.21 mm) (Fig. 5). Gut contents included gobies (Gobiidae) and eel-tail catfishes (Plotosidae). Based on *Cyt-b* analysis, the Sri Lankan population of *Hydrophis ornatus* forms a monophyletic group with other sampled IO *H. ornatus* populations. However, this IO lineage is genetically divergent from *H. ornatus* in Southeast Asia by a distance of 3.33–4.12% in the *Cyt-b* gene and does not show a sister species relationship (Ukuwela et al. 2016).

Hydrophis platurus

Four specimens (1.15% out of 346) were recorded from three locations from the southern and northern coasts. The total lengths ranged from 316 to 764 mm (Fig. 4f). Two females containing vitellogenic follicles were collected in May and had total lengths of 721 and 764 mm. Phylogenetic analyses of *Cyt-b*gene showed shallow genetic divergence (mean p-distance: 0.148%) for two populations of this species spanning the IO and WP (Ukuwela et al. 2016).

Hydrophis schistosus

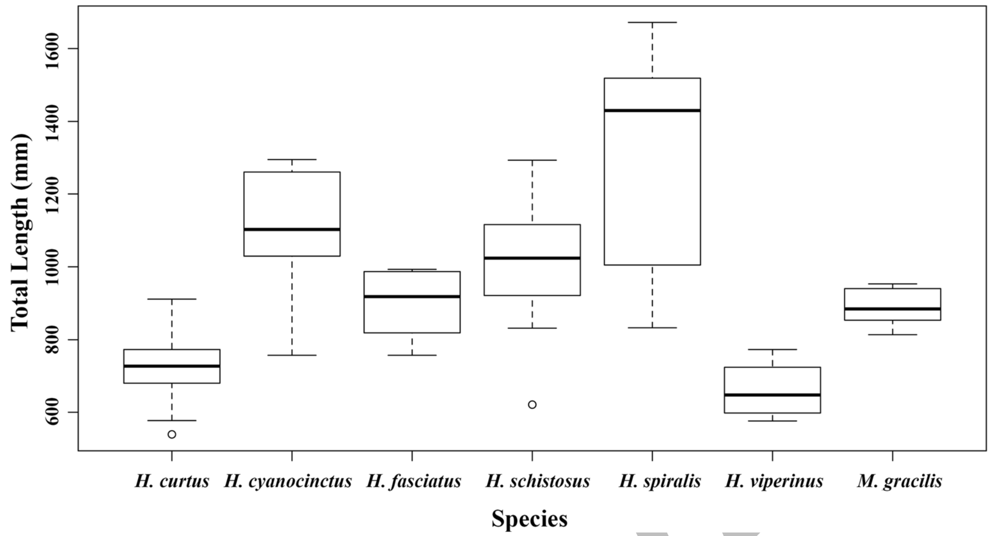
This common species (21 (6.1%) out of 346) was regularly collected from the by-catch mostly from brackish water habitats along the northwestern and western coasts during the study (Fig. 4g). However, four specimens were collected from trawl nets as far as 3 km off the coast of Kudiramale (north of Puttlam lagoon). The total length of the specimens ranged from 513 to 1293 mm. Females with vitellogenic follicles were collected in March while gravid females were collected in June and their total length ranged between 621 and 1293 mm (mean=1054.88 mm, SD=±238.81 mm) (Fig. 5). Litter sizes ranged between 7 and 16eggs/embryos per female (mean number of eggs and embryos =12.17, SD=±3.43). Gut contents were rabbit fish (Siganidae) and croakers (Sciaenidae). Phylogenetic analyses of the *Cyt-b* gene recovered two clades corresponding to populations in the IO (including Sri Lankan individuals) and Southeast Asia, with 4.06–4.96% divergence between the two clades (Ukuwela et al. 2016).

Hydrophis spiralis

This common species (28 (8.09%) out of 346) was regularly collected in coastal fisheries (3–5 km off the coast) from northern, southern, and western coasts (Fig. 4k). The total length of the specimens ranged from 451 to 1672 mm. Females with vitellogenic follicles were collected from January to October while gravid females were collected in January and October and the total length of females in reproductive condition ranged between 823 and 1672 mm (mean=1286.44 mm, SD=±297.11 mm) (Fig. 5). Litter sizes ranged between 7 and 13eggs/embryos per female (mean number of eggs and embryos =9.50, SD=±2.65). Gut contents were identified as eels in the families Ophichthidae and Muraenidae. Phylogenetic analysis of the *Cyt-b* gene indicates

Fig. 4 Viviparous sea snakes observed during the survey. **a** *Hydrophis curtus*; **b** *Hydrophis cyanocinctus*; **c** *Hydrophis fasciatus*; **d** *Hydrophis jerdonii*; **e** *Hydrophis lapemoides*; **f** *Hydrophis platurus*; **g** *Hydrophis schistosus*; **h** *Hydrophis ornatus*; **i** *Hydrophis viperinus* (striped form); **j** *Hydrophis viperinus* (plain form); **k** *Hydrophis spiralis*; **l** *Microcephalophis gracilis* (photos: a, j, k, l—K.D.B. Ukuwela; b, c, d, e, e, g, h, i—A. de Silva)

Fig. 5 Boxplot of the total length of seven species of female marine snakes in reproductive condition



weak population genetic structure between IO and Southeast Asian populations of this species (Ukuwela et al. 2016).

Hydrophis viperinus

This common species (37 (10.7%) out of 346) was regularly collected as fishery by-catch from coastal habitats (3–5 km off the coast) in the northern coast of Jaffna (Fig. 4 i and j). The total length of the specimens ranged from 505 to 773 mm. Females with vitellogenic follicles were observed between January and July while females with eggs (3–4) and embryos (2–6) were observed from April to August (mean number of eggs and embryos=3.60, SD=±1.52). The total length of the females in reproductive condition ranged between 576 and 773 mm (mean =663.71 mm, SD=±65.83 mm) (Fig. 5). Gut contents contained fish of the family Callionymidae (dragonets). *Hydrophis viperinus* populations in the IO and Southeast Asian seas form two corresponding reciprocally monophyletic groups and the populations are divergent in the *Cyt-b* gene by 4.05–4.85% (Ukuwela et al. 2016).

Microcephalophis gracilis

This uncommon species (16 (4.62%) out of 346) was recorded from the northern and southern coasts collected as fisheries by-catch approximately 3–5 km off the coast (Fig. 4l). The total length of the specimens ranged from 770 to 1244 mm. Females with eggs and vitellogenic follicles were observed in January, July, and December. Gravid females contained 4–7 eggs (mean number of eggs and embryos =5.00, SD =±1.41). The total length of the females in reproductive condition ranged between 813 and 953 mm (mean=887.83 mm, SD=±55.46 mm) (Fig. 5). Gut contents were identified as snake eels (Ophichthidae). *Microcephalophis gracilis* populations in the IO and Southeast Asian seas form reciprocally monophyletic groups and the populations are divergent in the *Cyt-b* gene by 4.53–5.44% (Ukuwela et al. 2016).

Discussion

The present study reports 14 species of marine snakes (Table 1) from Sri Lankan waters. This represents 16% of the currently known marine snake fauna in the world, 78% of the marine snake diversity previously reported from Sri Lanka, and 14% of the total snake fauna of Sri Lanka. We discuss these findings with respect to the diversity, ecology, systematics, distribution, and conservation of the marine snakes of Sri Lanka.

Diversity and systematics of marine snakes of Sri Lanka

The total diversity of marine snakes currently recognized in Sri Lanka is 18 species (15 elapids, 2 homalopsids, 1 acrochordid) (Wickramasinghe 2012). In one of the earliest reports on marine snakes, Wall (1921) listed all 22 of the known IO species of marine elapids as occurring in Sri Lanka. Subsequently, Deraniyagala (1955) revised this list to include only 18 species of marine snakes and later works by de Silva (1980) and (1990) listed 19 species. However, de Silva (1994) suspected the occurrence of *H. fasciatus*, *Hydrophis caerulescens*, *Hydrophis nigrocintus*, and *Lapemis hardwicki* (now synonymized with *H. curtus*) in Sri Lanka based on the records of these species by Murthy (1977) off the southeast coast of Madras, India. Subsequently, Balasubramaniam (2007) reported the occurrence of *Hydrophis mamillaris* and Abyerami and Sivashanthini (2008) confirmed the occurrence of *H. fasciatus* in Sri Lanka. Though *Laticauda colubrina* was added to the list of

Sri Lankan sea snakes by Das and de Silva (2005), no specimen has been found in Sri Lankan waters.

Our present survey failed to locate any specimens of *Hydrophis bituberculatus*, *H. mamillaris*, *Hydrophis stricticollis*, *Hydrophis stokesii*, and *L. colubrina*. Although the type locality of *H. bituberculatus* is Sri Lanka, it has not subsequently been collected in Sri Lanka but has been collected in Thailand (Rasmussen 1992). The most recent survey on marine snakes of Sri Lanka recorded *H. stricticollis* but failed to record *H. bituberculatus* and *H. stokesii* (Wickramasinghe & Rodrigo 2004). Historical surveys have also failed locate these species from the region (Hallermann et al. 2001; Kharin and Hallerman, 2009). Furthermore, we failed to locate any specimens of *H. bituberculatus* and *H. stokesii* in the collections of the National Museum of Sri Lanka in Colombo. Thus, the occurrence of *H. bituberculatus* and *H. stokesii* in Sri Lanka needs to be re-evaluated. A recent survey reported a single specimen of *Hydrophis caerulescens* from the Indian coast of the Gulf of Mannar (Lobo 2006). Thus, the absence of this species in Sri Lankan waters can be explained by its extreme rarity in the region. The same can be concluded for *H. mamillaris* that has only a single confirmed record in Sri Lanka but several records in neighboring India (Hallermann et al. 2001; Kharin and Hallerman, 2009). However, the occurrence of the banded sea krait (*L. colubrina*) in Sri Lanka is doubtful despite its addition to the Sri Lankan list by Das and de Silva (2005). Sea kraits are the most conspicuous of all marine snakes due to their close association with land as they come ashore to rest and lay eggs (Heatwole 1999). However, so far a specimen has never been observed in Sri Lanka nor seen resting or laying eggs in the coastal regions of Sri Lanka. The closest place to Sri Lanka where *L. colubrina* occurs is Andaman and Nicobar islands, which are more than 1200 km from the east coast of Sri Lanka. Since *L. colubrina* is a shallow water specialist, it is highly unlikely that it would cross this large expanse of deep sea that separates the two locations. Reasonably, Wickramasinghe (2012) did not include it in the recent most list of Sri Lankan snakes due to the lack of confirmed specimens from Sri Lankan waters.

Most abundant species (n>20) observed in the survey were *A. granulatus*, *H. curtus*, *H. cyanocinctus*, *H. schistosus*, *H. spiralis*, and *H. viperinus*. It is most likely that the populations of these species are high; however, it is also possible that it could be a sampling artefact as all these specimens were collected from artisanal fisheries by-catch and these fishers may be fishing in areas where these species are more abundant. However, *G. prevostiana*, *H. platurus*, and *H. jerdonii* were the least abundant species observed in the study. Our island-wide sampling in both open ocean and brackish waters indicates that both *G. prevostiana* and *H. jerdonii* could actually be very rare. However, the rarity of *H. platurus* could be most likely due to a sampling effect as this is the most widespread of all sea snakes in the world. *Hydrophis platurus* is a pelagic species that is usually observed in open ocean habitats about 5–10 km from the coast. The artisanal fishers we obtained our specimens from, rarely fish in the deeper open oceans. Thus, the rarity could most likely be due to this reason. The complete absence of *H. stricticollis* is however inexplicable given the fact that the species was found in the most recent marine snake survey (Wickramasinghe & Rodrigo 2004) and also by the availability of specimens in the National Museum of Sri Lanka collected from the northwestern coast.

Our phylogeographic analyses across the Indo-Pacific indicated the presence of strongly supported and reciprocally monophyletic lineages that correspond to the IO and Southeast Asia/WP for *G. prevostiana*, *H. curtus*, *H. schistosus*, *H. viperinus*, and *M. gracilis* (Ukuwela et al. 2014; Ukuwela et al. 2016; Ukuwela et al. 2017a). On average, the intraspecific corrected pairwise genetic divergences in the *Cytochrome b* gene ranged between 2.5 and 9.5% between the two lineages corresponding to the IO and Southeast Asia/WP. Further, our analyses recovered distantly related but cryptic lineages within both *H. cyanocinctus* and *H. ornatus* in the IO and WP. *Hydrophis cyanocinctus* sampled from the IO formed a sister lineage to a clade that contained three highly morphologically divergent species, including *H. cyanocinctus* from West Pacific (Southeast Asia and Australasia), *H. parviceps* and *H. coggeri* (Sanders et al. 2013; Ukuwela et al. 2016). Similarly, *H. ornatus* from Southeast Asia was sister to a clade that contained Southeast Asian species *H. lamberti* and *H. ornatus* from the IO (Ukuwela et al. 2016). Whether the paraphyly of *H. ornatus* reflects phenotypic convergence or whether it is due to incomplete lineage sorting of molecular markers needs to be tested using additional independent nuclear markers. This suggests that the actual diversity and regional endemism of viviparous sea snakes could be higher than currently known. Hence, broader sampling across each species' range and morphological examinations are needed to delimit cryptic species boundaries and their corresponding geographic ranges. Moreover, in addition to identifying morphological characters that may separate these cryptic lineages, it would be worthwhile to test for the presence of gene flow between them, which would provide further evidence that could be used in species delimitation.

Distribution of the marine snakes of Sri Lanka

Our by-catch data indicates that two species occur in many different coastal regions of the island while several other species are restricted to certain regions. The most widely distributed species, *Hydrophis spiralis* and *Hydrophis curtus*, were collected in our study from northern, southern, western, and eastern coasts of the island (Fig. 1). Museum records also indicate that these species have also been collected from all over the island (Deraniyagala 1955; De Silva 1980; de Silva 1990; Somaweera 2006; Somaweera & Somaweera 2009). *Gerarda prevostiana*, *H. fasciatus*, *H. jerdonii*, and *H. viperinus* were only recorded from a single site/region. The restricted distribution of *G. prevostiana* and *H. jerdonii* can be explained by their low number in our sampling in Sri Lanka (also see Ukuwela et al. 2017a; Karunarathna et al. 2018). However, our island-wide sampling suggests that *H. fasciatus* and *H. viperinus* are restricted to the northern coastal waters. Though *H. fasciatus* was rather an uncommon species, the latter was caught in considerable numbers in the northern coast of the Jaffna peninsula. This suggests that observation of *H. viperinus* only in the northern region during the study is due to restricted distribution of this species rather than rarity. Interestingly, *H. schistosus* was only observed in two locations in the west coast, while previous reports were also limited to lagoon and brackish water habitats of the west coast (Deraniyagala 1955; De Silva 1980; de Silva 1990; Somaweera 2006). Consistent with this, fishermen from many eastern coastal locations of the island failed to recognize photographs of *H. schistosus* despite its distinctiveness. This indicates that *H. schistosus* is most likely restricted in distribution to the west coast despite the presence of suitable habitats on the east coast. However, intense sampling in the coastal brackish water habitats in the east coast is necessary to verify this observation.

The findings of this study indicate that marine snake richness and abundances are differentially distributed across the eight main study sites. These differences are most likely due to the heterogeneity of the marine habitats at the study sites. The higher species richness in the northern coast of Jaffna could be explained by the large expanse of shallow seas (depth <120 m) in the region (Fig. 1). Given that hydrophiine sea snakes generally prefer waters shallower than 100 m except *H. platurus* (Heatwole, 1999), these shallow regions, which extend up to the coast of India, may provide a variety of habitats for sea snakes. The lowest species richness (2), which was recorded from Negambo, can be described by the presence of a narrow shallow coastal region in the area (Fig. 1). However, this region has significant areas of Mangroves, which provide ideal habitats for brackish water species such as *C. rhynchops*, *A. granulatus*, and *G. prevostiana* (Bambaradeniya et al. 2002). However, except the brackish water species *H. schistosus*, the latter three species were inexplicably absent in the fishery by-catch given that *C. rhynchops and A. granulatus* have been previously recorded from the region (Bambaradeniya et al. 2002). It is however possible that the fishery encountered in the survey were mainly open ocean fishers rather than lagoon fishers. By-catch of Puttlam lagoon consisted only of three brackish water species (*C. rhynchops*, *A. granulatus*, and *H. schistosus*) indicating that the fishing was restricted to the lagoon. As the specimens in the study were based on fisheries by-catch, information of exact site of collection in the sea, habitat, GPS coordinates, and depth are unavailable. Hence, it is impossible to explore the environmental determinants of species richness and abundances of marine snakes. These differences could also be due to differential fishing practices. Although fishing practices such as gill netting and angling by artisanal fishers and trawling were observed in the eight main study sites, except in one occasion, all the specimens obtained in the study were from gill nets laid by artisanal fishers. Hence, it is very unlikely that observed differences in the diversity and abundances were due to different fishing practices.

Natural history of the marine snakes of Sri Lanka

In contrast to the Southeast Asian region (Voris 1966; Voris et al. 1978; Voris & Jayne 1979; Voris & Glodek 1980; Voris & Moffett 1981; Voris & Voris 1983; Jayne et al. 1988), comparatively few studies have been conducted on the aspects of ecology and natural history on the marine snakes of the IO or the South Asian region (Lobo et al. 2004; Lobo et al. 2005). The few studies that are available are mostly preliminary or anecdotal observations on the natural history (Voris 1972; Karthikayan et al. 2008; Padate et al. 2009; de Silva et al. 2011b; Razzaque Sarker et al. 2017). Though the natural history observations reported here are also anecdotal, the information provided adds important insights to ever increasing knowledge on the aspects of natural history such as diet and reproduction of IO populations of many species of marine snakes. Our observations on the gut contents indicate that *H. curtus* is a generalist (Clupeidae, Engraulidae, Synodontidae, Gastropoda) in feeding habits while *M. gracilis*is a species that specializes on snake eels (Ophichthyidae). Both *M. gracilis* and *H. spiralis* seemed to be specializing on eel-type fish (i.e., fish with elongated bodies and no pelvic fins: Congridae, Ophichthyidae,). Similarly, *H. cyanocinctus* and *H. ornatus* seem to specialize on bottom dwelling fish (e.g., Congridae, Gobiidae, Plotosidae,). These observations in general are in agreement with Voris and Voris (1983).

Detailed information on the reproduction of marine snakes is scarce throughout their range and is available for *A. granulatus* (Voris & Glodek 1980), *Emydocephalus ijimae* (Masunaga & Ota 2003), *H. cyanocinctus* (Karthikayan et al. 2008), *H. schistosus* (Voris & Jayne 1979), *Aipysurus apraefrontalis*, *A. duboisii*, *A. mosaicus*, *H. caerulescens*, *H. czeblukovi*, *H. elegans*, *H. kingi*, *H. major*, *H. pacificus*, *Hydrophis peronii*, *H. platurus*, and *H. zweifeli* (Fry et al. 2001). Thus, relatively very little is known about the reproductive habits of other species of marine snakes and other studies have reported brief notes on the reproduction of marine snakes collected as by-catch (Ward 2001; Padate et al. 2009; de Silva et al. 2011b). However, with the exception of sea kraits (*Laticauda*), it is well known that all marine snakes are ovoviviparous and give birth to fully developed live young at the end of the gestation period (Heatwole 1999). The presence of mature eggs and embryos in marines snakes sampled in this study from December to August indicates almost year-round reproduction. However, our unevenly distributed sampling throughout the year makes it impossible for us to determine the reproductive seasonality of any of the species reported here. In this study, all the gravid females of *H. schistosus* were found in June and it has been stated that the gestation period of *H. schistosus* is from November to March in Southeast Asia (Voris & Jayne 1979; Lemen & Voris 1981). Though this might indicate a difference in the reproductive seasonality of the two populations in the IO and Southeast Asia, year-long multiyear sampling will be required to determine the reproductive cycles of this species and as well as other species in this region. The lowest number of eggs in gravid females was observed in *H. viperinus* (3.60) while the highest number was observed in *H. schistosus*(12.17). This is comparatively low when compared to *H. schistosus* populations in Southeast Asia that has high quantities (30) of mature eggs (Voris & Jayne 1979). However, thorough comparative studies are necessary to examine the differences in the reproductive biology of the two populations. The largest females in reproductive condition were observed in *H. spiralis* (mean total length of 1286.44 mm) (Fig. 5) and the smallest females in reproductive condition were observed in *H. viperinus* (mean total length of 663.71 mm) (Fig. 5). This can be expected given the large size of *H. spiralis* (average total length = 1600 mm) and the small size of *H. viperinus* (average total length = 800 mm) (Wall 1921; Smith 1926; Deraniyagala 1955). Given the availability of limited information of many species of marine snakes, we believe that the anecdotal observations on the reproduction of *H. curtus*, *H. fasciatus*, *H. spiralis*, *H. viperinus*, and *M. gracilis* reported here are significant contributions to the knowledge on the reproductive biology of marine snakes of the IO as well as the whole group.

Conservation of the marine snakes of Sri Lanka

The specimens reported in this study were collected as by-catch of local fishing during a period of 3 years with sporadic sampling distributed unevenly through the year. Although marine snakes are harvested for skins in other regions of Asia (Auliya 2011), there was no indication of deliberate harvest in Sri Lanka (also see de Silva et al. 2011a). However, our observations indicate that nearly 96% of the marine snakes captured by the artisanal fishers either were dead or died after retrieval from the nets. However, most of the snakes observed in the by-catch did not have visibly observable injuries (Fig. 6). This likely indicates that snakes either died due to drowning or due to suffocation as a result of strangulation in the nets. Such high rates of mortality must be definitely posing a major threat to these species in Sri Lanka (also see de Silva et al. 2010) (Fig. 6) and it is presumed to be the major threat for marine snakes in other regions of South Asia as well (Razzaque Sarker et al. 2017; Ganesh et al. 2019). A recent study in the western coast of India indicates comparatively higher annual by-catch (385 snakes per annum) (Rao et al. 2021) compared the findings of this study (138 snakes per annum). The reason for this discrepancy in the annual by-

Fig. 6 Marine snake by-catch in Sri Lanka; **a** Freshly caught *Microcephalophis gracilis* and *Hydrophis viperinus* in the northern coast of Jaffna peninsula; **b** carcasses of *Acrochordus granulatus* caught in a single net in Puttlam lagoon; **c** a pile of viviparous sea snake carcasses at a fish landing site in the northern coast of Jaffna peninsula (photos: **a** and c—K.D.B. Ukuwela; b—A. de Silva)

catch could be that the latter study examined a significantly higher number of trawls (65) (Rao et al. 2021) compared to that in this study (1). Many specimens reported here were gravid females and fully developed males that may be in reproductive condition. Thus, continuous removal of sexually mature individuals in reproductive condition could have drastic effects on the population sizes of these marine snakes. Further, changes in the coastal environment such as destruction of mangrove habitats may also pose a significant threat to brackish water species such as *A. granulatus*, *C. rynchops*, and *G. prevostiana*. Though we found several cases of mangrove habitat destruction, our sampling was inadequate to find direct evidence for effects of habitat destruction on the population declines of marine snakes. Thus, a continuous monitoring strategy needs to be implemented immediately to document the long-term effects of by-catch and habitat destruction on population dynamics and recruitment of marine sea snakes in Sri Lanka as well as the rest of South Asia.

It was also revealed during discussions with fishers at the study sites that entangled marine snakes are deliberately killed at sea to avoid being bitten. Bites from highly venomous elapid sea snake are not very common in Sri Lanka despite the routine exposure to highly venomous elapid sea snakes during fishing activities (de Silva & Fernando 2018). However, during the past 30 years, only a handful of sea snake bites have been reported in the island (de Silva & Fernando 2018) which has also resulted in a low number of mortalities (Kularatne et al. 2014; Vithanage & Thirumalavan 2013). This suggests that envenoming and life-threatening conditions due to sea snake bites in Sri Lanka are less prevalent in comparison to bites by venomous terrestrial snakes (Ediriweera et al. 2016).

Our findings are important in light of the fact that many species of IO marine snakes that are co-distributed in Southeast Asia and Australasia are genetically divergent from their conspecifics, with many forming cryptic lineages (see above and also (Ukuwela et al. 2014; Ukuwela et al. 2016; Ukuwela et al. 2017a). Although these cryptic lineages are not yet confirmed as valid species, due to their genetic distinctiveness from their conspecifics from Southeast Asia/WP, they qualify as "evolutionary significant units" (ESU) (Ryder 1986; Moritz 1994). Comparative phylogeographic data from many species of viviparous sea snakes suggest the presence of at least two ESU's that correspond to the IO and Southeast Asia/WP (Ukuwela et al. 2014; Ukuwela et al. 2016; Ukuwela et al. 2017a). Divergence dating indicates that the viviparous sea snakes spanning the IO and WP have long (between 2.5 and 0.5 million years) and complex evolutionary histories in the region (Ukuwela et al. 2014; Ukuwela et al. 2016) with a unique conservation value and thus should be considered separate conservation management units. Marine protected area networks currently ignore marine snakes due to the lack of data for these potentially vulnerable species. Further, there are currently no conservation policies that target sea snakes in terms of fishing practices, trade restrictions, or protected areas (Livingstone 2009). On a broader scale, results from our studies indicate significant limits to genetic connectivity among marine snake populations (e.g., *H. curtus*) spanningthe Indo-West Pacific (Ukuwela et al. 2014). Hence, the identification of these distinct phylogeographic regions through comparative phylogeographic approaches is critical for regional-scale marine conservation planning in the IO and the WP (Sala et al. 2002; Reaka & Lombardi 2011). Thus, findings on the systematics and population genetic structure (reported elsewhere) of marine snakes can be used not only to inform future marine snake-oriented conservation, but may also be used to inform marine reserve planning in the IO, Sri Lanka, and the WP.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s12526-022-01259-3.

Acknowledgements We thank the Department of Wildlife Conservation, Sri Lanka, for the research and tissue exportation permits (WL/3/2/1/14/12). We are grateful to many fishermen all over the island for their kind assistance and hospitality. Naval Officers including Lt. Commander Pradeep Bandara of Sri Lanka Navy are gratefully acknowledged for their cooperation and hospitality at many sites. We appreciate the assistance given by Manori Goonetilake and Chandrika Munasinghe at the National Museum of Sri Lanka and the officials at the National Wildlife Research and Training Center at Girithale during specimen deposition. Our sincere thanks go to our colleagues Imesh Nuwan Bandara, Chamara Amarasinghe, Gajaba Ellepola, Pushpalingam Surenthar, Kamalakkannan Rahavan, and Tharmeka Selvaraja for accompanying us in the field, collecting specimens, and for the long hours spent processing and preserving specimens. We are highly grateful to Ralph Foster (South Australian Museum) for identifying the fish in marine snake diet and Krishantha Sameera De Zoysa for preparing the map. Jakob Hallermann is gratefully acknowledged from providing some important literature. The Australian Research Council and the Mohamed Bin Zayed Species Conservation Fund are thanked for funding this study. Finally, we appreciate the editor and two anonymous reviewers for on their comments on the manuscript.

Funding This survey on the marine snakes of Sri Lanka was supported by an Australian Research Council Discovery grant to KLS and a Mohomed Bin Zayed species conservation grant to AdeS.

Declarations

Conflict of interest The authors declare no competing interests.

Ethics approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed by the authors.

Sampling and field studies Sampling and field studies were carried out with permission from the Department of wildlife Conservation in Sri Lanka (Permit No: WL/3/2/1/14/12).

Data availability Not applicable

Author contribution KDBU, AdeS, and KLS conceived the study. AdeS and KLS obtained funding for the study. KDBU, AdeS, KLS, and AS conducted fieldwork. KDBU generated the data and wrote the first draft of the manuscript. All other authors contributed to the writing.

References

Abyerami S, Sivashanthini K (2008) Current status of marine snakes from Jaffna Peninsula, Sri Lanka with description of hitherto unrecorded Hydrophis fasciatus fasciatus (Schneider, 1799). Int J Zool Res 4: 214–224. https://doi.org/10.3923/ijzr.2008.214.224

Anonymous (1997) Revised Coastal Zone Management Plan. Coastal Conservation Department. Ministry of Fisheries and Aquatic resources development of Sri Lanka, Colombo

Auliya M (2011) Lapemis Curtus (Sepentes: Elapidae) harvested in West Malaysia. Seas snake specialist group Newsletter March issue: 6-8.

Balasubramaniam A (2007) Status and taxonomy of herpetofauna and their conservation in the Jaffna Peinsula, Sri Lanka. University of Jaffna, Dissertation

Bambaradeniya CNB, Ekanayake SP, Kekulandala LDCB, Samarawickrama VAP, Ratnayake ND, Fernando RHSS (2002) An assessment of the status of biodiversity in the Muthurajawela Wetland Sanctuary, vol 3. Occasional Papers of the IUCN, Sri Lanka, p iv-pp48

Das I, De Silva A (2005) A photographic guide to snakes and other reptiles of Sri Lanka. New Holland, London, UK

De Silva PHDH (1980) Snake fauna of Sri Lanka: with special reference to skull, dentition, and venom in snakes. National Museums of Sri Lanka. Colombo, Sri Lanka

de Silva A (1990) Colour guide to the snakes of Sri Lanka. R & A Publishing Limited, Avon, England

de Silva A (1994) An account of sea snakes (Serpentes: Hydrophiidae) of Sri Lanka. In: Gopalkrishnakone P (ed) Sea snake toxinology. National University of Singapore press Singapore, pp 234–249

de Silva A, Fernando M (2018) Seasnakes and their bites. Sri Lanka Medical Association, Colombo, Sri Lanka

de Silva A, Freed P, Rudge J, Rasmussen AR, Sanders K (2010) Some observations on the wart snake Acrochordus granulatus (Schneider, 1799) (Squamata: Serpentes) in Sri Lanka. Lyriocephalus 7:203–206

de Silva A, Sivaruban A, Ukuwela KDB, Rasmussen AR, Sanders KL (2011a) First record of a sea snake (Lapemis Curtus) feeding on a gastropod. Herp Notes 4:373–375

de Silva A, Ukuwela KDB, Sivaruban A, Sanders KL (2011b) Preliminary observations on the reproductive biology of six species of Sri Lankan sea snakes (Elapidae: Hydrophiinae). Salamandra 47: 193–198

Deraniyagala PEP (1955) A coloured atlas of some vertebrates from Ceylon. Ceylon National Museums, Colombo, Ceylon

Dunson WA (1975) The Biology of Sea snakes. University Park Press, Baltimore, USA

Ediriweera DS, Kasturiratne A, Pathmeswaran A, Gunawardena NK, Wijayawickrama BA, Jayamanne SF, Isbister GK, Dawson A, Giorgi E, Diggle PJ, Lalllo DG, de Silva HJ (2016) Mapping the risk of snakebite in Sri Lanka - a national survey with geospatial analysis. PLOS Negl Trop Dis 10(7):e0004813. https://doi.org/10.1371/journal.pntd.0004813

Fry GC, Milton A, Wassenberg TJ (2001) The reproductive biology and diet of sea snake bycatch of prawn trawling in Northern Australia: characteristics important for assessing the impacts on populations. Pac Conserv Biol 7:55–73. https://doi.org/10.1071/PC010055

Ganesh SR, Nandhini T, Samuel VD, Sreeraj CR, Abhilash KR, Purvaja R, Ramesh R (2019) Marine snakes of Indian Coasts: historical resume, systematic checklist, toxinology, status, and identification key. Journal of Threat Taxa 11: 13132-13150. 10.11609/jott.3981.11.1.13132-13150

Hallermann J, Ananjeva NB, Orlov NL (2001) On a remarkable collection of repiles and amphibians collected by the German Indian Expedition 1955-1958. Russ. J. Herp 8:59–68. https://doi.org/10.30906/1026-2296-2001-8-1-59-68

Heatwole H (1999) Sea Snakes. University of New South Wales Press. Sydney, Australia

IUCN (2010) IUCN Red List of Threatened Species (ver. 2010.4). Available at: https://www.iucnredlist.org. Accessed 20 Oct 2014

Jayne BC, Voris HK, Heang KB (1988) Diet, feeding behavior, growth, and numbers of a population of Cerberus Rynchops (Serpentes : Homalopsinae) in Malaysia. Fieldiana: Zoology 50:1–15. https://doi.org/10.5962/bhl.title.2872

Karthikayan R, Vijayalakshmi S, Balasubramanian T (2008) Feeding and parturition of female annulated sea snake Hydrophis Cyanocinctus in captivity. Curr Sci 95:660–664

Karunarathna S, Surasinghe T, Botejue M, Madawala M (2018) Gerarda Prevostiana (Serpentes: Homalopsidae) in Sri Lanka: distribution and behaviour. The Herpet Bull 145:8–13

Kharin V, Hallerman J (2009) Annotated catalogue of sea kraits (Laticaudidae) and sea snakes (Hydrophiidae) of the herpetological collection of the Zoological Museum, University of Hamburg. Mitt. Hamb. Zool. Mus. Inst. 106:51–67

Kularatne SAM, Hettiarachchi R, Dalpathadu J, Mendis ASV, Appuhamy PDSAN, Zoysa HDJ, Maduwage K, Weerasinghe VS, de Silva A (2014) *Enhydrina schistosa* (Elapidae: Hydrophiinae) the most dangerous sea snake in Sri Lanka: three case studies of severe envenoming. Toxicon 77:78–86. https://doi.org/10.1016/j.toxicon.2013.10.031

Lemen CA, Voris HK (1981) A comparison of reproductive strategies among marine snakes. J Anim Ecol 50:89–101. https://doi.org/10.2307/4033

Livingstone SR (2009) Status of the world's sea snakes Iucn Red List Assessment: Final Report. IUCN, p 18

Lobo AS (2006) Sea Snakes of the Gulf of Mannar Marine National Park. The species and their conservation. A Technical Report Submitted to the Rufford Foundation, p 66

Lobo A, Pandav B, Vasudevan K (2004) Weight–length relationships in two species of marine snakes along the Coast of Goa, Western India. Hamadryad 29:89–93

Lobo A, Vasudevan K, Pandav B (2005) Trophic ecology of Lapemis Curtus (Hydrophiinae) along the western coast of India. Copeia 2005:636–640. https://doi.org/10.1643/CH-04-076R1

Masunaga G, Ota H (2003) Growth and reproduction of the sea snake, Emydocephalus Ijimae, in the Central Ryukyus, Japan: A Mark and Recapture Study. Zool Sci 20:461–470. https://doi.org/10.2108/zsj.20.461

Moritz C (1994) Defining 'evolutionarily significant units' for conservation. Trends in Ecol and Evol 9:373–375. https://doi.org/10.1016/0169-5347(94)90057-4

Murthy TSN (1977) On sea snakes occurring in Madras waters. J Mar Biol Assoc India 19:68–72

Padate VP, Baragi LV, Rivonker CU (2009) Biological aspects of sea snakes caught incidentally by commercial trawlers off Goa, West Coast of India. J of Threat Taxa 1:609–616. https://doi.org/10.11609/JoTT.o2253.609-16

Rao C, Dsouza S, Gupta T, Manoharikrishnan M, Lobo AS (2021) Fisheries induced shift in sea snake community assemblages along the Konkan coast, India. Aquatic Conservation 31:2402–2411. https://doi.org/10.1002/aqc.3658

Rasmussen AR (1992) Rediscovery and redescription of Hydrophis tuberculatus Peters, 1872 (Serpentes: Hydrophidae). Herpetologica 48:85–97 https://www.jstor.org/stable/3892922

Rasmussen AR (2001) Sea Snakes. In: Carpenter KE, Niem VH (eds) Living marine resources of the Western Central Pacific. Food and Agriculture Organization, Rome, pp 3987–4000

Rasmussen AR, Murphy JC, Ompi M, Gibbons JW, Uetz P (2011) Marine reptiles. PLoS ONE 6:e27373. https://doi.org/10.1371/journal.pone.0027373

Razzaque Sarker MA, Sanders KL, Ukuwela KDB, Jamam FJ (2017) Sea snakes of Bangladesh: a preliminary survey of Cox's Bazar district with notes on diet, reproduction, and conservation status. Herpetol Conserv and Biol 12:384–393

Reaka M, Lombardi S (2011) Hotspots on global coral reefs. In: Zachos FE, Habel JC (eds) Biodiversity hotspots. Springer, Berlin Heidelberg, pp 471–501

Rezaie-Atagholipour M, Ghezellou P, Hesni MA, Dakhteh SMHD, Ahmadian H, Vidal N (2016) Sea snakes (Elapidae, Hydrophiinae) in their westernmost extent: an updated and illustrated checklist and key to the species in the Persian Gulf and Gulf of Oman. Zookeys 622:129–164

Ryder OA (1986) Species conservation and systematics - the dilemma of subspecies. Trends Ecol Evol 1:9–10. https://doi.org/10.1016/0169-5347(86)90059-5

Sala E, Aburto-Oropeza O, Paredes G, Parra I, Barrera JC, Dayton PK (2002) A general model for designing networks of marine reserves. Science 298:1991–1993. https://doi.org/10.1126/science.1075284

Sanders KL, Rasmussen AR, Mumpuni EJ, de Silva A, Guinea ML, Lee MSY (2013) Recent rapid speciation and ecomorph divergence in Indo-Australian sea snakes. Mol Ecol 22:2742–2759. https://doi.org/10.1111/mec.12291

Smith M (1926) Monograph of the sea-snakes (Hydrophiidae). Trustees of the British Museum. England, London

Somaweera R (2006) Sri Lankawe Sarpayin ('the Snakes of Sri Lanka'). Wildlife Heritage Trust of Sri Lanka, Colombo

Somaweera R, Somaweera N (2009) An overview of sri lankan sea snakes with an annotated checklist and a field key. Taprobanica 1: 43–54

Somaweera R, Ukuwela K, Alagoda T (2006) A note on specimens of Gerarda Prevostiana (Colubridae: Serpentes) collected from Sri Lanka. Ceyl J Science (Biol Sci) 35:91–93

Ukuwela KDB, de Silva A, Mumpuni FBG, Lee MSY, Sanders KL (2013) Molecular evidence that the deadliest sea snake Enhydrina Schistosa (Elapidae: Hydrophiinae) consists of two convergent species. Mol Phylogen Evol 66:262–269. https://doi.org/10.1016/j.ympev.2012.09.031

Ukuwela KDB, de Silva A, Mumpuni FBG, Sanders KL (2014) Multilocus phylogeography of the spine-bellied sea snake (Hydrophis Curtus, Elapidae) reveals historical vicariance and cryptic lineage diversity. Zool Scr 43:472–484. https://doi.org/10.1111/zsc.12070

Ukuwela KDB, Lee MSY, Rasmussen AR, de Silva A, Mumpuni FBG, Ghezellou P, Rezaie-Atagholipour M, Sanders KL (2016) Evaluating the drivers of Indo-Pacific biodiversity: speciation and dispersal of sea snakes (Elapidae: Hydrophiinae). J Biogeogr 43: 243–255. https://doi.org/10.1111/jbi.12636

Ukuwela KDB, de Silva A, Sanders KL (2017a) Further specimens of the mud snake, Gerarda Prevostiana (Homalopsidae) from Sri Lanka with insights from molecular phylogenetics. Raffles Bull Zool 65: 29–34

Ukuwela KDB, Lee MSY, Rasmussen AR, de Silva A, Sanders KL (2017b) Biogeographic origins of the Viviparous sea snake assemblage (Elapidae) of the Indian Ocean. Ceyl J Sci 46:101–110. https://doi.org/10.4038/cjs.v46i5.7457

Vithanage K, Thirumavalavan KA (2013) A case of a sea snake bite resulting in fatal envenoming. Ceylon. Med. J. 57:174–175. https://doi.org/10.4038/cmj.v57i4.5089

Voris HK (1966) Fish eggs as the apparent sole food item for a genus of sea snake, Emydocephalus (Krefft). Ecology 47:152–154. https://doi.org/10.2307/1935755

Voris HK (1972) The role of sea snakes (Hydrophiidae) in the trophic structure of coastal ocean communities. Journal of marine biological Association of India 14:429–442

Voris HK, Glodek GS (1980) Habitat, diet and reproduction of the file snake, Acrochordus Granulatus, in the Straits of Malacca. J Herpetol 14:108–111. https://doi.org/10.2307/1563896

Voris HK, Jayne BC (1979) Growth, reproduction and population structure of a marine snake Enhydrina Schistosa (Hydrophidae). Copeia 2:307–318. https://doi.org/10.2307/1443419

Voris HK, Moffett MW (1981) Size and proportion relationship between the beaked sea snake and its prey. Biotropica 13:15–19. https://doi.org/10.2307/2387866

Voris HK, Voris H (1983) Feeding stratergies in marine snakes: an analysis of evolutionary, morphological, behavioural and ecological relationships. Am Zool 23:411–425. https://doi.org/10.1093/icb/23.2.411

Voris HK, Voris HH, Liat LB (1978) The food and feeding behavior of a marine snake, Enhydrina Schistosa (Hydrophiidae). Copeia 1978: 134–146. https://doi.org/10.2307/1443834

Wall F (1921) Ophidia Taprobanica or the snakes of Ceylon. H.R. Cottle, Govt. printer, Colombo, Ceylon

Ward TM (2001) Age structures and reproductive patterns of two species of sea snakes, Lapemis Hardwickii Gray (1836) and Hydrophis Elegans (Grey 1842), incidentally captured by prawn trawlers in Northern Australia. Mar Freshwat Res 52:193–203. https://doi.org/10.1071/MF00025

Wickramasinghe LJM (2012) The taxonomy and conservation status of the reptile fauna in Sri Lanka. In: Weerakoon DK, Wijesundara S (eds) The National Red List of Sri Lanka: conservation status of the fauna and flora. Ministry of Environment, Colombo, Sri Lanka, pp 99–113

Wickramasinghe LJM, Rodrigo RK (2004) Taxonomy and current status of marine snake fauna of Sri Laka. National Workshop on current status of the Marine fauna of Sri Lanka.

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.