

Observations of marine elapid snakes in the mesophotic zone in the Ryukyu Islands, Japan, with the deepest records for three species

Kanta Fujishima

kantafujishima606@gmail.com

Kyoto Daigaku Rigaku Kenkyuka Rigakubu <https://orcid.org/0009-0002-9813-9950>

Takuo Higashiji

Okinawa Churashima Foundation

Frederic Sinniger

University of the Ryukyus: Ryukyu Daigaku

Saki Harii

University of the Ryukyus: Ryukyu Daigaku

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Abstract

Marine snakes in the Family Elapidae are key mesopredators in tropical and subtropical Indo-Pacific ecosystems. While some species have been recorded in the mesophotic zone (30–150 m) and in even deeper water, such observations remain rare and limit our understanding of habitat use and the ecological role of these snakes. We present 15 observations of marine elapids at depths > 50 m in the Ryukyu Islands of southwestern Japan, obtained through rebreather diving and remotely operated vehicles. Black-banded Sea Kraits (*Laticauda semifasciata*) were observed at depths of 50–112 m across both hard and soft substrates ($n = 13$), and one Blue-lipped Sea Krait (*L. laticaudata*) was observed at 122 m depth. Four of the observed *L. semifasciata* exhibited foraging behavior. Additionally, one Ornate Reef Sea Snake (*Hydrophis ornatus*) was recorded at 95 m. These represent the deepest known records for all three species. As benthic foragers, these marine elapids may play a role in nutrient transfer between deep and shallow habitats. Furthermore, deep-water environments may serve as foraging refugia, offering protection from predators such as sharks, as well as the impacts of marine heatwaves and coastal development.

Introduction

Snakes of the family Elapidae include two major clades that have independently colonized the marine environment: sea kraits (genus *Laticauda*) and sea snakes in the subfamily Hydrophiinae. Sea kraits are oviparous and periodically return to land for digestion, mating, and oviposition, while sea snakes are viviparous and fully aquatic. Both groups have a convergently evolved paddle-shaped tail that enhances swimming, and exhibit various morphological and physiological adaptations to the marine environment. These marine elapids play crucial roles as mesopredators in tropical and subtropical coastal marine ecosystems in the Indo-Pacific (Voris and Voris 1983; Heatwole 1999). Furthermore, many marine elapids prey on rare or cryptic fish such as eels and gobies, and have the potential as bioindicators to help monitor the effects of climate change and habitat change on marine fish assemblages (Brischoux et al. 2009; Rasmussen et al. 2011). Most ecological studies of marine elapids have focused on shallow waters (< 15 m) due to logistical constraints (e.g., Lukoschek et al. 2013; Udyawer et al. 2015; Shine et al. 2020). However, recent remotely operated vehicle (ROV) observations have recorded sea snakes at depths down to 250 m, significantly expanding their known depth range (Crowe-Riddell et al. 2019). Additionally, surveys using baited remote underwater video stations (BRUVS) and ROVs have revealed the presence of sea snakes in the mesophotic zone (30–150 m) in Ashmore Reef, Australia, underscoring the significance of deep-water habitats in the ecology of marine elapids (Udyawer et al. 2014; Speed et al. 2022). Speed et al. (2022) further proposed that these deep zones may offer refuge from predators, particularly sharks, which are more abundant in shallower waters. Given the recent decline of marine elapid abundance in global hotspots (Goiran and Shine 2013; Somaweera et al. 2021), it is essential to assess their distribution across their full spatial range.

The Ryukyu Islands in southwestern Japan represent one of the northernmost areas with breeding populations of marine elapids: records further north in mainland Japan and Korea are considered waif

dispersals (Hecht et al. 1974; Masunaga et al. 2005; Ota and Yamadashima 2012; but see Park et al. 2017). Although marine elapids are regularly observed during benthic surveys in the mesophotic zone in this region (Sinniger et al. 2019), detailed accounts of their species composition, habitat use, and behavior are lacking. Here, we present new records of marine elapids in the mesophotic zone of the Ryukyu Islands based on ROV and scuba surveys, including the deepest known occurrences of three species.

Materials and methods

Observations were conducted in coastal waters off northwestern Okinawa Island and near Kodakara Island, Japan (Fig. 1). The coastlines are predominantly surrounded by fringing reefs. In our study site around Okinawa Island, the area surrounded by Okinawa, Ie, Minna, and Sesoko Islands is relatively flat and comprises mesophotic coral reefs and soft substrate. At the outer coasts of the islands, steep reef slopes occur, and depths rapidly drop off to > 100 m within ca. 3 km from land. Several topographic features raising a few hundred meters above the seafloor with large flat tops reaching 65 m depth are located in the survey area, and provide extensive habitats for benthic invertebrates. Around Kodakara Island, the depths similarly rapidly increase from the coast. Videos and photos of marine elapid snakes were opportunistically taken during technical scuba diving surveys for mesophotic corals led by FS and SH, and during benthic surveys using ROVs conducted by the Okinawa Churashima Foundation. Images from Kodakara Island were obtained from the JAMSTEC E-library of Deep-sea Images (<https://www.godac.jamstec.go.jp/jedi/e/index.html>). In the scuba surveys, depth, time, and water temperature were obtained from the dive computers (Shearwater Research, Canada). In the ROV surveys, depth was recorded. From the video footage, we visually categorized the substrate as rock, rock plus sand, sand plus coral rubble, non-branching hard coral, or soft sediment.

Results and discussion

We made 15 observations of marine elapids between October 2011 and August 2024 in the daytime. Observations included 13 Erabu Sea Kraits *Laticauda semifasciata*, one Blue-banded Sea Krait *L. laticaudata*, and one Ornate-reef Sea Snake *Hydrophis ornatus* (Table 1, Fig. 2). One *L. laticaudata* was found near Kodakara Island, and the others around Okinawa Island. Observations ranged from 50 to 122 m depth, with ambient temperatures of 21.6–24.6°C (where recorded). *Laticauda semifasciata* was found on a variety of hard and soft substrates, while *L. laticaudata* was found in rock plus sand substrate, and *H. ornatus* in soft sediment substrate. The snakes were either foraging (indicated by the snout repeatedly touching the substrate) or swimming. Three individuals of *L. semifasciata* approached the diver or the ROV.

Table 1

List of observations of marine elapid snakes in the mesophotic zone in the Ryukyu Islands, Japan.

Species	Date	Time	Habitat	Depth (m)	Temperature (°C)	Behavior
<i>Laticauda laticaudata</i>	15 Oct 2011	14:05	Rock plus sand	122	22	Swimming
<i>Laticauda semifasciata</i>	8 Sep 2015	10:20	Sand plus coral rubble	50	N/A	Foraging; approaching ROV
<i>Laticauda semifasciata</i>	27 Sep 2019	11:37	Sand plus coral rubble	112	24.6	Swimming
<i>Laticauda semifasciata</i>	9 Jul 2021	10:36	Sand plus coral rubble	85	22.5	Approaching ROV; fleeing
<i>Laticauda semifasciata</i>	18 Oct 2021	10:15	Non-branching hard coral	67	21.7	Foraging
<i>Laticauda semifasciata</i>	24 Mar 2022	11:16	Non-branching hard coral	75	N/A	Foraging
<i>Laticauda semifasciata</i>	24 Mar 2022	11:27	Non-branching hard coral	70	N/A	Foraging
<i>Laticauda semifasciata</i>	29 Apr 2022	12:24	Sand plus coral rubble	88	21.6	Swimming
<i>Laticauda semifasciata</i>	22 Jul 2022	13:35	Non-branching hard coral	57	22	Swimming
<i>Laticauda semifasciata</i>	8 Aug 2022	13:49	Rock	81	22	Approaching diver
<i>Laticauda semifasciata</i>	20 Aug 2022	9:47	Rock plus sand	72	23	Swimming
<i>Laticauda semifasciata</i>	20 Aug 2022	10:13	Rock plus sand	70	23	Swimming
<i>Laticauda semifasciata</i>	30 Jul 2024	9:56	Rock plus sand	77	22	N/A
<i>Hydrophis ornatus</i>	14 Aug 2024	14:43	Soft sediment	95	N/A	Swimming
<i>Laticauda semifasciata</i>	14 Aug 2024	NA	Soft sediment	95	N/A	Swimming

Laticauda semifasciata is a dietary generalist that feeds on fish from a wide range of families and body shapes (Su et al. 2005; Tabata et al. 2017). The spatial ecology of *L. semifasciata* is largely unknown, but

they have been observed to forage at < 45 m depth (Somaweera et al. 2023). In our observations, about one-third of the individuals were found during foraging behavior, suggesting that *L. semifasciata* is a predator of a wide array of fish in mesophotic reef communities. A *L. laticaudata*, a known eel specialist (Brischoux et al. 2007; Tabata et al. 2017), was observed at 122 m, also far deeper than previous records for this species (maximum 32.4 m in New Caledonia; Cook et al. 2016). Several physiological adaptations enable marine elapids to perform deep dives. A large cardiac shunt coupled with high skin permeability to gases are thought to allow *Hydrophis* sea snakes to avoid forming nitrogen bubbles in the bloodstream after deep dives (i.e., decompression sickness). Sea kraits also possess these traits, albeit to a lesser extent, and simulated pressurization experiments have estimated that they may be at risk of decompression sickness at depths of 30–70 m. (Seymour 1978). However, our observation of sea kraits occurring at > 100 m depth demonstrates that the diving capacity of sea kraits is underestimated. This calls for further assessment of their physiological adaptations for diving.

Hydrophis ornatus is a widespread sea snake that, in the Ryukyu Islands, has been predominantly observed in relatively enclosed bay-like waters with soft substrates at depths of less than 25 m, where it primarily feeds on burrowing gobies (Kidera et al. 2015; Fujishima et al. 2021). Consistent with these observations, we found an *H. ornatus* on soft substrate, but at a greater depth of 95 m. The habitat use of *H. ornatus* is largely unknown, and to our knowledge, this represents the deepest recorded occurrence of this species.

Our observations with temperature records showed that the water temperatures at the depth of the observations were 22–23°C in July, August, and October. Surface water temperature around Okinawa Island range around 21–29°C peaking during August and September, and 21–24°C at 100 m depth (Japan Oceanographic Data Center, <http://www.jodc.go.jp/service.htm>). Diving to deeper, cooler waters may benefit snakes, particularly in warmer months, by lowering their metabolic rate, which reduces energy expenditure and extends dive duration, thereby allowing more time for foraging (Cook and Brischoux 2014).

In conclusion, our observations substantially expand the depth range of three species of marine elapid snakes.

In particular, sea kraits regularly move across large areas (> 20 km from the home island) of the reef to forage on the bottom and return to land (Brischoux et al. 2007). Our observations of sea kraits occurring in the mesophotic zone suggests their role in translocating nutrients between mesophotic and shallow reef systems, as well as with the terrestrial habitat that they utilize (Slattery et al. 2011; Estupiñán-Montaña et al. 2023).

In Ashmore Reef in north-western Australia, where the once abundant sea snakes have largely disappeared from shallow waters, sea snake populations were found to persist in the mesophotic zone (Speed et al. 2022). The increase in numbers of top predators, namely sharks, has been a major plausible explanation for the drastic decline of sea snakes in Ashmore Reef (Somaweera et al. 2021). The mesophotic zone may have acted as a refuge for sea snakes from predatory sharks, which are

significantly more abundant in shallow waters (Speed et al. 2022). Similarly in the Ryukyu Islands, sharks, particularly tiger sharks *Galeocerdo cuvier*, are known to be a major predator of sea kraits and sea snakes (Masunaga et al. 2008), and deep diving by snakes may serve to avoid predation by sharks.

Coral reefs have experienced widespread habitat degradation, notably through heat-induced bleaching events caused by elevated ocean temperatures (Hoegh-Guldberg et al. 2007; Hughes et al. 2017). While the direct impacts of reef degradation on marine elapids remain poorly quantified, declines in the abundance of reef-associated fishes following habitat loss are relatively well documented, though the magnitude varies across taxa (Prachett et al. 2011; Huang et al. 2023). Marine elapids that primarily feed on coral reef fishes (e.g., sea kraits) may be indirectly affected by such declines (Ota 2014). Mesophotic reefs represent a major habitat type that may be less impacted by heat-induced bleaching events that severely affect shallow reefs (Bongaerts and Smith 2019; Pérez-Rosales et al. 2021). These deep areas may serve as important refugial foraging habitats for reef-associated snakes. Future research integrating standardized visual survey methods using ROVs and/or BRUVS and implanted data loggers are needed to understand the population trends, diving behavior, and ecological roles of marine elapids in mesophotic systems. Such information will be crucial in informing conservation policies such as marine protected areas (MPAs) regarding mesophotic habitats (Gress et al. 2018; Pulido Mantas et al. 2024).

Declarations

Compliance with Ethical Standards

No ethics approval was required for the present study as all sampling was conducted using non-invasive underwater video and photography techniques.

Competing interests

The authors declare that they have no competing interests.

Author contributions

All authors contributed to the study conception and design. Kanta Fujishima carried out video analysis, species identification, and writing of the first manuscript draft. Takuji Higashiji provided resources for ROV surveys at the Churashima Foundation, and associated data. Frederic Sinniger conceived scuba diving field work and provided the records and associated data. Saki Harii supported the field work. All authors contributed and reviewed the final version of the manuscript.

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Data availability

All raw data supporting the conclusions of this study are available from the corresponding author upon reasonable request.

References

1. Bongaerts P, Smith TB (2019) Beyond the “deep reef refuge” hypothesis: a conceptual framework to characterize persistence at depth. In: Mesophotic Coral Ecosystems. Springer, Cham, pp 881–895
2. Brischoux F, Bonnet X, Shine R (2007) Foraging ecology of sea kraits *Laticauda* spp. in the Neo-Caledonian Lagoon. Mar Ecol Prog Ser 350:145–151. <https://doi.org/10.3354/meps07133>
3. Brischoux F, Bonnet X, Legagneux P (2009) Are sea snakes pertinent bio-indicators for coral reefs? a comparison between species and sites. Mar Biol 156:1985–1992. <https://doi.org/10.1007/s00227-009-1229-7>
4. Cook TR, Brischoux F (2014) Why does the only “planktonic tetrapod” dive? Determinants of diving behaviour in a marine ectotherm. Anim Behav 98:113–123. <https://doi.org/10.1016/j.anbehav.2014.09.018>
5. Cook TR, Bonnet X, Fauvel T, Shine R, Brischoux F (2016) Foraging behaviour and energy budgets of sea snakes: Insights from implanted data loggers. J Zool 298:82–93. <https://doi.org/10.1111/jzo.12286>
6. Crowe-Riddell JM, D’Anastasi BR, Nankivell JH, Rasmussen AR, Sanders KL (2019) First records of sea snakes (Elapidae: Hydrophiinae) diving to the mesopelagic zone (>200 m). Austral Ecol 44:752–754. <https://doi.org/10.1111/aec.12717>
7. Estupiñán-Montaña C, Zetina-Rejón MJ, Galván-Magaña F, Delgado-Huertas A, Elorriaga-Verplancken FR, Polo-Silva CJ, Rojas-Cundumí J, Villalobos-Ramírez DJ, Sánchez-González A (2023) Trophic connectivity between the terrestrial and marine ecosystems of Malpelo Island, Colombia, evaluated through stable isotope analysis. Mar Biol. <https://doi.org/10.1007/s00227-022-04157-1>
8. Fujishima K, Sasai T, Hibino Y, Nishizawa H (2021) Morphology, diet, and reproduction of coastal *Hydrophis* sea snakes (Elapidae: Hydrophiinae) at their northern distribution limit. Zoolog Sci 38:405–415. <https://doi.org/10.2108/zs210010>

9. Goiran C, Shine R (2013) Decline in sea snake abundance on a protected coral reef system in the New Caledonian Lagoon. *Coral Reefs* 32:281–284. <https://doi.org/10.1007/s00338-012-0977-x>
10. Gress E, Arroyo-Gerez MJ, Wright G, Andradi-Brown DA (2018) Assessing mesophotic coral ecosystems inside and outside a Caribbean marine protected area. *R Soc Open Sci.* 5:180835. <http://dx.doi.org/10.1098/rsos.180835>
11. Heatwole H (1999) Sea snakes. Krieger Publishing Company, Florida
12. Hecht MK, Kropach C, Hecht BM (1974) Distribution of the yellow-bellied sea snake, *Pelamis platurus*, and its significance in relation to the fossil record. *Herpetologica* 30: 387–396.
13. Hinderstein LM, Marr JCA, Martinez FA, Dowgiallo MJ, Puglise KA, Pyle RL, Zawada DG, Appeldoorn R (2010) Theme section on “Mesophotic Coral Ecosystems: Characterization, Ecology, and Management.” *Coral Reefs* 29:247–251.
14. Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, Greenfield P, Gomez E, Harvell CD, Sale PF, Edwards AJ, Caldeira K, Knowlton N, Eakin CM, Iglesias-Prieto R, Muthiga N, Bradbury RH, Dubi A, Hatziolos ME (2007) Coral reefs under rapid climate change and ocean acidification. *Science* 318:1737–1742. <https://doi.org/10.1126/science.1152509>
15. Huang M, Wei S, Li Q, Gao K, Peng Z, Chen Y, Zhou W, Wei F (2023) Degradation of coral reefs altered the community trophic structure and reduced the shoaling size of fish. *Front Conserv Sci.* <https://doi.org/10.3389/fcosc.2023.1229513>
16. Hughes T, Barnes M, Bellwood D, Cinner J, Cumming G, Jackson JBC, Kleypas J, van de Leemput I, Lough JM, Morrison TH, Palumbi SR, van Nes EH, Scheffer M (2017) Coral reefs in the Anthropocene. *Nature* 546:82–90. <https://doi.org/10.1038/nature22901>
17. Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, Greenfield P, Gomez E, Harvell CD, Sale PF, Edwards AJ, Caldeira K, Knowlton N, Eakin CM, Iglesias-Prieto R, Muthiga N, Bradbury RH, Dubi A, Hatziolos ME (2007) Coral reefs under rapid climate change and ocean acidification. *Science* (1979) 318:1737–1742. doi: 10.1126/science.1152509
18. Hughes TP, Barnes ML, Bellwood DR, Cinner JE, Cumming GS, Jackson JBC, Kleypas J, Van De Leemput IA, Lough JM, Morrison TH, Palumbi SR, Van Nes EH, Scheffer M (2017) Coral reefs in the Anthropocene. *Nature* 546:82–90. doi: 10.1038/nature22901
19. Huang M, Wei S, Li Q, Gao K, Peng Z, Chen Y, Zhou W, Wei F (2023) Degradation of coral reefs altered the community trophic structure and reduced the shoaling size of fish. *Frontiers in Conservation Science.* doi: 10.3389/fcosc.2023.1229513
20. Kidera N, Uyeno D, Naruse T (2015) Notes on the occurrence and habitat of *Hydrophis ornatus* (Gray, 1842) (Reptilia: Squamata: Elapidae) in the Ryukyu Islands, Japan. *Fauna Ryukyuana* 20:7–13.
21. Lukoschek V, Beger M, Ceccarelli D, Richards Z, Pratchett M (2013) Enigmatic declines of Australia’s sea snakes from a biodiversity hotspot. *Biol Conserv* 166:191–202. <https://doi.org/10.1016/j.biocon.2013.07.004>
22. Masunaga G, Ota H, nagai Y, Tanase H (2005) A record of the black-headed sea snake, *Hydrophis melanocephalus* (Reptilia: Elapidae), from Wakayama Prefecture, Japan. *Curr Herpetol* 24:37–41.

<https://doi.org/10.5358/hsj.24.37>

23. Masunaga G, Kosuge T, Asai N, Ota H (2008) Shark predation of sea snakes (Reptilia: Elapidae) in the shallow waters around the Yaeyama Islands of the southern Ryukyus, Japan. *Mar Biodivers Rec* 1, e96:e96. <https://doi.org/10.1017/s1755267207009700>
24. Ota H (2014) *Laticauda semifasciata*: In: Japanese Red Data Book of Japan: Fauna, Wildlife Division, Japan's Ministry of Environment, Tokyo (in Japanese).
25. Ota H, Yamadashima T (2012) Notes on the previous records of two sea snakes from the southwestern islands of Kagoshima. *Bulletin of the Kagoshima Prefectural Museum* 31:59–65.
26. Park J, Kim I, Fong JJ, Koo K, Choi W, Tsai S, Park D (2017) Northward dispersal of sea kraits (*Laticauda semifasciata*) beyond their typical range. *PLoS One* 12:e0179871. <https://doi.org/10.1371/journal.pone.0179871>
27. Pérez-Rosales G, Rouzé H, Torda G, Bongaerts P, Pichon M, Parravicini V, Hédouin L (2021) Mesophotic coral communities escape thermal coral bleaching in French Polynesia. *R Soc Open Sci.* 8: 210139. <https://doi.org/10.1098/rsos.210139>
28. Pratchett MS, Hoey AS, Wilson SK, Messmer V, Graham NAJ (2011) Changes in biodiversity and functioning of reef fish assemblages following coral bleaching and coral loss. *Diversity* 3:424–452. <https://doi.org/10.3390/d3030424>
29. Pulido Mantas T, Roveta C, Calcinai B, Campanini C, Coppari M, Falco P, Di Camillo CG, Garrabou J, Lee MC, Memmola F, Cerrano C (2024) Mesophotic zone as buffer for biodiversity protection: A promising opportunity to enhance MPA effectiveness. *Mar Environ Res* 201:106676 <https://doi.org/10.1016/j.marenvres.2024.106676>
30. Rasmussen AR, Hay-Schmidt A, Boneka F, Allentoft ME, Sanders KL, Elmberg J (2020) Viviparous sea snakes can be used as bioindicators for diverse marine environments. *Philipp J Syst Biol* 19:1–16. <https://doi.org/10.26757/pjsb2020b14013>
31. Seymour RS (1978) Gas Tensions and blood distribution in sea snakes at surface pressure and at simulated depth. *Physiol Zool* 51:388–407.
32. Shine R, Shine TG, Brown GP, Goiran C (2020) Life history traits of the sea snake *Emydocephalus annulatus*, based on a 17-yr study. *Coral Reefs* 39:1407–1414. <https://doi.org/10.1007/s00338-020-01974-y>
33. Sinniger F, Harii S, Humblet M, Nakamura Y, Ohba H, Praselia R (2019) Ryukyu Islands, Japan. In: *Mesophotic Coral Ecosystems*. Springer, Cham, pp 231–247
34. Slaterry M, Lesser MP, Brazeau D, Stokes MD, Leichter JJ (2011) Connectivity and stability of mesophotic coral reefs. *J Exp Mar Biol Ecol* 408:32–41. <https://doi.org/10.1016/j.jembe.2011.07.024>
35. Somaweera R, Udyawer V, Guinea ML, Ceccarelli DM, Clarke RH, Glover M, Hourston M, Keesing J, Rasmussen AR, Sanders K, Shine R, Thomson DP, Webber BL (2021) Pinpointing drivers of extirpation in sea snakes: a synthesis of evidence from Ashmore Reef. *Front Mar Sci* 8:658756. <https://doi.org/10.3389/fmars.2021.658756>

36. Somaweera R, Udyawer V, Fresnes J De, Amarasinghe AAT, Molchanova G (2023) Coordinated and communal hunting behaviours by Erabu sea krait *Laticauda semifactiata*. Sci Rep 1–7. <https://doi.org/10.1038/s41598-023-48684-3>
37. Speed CW, Wilson NG, Somaweera R, Udyawer V, Meekan MG, Whisson C, Miller K (2022) Video surveys of sea snakes in the mesophotic zone shed light on trends in populations. Front Mar Sci 9:1–10. <https://doi.org/10.3389/fmars.2022.921542>
38. Su Y, Fong SC, Tu MC (2005) Food habits of the sea snake, *Laticauda semifasciata*. Zool Stud 44:403–408.
39. Tabata R, Tashiro F, Nishizawa H, Takagi J, Kidera N, Mitamura H (2017) Stomach contents of three sea kraits (Hydrophiinae: *Laticauda* spp.) in the Ryukyu Islands, Japan. Curr Herpetol 36:127–134. <https://doi.org/10.5358/hsj.36.127>
40. Udyawer V, Cappo M, Simpfendorfer CA, Heupel MR, Lukoschek V (2014) Distribution of sea snakes in the Great Barrier Reef Marine Park: observations from 10 yrs of baited remote underwater video station (BRUVS) sampling. Coral Reefs 33:777–791. <https://doi.org/10.1007/s00338-014-1152-3>
41. Udyawer V, Simpfendorfer CA, Heupel MR (2015) Diel patterns in three-dimensional use of space by sea snakes. Animal Biotelemetry 3:1–9. <https://doi.org/10.1186/s40317-015-0063-6>
42. Voris HK, Voris HH (1983) Feeding strategies in marine snakes: an analysis of evolutionary, morphological, behavioral and ecological relationships. Am Zool 425:411–425.

Figures

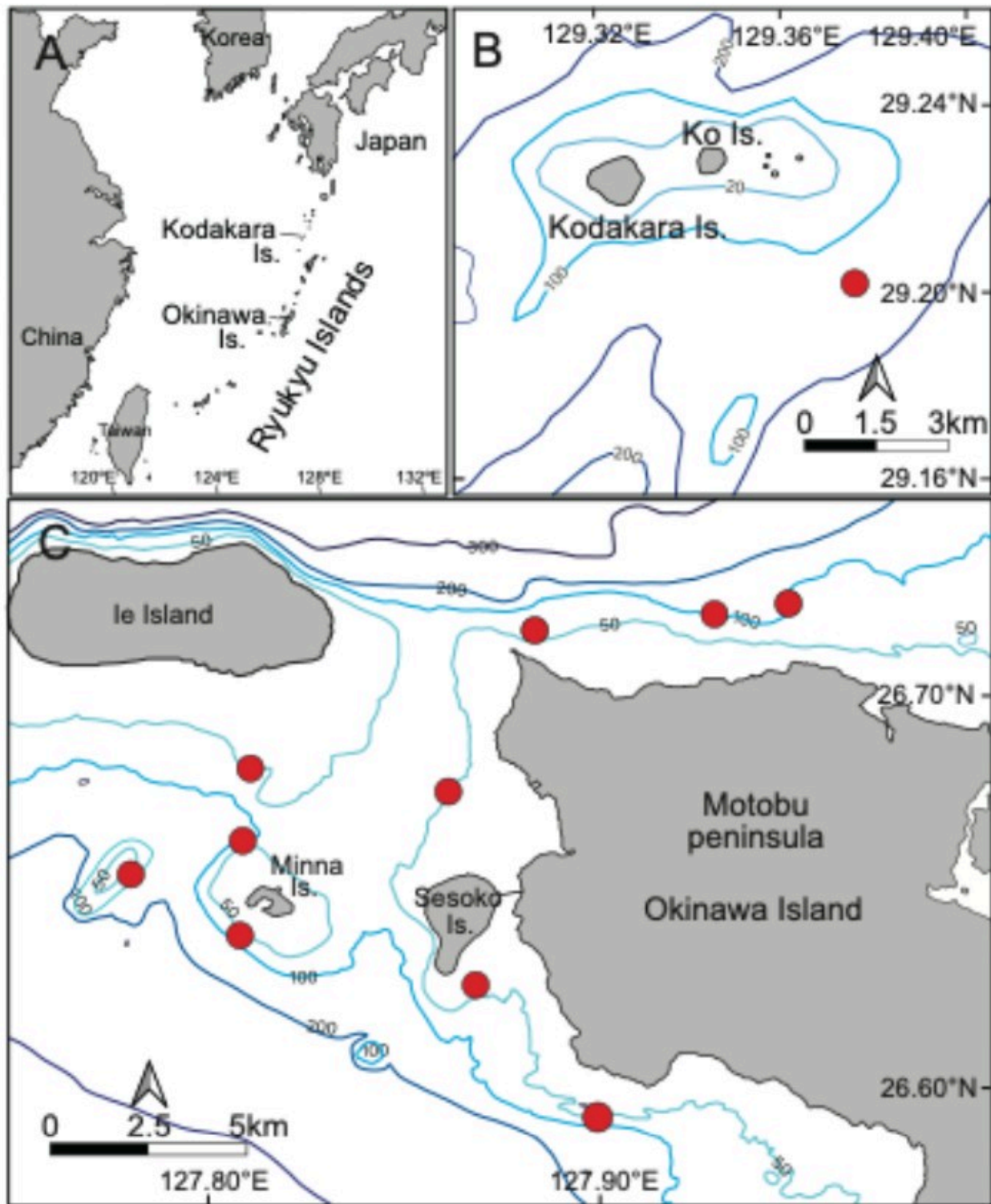


Figure 1

Map showing the Ryukyu Islands (A) and the study sites (B and C). The locations where marine elapids were observed in the mesophotic zone are indicated by red dots.

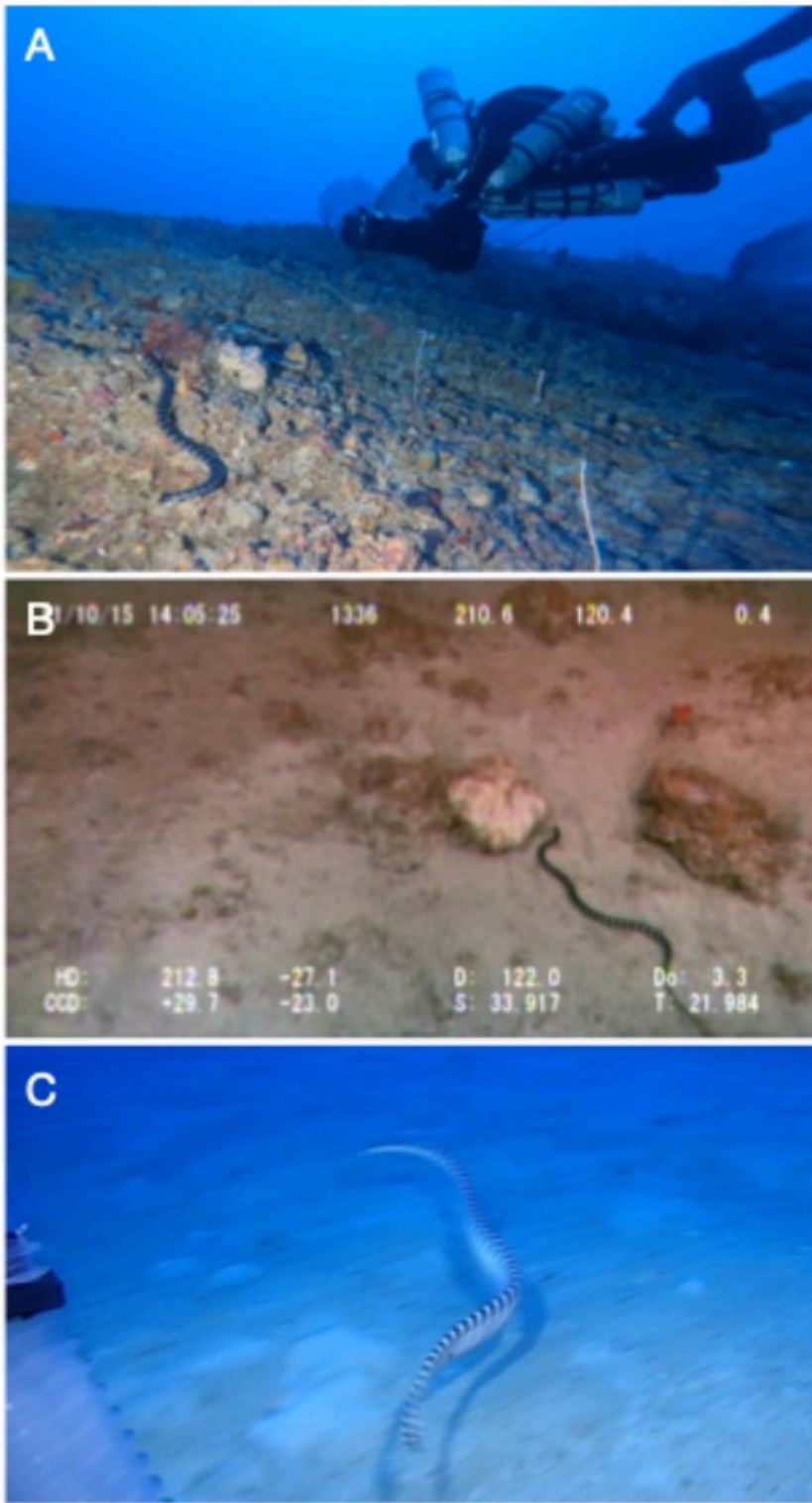


Figure 2

Marine elapid snakes observed in the mesophotic zone of the Ryukyu Islands, Japan. (A) *Laticauda semifasciata* photographed with a mixed-gas rebreather diver at 75 m depth. (B) *Laticauda laticaudata* at 122 m depth, recorded by a remotely operated vehicle (ROV). (C) *Hydrophis ornatus* at 95 m depth, recorded by an ROV. Photographs courtesy of Thomas Jonsson (A) and the Okinawa Churashima Foundation (C). Image in (B) was derived from a video by the Japan Agency for Marine-Earth Science

and Technology (JAMSTEC;
https://www.godac.jamstec.go.jp/jedi/static_player/e/HPD1336HDDDB10_00420900).

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