

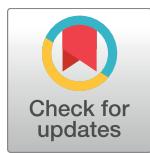
RESEARCH ARTICLE

Northward dispersal of sea kraits (*Laticauda semifasciata*) beyond their typical range

Jaejin Park¹, Il-Hun Kim^{1✉}, Jonathan J. Fong², Kyo-Soung Koo¹, Woo-Jin Choi¹, Tein-Shun Tsai³, Daesik Park^{4*}

1 Department of Biology, Kangwon National University, Chuncheon, Kangwon, South Korea, **2** Science Unit, Lingnan University, Tuen Mun, New Territories, Hong Kong, **3** Department of Biological Science and Technology, National Pingtung University of Science and Technology, Neipu Township, Pingtung County, Taiwan (Republic of China), **4** Division of Science Education, Kangwon National University, Chuncheon, Kangwon, South Korea

✉ Current address: National Marine Biodiversity Institute of Korea, Seochun, Chungnam, South Korea
* parkda@kangwon.ac.kr



Abstract

Marine reptiles are declining globally, and recent climate change may be a contributing factor. The study of sea snakes collected beyond their typical distribution range provides valuable insight on how climate change affects marine reptile populations. Recently, we collected 12 *Laticauda semifasciata* (11 females, 1 male) from the waters around southern South Korea—an area located outside its typical distribution range (Japan, China including Taiwan, Philippines and Indonesia). We investigated the genetic origin of Korean specimens by analyzing mitochondrial cytochrome b gene (*Cytb*) sequences. Six individuals shared haplotypes with a group found in Taiwan-southern Ryukyu Islands, while the remaining six individuals shared haplotypes with a group encompassing the entire Ryukyu Archipelago. These results suggest *L. semifasciata* moved into Korean waters from the Taiwan-Ryukyu region via the Taiwan Warm Current and/or the Kuroshio Current, with extended survival facilitated by ocean warming. We highlight several contributing factors that increase the chances that *L. semifasciata* establishes new northern populations beyond the original distribution range.

OPEN ACCESS

Citation: Park J, Kim I-H, Fong JJ, Koo K-S, Choi W-J, Tsai T-S, et al. (2017) Northward dispersal of sea kraits (*Laticauda semifasciata*) beyond their typical range. PLoS ONE 12(6): e0179871. <https://doi.org/10.1371/journal.pone.0179871>

Editor: Yan Ropert-Coudert, Centre National de la Recherche Scientifique, FRANCE

Received: January 23, 2017

Accepted: June 6, 2017

Published: June 23, 2017

Copyright: © 2017 Park et al. This is an open access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Data Availability Statement: All relevant data are within the paper and its Supporting Information files. All sequence data obtained and used in this study were deposited at GenBank (Accession numbers: KY445753 to KY445768).

Funding: Research was supported by Basic Science Research Program through the National Research Foundation of Korea (NRF) funded by the Ministry of Education (2014R1A1A4A01005302). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Introduction

Reptiles, both terrestrial [1] and marine [2–4], are declining on a global scale. The major contributing factors for marine reptile declines include climate change, deterioration of habitat quality and overexploitation [5,6]. In particular for marine reptiles, ocean warming due to climate change could widely affect breeding patterns, abundance and distribution [2,7]. To understand how climate change affects marine reptile populations, data on changes in geographic distribution (e.g. records of individuals beyond the typical range) are useful.

In this study, we focus on sea snakes. For marine reptiles, sea turtles are the common example for population declines [3], but sea snakes are also decreasing [3,8,9]. Sea snakes primarily inhabit tropical and subtropical regions of the Indian and Pacific Oceans and consist of two

Competing interests: The authors have declared that no competing interests exist.

major groups: true sea snakes (Hydrophiinae), which exclusively use marine environments, and sea kraits (Laticaudinae), which use both marine and terrestrial habitats [10,11]. Based on recent reports, sea snake captures outside the typical distribution range are increasing: *Hydrophis platurus* from California, USA [12], *Laticauda semifasciata* and *L. laticaudata* from mainland Japan [13], *L. semifasciata* and *H. platurus* from Russia [14] and *L. semifasciata* from Korea [15–17]. It has been suggested that these new records are a result of ocean warming following recent climate change.

Historically, only three Hydrophiine species (*H. platurus*, *H. cyanocinctus*, *H. melanocephalus*) were reported from Korea [18–21]. The capture of *L. semifasciata* in Korean waters represents a new and recent appearance [15–17]; *Laticauda semifasciata* is typically found in the waters around Japan, China including Taiwan, Philippines and Indonesia [22]. Tandavanitj et al. [23] found that despite its dispersal abilities, *L. semifasciata* showed distinctive genetic structure between island groups in Taiwan and Japan. In this study, we use molecular methods to determine the geographic origin and cause of *L. semifasciata* recently collected from Korean waters.

Materials and methods

Collection of sea snake samples

Animal handling and experimental procedures were conducted in accordance with guidelines established by the Kangwon National University Institutional Animal Care and Use Committee (Permit Number: KW-161108-1). *Laticauda semifasciata* is not protected in South Korea, so the collection of sea snakes does not require a permit. The individuals were caught from open waters, which are not privately owned or protected.

To obtain sea snake samples from Korean waters, we placed more than 200 posters and 50 banners around coastal towns of southern South Korea bordering the South Sea (including Jeju Island) between April 2015 and October 2016. A total of 12 *L. semifasciata* (six dead, six alive) were collected and donated by local fishermen—nine from Jeju Island and three from the Korean Peninsula. For convenience, we named the locality based on the nearest port to the capture site. All specimens were delivered to the Herpetological Lab of Kangwon National University (KNU). Upon arrival, we collected basic data on the specimens: sex (using a probe), snout-vent length (SVL; using a tape measure up to 0.1 cm) and body weight (using a digital balance up to 0.1 g; ELT 4001, Sartorius-Korea, Seoul Korea). For tissue collection, we took a tail clip (usually only the terminal scale) using scissors [24]. Additional tail tissue samples from four *L. semifasciata* specimens (from Orchid Island, Taiwan) were included in our study to increase geographic sampling. Sequences from the Ryukyu Islands, Japan were obtained from GenBank [23].

DNA extraction and PCR

We extracted whole genomic DNA from tissue samples using the QIAGEN DNeasy Blood & Tissue kit (QIAGEN, Hilden, Germany) following the manufacturer's instructions. For this study, we targeted *Cytb* because there are comparable data in GenBank. We amplified partial sequences of the *Cytb* gene using the primers L14910 and H16064 [25]. DNA was amplified using a SimpliAmp Thermal Cycler (Life Technologies, Carlsbad, CA, USA) in 25 μ l reaction volumes, consisting of 10 ng of template DNA, 1.25 U of ELPIS rTaq DNA polymerase (ELPIS, Daejeon, South Korea), 2.5 μ l of 10x PCR buffer, 2 μ l of 10 mM dNTP mix (2.5 mM each) and 0.5 μ l of each primer (10 pmol). The cycling conditions for PCR were as follows: 94°C for 4 min, followed by 35 cycles at 94°C for 30 s, 57°C for 30 s and 72°C for 1 min with a final extension step of 72°C for 7 min [25]. We verified PCR products by electrophoresis on

1.5% agarose gels, and purified products using an AccuPrep[®] PCR Purification Kit (Bioneer, Daejeon, South Korea). PCR products were sequenced in both directions using the same PCR primers at Macrogen (Seoul, South Korea) on a 3730xl DNA analyzer (Applied Biosystems, Foster City, CA, USA).

Sequence data analysis

We edited and assembled sequences using Geneious v5.3.6. To verify our specimens were all *L. semifasciata*, we constructed a phylogenetic tree using 16 new sequences (GenBank accession numbers KY445753 to KY445768), 11 *Laticauda* sequences from GenBank (5 of *L. semifasciata*, 4 of *L. laticaudata* and 2 of *L. colubrina*) and 3 *Hydrophis* sequences as outgroups. ([S1 Fig](#)). Sequences were aligned using MUSCLE [26], and the alignment was analyzed using both maximum likelihood (ML) and Bayesian inference (BI) methods. ML analyses were run in RAxML v8.2.4 [27] inferring the best-scoring ML tree with 100 replicates followed by a non-parametric bootstrap analysis of 1000 replicates evaluate node robustness of the ML tree. All replicates were run under the GTR + gamma model of sequence evolution. For BI analyses, Markov Chains Monte Carlo chains were run for 2 million generations, sampling every 1000 generations, implemented in MrBayes v.3.2.4 [28]. Models of nucleotide substitution were chosen within MrBayes using the reversible jumping model choice (nst = mixed) with both rate variation and invariable sites (rates = invgamma). Stationarity was checked graphically by plotting log-likelihood scores in Tracer v.1.5 (<http://tree.bio.ed.ac.uk/software/tracer>). The first 500,000 generations were discarded as burn-in and the remaining trees were used to build a consensus tree.

For population genetic analyses, we built a haplotype network using a median joining method in PopArt 1.7.2 (<http://popart.otago.ac.nz>). The dataset analyzed is a combination of our data (16 individuals) with data from Tandavanitj et al. [23] (16 haplotype sequences from 177 individuals).

Results

Of the 12 snakes from Korea, 11 individuals were female and one was male. Detailed morphological information of each snake is provided in [S1 Table](#).

The phylogenetic trees inferred using ML and BI were highly similar, only differing by support values and the relationships of some terminal branches. Phylogenetic analyses verified the identity of the 16 new specimens (12 Korea, 4 Taiwan) to be *L. semifasciata* ([S1 Fig](#)).

We identified three different *Cytb* haplotypes from our specimens, all which were previously reported from the Taiwan-Ryukyu Archipelago ([Fig 1](#)); we adopted the same haplotype names as the previous study [23]. Three specimens from Aewol, Moseolpo, and Gangjeong 2 (Jeju Island) and one from Gori (Korean Peninsula) had the Semi-1 haplotype, a haplotype primarily from the southern Ryukyu Islands (37 out of 38 specimens; [23]). One specimen from Wimi (Jeju Island), one from Ilgwang (Korean Peninsula), and four from Taiwan had the Semi-3 haplotype, a haplotype from Taiwan and the southern Ryukyu Islands (27 from Taiwan and 5 from southern Ryukyu; [23]). The five remaining specimens from Jeju Island (Marado, Gangjeong 1, Seogwipo, Dukdol, and Udo) and one from the Korean Peninsula (Yeosu) had the Semi-5 haplotype, a haplotype found throughout the Ryukyu Archipelago ([Fig 1](#)).

The 12 Korean samples had only three haplotypes (Semi-1, 3 and 5), which could be placed into two major groups based on geography: (1) Semi-1 and Semi-3 haplotypes originating from Taiwan-southern Ryukyu (Aewol, Moseulpo, Gangjeong 2, Gori, Wimi, Ilgwang) and (2) Semi-5 haplotype originating from the entire Ryukyu Archipelago (Yeosu, Udo, Dukdol,

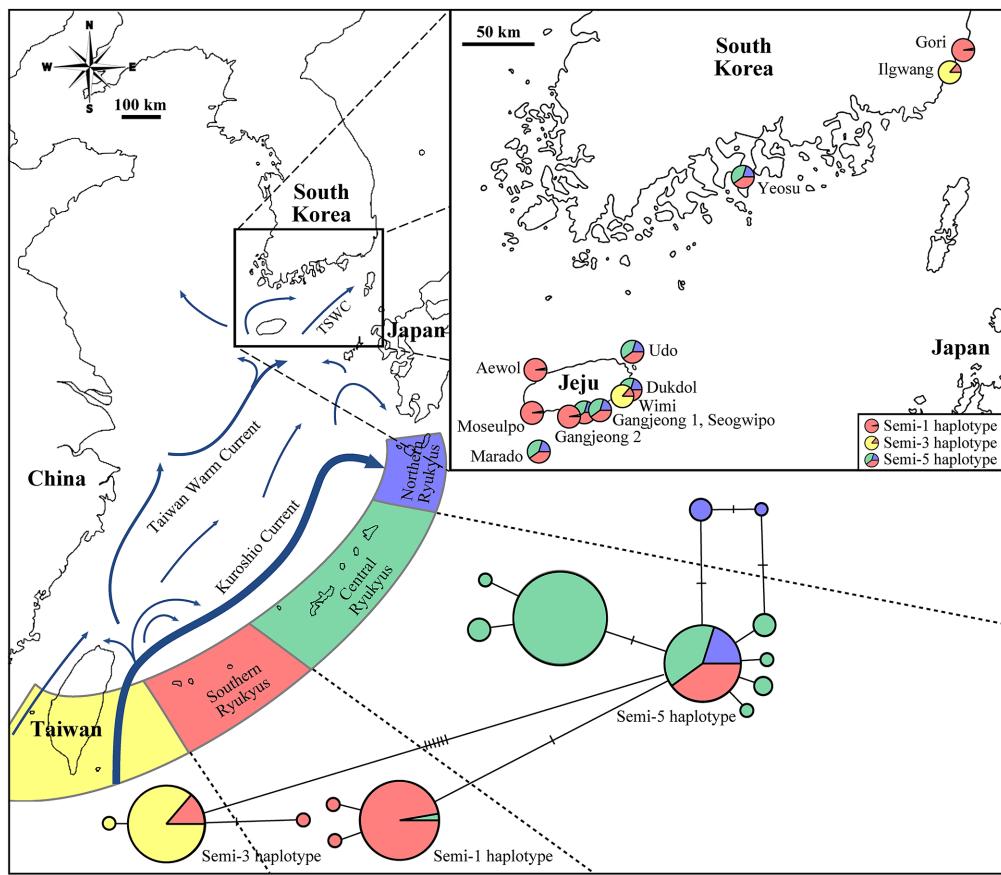


Fig 1. Haplotype network (Cytb) of *Laticauda semifasciata* from East Asia. The four major geographic areas in Taiwan-Ryukyu Archipelago (Taiwan, southern, central and northern Ryukyu) are color-coded. Each circle in the network represents a haplotype, and the color represent the geographic origin, while the size represents the frequency of the haplotype. For clarity, we only label three haplotype names, which were found in new specimens examined in this study. The map of Korea indicates the location of each individual, as well as its matching haplotype in Taiwan and the Ryukyu Archipelago. Arrows indicate the path of the major ocean currents in the region. TSWC; Tsushima Warm Current.

<https://doi.org/10.1371/journal.pone.0179871.g001>

Gangjeong 1, Seogwipo, Marado). Korean samples did not have any haplotypes restricted to either central or northern Ryukyu.

Discussion

We identify two genetic groups of *L. semifasciata* from Korean waters: one group (6 individuals) is closely related to the entire Ryukyu Archipelago (Semi-5), while the second group (6 individuals) has genetic affinity to Taiwan and the southern Ryukyu Islands (Semi-1, Semi-3). For the first group, there is not enough genetic structure to infer the specific geographical origin beyond the Ryukyu Islands. However, for the second group, the available data suggest that the genetic origin of these individuals is either Taiwan or the southern Ryukyu. It is possible, based on the pathways of the Kuroshio Current [29], that the origin of Korean individuals is from further south (Philippines and Indonesia), but genetic data from this region are needed to evaluate this possibility. Ocean currents play a key role in dispersal genetic differentiation in various marine animals, through allowing passive drifts and active swimming of animals in the currents [30–32], and the Taiwan Warm Current and the Kuroshio Current seem to be

important for northward dispersal of *L. semifasciata*. The presence of *L. semifasciata* in Korea was previously undetected, but becoming more common, and we believe that these currents along with recent climate change have contributed to increased records.

In the past, only Hydrophiine species were known to occur in Korea, with fewer than seven observations [20,21], while the first record of Laticaudine sea snakes was in 1995 [16]. The frequency of *L. semifasciata* sightings has increased, while *H. platurus* observation and capture has been relatively steady [17,33]. To explain the occurrence of *L. semifasciata* in Korean waters, we consider three contributing factors: 1) increased effort, 2) northward expansion of prey fish and 3) higher ocean temperatures in Korean waters.

First, increased observation of Laticaudine snakes may be attributed to increased effort in sea snake research relative to the past. We do not believe this to be a major factor because increased effort should also increase observations of Hydrophiine sea snakes known to exist in Korea; during our study period, we had only two reports of *H. platurus*, while we collected 12 *L. semifasciata* and had greater than six observations. The increased numbers of *L. semifasciata* in Korean waters is likely a true pattern.

Second, the northward expansion of prey fish species due to climate change in the East China Sea might increase survival of the sea kraits in northern areas by providing suitable prey. Previous studies showed that global climate change actively or passively expanded various marine fish species beyond their typical distribution ranges [34–36]. In the waters around Jeju Island, subtropical and tropical fish are being captured more frequently [37,38], such as *Chromis notatus* and *Halichoeres tenuispinis* (family Labridae). Previous studies found *L. semifasciata* consume these two fish species [39,40]. So, when *L. semifasciata* are in waters around Korea, they can feed on familiar prey fish, resulting in longer survivorship and more sea krait records.

Third, higher ocean temperatures could contribute to survival of *L. semifasciata* in northern waters. In such a situation, *L. semifasciata* are occasionally dispersed northward, but it is only recently with warmer temperatures that individuals could survive, at least temporarily. The annual mean ocean surface temperature around Jeju Island has increased at a rate of 0.024°C/year (from 17.9°C to 18.6°C) between 1971 and 2000. Winter temperatures are colder and more critical for survival, and these temperatures have also increased (December: 15.41 to 16.52°C; February: 12.71 to 13.32°C) [41]. This suggests that *L. semifasciata* that moved into Korean waters should survive for a longer period than previous, resulting in increased observation of sea kraits.

Our study raises two additional questions: (1) why was *L. semifasciata* the only collected sea krait species? and (2) why were more female *L. semifasciata* captured? We provide potential explanations for these questions. There are three *Laticauda* species found in Northeast Asia: *L. semifasciata*, *L. colubrina* and *L. laticaudata* [42–44]. The capture of only *L. semifasciata* in Korean waters might be due to the geographic distribution, habitat use and physical characteristics of the three species. At a global scale, *L. colubrina* and *L. laticaudata* have a wide regional distribution throughout Southeast Asia, whereas *L. semifasciata* has a more restricted, northeastern distribution (Taiwan, the Ryukyu Islands, Philippines and Indonesia) [22,45]. The core and largest populations of *L. semifasciata* are located in Taiwan and the Ryukyu Islands [22]. If the Taiwan Warm Current and the Kuroshio Current play a major role in northward dispersal, *L. semifasciata* should have the highest chance to move into Korean waters. In addition, of the three *Laticauda* species, *L. semifasciata* is the most adapted to marine environments: spends the more time in the water [10,45,46], has the lowest net water loss [47] and has a wider tail and more cylindrical body trunk [46]. These factors increase the chance that *L. semifasciata* drifts or moves into ocean currents.

Why were more female *L. semifasciata* captured? Of the 12 total sea kraits collected in this study, 11 sea kraits were female (92%). We hypothesize that different feeding behavior and abilities contribute to the skew of females found in Korean waters. *Laticauda* species are benthic feeders and often make trips to the deep bottom (> 80 m) of the ocean for an extended time (> 130 min) to obtain their food [48,49]. Because of a larger body size [50], females need larger and more prey items, and likely have better diving performance (deeper and for longer duration) [49]. Such foraging patterns would result in female *L. semifasciata* more frequently drifting into the rapid ocean currents or seasonal typhoons [51].

Findings from this study have three important ecological implications. First, northward dispersal of *L. semifasciata* is a real phenomenon, and has the potential to establish a new population beyond the typical distribution range. Second, relatively long-distance dispersal of *L. semifasciata* confirms the importance of ocean currents in the dispersal of marine animals, as recently shown in *H. platurus* [32]. Third, because *L. semifasciata* are venomous sea kraits (although they are less likely to bite) [10], appropriate education on sea snake bites is immediately necessary at the coastal towns in South Korea. Questions still remain on whether *L. semifasciata* in Korea originate from specific population or various populations, how long *L. semifasciata* survive at the new northern sites, whether new breeding populations are being established, and how this species as a new predator impact local marine ecosystems [52]. Detailed studies on *L. semifasciata* in Korea and other worldwide sea snake populations beyond typical the distribution range will help clarify these issues.

Supporting information

S1 Fig. Maximum likelihood (ML) tree inferred from a dataset of partial sequences of mitochondrial cytochrome b (*Cytb*) gene. The new specimens collected in our study (12 from Korea, 4 from Taiwan) are in larger, bold font. All were identified as *Laticauda semifasciata*. Numbers at the end of the taxon name refer to GenBank accession numbers. Numbers on the branches represent support values for the major groups—ML bootstrap support, followed by Bayesian posterior probabilities.
(TIFF)

S1 Table. Collection information, morphological characters and mitochondrial cytochrome b (*Cytb*) haplotype of the 12 *Laticauda semifasciata* collected in Korean waters. The haplotype names of *Cytb* are based on [23].
(DOCX)

Acknowledgments

We thank the fishermen who donated valuable sea krait samples, Dr. Ming-Chung Tu for his support in collecting samples in Taiwan and Jong-Sun Kim, Il-Kook Park and Sera Kwon for their help during the field surveys. Research was supported by Basic Science Research Program through the National Research Foundation of Korea (NRF) funded by the Ministry of Education (2014R1A1A4A01005302). In special, we dedicate this manuscript to Heon-Joo Lee, who passed away in car accident during a field survey on Jeju Island.

Author Contributions

Conceptualization: Jaejin Park, Il-Hun Kim, Daesik Park.

Formal analysis: Jaejin Park, Il-Hun Kim, Jonathan J. Fong.

Funding acquisition: Daesik Park.

Investigation: Jaejin Park, Il-Hun Kim, Kyo-Soung Koo, Woo-Jin Choi, Daesik Park.

Project administration: Jaejin Park, Kyo-Soung Koo, Daesik Park.

Resources: Tein-Shun Tsai.

Supervision: Daesik Park.

Writing – original draft: Jaejin Park, Il-Hun Kim, Daesik Park.

Writing – review & editing: Jonathan J. Fong, Kyo-Soung Koo, Woo-Jin Choi, Tein-Shun Tsai, Daesik Park.

References

1. Reading CJ, Luiselli LM, Akani GC, Bonnet X, Amori G, Ballouard JM, et al. Are snake populations in widespread decline? *Biol Letters*. 2010; 6:777–80.
2. Hamann M, Limpus CJ, Read MA. Chapter 15: Vulnerability of marine reptiles in the Great Barrier Reef to climate change. Townsville; Australia: The Great Barrier Reef Marine Park Authority; 2007.
3. Rasmussen AR, Murphy JC, Ompi M, Gibbons JW, Uetz P. Marine reptiles. *PLoS ONE*. 2011; 6(11): e27373. <https://doi.org/10.1371/journal.pone.0027373> PMID: 22087300
4. Wallace BP, Dutton PH, Marcovaldi MA, Lukoschek V, Rice J. Marine reptiles. Chapter 39. The First Global Integrated Marine Assessment. 2016 [cited 2017 Jan 13]. http://www.un.org/depts/los/global_reporting/WOA_RegProcess.htm.
5. Cao NV, Tao NT, Moore A, Montoya A, Rasmussen AR, Broad K, et al. Sea snake harvest in the gulf of Thailand. *Conser Biol*. 2014; 28:1677–87.
6. Great Barrier Reef Marine Park Authority. A vulnerability assessment for the Great Barrier Reef. Townsville; Australia: The Great Barrier Reef Marine Park Authority; 2012.
7. Hawkes LA, Broderick AC, Godfrey MH, Godley BJ. Investigating the potential impacts of climate change on a marine turtle population. *Glob Change Biol*. 2007; 13:923–32.
8. Goiran C, Shine R. Decline in sea snake abundance on a protected coral reef system in the New Caledonian lagoon. *Coral Reefs*. 2013; 32:281–4.
9. Lukoschek V, Beger M, Ceccarelli D, Richards Z, Pratchett M. Enigmatic declines of Australia's sea snakes from a biodiversity hotspot. *Biol Conserv*. 2013; 166:191–202.
10. Heatwole H. Sea snakes. Sydney; Australia: University of New South Wales Press; 1999.
11. Dunson WA. The biology of sea snakes. Baltimore; MD: University Park Press; 1975.
12. Gordon L. Blame El Niño for poisons sea snake found on Ventura County Beach. Los Angeles Times. 2015 Oct 16. <http://www.latimes.com/local/lanow/la-me-ln-venomous-sea-snake-found-20151016-story.html>.
13. Tandavanitj N, Mitani S, Toda M. Origins of *Laticauda laticaudata* and *Laticauda semifasciata* (Elapidae: Laticaudinae) individuals collected from the main islands of Japan as inferred from molecular data. *Curr Herpetol*. 2013; 32:135–41.
14. Kharin VE. Redescription of a Russian finding of the Erabu sea krait *Pseudolaticauda semifasciata* (Reinwardt in Schlegel, 1837), with remarks about species composition of sea snakes (Serpentes: Laticaudidae, Hydrophiidae) in Russian and adjacent waters. *Russ J Mar Biol*. 2009; 35:8–14.
15. Lee JN, Kang SH, Moon SG, Lee IS. On the reptiles of 8 species collected in Busan area—*Caretta caretta*, *Clemmys japonica*, *Trachemys scripta elegans*, *Gekko japonicus*, *Eremias argus*, *Elaphe schrenckii*, *Dinodon rufozonatum*, *Hydrophis melanocephalus*. *Bull Basic Sci Res Cent Kyungsung Univ*. 2003; 15:153–60. Korean with English abstract.
16. Kim IH, Park J, Kaplan RH, Lee JN, Park D. Chinese sea snake (*Laticauda semifasciata*) misidentified as slender-necked sea snake in previous published account in Korea. *J Ecol Environ*. 2016; 40:1. <https://doi.org/10.1186/s41610-016-0002-3>
17. Park J, Kim IH, Koo KS, Park D. First record of *Laticauda semifasciata* (Reptilia: Squamata: Elapidae: Laticaudinae) from Korea. *ASED*. 2016; 32:148–52.
18. Stejneger L. Herpetology of Japan and adjacent territory. Washington; USA: Government Printing Office; 1907.
19. Shannon FA. The reptiles and amphibians of Korea. *Herpetologica*. 1956; 12:22–49.
20. Kang YS, Yoon IB. Illustrated encyclopedia of fauna and flora of Korea. Vol. 17. Amphibia and reptilian. Seoul; South Korea: Sam Hwa Press; 1975. Korean.

21. Kim LT, Han HG. 2009. Fauna of Chosun: amphibia and reptilia. Pyeongyang; DPR Korea: Science and Technology Press; 2009. Korean.
22. Heatwole H, Lillywhite H, Grech A. Physiological, ecological, and behavioral correlates of the size of the geographic ranges of sea kraits (*Laticauda*: Elapidae, Serpentes): A critique. *J Sea Res.* 2016; 115:18–25.
23. Tandavanitj N, Ota H, Cheng YC, Toda M. Geographic genetic structure in two Laticaudine sea kraits, *Laticauda laticaudata* and *Laticauda semifasciata* (Serpentes: Elapidae), in the Ryukyu-Taiwan region as inferred from mitochondrial cytochrome b sequences. *Zool Sci.* 2013; 30:633–41. <https://doi.org/10.2108/zsj.30.633> PMID: 23915156
24. Sheehy CM III, Solórzano A, Pfaller JB, Lillywhite HB. Preliminary insights into the phylogeography of the Yellow-bellied sea snake, *Pleamis platurus*. *Integ Comp Bio.* 2012; 52:321–30.
25. Burbrink FT, Lawson R, Slowinski JB. Mitochondrial DNA phylogeography of the polytypic North American rat snake (*Elaphe obsoleta*): a critique of the subspecies concept. *Evolution.* 2000; 54:2107–18. [https://doi.org/10.1554/0014-3820\(2000\)054\[2107:MDPOTP\]2.0.CO;2](https://doi.org/10.1554/0014-3820(2000)054[2107:MDPOTP]2.0.CO;2) PMID: 11209786
26. Edgar RC. Muscle: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Res.* 2004; 32:1792–7. <https://doi.org/10.1093/nar/gkh340> PMID: 15034147
27. Stamatakis A. RAxML Version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics.* 2014; 30:1312–3. <https://doi.org/10.1093/bioinformatics/btu033> PMID: 24451623
28. Ronquist F, Huelsenbeck JP. MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics.* 2003; 19:1572–4. PMID: 12912839
29. Barkley RA. The Kuroshio Current. *Curr Sci.* 1970; 6:54–60.
30. Kobayashi DR, Cheng IJ, Parker DM, Polovina JJ, Kamezaki N, Balazs GH. Loggerhead turtle (*Caretta caretta*) movement off the coast of Taiwan: characterization of a hotspot in the East China Sea and investigation of mesoscale eddies. *ICES J Mar Sci.* 2011;fsq185. <https://doi.org/10.1093/icesjms/fsq185>
31. Chapman JW, Klaassen RHG, Drake VA, Fossette S, Hays GC, Metcalfe JD, et al. Animal orientation strategies for movement in flows. *Curr Biol.* 2011; 21:R861–70. <https://doi.org/10.1016/j.cub.2011.08.014> PMID: 22032194
32. Brischoux F, Cotté C, Lillywhite HB, Bailleul F, Lalire M, Gaspar P. Oceanic circulation models help to predict global biogeography of pelagic Yellow-bellied sea snake. *Biol Lett.* 2017; 12:20160436. <https://doi.org/10.1098/rsbl.2016.0436> PMID: 27555651
33. Lee HJ, Kim IH, Park D. Telephone inquiry and local interview on the observation of Korean sea snakes. *Korean J Herpet.* 2013; 5:45–52. Korean with English abstract.
34. Perry AL, Low PJ, Ellis JR, Reynolds JD. Climate change and distribution shifts in marine fishes. *Science.* 2005; 308:1912–5. <https://doi.org/10.1126/science.1111322> PMID: 15890845
35. Last PR, White WT, Gledhill DC, Hobday AJ, Brown R, Edgar GJ, et al. Long-term shifts in abundance and distribution of a temperate fish fauna: a response to climate change and fishing practices. *Global Ecol Biogeogr.* 2011; 20:58–72.
36. Jung S, Pang IC, Lee JH, Choi I, Cha HK. Latitudinal shifts in the distribution of exploited fishes in Korean waters during the last 30 years: a consequence of climate change. *Rev Fish Biol Fisheries.* 2014; 24:443–462.
37. Choi Y, Kim B, Lee HH. The fish fauna of little Munsom in Jeju-do, Korea. *Korean J Environ Biol.* 2013; 31:45–52. Korean with English abstract.
38. Ko JC, Kim BY, Kim MJ, Park SE, Kim JB, Cho HK. A seasonal characteristic of marine environment and fish assemblage in the coastal waters Jeju Island, Korea from 2012–2013. *JFMSE.* 2015; 27:319–44. Korean with English abstract.
39. Su Y, Fong SC, Tu MC. Food habits of the sea snake, *Laticauda semifasciata*. *Zool Stud.* 2005; 44:403–8.
40. Park J, Koo KS, Choi WJ, Kim IH, Park D. Report on the activity patterns of a Chinese sea snake (*Laticauda semifasciata*) in rearing captivity. *Korean J Herpetol.* 2016; 7:6–14. Korean with English abstract.
41. Jang SM, Kim SS, Choi YC, Kim SG. A study of correlations between air-temperature of Jeju and SST around Jeju Island. *JKOSME.* 2006; 9:55–62. Korean with English abstract.
42. Mao SH, Chen BY. Sea snakes of Taiwan: a natural history of sea snakes. Taipei; Taiwan Republic of China: The National Science Council; 1980.
43. Zhao EM, Adler K. Herpetology of China. Oxford; Ohio; USA: Society for the Study of Amphibians and Reptiles and Chinese Society for the Study of Amphibians and Reptiles; 1993.
44. Toriba M. Sea snakes of Japan. In: Gopalakrishnakone P, editor. *Sea snake toxinology.* Singapore: Singapore University Press; 1994. p. 206–11.

45. Heatwole H, Busack S, Cogger H. Geographic variation in sea kraits of the *Laticauda* colubrine complex (Serpentes: Elapidae: Hydrophinae: Laticaudini). *Herpetol Monogr*. 2005; 19:1–136.
46. Wang S, Lillywhite HB, Tu MC. Locomotor performance of three sympatric species of sea kraits (*Laticauda* spp.) from Orchid Island, Taiwan. *Zool Stud*. 2013; 52.1:43. <https://doi.org/10.1186/1810-522X-52-43>
47. Brischoux F, Tingley R, Shine R, Lillywhite HB. Behavioral and physiological correlates of the geographic distributions of amphibious sea kraits (*Laticauda* spp.). *J Sea Res*. 2013; 76:1–4.
48. Brischoux F, Bonnet X, Shine R. Foraging ecology of sea kraits *Laticauda* spp. in the Neo-Caledonian lagoon. *Mar Ecol Prog Ser*. 2007; 350:145–51.
49. Brischoux F, Bonner X, Cook T, Shine R. Snakes at sea: diving performance of free-ranging sea kraits. *Proceedings of the 11th Annual Meeting on Health, Science and Technology*; 2007; Tours University, France.
50. Tu MC, Fong SC, Lu KY. Reproductive biology of the sea snake, *Laticauda semifasciata*, in Taiwan. *J Herpetol*. 1990; 24:119–26.
51. Liu YL, Lillywhite HB, Tu MC. Sea snakes anticipate tropical cyclone. *Mar Biol*. 2010; 157:2369–73.
52. Ineich I, Bonnet X, Brischoux F, Kulbicki M, Séret B, Shine R. Anguilliform fishes and sea-kraits: neglected predators in coral reef ecosystems. *Mar Biol*. 2007; 151:793–802.