Why Are There No Sea Snakes in the Atlantic?

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Roughly 70 species of sea snakes inhabit the Indo-Pacific but are absent from the Atlantic Ocean. Paleoclimatic conditions in the Coral Triangle were favorable for evolutionary transitions to the sea, while those in the Caribbean region and coastlines bordering the Atlantic Ocean were less favorable. The dispersal of sea snakes from the Indian to Atlantic Oceans around the Cape of Good Hope has been prevented by low water temperatures and a lack of precipitation related to the presence of the Benguela Current along the Atlantic coast of southern Africa. The Isthmus of Panama fully separated the Pacific and Atlantic Oceans before the speciation and dispersal of the sole pelagic species of sea snake to reach the Central American Pacific shoreline. Future climatic changes could bring declines or extinctions of sea snakes within their present ranges, but they appear unlikely to favor the dispersal and establishment of sea snakes in the Atlantic Ocean.

Keywords: sea snakes, Atlantic, Coral Triangle, distribution, paleoclimate

Now that the Mesozoic plesiosaurs, mosasaurs, and ichthyosaurs are long extinct, the most conspicuous and generally familiar marine reptiles are the sea turtles, consisting of seven species in six genera and two families (TTWG 2017). Sea turtles occupy tropical and subtropical marine habitats in all of the world's oceans. Interestingly, by far the most species-rich group of marine reptiles, the sea snakes (Elapidae: Hydrophiinae), do not occur anywhere in the Atlantic Ocean, a biogeographic curiosity that we will attempt to explain in this article.

Sea snakes are represented by eight species of semiaquatic oviparous sea kraits (*Laticauda* spp.) and 60 species of fully marine viviparous "true" sea snakes (figures 1 and 2; Heatwole 1999, Sanders et al. 2008). The sea kraits are an independent marine lineage that is a close sister to terrestrial Australasian elapids plus the true sea snakes (Lukoschek and Keogh 2006, Sanders et al. 2008, 2010, Lee et al. 2016, Ukuwela et al. 2016). The two lineages of marine snakes independently adapted to the sea and did not share a common marine ancestor. Their most recent (Asian) common terrestrial ancestor lived approximately 26 to 14 million years ago (Ma), and the viviparous clade of true sea snakes diverged at approximately 8 to 6 Ma (Sanders et al. 2008, Lee et al. 2016). The majority of speciation events occurred during changes of sea level that generated and dissolved barriers between marine basins during the last 2.5 million years (Ukuwela et al. 2016). Therefore, the fully marine sea snakes represent a recent, rapid radiation and evolutionary transition from land to sea.

The evolutionary origin and diversification of the viviparous sea snakes were in the region of southeastern Asia known as the Coral Triangle, at the Sahul and Sunda Shelves (Sanders et al. 2008), and Australasia (figure 3; Ukuwela et al. 2016). Speciation within the sea-snake lineages (including *Laticauda*) involved trophic associations with coral reefs and numerous islands, generally extending outward from the Coral Triangle to other parts of southern Asia, Australia, the Pacific Ocean to the east, and the Indian Ocean to the west (Heatwole 1999, 2010, Sanders et al. 2008, Ukuwela et al. 2016). The single pelagic and planktonic species, *Hydrophis platurus*, drifts with surface and subsurface currents and shows relatively high dispersal rates (figures 4 and 5; Sheehy et al. 2012, Brischoux et al. 2016, Ukuwela et al. 2016). Consequently, it has the broadest distribution of any squamate reptile, ranging from coastal southern Africa across the Indo-Pacific to the western coasts of Central America (Heatwole 1999, Sheehy et al. 2012). This species is the only sea snake geographically poised to invade the Atlantic via dispersal from its Pacific origin.

Although no species of marine snake currently inhabits the Atlantic Ocean (figure 3), this was not always the case. The extinct (and unrelated) family Palaeopheidae contains at least 20 species of fully aquatic snakes that inhabited offshore marine, estuarine, or riverine habitats in the eastern and western Atlantic Ocean (Holman 2000). These diverse habitats suggest that various species or populations were

*Figure 1. An amphibious sea krait (*Laticauda semifasciata*) and its coastal habitat at Orchid Island, Taiwan. Photographs: Ming-Chung Tu (upper) and Harvey B. Lillywhite (lower).*

and many other lineages of vertebrates correlates with the rapid cooling of the Earth at the end of the Eocene, and the palaeopheid lineage left behind no extant relatives.

Sea snakes are absent from colder water associated with the polar seas, areas of high salinity such as the Red Sea, and the entire Atlantic Ocean and Caribbean Sea. The tropical and subtropical Atlantic and Caribbean have appropriate habitat for sea snakes, so the question arises why no sea snakes are there. Here, we address five focal topics; (1) the importance of viviparity in lineages ancestral to sea snakes; (2) why sea snakes have not dispersed from the Indian Ocean to the South Atlantic Ocean around the African Cape of Good Hope; (3) why dispersal had not occurred from the Pacific to the Caribbean before completion of the Panama Isthmus; (4) why colubrid or other taxa of snakes have not transitioned from terrestrial to marine habitats in the Caribbean region, similarly to marine radiations of elapids in southeastern Asia; and (5) what might happen should sea snakes enter the tropical Caribbean, either through dispersal of waifs through the Panama Canal or as a result of global warming possibly eliminating thermal barriers.

Viviparity

Viviparity is an important attribute in the evolutionary adaptation of marine snakes. The cleidoic egg does not develop in water; therefore, amniotes have two avenues of adaptation to aquatic life: (1) lay their eggs on land despite whatever other aquatic tendencies they may have (e.g., seabirds, marine iguanas, and turtles) or (2) viviparity (e.g., all aquatic mammals). Like sea turtles, the sea kraits have followed the former mode: They feed in the sea but oviposit on land, thereby retaining the oviparous traits of their immediate elapid ancestors. By contrast, the true sea snakes descended from a lineage of viviparous terrestrial elapids and in that sense were pre-adapted to marine life, much as aquatic mammals descended from already-viviparous terrestrial lineages. Murphy (2012) reviewed the reproductive mode of 2552 species of aquatic and semiaquatic snakes and found that they were about equally divided as to their mode of reproduction (48% oviparous; 52% viviparous). However, in the family Elapidae, all

adapted to water salinities ranging from low to very high (Hutchison 1985). Fossils and the sediments that contain them indicate that some palaeopheids were entirely marine and that most species were very large, with some exceeding 9 meters in total length. Palaeopheids lived during the Paleocene–Eocene Thermal Maximum, when global temperatures increased by 5 degrees Celsius (°C)–8°C (McInerney and Wing 2011) and caused oceanic surface temperatures near the North Pole to increase from about 18°C to over 23°C (Sluijs et al. 2006). The extinction of these

Figure 2. Hydrophiine sea snakes swimming over coral reefs in the Timor Sea. Upper photo, **Hydrophis stokesii;** *Lower photo,* **Emydocephalus annulatus;** *Inset,* **Aipysurus laevis.** *Photographs: Chris Malam, with permission.*

of snakes having potential for evolving marine habits (table 1).

Indian Ocean to the South Atlantic Corridor

Sea snakes are present in various parts of the Indian Ocean, and the pelagic *Hydrophis platurus* in particular occurs at the southern tip of Africa. Insofar as this species occurs to the east of this location, what has prevented its distribution from extending westward into the Atlantic? Two factors are likely to be important. First, the prevailing oceanic temperatures are relatively low and are not favorable for survival, and especially not for reproduction, of *H. platurus* along the southern coast of South Africa (Dunson and Ehlert 1971). Second, there is a stable trough of high pressure along the western coast of South Africa that extends northward along the coast of Namibia. The South Atlantic high pressure covers an area from approximately 35° W eastward to 12° E and from approximately 18° S to 40° S. A second semipermanent trough of high pressure is located in the Indian Ocean and covers an area from approximately 30° E eastward to 110° E and from approximately 20° S to 43° S. The high-pressure cell in the South Atlantic drives winds that spiral outward in an anticlockwise direction, and consequently, strong winds move up the Namibian coast from the south and southwest (figure 3).

Oceanic temperatures for Cape Town average roughly between 15°C during July–September and 18.5°C during January–March, with an overall mean annual temperature of 16.7°C. Surface temperatures off coastal Namibia are influenced by upwelling of the cold Benguela Current, which is the eastern boundary current of the South Atlantic subtropical gyre (Wedepohl et al. 2000). The Benguela upwelling replaces surface waters with deep, cooler layers of water, and the temperatures of the sea's surface typically range between 13°C and 18°C. The Benguela Current has a well-defined flow northward along the western coast of southern Africa (from 15° S to 35° S; figure 3), mostly confined near the continent and having a more variable flow on its western side (Garzoli and Gordon 1996). The Benguela Current is 200 to 300 kilometers wide, broadening as it flows northwest along the coast of South Africa and Namibia. Considerable fossil evidence from both

of the more than 70 species of true sea snakes are viviparous, whereas all eight species of sea kraits are oviparous, reflecting their respective genetic heritages from ancestral viviparous and primarily oviparous lineages (Sanders et al. 2008). It is tempting to speculate that the adaptive radiation of the true sea snakes into various marine niches, in comparison with the less diverse lineage of sea kraits, might be related to the degree to which true sea snakes' mode of reproduction freed them from dependence on land. This topic is discussed further below in relation to the Coral Triangle and its relative predominance of viviparous coastal lineages
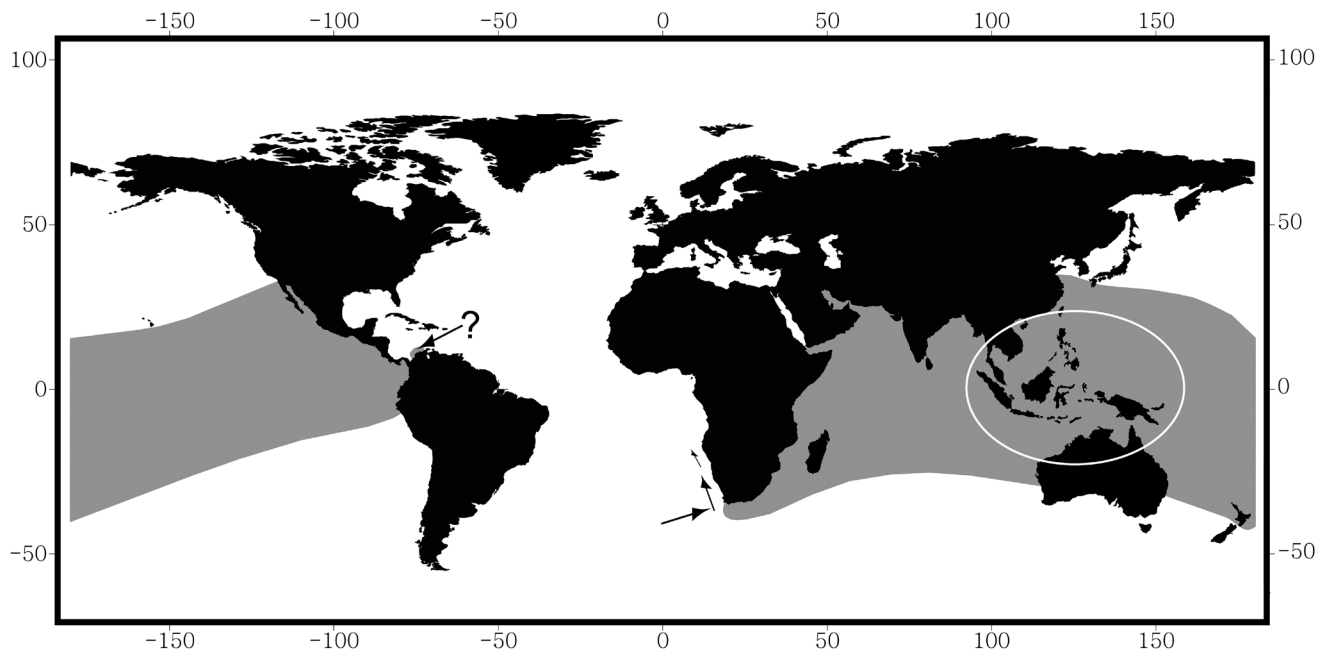
Figure 3. Map of the Earth emphasizing the oceanic distribution of sea snakes (gray swaths) and the dearth of sea snakes in the Atlantic and Caribbean Oceans (center of figure). Surrounding numbers are latitude and longitude. Note that the areas in gray enclose known distributions of sea snakes based on locations of known specimens and thus include waifs and potential distribution of Hydrophis platurus*, which is pelagic and drifts on oceanic currents. Thus, the distribution shown is a polygon that encloses known records without confirmation of breeding populations. The displayed range is not equivalent to the extent of occurrence (EO) or the area of occupancy (AO) as are used by the International Union for Conservation of Nature. The question mark denotes the questionable possibility of a population of* Hydrophis platurus *off the coast of northern Columbia. The other arrows depict the southeasterly part of the South Atlantic Gyre and the Benguela current of cold water along the western coast of southern Africa. The white ellipse encloses the region of origins and highest diversity of sea snakes. Map modified from figure 6 in Rasmussen et al. (2011).*

marine and terrestrial vertebrates suggests that the cold Benguela Current has been operative for at least 5 million years (Olson 1983, Lehmann et al. 2016).

Hydrophis platurus (and other sea snakes) are sensitive to thermal conditions; breeding populations occur only in waters where the monthly temperatures exceed 20°C (Dunson and Ehlert 1971), and temperatures below 18°C generally are lethal. Thus, the latitudinal limit of distribution coincides with the 18°C surface isotherm (Graham et al. 1971). Feeding ceases in water with temperatures below 19°C, which also reduce locomotor abilities and cause death within 5 to 12 days (Graham et al. 1971, Heatwole et al. 2012). The upper thermal limit of *H. platurus* is about 36°C, and high temperatures probably are not a significant factor limiting geographic distribution (Hecht et al. 1974). Simulations of drifting snakes suggest that sea snakes can potentially disperse as waifs around the Cape of Good Hope into the southern Atlantic, but survival is estimated to be less than 1 year, attributable solely to low prevailing temperatures (Brischoux et al. 2016).

The average rainfall near the coast of Namibia is less than 20 millimeters per year, and all of the precipitation falls during a very small number of days. Many years may pass without significant rain. Sea snakes, including *H. platurus*, depend on fresh water and dehydrate at sea during periods without significant precipitation (Lillywhite et al. 2008, 2012, 2014, 2015). Thus, snakes are without access to fresh water from rainfall west of the Cape of Good Hope, and currents will carry them in a prevailing northward direction, where conditions of cold water and dry air continue for considerable distances. This environment is not favorable to the survival of sea snakes and likely explains why *H. platurus* has not established breeding populations in the western Atlantic Ocean.

The Isthmus of Panama

The Isthmus of Panama may have started to emerge as early as approximately 15 to 12 Ma ago (Bacon et al. 2015), thereby fully separating the Pacific and Atlantic Oceans no later than 4.5 Ma ago. This was much earlier than the speciation of *H. platurus* (1.3–3 Ma ago; Sanders et al. 2013,

completion of the Panama Canal raised the possibility of present-day dispersal of individuals into the Caribbean (Graham et al. 1971). The susceptibility of this species to drifting with currents, however, led Sheehy and colleagues (2012) to suggest that establishment of a breeding population originating from rare dispersal events would be highly improbable. The fact that no populations have been established on the Caribbean side of the canal since its completion in 1914 lends credence to this opinion. We note, however, that four sight records of individual *H. platurus* on the Caribbean coast of Colombia (Hernández-Camacho et al. 2006) suggest that establishment is at least a remote possibility (figure 3).

One of the concerns arising from the never-realized plans of building a sea-level canal through Central America was that an invasion by sea snakes into Western-Hemisphere marine waters would have an impact on the tourist industry of Caribbean beaches and resorts. The fact that various Indonesian, Fijian, and Australian tourist islands, reefs, and dive sites maintain thriving businesses despite the presence of several species of sea snakes suggest that such fears are groundless. Indeed, the snakes seem to be an attraction for diving photographers.

Evolution of marine snakes from nonelapid taxa bordering the Atlantic and Caribbean Oceans: Comparisons with Coral Triangle

The taxa of marine or brackish-water snakes other than sea snakes probably include fewer than 40 species representing other families: Homalopsidae, Acrochordidae, Dipsadidae, the African Grayidae, and Colubridae (table 1; Murphy 2012, Vitt and Caldwell 2014). Most of these species are Asian and are associated with the Indian and Pacific Oceans (table 1). Relatively few species utilize the brackish water associated with North and South America, west-central Africa, and the Mediterranean, with connections or association with the Atlantic Ocean (table 1).

Nearly all nonelapid snakes that have some marine association are found in mangrove environments, which likely acted as transitional settings for aquatic snakes evolving marine habits (Murphy 2012). The more dramatic

Figure 4. The pelagic sea snake, Hydrophis platurus, *showing both dorsal and ventral (underwater) aspects of the snake. Photographs: Harvey B. Lillywhite (upper) and Joseph B. Pfaller (middle and lower photographs, used with permission).*

Ukuwela et al. 2016), so there was no dispersal corridor to the Atlantic Ocean when this pelagic species reached the Central American coastline (but see the primary calibrations in Lee et al. 2016, which extend the divergence dating of *H. platurus* to about 6 Ma ago). Nevertheless, reconnection of the Pacific Ocean and Caribbean Sea occasioned by the

Figure 5. Planktonic behavior of **Hydrophis platurus** *in coastal waters offshore from northwestern Costa Rica. Photographs: Harvey B. Lillywhite.*

evolutionary radiations from terrestrial or freshwater habitats to marine ones occurred in the vast wetland complex associated with the Sunda Shelf (1.85 million square kilometers), southeast Asia, and Australasia, where sea snakes no doubt originated (figure 3; Ukuwela et al. 2016).

The Coral Triangle/Sahul/Sundaland areas have the highest diversity of elapid sea snakes (Heatwole 1999, Elfes et al. 2013, Ukuwela et al. 2016) and sea kraits (Gherghel et al. 2016), and the latter taxon almost certainly originated and diversified there (Heatwole et al. 2017). Inspection of a world map shows that at present, this area has the greatest interdigitation of land and sea of anywhere in the world, and this condition has extended into the past (e.g., Sathiamurthy and Voris 2006). Thus, the evolutionary transitions to and from marine habitats may be related to an extensive interface between land and sea across a very large geographic region with dynamic historical changes and presence of multiple ancestral snake lineages. High precipitation and relatively low salinities within the Coral Triangle also provided favorable conditions for evolutionary transitions to the sea (Brischoux et al. 2012a, 2012b). The Coral Triangle/Sundaland also experienced numerous cycles of changes in sea level during the 20 or more Pliocene and Pleistocene glacial–interglacial intervals, driving major geographic changes favorable to speciation, such as the appearance and disappearance of islands, the opening and closing of marine corridors and bridges (Voris 2000, Heatwole 2010, Heatwole et al. 2016, 2017), alternating higher and lower salinities (Brischoux et al. 2012a, 2012b), and the rapid formation or disappearance of mangrove fringes and mud flats (Hanebuth et al. 2011). In spite of these fluctuating sea levels, the Coral Triangle has been thermally stable since the Pliocene (Kent and Muttoni 2008), leading to a favorable setting for marine transitions and the speciation of estuarine species of snakes having the breadth of niche and capabilities for dispersal (Hanebuth et al. 2011). Reduced extinctions attributable to the persistence of stable shallow marine habitats might also have been important during the past 3 million years (Pellissier et al. 2014).

Roughly one-third of the approximately 160 shallow marine fish families in the Coral Triangle are preyed on by sea snakes (Voris and Voris 1983). Although many aspects of ecology related to the partitioning of niches are not well known in sea snakes, clearly, assemblages of species of sea snakes involve differences in diet, feeding behavior, and morphology that evolved relatively rapidly in the center of their distribution.

The Caribbean ostensibly provides a region that is similar to the Coral Triangle, with historical changes in sea level,

Table 1. Nonelapid, estuarine, or marine snakes by region.

Region	Family, Species	Total species	Endemic?	Reproductive mode	Reference
Coral Triangle	**Homalopsidae**				
	Bitia Hydroides		yes	V	Murphy 2007
	Cantoria annulata		yes	V	Murphy 2007
	C. violacea		yes	V	Murphy 2007
	Cerberus australis		?	V	Murphy 2007
	C. microlepis		?	V	Murphy 2012
	C. rhynchops		yes	V	Murphy 2007
	Djakoiskandanus annulatus		?	V	Murphy 2012
	Enhydris albomaculata		?	V	Murphy 2007
	E. bennettii		yes	V	Murphy 2007
	Erpeton tentaculatus		no	V	Murphy 2012
	Fordonia leucobalia		yes	V	Murphy 2007
	Gerarda prevostiana		yes	V	Murphy 2007
	Myron karnsi		?	V	Murphy 2012
	M. resetari		?	V	Murphy 2012
	M. richardsonii		yes	V	Murphy 2007
	Acrochordidae				
	Acrochordus arafurae		no	V	Murphy 2012
	A. granulatus		yes?	V	Murphy 2012
	A. javanicus		no	V	Murphy 2012
	Colubridae				
	Ahaetulla fronticincta		?	V	Rasmussen et al. 2011
	Macropisthodon flaviceps	20	no	?	Rasmussen et al. 2011
Mediterranean and Africa	**Colubridae**				
	Grayia smythii		no	O	Murphy 2012
	Crotaphopeltis hotamboeia		no	O	Rasmussen et al. 2011
	Natrix maura		no	O	Galan 2012; Fuentes and Escoriza 2015
	N. natrix		no	O	Baker 2015
	N. tessellata	5	no	O	Rasmussen et al. 2011
Caribbean and Gulf of Mexico	**Colubridae**				
	Farancia erytrogamma		no	O	Palmer and Braswell 1995
	Nerodia clarkii		yes	V	Rasmussen et al. 2011
	N. fasciata		no	V	Heatwole 1999
	N. sipedon		no	V	Heatwole 1999
	N. valida		no	V	Heatwole 1999
	Tretanorhinus nigroluteus		no	O	Murphy 2012
	T. variabilis	7	no	O	Murphy 2012
South America	**Colubridae**				
	Helicops angulatus		no	O, V	Rasmussen et al. 2011
	H. infrataeniatus		no	V	Rasmussen et al. 2011
	Hydrops triangularis		no	O	Rasmussen et al. 2011
	H. martii	4	no	O	Rasmussen et al. 2011

Note: Endemism refers to estuarine or coastal waters, and reproductive modes are indicated as oviparous (O) or viviparous (V).

cyclic submergence and reemergence of islands, and extensive coral reefs and mangroves (Lin et al. 1997, Hearty et al. 1998, Steadman et al. 2015). The question why American, Caribbean, or African taxa of snakes did not undergo evolutionary transitions to occupy marine habitat as did those in Asia is likely related to the Coral Triangle representing a much larger and more complex system. Other possible reasons could be related to subtle or unrecognized aspects of geologic and climatic history, unknown evolutionary constraints within the various taxa of New World snakes, or simply historical

accident. Closure of the Isthmus of Panama, which sealed off the tropical Pacific from the tropical Atlantic, may have been involved (see previous section). The Coral Triangle, by contrast, has always maintained direct connections between the tropical Pacific and tropical Indian oceans.

The Pliocene and Pleistocene paleoclimate in the Caribbean may have provided conditions (e.g., salinity and/or rainfall, water temperature) less favorable to transitions to marine life than in the Coral Triangle/Sundaland. For example, the Pliocene paleoclimate was characterized by an increase in the salinity of the surface of the sea and a decrease in sea-surface temperatures as a consequence of the emergence of the Central American Isthmus and the restricted exchange of surface water through the Panama Strait (Gussone et al. 2003). Contrasts in paleoclimates between these two biogeographic areas also occurred more recently during the middle Pleistocene transition that was characterized by decreases in sea-surface temperatures in the Atlantic versus an increase in Asian monsoonal intensity (Clark et al. 2006).

Roberts and colleagues (2002) analyzed the geographic ranges of 3235 species of fish, corals, snails, and lobsters to explore the importance of coral-reef habitats to shallow-water marine biodiversity and the locations of marine biodiversity hotspots. For all taxa, species richness was highest in the Coral Triangle region of Southeast Asia. They also identified centers of endemism involving multiple taxa and demonstrated they occur in many places that are highly interconnected with other regions, again predominantly in the Coral Triangle. Their findings accord with growing evidence that species with pelagic larval stages do not always disperse widely (Jones et al. 1999, Robertson 2001). In the case of sea snakes, it is noteworthy that rapid and recent speciation events have produced only a single pelagic species (*H. platurus*). Thus, sea snakes have remained most diverse near their centers of origin.

We note that mangroves are much more diverse in the Coral Triangle (13 genera) than in the Caribbean, where only 4 genera exist and none are endemic (Hutchings and Saenger 1987). Similarly, the number of species of snakes that are endemic to estuarine and marine waters in the Coral Triangle exceeds that in the Caribbean and the adjacent Gulf of Mexico by about 20:1, although a number of snakes extend into mangroves from other habitats (table 1). No species of tetrapod vertebrate is confined to mangroves or other estuarine habitats in the Caribbean. By contrast, mangroves in Australia have an avifauna of over 200 species, of which about 7% are restricted to mangroves and about an additional 6% use it as their primary habitat (Hutchings and Saenger 1987). Few, if any, mammals, reptiles, or amphibians are restricted to mangroves (Hutchings and Saenger 1987), even in Australia.

Other types of coastlines bordering the Atlantic Ocean also failed to produce significant numbers of snakes that tolerate estuarine or marine waters (table 1). Moreover, the Coral Triangle (broadly defined) appears to be the only region where viviparity is characteristic of the estuarine species, including the ancestral lineages giving rise to sea snakes, as well as extant species that could potentially adapt to marine habitats (table 1). Understanding these differences in relation to marine invasions by snakes will require much further research concerning the adaptive variation, physiological tolerances, and epigenetic processes in the respective taxa, as well as the local opportunities for adaptation and dispersal (Sherman et al. 2016).

Prospects for snakes reaching the tropical Atlantic or Caribbean waters

Talk of constructing a sea-level canal between the Caribbean Sea and the Pacific Ocean arises periodically. Because of the pelagic habits of *Hydrophis platurus*, such a canal would be more likely to provide passage for it than would the present canal. There are two hypothetical effects of such an invasion into the Caribbean. First, populations of sea snakes could increase predation on native populations of fish. *H. platurus* inhabits slicks at the surface of the sea and preys on fish seeking shelter beneath floating debris. These are mainly the juvenile stages of pelagic fish, and their proportional species composition in the stomachs of snakes is similar to that of the assemblage of fish sheltering under debris (Hunter and Mitchell 1967, Brischoux and Lillywhite 2013). Thus, it is likely that the direct effect of *H. platurus* would be on pelagic fish rather than benthic fish. Furthermore, if species of sea snakes with a distinctive type of venom invade new areas, they might encounter a pool of prey that are relatively defenseless against their venom and therefore could be easily overcome by a bite. For example, species of eel normally included in the diet of sea kraits have high resistance to the snake's venom, whereas allopatric eels of the same genus are highly sensitive to the venom of sea kraits (Heatwole and Poran 1995, Heatwole and Powell 1998).

Second, predators of the invasive snakes might be adversely affected. This could occur either through envenomation via a counter attack by a captured snake (Rubinoff and Kropach 1970) or by the predator being sickened by consuming a snake. Avian and piscine predators in the native habitat of *H. platurus* either do not attack these snakes, or they soon release such prey (Weldon and Vallarino 1988, Sheehy et al. 2011). Rubinoff and Kropach (1970) found that when offered yellow-bellied sea snakes, naïve predatory fish from the Atlantic would eat them and subsequently either regurgitate them or die, whereas predatory fish from the Pacific would avoid the snakes. Clearly, invasion of the Caribbean or Atlantic would result in new interactions between predator and prey—some operating over short timescales, others requiring a new evolutionary equilibrium.

There is some evidence that expansion of sea kraits' geographic range is occurring in response to global warming at the northern border of their present distribution (see Heatwole et al. 2016). The pool of species available for invasion of the Caribbean or Atlantic could change should such expansion of range occur in the south, either in response to global warming or to other environmental changes. At present, the cold Benguela and Humboldt currents respectively prevent entry around the Cape of Good Hope and

Cape Horn into the Atlantic. Moreover, recent analyses on the effects of climatic changes on upwelling systems, such as the Benguela Current, suggest that changes in coastal winds tend to intensify rather than weaken upwellings in eastern boundary current systems (Sydeman et al. 2014). Thus, future climatic changes are not expected to increase potential dispersal of sea snakes from the Indian to Atlantic Ocean via the Cape of Good Hope.

Conversely, persistence of sea-snake populations could be jeopardized, even in present ranges, by current and future global changes owing to the implications of changes in patterns of rainfall (Lillywhite et al. 2015), thermal conditions (Heatwole et al. 2012), or contamination (Sereshk and Bakhtiari 2014). Strong declines of protected populations of sea snakes suggest this may be occurring at present (Lukoschek et al. 2013). Thus, future climatic changes might have both negative and positive impacts on the biogeography of sea snakes. The former might involve declines or extirpations of populations within present ranges, and the more dramatic aspect of the latter could involve invasion and establishment of sea snakes in the Atlantic Ocean.

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