JOURNAL OF HERPETOLOGY

Slithering sentinels: assessing the relevance of sea snakes as bioindicators for monitoring New Caledonia's lagoon

David Hudry[1,2*]

[1]*CEBC, Centre d'étude Biologiques de Chizé, UMR7372, CNRS, La Rochelle University, France*

[2]*Institute for Biodiversity and Ecosystem Dynamics (IBED), University of Amsterdam, 1098 XH Amsterdam, The Netherlands*

[3]*Present address: Institute for Biodiversity and Ecosystem Dynamics (IBED), University of Amsterdam, 1098 XH Amsterdam, The Netherlands*

Corresponding author. E-mail: hudry.david@yahoo.com

LRH: Hudry David et al.

RRH: True marine snakes as bioindicators

Abstract. Coral reefs are vital ecosystems, rich in biodiversity and economically significant. However, they face severe threats from human activities such as climate change, pollution, and overfishing. Large-scale monitoring is crucial for their conservation. Integrative bioindicators are needed to better assess their health. Marine snakes, as high-level predators with strong site fidelity, are excellent bioindicators. Their health and population status can accurately reflect local environmental conditions. Their long lifespan allows for long-term monitoring, helping to detect human-induced impacts on coral reef ecosystems. Sea kraits, which are amphibious and well-studied, play a key role in reef monitoring. They are abundant, easy to observe, and provide valuable ecological insights. Most research has focused on their relevance as bioindicators, but broader studies on aquatic snakes are necessary. Fully marine snakes (viviparous species) share habitats with sea kraits but have a wider ecological range. They expand the spectrum of prey types, foraging behaviors, and sensitivity to human activities. Their Indo-Pacific distribution makes them essential for coral reef monitoring. Despite their ecological importance, truly marine snakes remain understudied. Their populations are vulnerable to environmental changes, yet their role in coral reef ecosystems is not fully understood. Research on their conservation is essential, as they could be key indicators of reef health in biodiversity hotspots like New Caledonia.

Keywords: Aipysurines, Biodiversity monitoring, Coral reef ecosystems, Hydrophiinae, Marine conservation

The need of bioindicators for monitoring marine ecosystems. – In a world of constant anthropogenic pressures, we need more and more tools to protect, manage and monitor habitats. Particularly those that are home to rich biodiversity and complex ecosystems. Bioindicators are particularly useful for this purpose (Cooper et al., 2009). These are species, or a species community, that are the main indicator of environmental quality, ecology and biodiversity because of their ability to tolerate disturbance to a moderate degree (Holt & Miller, 2011). They act as early warning predictors for ecological changes in the environment. As bioindicator study method is cost-effective, its development is increasingly becoming a valuable means of monitoring the state of current ecosystems (Siddig et al., 2015). However, some ecosystems are difficult to monitor and protect, such as coral reefs (Bispo et al., 2009; Phillips & Rainbow, 2013; Thakur et al., 2013). The development of useful bioindicators in marine ecosystems is vital, as they are home to world biodiversity hotspots (Terry et al., 2002). Various criteria are needed to identify appropriate bioindicators. The taxonomy of the species (or group of species) must be well known and stable, as must its ecology and natural history. Individuals must be easy to count, widely distributed in space and in different habitats. It is preferable to study a group of specialized species with different sensitivities to habitat modifications. Finally, potential economic importance could be useful (Rasmussen et al., 2021). It turns out that many snake species meet these criteria. In fact, several studies have used snakes as bioindicators, for example to monitor heavy metal concentrations, as they are top predators in many ecosystems (Frossard et al., 2019; Lettoof et al., 2020). However, few studies have focused on aquatic snakes (Hurtado-Morales, 2022), and even fewer on sea snakes as environmental indicators (Udyawer et al., 2018; Rasmussen et al., 2021).

Unique evolution linked to geological events and marine ecosystems. – In the course of evolution, different lineages of snakes have returned to marine life. Various aspects need to be taken into account to understand how sea snakes adapted to their new environment and how they became the largest group of marine reptiles. From morphology, paleontology and molecular phylogeny, we know that the ancestors of snakes were probably terrestrial (Vidal & Hedges, 2004; Gearty et al., 2021). Over the last 10 Ma, more than 100 snake species have adapted to marine habitats (Bonnet, 2012). Of these 100 species, more than 60 are fully adapted to the marine environment and are referred to as 'true' sea snakes. All these sea snakes belong to the taxon Elapidae. Their common ancestor with their Australian neighbors dates from between 10.6 and 6.5 Ma ago (Ukuwela et al., 2016). Recent research indicates that sea snakes have undergone rapid radiation and a recent evolutionary transition, with a return to the sea occurring around four times throughout history (Bonnet, 2012; Lillywhite et al., 2018). The emergence of several physiological and reproductive traits has provided significant advantages in exploiting new foraging niches (Bonnet, 2012; Cook et al., 2016). The vertically flattened paddle-shaped tail (Rasmussen, 2000) and viviparity (Bonnet, 2012) are very good examples. In these taxa, we find the whole spectrum of marine lifestyles with different degrees of dependence on the marine habitat, from amphibious snakes that return to land daily, such as the sea kraits of the genus *Laticauda*, to entirely pelagic snakes that live only in the ocean and never come ashore, such as the yellow-bellied sea snake of the genus *Hydrophis* (Heatwole, 1999). Sea snake species are found in large numbers in the "coral triangle". This area, located in the Indo-Australian archipelago, is one of the world's main marine biodiversity hotspot (Gherghel et al., 2016; Udyawer et al., 2018). The Coral Triangle has experienced a significant sequence of geological events, including climatological, paleogeographic and sea-level fluctuations in the past (Heatwole et al., 2017). It presents an exceptional mix of land and sea and, as a result, a unique environment on Earth (e.g. Fig.1). Past major geographical disturbances have favored speciation and the marine transition (Ukuwela et al., 2016; Lillywhite et al., 2018). Therefore, the presence of diverse ancestral lineages of snakes, added to this complex interplay of geographical and geological elements, highlights the complexity of these evolutionary processes. Moreover, sea snakes are also found from South Asia to Australia, via the eastern Pacific Ocean and the western Indian Ocean (Lillywhite et al., 2018).

Ecology and taxonomy of sea snakes. – Studies show that there are two distinct taxonomic groups of marine snakes: truly marine snakes (>60 species) and sea kraits (8 species). They provide three distinct lineages of snakes: *Aipysurus*, *Hydrophis* and *Laticauda*. These genera are of major interest in answering our main question on monitoring coral reef ecosystems. We found amphibious snakes that share their lives between land and sea (*Laticauda*) and truly marine snakes that never return to land (*Aipysurus* and *Hydrophis*). However, recent molecular studies have shown that almost twenty more species have yet to be discovered in the genus *Hydrophis* (Udyawer et al., 2018). This information could increase the diversity of sea snakes by up to 30%, which is very important for our understanding of sea snake biology.

The *Laticauda* clade contains 8 species distributed in the warm, shallow waters of the Indo-Pacific Ocean (Heatwole et al., 2005-2013). They are packed into 3 main clades of *Laticauda* (Udyawer et al., 2018). Commonly known as sea kraits, *Laticauda spp* are mainly distributed over a wide geographical area and are found close to the coast (Bonnet et al., 2006). Their amphibious lifestyle has shaped their unique ecology: sea kraits prey on anguilliform fish species, such as eels and congers. As most of their prey remains in the coral matrix, sea kraits are limited by coral reefs (Brischoux & Bonnet, 2009). They return to land to rest, digest, shed their skin, mate and lay their eggs (Bonnet et al., 2006). In addition, a study shows that sea kraits show a very strong philopatry towards a specific shoreline and area. In fact, they can identify their terrestrial environment and select specific routes in order to avoid predation and optimize the time needed to reach the thermal optimum on land

(Brischoux et al., 2009). However, a study suggests that philopatry develops over time after settling on a specific patch, with juveniles appearing to be more adventurous than adults (Bech et al., 2016). Indeed, sea kraits are highly dispersive species, forming colonies spread over several islands in the Indo-Pacific Ocean (Heatwole, 1999). However, the extent of occurrence of sea kraits is strongly affected by food resources (Brischoux et al., 2007). Foraging ecology differs between the sexes and may be a consequence of sexual size dimorphism. Females feed on large conger eels in deep water, while males feed on moray eels in shallow water (Shine et al., 2002; Brischoux & Bonnet, 2006). These predator-prey interactions are not yet fully understood, as reef seabed ecosystems may harbor complex food webs, comparable in complexity to those found in the wider spatial extent of the water column (Brischoux et al., 2011). It seems that there is still much to be discovered about the behavior of sea kraits. For example, articles have recently been published on coordinated pack hunting behavior (Doody et al., 2013; Somaweera et al., 2023). Sea kraits are present in large numbers in the lagoon of New Caledonia, where two main species occupy the area (e.g. Fig. 2): *L. saintgironsi* and *L. laticaudata.* They differ in their genetics (Bech et al., 2016), feeding habits (Brischoux et al., 2007), coloration (Bonnet et al., 2006), diving behavior (Cook et al., 2016), physiological performance on land and underwater (Bonnet et al, 2005), their trophic level (Brischoux et al., 2011), their diet (Bonnet et al., 2006), their metabolic rate (Brischoux et al., 2007), their shelter on land (Bonnet et al., 2009), and even their mating ecology (Bonnet et al., 2006).

The *Aipysurus* and *Hydrophis* clades contain a vast majority of sea snake species (Udyawer et al., 2018). The main differences between truly marine snake (*Aipysurus* & *Hydrophis*) and *Laticauda* species can be linked to greater diversity in terms of morphology, behavior and ecology (Rasmussen et al., 2021). For example, the diet of truly marine snakes is based on various components, such as fish eggs for *E. annulatus* (Lukoschek & Shine, 2012) or catfish species for *H. major* (Shine et al., 2019). However, all species are strictly adapted to a marine lifestyle. Some of them show a strong philopatry towards specific coral reefs (Lukoschek & Shine, 2012). The *Aipysurus* group exploits various coral reefs and sandy bottom environments, while the *Hydrophis* group is present in a plurality of micro-habitats, such as seagrass beds, freshwater rivers, river mouths and sediments (Rasmussen et al., 2021). Although sea snake spatial ecology appears to be restricted to shallow waters and coral reefs in the nearshore zone, observations of *Hydrophis* at depths of 245 m and 239 m in the mesopelagic zone raise new questions (Crowe-Riddell et al., 2019). In addition, we found the only fully pelagic sea snake in this group: *H. platurus* (Linnaeus, 1766). This species has the most extensive distribution range of all sea snakes (Lillywhite et al., 2018; Bessesen et al., 2020-2023). A total of 10 species of the *Aipysurus* and *Hydrophis* group have been recorded in the lagoon of New Caledonia (Ineich & Laboute, 2002; Goiran et al., 2022). Few studies have focused on these species in the New Caledonian lagoon, unlike sea kraits (Goiran et al., 2022). As a result, it is difficult to effectively assess their ecological importance in the marine ecosystem.

In this review, I only focus on the 2 main species of sea kraits and the 10 species of truly marine snakes present in the New Caledonian lagoon (e.g. Tab. S1 & Tab. S2). I aim to assess the effectiveness of true sea snakes as bioindicators compared to sea kraits, which have been well-established as bioindicators for reef monitoring in New Caledonia (Brischoux et al., 2009). I hypothesize that true sea snakes may not be better indicators but could nicely complement sea kraits in monitoring secretive fish species, such as gobies, moray eels, and other anguilliform fishes in New Caledonia.

Analysis

Established and stable taxonomy – A well-established and stable taxonomy of sea snakes is crucial for effective bioindication, as it provides a foundation for understanding the relationships between different species and their roles in marine ecosystems (Voris et al., 1977). This understanding is essential for accurately interpreting the presence, absence, or behavior of specific sea snake species as indicators of environmental health (Rasmussen et al, 2021).

Truly marine sea snake taxonomy is now clearer than ever, as many genetic studies focused on this topic, with 85% of the genomic DNA included in genetic database (Sanders et al., 2013). The revised taxonomy of truly marine snakes invalidates the previously recognized genera *Acalyptophis*, *Astrotia, Disteira, Enhydrina, Kerilia, Lapemis, Kolpophis*, and *Thalassophina*, as these taxa are now nested within the single genus *Hydrophis*, eliminating the need for the creation of multiple new genera (Sanders et al., 2013; Lee et al., 2016).

On the other side, sea krait's taxonomy is well-known and very stable, as we discovered all the species from this genus (Sanders et al., 2013). The Laticaudinae are considered as the most primitive genus, making part of a single family (Hydrophiidae) and have evolved from separate terrestrial ancestors compared to the Hydrophiinae (Rasmussen, 2000). Further taxonomic studies need to be done to see if *L. laticaudata* could be endemics from New Caledonia (Brischoux et al., 2006-2009). However, sea kraits phylogeny is still well-known and no other lineages seems to be undiscovered in the genus (Heatwole et al., 2005; Sanders et al., 2013). As they are easy to study and found on land, most potential sample sites in the Pacific have been visited. This allowed to build a strong and stable phylogeny (Heatwole et al., 2005; Cogger & Heatwole, 2006; Brischoux et al., 2006-2009; Tandavanitj et al., 2013; Udyawer et al., 2018; Il-Hun Kim et al., 2018).

Recognized ecology and natural history – The yellow sea kraits, *L. saintgironsi*, are easy to recognize, with banded black and yellow patterns (Brischoux & Bonnet, 2006). Background color's variation occurs, including greyish, brown, orange, and even bright red individuals. On the other side, blue sea kraits, *L. laticaudata,* have blue background and the usual banded black patterns (Brischoux & Bonnet, 2006). These black patterns could be a main strategy for controlling predators, but no cases have been reported of the effectiveness of these patterns (Lorioux et al, 2008). Their color vary from dark to light blue, including melanistic specimens apparently turning from blue to black coloration in 9 months. Intriguing fact, no fully melanistic specimens have been recorded in the yellow sea kraits species (Brischoux & Bonnet, 2006). Through time, coloration is not changing and is not depending on specimen's age, except for melanism. Additionally, yellow sea kraits present less black rings than blue sea kraits. We observe white dots in black rings on the belly of yellow sea kraits and black dots in white rings in blue sea kraits, providing individual patterns. Blue sea kraits are slender animals and longer on average, compared to their yellow neighbors (Brischoux & Bonnet, 2006).

Yellow sea kraits feed on anguilliform fishes from hard-bottom substrate, where blue sea kraits forage on soft-bottom substrate (Brischoux et al., 2007-2009; Bonnet, 2012). Their prey are found in the coral matrix and are varied and numerous, including species of anguilliform fish which are themselves predators. Yellow sea kraits feed on much more eel's species and larger specimens than blue sea kraits. They are actively exploring the coral matrix, within the cavities and crevices. On the opposite, blue sea kraits searched for fishes hidden in burrows, seagrass beds, mud flats and sandy environment. Once found, preys are bitten and the snake inject its venom (Brischoux & Bonnet, 2006). The venom allows the snake to kill rapidly its prey, as some specimens can be deadly injured by massive moray eels which retaliate during the attack, but also to prevent the prey from escaping far away. From F.

Brischoux (2009), yellow sea kraits seems to be “the best candidate to gauge anguilliform fish associated with Neo-Caledonian coral reef ecosystems”. In order to get their foraging habitat, yellow sea kraits can travel long distances, with a mean of 3km, in a radius of 21km from their initial islet (Brischoux et al., 2007; Bonnet, 2012). In comparison, blue sea kraits travel in a radius of 14km to reach their foraging habitat with mean travel of 1km. Both species have similar trip duration (Brischoux et al., 2007). Both species feed over more than 45 eel’s species, with 13 shared by the two species, and play significant role in the food chain of New Caledonia’s lagoon (Ineich et al., 2007; Briand et al., 2015-2016-2018). The connections in trophic relationships between sea kraits and their prey seemed remarkably close. In fact, both species found 1/3 of their preys close from the islets where they are established, implying a spatial connection between the habitat of sea kraits and the distribution of their prey (Brischoux et al., 2007). The combination of blue and yellow sea kraits enables us to get a broader view on the anguilliform fishes assemblage of the neo-caledonian lagoon (Brischoux et al., 2009). It remains plausible that some sea kraits travel in deeper water and further than studies assumed, as only one study has tried to implant data loggers in order to understand their diving patterns (Cook et al., 2016).

In contrast, the truly marine snakes found in New Caledonia's lagoon are mostly generalists, but some are specialized in feeding (Voris & Voris, 1983; Rasmussen et al., 2021). They prey on secretive fish, hidden in crevices and burrows among the reefs. Foraging mode and prey type vary among truly marine snake, influenced by body-plan (Sanders et al., 2013; Rasmussen et al., 2021). Sexual dimorphism is occurring as well within truly marine snake (Shine et al., 2002-2019).

Mating and courtship in yellow sea kraits occur mainly in November-December and last until February during the warm season, as vitellogenic females were observed in this period (Brischoux & Bonnet, 2006; Rasmussen et al., 2021). Couples, mating, are observed under rocks or inside of wedge-tailed shearwater's burrows, located on dry and sandy environment inside islets. On the other side, blue sea krait females are gravid between the beginning of December and mid-March, peaking at January. Recordings describe five males attempting to copulate with a female on a damp substrate close to the coast, almost underwater at night. In both species, no male combats have been recorded. Once gravid, females lay their eggs in coastal nurseries located on specific islands, travelling over 50km seasonally (Bonnet et al., 2014). These nurseries are still under study, notably to examine why and how females decide to use certain sites instead of others to lay their eggs. Scientists suspect that environmental parameters are the main drivers of these seasonal egg-laying periods. Breeding biology of truly marine snakes species occurring in New Caledonia's waters still needs to be investigated (Rasmussen et al., 2021). Once on land, both sea kraits species exhibit behavioral variations. *L. saintgironsi* individuals undertake long terrestrial trip (Brischoux & Bonnet, 2006; Brischoux et al., 2009). Moreover, yellow sea kraits present high terrestrial locomotor performances. They are very good crawlers inside the vegetation, and excellent rock/tree climbers, looking for shelters to rest (Bonnet et al., 2004). In fact, yellow sea kraits land performances may indicate that they could be subject to intense selection pressure favoring the use of terrestrial habitats (Brischoux et al., 2009; Bonnet, 2012). On the other side, *L. laticaudata* undertake short terrestrial trips and are relatively less agile once on land compared to their yellow neighbors (Bonnet et al., 2004). They tend to remain mainly close to the shores, between and under beach-rocks, and show less terrestrial site fidelity (Bonnet et al., 2009). Active on land, both species are frequently cruising on the shore of islands, going to the ocean or coming back on land during sunset (Brischoux & Bonnet, 2006). It also seems that the predation rate is very low, if not zero on land, but probably higher underwater (e.g. tiger sharks, even sea anemones) as sea kraits are easy to catch.

An easy survey – Both species of sea kraits are easy to spot on land (Brischoux & Bonnet, 2006). It is also possible to catch them underwater, even though this technique is not as efficient as land catching. They are easy to handle and resilient to handling stress (Fauvel et al., 2012). Even though they remain venomous snakes, their docile behavior towards humans facilitates field procedures (Brischoux & Bonnet, 2006). Thus, New Caledonia stands out as one of the rare places on Earth where a significant population of venomous snakes, including sea kraits and truly marine snakes, coexists harmoniously with human communities (Udyawer et al., 2021).

The distribution and habitat preferences of marine snakes are influenced by a variety of factors, including habitat structure, spatial factors, and prey availability. X. Bonnet (2009) found that sea kraits of New Caledonia have specific habitat requirements. Yellow sea kraits are generally found in inland vegetation and on the shores of islets, while blue sea kraits are generally found in the intertidal zone. The sea kraits database is one of the largest databases in the world for long-term monitoring of a snake population. Islets located in New Caledonia's lagoon like Signal, Amédée, Améré, M'ba, M'bo, Porc epic, N'da or Redika are all full of sea kraits (Brischoux et al., 2009). Another aspect of the study of sea kraits is that it is easy to make them regurgitate their prey once they have returned from the sea, as this manipulation is harmless for the snakes (Brischoux & Bonnet, 2006; Bonnet, 2012; Fauvel et al., 2012). A large number of anguilliform fish species have been discovered using this technique, demonstrating the diversity of this overlooked assemblage (Ineich et al, 2007; Bonnet et al, 2014).

For truly marine snakes, as it is impossible to capture these species on land, studies must be carried out from a boat for species inhabiting coral reefs or by scuba diving/snorkeling near the coast (Shine et al., 2019; Rasmussen et al., 2021). More specifically, boat surveys can be carried out during the day or at night, as some species are more or less active at certain times of the day (Rasmussen et al, 2020; Bessesen et al, 2022). Most studies of the truly marine snakes present in the lagoon have been carried out on collections held by Museums, but very few studies have attempted to study the populations directly in their natural environment (Shine et al, 2019-2023; Udyawer et al., 2023). V. Udyawer (2014) observed a strong latitudinal effect on the distribution of sea snakes in the Great Barrier Reef Marine Park, with shallow inshore areas being key habitats for some species. Within a population of sea snakes, habitat selection varied among individuals, but with a preference for coral-dominated substrates (Goiran et al., 2020). Other methods exists to survey sea snake species, like underwater video (Goiran et al., 2022) or passive acoustic survey (Udyawer et al., 2018), providing different ways of gathering data on sea snakes ecology. The use of environmental DNA is the last monitoring tools taking place in sea snake survey as it is tremendously useful for monitoring species occurring in low densities like truly marine snakes, yet little information (presence/absence) can be gathered (Rasmussen et al., 2021).

Higher taxa widely distributed geographically and over a breadth of habitats – Sea kraits are well spread across the Indo-Pacific (Ineich, 2007). We found the 8 species of sea kraits in various places, such as New Guinea, Ryukyu Islands, Sumatra, Taiwan, Philippines, and (Heatwole et al., 2017).

Truly marine snakes occur in almost all aquatic habitats in tropical and subtropical areas of the Indo-Pacific regions (Rasmussen et al., 2021). Along with *H. platurus*, truly marine snakes have the widest range of distribution among snakes (Lillywhite et al., 2015-2018). Some species are found over vast regions, such as certain species of *Hydrophis* found in Asian and Australian waters, and others are localized in very specific places in Indonesia, Vietnam or Australia (Rasmussen et al., 2021). There are still many places that are likely to host a large number of species of truly marine snakes that have yet to be discovered. New data on the distribution of certain species confirm the need for exploratory studies on the distribution of species (Gherghel et al., 2018). We could be missing part of the ecology of sea snakes, as some have been observed at unsuspected depths (Crowe-Riddell, 2019) and others could be found in habitats such as mangroves, river mouths and deeper waters. Truly marine snakes appear to be widely distributed in diverse ecological niches relative to sea kraits in the marine biodiversity hotspot.

Diverse number of species specialized and sensitive to habitat changes – Sea kraits are very sensitive to environmental changes and pollution occurring in shallow habitats (Rasmussen et al., 2021). One study showed extremely high bio- accumulation of mining trace elements, such as Ni and Cr, in sea kraits and their prey (Bonnet et al., 2014). As a top predator, sea kraits are sensitive to heavy metal contamination. In addition, tourist activity has a major impact on the populations of both species of sea kraits through the destruction of their habitat (Bonnet et al., 2009). The yellow sea krait seems to be able to withstand tourist pressures thanks to its ability to crawl, climbing trees and moving around on land, and its capacity to use various terrestrial shelters, such as seabird burrows, debris, large tree trunks, etc. On the other hand, blue sea kraits are not as adept as their yellow cousins at adapting to different coastal features. They are heavily dependent on the presence of beach rocks, which provide stable thermal and hygrometric conditions (Bonnet et al., 2009). Overall, both species of sea kraits are affected by human activities, to a greater or lesser extent depending on the species. Habitat destruction strongly affects the distribution of sea kraits, as it can have an impact on water resources, the availability of refuges and mating opportunities (Bonnet et al., 2009; Gherghel et al., 2018). The scarcity of favorable terrestrial environments makes sea kraits highly sensitive to disturbance, as they have no other accessible shelters.

Truly marine snake are also very sensitive to environmental perturbations, like in the Ashmore reef in the Timor sea where 14 species disappearance have been recorded in 2013 with no any clues for explanations (Lukoschek et al., 2013). Nonetheless, pollution, seabed destruction and bycatch are important pressures from human activities but might not explain the mentioned phenomenon. In several regions, such as South China, the loss of sea snakes and their disappearance might act as an "*early warning system for unknown processes as indicators of localized ecosystem change*" as M. Guinea said in 2020 at the World Congress of Herpetology. Furthermore, truly marine snakes are greatly impacted by trawlers activities (Wassenberg et al., 2000; Dsouza & Rao, 2021). All populations tends to be affected negatively by this fisheries activity, with a mortality up to 50% when snakes are caught in commercial prawn trawling. Fisheries could have the most dramatic impact on the sea snake population, as some people consume them and bycatch is high. The impact of tourism on truly marine snake species has not yet been studied except for one species, but could also be a significant pressure on populations (Ineich, 2007; Goiran & Shine, 2013).

Patterns observed in indicator taxa are also observed in other related and unrelated taxa – True marine snakes observed in the neo-caledonian lagoon mainly feed on catfishes and anguilliform fishes. *A. duboisi* is generalist that feeds on small fish and on anguilliform fishes, like *A. laevis* (Laboute & Ineich, 2002). *H. peroni* feeds on shrimps when young and then on gobies when adult. *H. coggeri* feeds on small eel species in seagrass substrates (Udyawer et al., 2023), such as *H. macdowelli* (Sherratt & Sanders, 2020). *H. major* is mainly preying on striped eel catfish (Shine & Goiran, 2019) where *H. ornatus* preys on spinecheek gobies or goat fish (Fujishima et al., 2021). Finally, *H. spiralis* feeds on eels (Ukuwela et al., 2022) and the pelagic species *H. platurus* is preying on spiny catfishes and small pelagic fishes (Voris & Voris, 1983). Overall, truly marine snakes are feeding on small fishes, gobies and anguilliform fishes, such as moray eels, creating a general prey item pattern. As true marine snakes live in marine biodiversity hotspots, anthropogenic pressures can also be observed in many other taxa, like moray eels (Kannan et al., 2019), corals (Anthony, 2016), etc.

R. Somaweera (2021) highlighted the potential drivers of extirpation in sea snakes, including stochastic environmental events, resurgence of top predators, and increased boat traffic, which may also impact other species. Moreover, longitudinal datasets on truly marine snakes are accessible from various locations, including New Caledonia (Rasmussen et al., 2021). These datasets can be employed to investigate potential correlations with alterations in population size, relative abundances, and the demography of elusive fish species.

Present or potential economic importance – The economic importance of marine sea snakes is a complex issue. Potential impact of prawn trawling on sea snake populations are occurring, suggesting that by- catch harvesting could significantly increase this impact (Heatwole, 1997). However, this is tempered by the need for a management scheme that considers the biology of different species. Another aspect is the consumption of sea snakes flesh and skin by Indo-Pacific nations, as sea snake harvesting by fisheries could be "one of the largest harvest activities of venomous snakes and marine reptile in the world today" (Rasmussen et al., 2021). N. Cao (2014) provides a sobering perspective, noting the large-scale harvest of sea snakes in the Gulf of Thailand for human consumption and traditional remedies, and the need for conservation efforts.

For sea kraits, there is another economic aspect to consider. They are popular icons in New Caledonia. Everyone knows these animals and respects them when they meet them. They are one of the few animals that are very famous in New Caledonia and promoted by the country. Their presence is synonymous with healthy coral reefs and populations of anguilliform fish (Brischoux & Bonnet, 2006; Brischoux et al., 2007). They are of major interest for monitoring the health of coral reefs and are therefore powerful tools for eco-tourism in New Caledonia.

Historical research and scientific interest – Scientific interest in the study of sea snake's ecology has recently attracted strong attention. Historical research on sea snakes has been significant in scientific literature, with a focus on their conservation, venom, natural history, and bite treatment. Initial investigations centered on descriptive studies, field observations, and the general biology of snakes. In 1993, W. A. Culotta provided a comprehensive bibliography of sea snake literature, covering a wide range of topics. Similarly, H. Heatwole, in 1999, provided a more in-depth and comprehensive view of the biology of marine snakes by publishing a complete book on the subject. And more recently, V. Udyawer (2018) identified key research questions to guide future studies, based on the recent bibliography, highlighting the need for more information on this group. With the development of new technologies, new studies have appeared, focusing on complex evolutionary questions, physiology, toxicology, ecology, behavior, and resolution of systematics (Udyawer et al., 2018). The dearth of long-term field data should promote further research as there is a strong need of gathering scientific dataset. Anthropic pressures are so significant on world biodiversity that scientific interest is becoming more and more important about these animals (Rasmussen et al., 2021).

Prospective projects and new methodologies – In the perspective of all existing species of sea snakes, we have little information about all species currently known (Shine, 2019). True marine snake data are especially lacking in many places of the planet. Some specific areas needs to be discovered, especially in South China and Northern Australia where new species might occur (Rasmussen et al., 2021). These areas are suspected to host a huge number of sea snakes. As they might occur in very various type of microhabitat that we do not suspect, there is a strong need of improving current methodologies for monitoring sea snakes (Brischoux & Bonnet, 2006; Crowe-Riddell, 2019). Indeed, effective monitoring of marine snakes through standardized methods is essential for evaluating patterns in community composition, population structure, and the proportional impact of both natural and human-induced pressures over time (Udyawer et al., 2018). Some of the methods used may bias our view, like remote-underwater-camera and direct underwater observations. These methods only allow individuals to be observed in underwater areas that are not remote and accessible, and during specific periods of the day. It is possible that the activity of some marine snake species also fluctuates at night and with tidal cycles, as only recent published papers has ever attempted to explore this aspect of their ecology (Goiran et al., 2020; Lynch et al. 2023).

The current focus of sea snake study in 2023 addresses different aspects such as distribution (Bessesen et al., 2023), genomic (Zheng et al., 2023), the impact of human activity (Zhong et al., 2023), species ecology (Shine et al., 2023) and genetic diversity (Yousefkhani et al, 2023). More studies needs to initiate monitoring populations of sea snakes, as this has been only the case in New Caledonia for now...

Potential expansive geographical distribution and global warming impact – Climate change is expected to have a significant impact on the distribution and population of venomous terrestrial species, including sea snakes (Needleman et al., 2018). This is particularly concerning given the potential for increased human encounters and the threat to human health. As sea snakes are poikilotherm animals, the temperature is playing a huge role in their distribution range (Bonnet, 2012; Heatwole et al., 2017; Lillywhite et al., 2018). Thus, global warming might have an indirect impact on sea snake distribution around the Indo-Pacific waters. For amphibious species, like sea kraits, these changes in global water temperature might favors colonization of new islands and creation of new underwater pathway to new terrestrial environment (Heatwole et al., 2017). However, the increase in temperature could have a negative impact on the distribution of sea kraits due to coral bleaching. Populations of the elusive anguilliform fish that live in the coral matrix would be negatively affected by the loss of their habitat, which would drastically reduce food resources (Lillywhite et al., 2018).

Differently, truly marine snake species distribution could have another impact, as recent studies demonstrated the potential establishment and invasiveness of some specific species (Bessesen et al., 2022; Razzaque Sarker et al., 2023). For example, *H. platurus xanthos* could be invasive in Caribbean waters, as this area provides similar environmental factors than the Coral Triangle and could potentially impact fishes communities negatively. New interactions between preys and predators are to be expected with global warming. New species occurrence are already been reported and this might be more and more common in the future (Razzaque Sarker et al., 2023).

Requirement of scientific understandings for sea snake's population decline management – The majority of snake's populations are declining continuously and can have serious impacts for the ecosystems where they occur (Reading et al., 2010). Studies emphasized the urgent need of developing methods for monitoring and protecting snake's population around the world. This aspect is especially true for sea snake's population, where population's declines are widespread, with several reports recording dramatic and unexpected declines of sea snake's biodiversity hotspots (Lukoschek et al., 2013). The decline in sea snake populations is a significant concern, with potential causes including stochastic environmental events, changes in trophic structure, and increased boat traffic (Somaweera et al., 2021). This decline has been observed in various locations, including the New Caledonian Lagoon (Goiran & Shine, 2013) and Ashmore Reef in Australia (Lukoschek et al., 2013). To effectively manage this decline, it is crucial to address critical knowledge gaps, such as the specific causes of the decline and the potential impacts of protected areas. A study conducted by Van Cao in 2014 has shown the decrease of sea snake mass in in Thai fisheries, the same area where sea snake are foraging (Cao et al., 2014). Today, fisheries are reporting a decline in capturing sea snakes since they began their activity. Another report from Goiran and Shine (2013) shown a decrease of turtle-head snake's population in marine protected areas of New Caledonia's lagoon near from human infrastructures. Many anthropic factors are pointed out but we are lacking of information to explain precisely sea snake's populations decline.

For now, the best policy for managing sea snake's populations decline is the design of new protected areas and marines reserves (Udyawer et al., 2018). Unfortunately, existing protected areas are rarely designed for sea snake's population conservation and seems to be insufficient for monitoring effectively sea snake's population decline. As some truly marine snakes and sea kraits have low-dispersal rate, their resilience to such decline might permanent for their populations and such local extinctions are making sea snake's populations in great danger (Goiran & Shine, 2013). We still know very little about the ability of sea snakes to recover, hence the need to monitor populations in order to answer this pressing question. Indeed, the little data we have on certain species does not bode well for the time being.

Sea snakes as pertinent indicators for monitoring reef ecosystems – Various gaps must be filled for a species to become a good bioindicator (Brischoux et al., 2009; Kristen et al., 2017). A. Rasmussen (2021) and X. Bonnet (2012) both highlight the great potential of sea snakes as bioindicators of the health of marine ecosystems, including the effects of climate change, habitat modification and biodiversity decline. Sea kraits have been extensively studied in this field in New Caledonia by F. Brischoux and X. Bonnet, but truly marine snakes have been studied briefly by researchers such as R. Shine, C. Goiran, A. Rasmussen and V. Udyawer.

For the time being, New Caledonia is the place of origin for long-term field studies on sea snakes. However, true sea snake should attract greater interest in monitoring coral reef ecosystems, as it is strongly suspected of seeking more varied habitats and prey types than sea kraits (Harold et al., 1983; Goiran & Shine, 2019; Goiran et al., 2022; Udyawer et al., 2023). Only the turtle-head sea snake *E. annulatus* has been monitored, showing great potential as an excellent bioindicator (Shine et al; 2003- 2004-2020; Goiran et al, 2022). Some true sea snake species may seem more interesting than other candidates for population monitoring because their ecology has been briefly studied, such as the great sea snake *H. major* (Shine et al., 2019; Udyawer et al., 2020-2023) and *A. laevis* (Heatwole et al., 1998; Wirsing et al, 2009; Lynch et al., 2023). The yellow-bellied sea snake *H. platurus* could also be an excellent candidate due to its unique ecology within sea snakes, offering a global view across multiple ecosystems (Lillywhite et al., 2015-2018).

The use of sea snakes as a relevant bioindicators needs to be considered more than ever as it is a powerful tool for monitoring tropical coral reef ecosystems in the Indo-Pacific region. This could be of great interest for marine conservation and therefore of economic interest for tourism and the fish industry. Sea snakes can indicate the state of marine biodiversity and enable marine tourism infrastructures, such as those in the scuba diving sector, to monitor the health of the marine ecosystem. However, new studies need to collect long-term monitoring data in the field in order to observe population patterns.

Current studies have shown the unusual ecology of sea snake species and the foraging habits and life history of different species. Yet, research projects have been biased towards species with vast geographic distribution in shallow waters where visibility is good. This is especially true for the amphibious sea kraits that have been widely studied in New Caledonia's lagoon. Nevertheless, few dataset have been built around "true" marine snakes and we can observe today a huge gap between the biggest dataset ever built on an amphibious sea snake population, and almost no long- term field dataset on more than 60 species of truly marine snakes spread around the Indo-Pacific oceans. The few studies carried out on true marine snake species give good reason to say that true marine snakes are better bioindicators for monitoring coral reefs than amphibian snakes.

Acknowledgments

The authors would like to thank Xavier Bonnet from the CEBC, for his supervision during fieldwork and writing process, Olivier Chateau from the Aquarium des Lagons in Nouméa, for welcome and administrative authorization for fieldworking in New Caledonia, and Verena Schoepf for academic supervision on this review.

Literatures cited

Anthony, K. R. N. 2016. Coral Reefs under Climate Change and Ocean Acidification: Challenges and Opportunities for Management and Policy. Annual Review of Environment and Resources, 41, 59–81.

Bech, N., T. Foucart, T. Fauvel, F. Brischoux, D. Bouchon, & X. Bonnet. 2016. Phenotypic variation contrasts with genetic homogeneity across scattered sea snake colonies. Journal of Biogeography, 43(8), 1573–1582.

Bessesen, B. L., C. Garrido-Cayul, & M. González-Suárez. 2023. Habitat suitability and area of occupancy defined for rare New World sea snake. Conservation Science and Practice, 5(1).

Bessesen, B. L., C. S. Oedekoven, G. J. Galbreath, & M. González-Suárez. 2022. Population Abundance and Density Estimates for Costa Rica's Endemic Sea Snake, Hydrophis platurus xanthos. Frontiers in Marine Science, 9.

Bessesen, B. L. 2012. Geospatial and behavioral observations of a unique Xanthic colony of pelagic sea snakes, Pelamis platurus, residing in Golfo Dulce, Costa Rica. Herpetological Review, 43(1), 22–26.

Bispo, A., D. Cluzeau, R. Creamer, M. Dombos, U. Graefe, P. H. Krogh, J. P. Sousa, G. Peres, M. Rutgers, A. Winding, & J. Römbke. 2009. Indicators for monitoring soil biodiversity. Integrated Environmental Assessment and Management, 5(4), 717–719.

Bonanno, G., & M. Orlando-Bonaca. 2018. Perspectives on using marine species as bioindicators of plastic pollution. Marine Pollution Bulletin, 137, 209–221.

Bonnet, X., M. J. Briand, F. Brischoux, Y. Letourneur, T. Fauvel, & P. Bustamante. 2014. Anguilliform fish reveal large scale contamination by mine trace elements in the coral reefs of New Caledonia. Science of the Total Environment, 470–471, 876–882.

Bonnet, X., F. Brischoux, D. Pearson, & P. Rivalan. 2009. Beach rock as a keystone habitat for amphibious sea snakes. Environmental Conservation, 36(1), 62–70.

Bonnet, X., F. Brischoux, C. Bonnet, P. Plichon, & T. Fauvel. 2014. Coastal nurseries and their importance for conservation of sea kraits. PLoS ONE, 9(3).

Bonnet, X., R. Shine, & I. Ineich. 2004. Terrestrial locomotion in sea snakes: the effects of sex and species on cliff-climbing ability in sea kraits (Serpentes, Elapidae, Laticauda).

Briand, M. J., P. Bustamante, X. Bonnet, C. Churlaud, & Y. Letourneur. 2018. Tracking trace elements into complex coral reef trophic networks. Science of the Total Environment, 612, 1091–1104.

Briand, M. J., X. Bonnet, G. Guillou, & Y. Letourneur. 2016. Complex food webs in highly diversified coral reefs: Insights from δ13C and δ15N stable isotopes. Food Webs, 8, 12–22.

Briand, M. J., X. Bonnet, C. Goiran, G. Guillou, & Y. Letourneur. 2015. Major sources of organic matter in a complex coral reef lagoon: Identification from isotopic signatures (δ13C and δ15N). PLoS ONE, 10(7).

Brischoux, F., X. Bonnet, & P. Legagneux. 2009. Are sea snakes pertinent bio-indicators for coral reefs? A comparison between species and sites. Marine Biology, 156(10), 1985–1992.

Brischoux, F., X. Bonnet, & R. Shine. 2007. Foraging ecology of sea kraits Laticauda spp. in the Neo-Caledonian Lagoon. Marine Ecology Progress Series, 350, 145–151.

Brischoux, F., X. Bonnet, Y. Cherel, & R. Shine. 2011. Isotopic signatures, foraging habitats, and trophic relationships between fish and sea snakes on the coral reefs of New Caledonia. Coral Reefs, 30(1), 155–165.

Brischoux, F., X. Bonnet, & D. Pinaud. 2009. Fine scale site fidelity in sea kraits: Implications for conservation. Biodiversity and Conservation, 18(9), 2473–2481.

Brischoux, F., V. Rolland, X. Bonnet, M. Caillaud, & R. Shine. 2012. Effects of oceanic salinity on body condition in sea snakes. Integrative and Comparative Biology, 52(2), 235–244.

Burns, G., & H. Heatwole. 1998. Home range and habitat use of the olive sea snake, Aipysurus laevis, on the Great Barrier Reef, Australia. Journal of Herpetology, 32(3).

Cogger, H. G., & H. F. Heatwole. 2006. Laticauda frontalis (de Vis, 1905) and Laticauda saintgironsi n. sp. from Vanuatu and New Caledonia (Serpentes: Elapidae:

Laticaudinae)—a new lineage of sea kraits? Records of the Australian Museum, 58, 245–256.

Cook, T. R., X. Bonnet, T. Fauvel, R. Shine, & F. Brischoux. 2016. Foraging behaviour and energy budgets of sea snakes: Insights from implanted data loggers. Journal of Zoology, 298(2), 82–93.

Crowe-Riddell, J. M., B. R. D'Anastasi, J. H. Nankivell, A. R. Rasmussen, & K. L. Sanders. 2019. First records of sea snakes (Elapidae: Hydrophiinae) diving to the mesopelagic zone (>200 m). Austral Ecology, 44(4), 752–754.

Doody, J. S., G. M. Burghardt, & V. Dinets. 2013. Breaking the social-non-social dichotomy: A role for reptiles in vertebrate social behavior research? Ethology, 119(2), 95–103.

Dsouza, S., & C. Rao. 2021. Demographics and reproductive biology of Hydrophis schistosus may make it more resilient to bycatch effects than other sea snakes. Regional Studies in Marine Science, 47.

Emily, A. Holt, & S. W. Miller. 2011. Bioindicators: Using organisms to measure environmental impacts.

Frossard, A., F. L. G. Leite, E. L. F. Silva, M. T. W. D. Carneiro, J. L. R. Júnior, L. C. Gomes, & D. C. Endringer. 2019. The snake Bothrops jararaca (Squamata: Viperidae) is a suitable bioindicator of environmental exposure to cadmium: An experimental study. Ecological Indicators, 104, 166–171.

Fujishima, K., T. Sasai, Y. Hibino, & H. Nishizawa. 2021. Morphology, diet, and reproduction of coastal Hydrophis sea snakes (Elapidae: Hydrophiinae) at their northern distribution limit. Zoological Science, 38(5), 405–415.

Gearty, W., E. Carrillo, & J. L. Payne. 2021. Ecological filtering and exaptation in the evolution of marine snakes. *American Naturalist*, 198(4), 506–521.

Gherghel, I., F. Brischoux, & M. Papeș. 2018. Using biotic interactions in broad-scale estimates of species' distributions. *Journal of Biogeography*, 45(9), 2216–2225.

Goiran, C., P. Bustamante, & R. Shine. 2017. Industrial melanism in the seasnake *Emydocephalus annulatus*. *Current Biology*, 27(16), 2510-2513.e2.

Goiran, C., D. Mallet, N. Lanos, R. Shine, V. Udyawer, & L. Wantiez. 2022. Sea snake diversity at the Entrecasteaux atolls, Coral Sea, as revealed by video observations at unbaited stations. *Coral Reefs*, 41(6), 1551–1556.

Goiran, C., & R. Shine. 2013. Decline in sea snake abundance on a protected coral reef system in the New Caledonian Lagoon. *Coral Reefs*, 32(1), 281–284.

Goiran, C., G. P. Brown, & R. Shine. 2020. Niche partitioning within a population of sea snakes is constrained by ambient thermal homogeneity and small prey size. *Biological Journal of the Linnean Society*, 129.

Goiran, C., G. P. Brown, & R. Shine. 2020. The behaviour of sea snakes (*Emydocephalus annulatus*) shifts with the tides. *Scientific Reports*, 10(1).

Heatwole, H. 1999. *Sea Snakes*. Sydney, SA: University of New South Wales Press.

Heatwole, H., & H. Cogger. 2013. Provenance errors and vagrants: Their role in underestimating the conservation status of sea kraits (*Elapidae: Laticaudinae*). *Pacific Conservation Biology*, 19.

Heatwole, H., A. Grech, & H. Marsh. 2017. Paleoclimatology, paleogeography, and the evolution and distribution of sea kraits (*Serpentes; Elapidae; Laticauda*). *Herpetological Monographs*, 31(1), 1–17.

Heatwole, H., & S. Busack. 2005. Geographic variation in sea kraits of the *Laticauda colubrina* complex (*Serpentes: Elapidae: Hydrophiinae: Laticaudini*).

Heatwole, H. 1973. Marine snakes: Are they a sustainable resource? *Source*, 25(4).

Hughes, T. P., D. R. Bellwood, & S. R. Connolly. 2002. Biodiversity hotspots, centres of endemicity, and the conservation of coral reefs. *Ecology Letters*, 5(6), 775–784.

Hurtado-Morales, M. J., M. R. Susa, & A. Amézquita. 2022. Heavy metal concentration in neotropical aquatic snakes (*Helicops pastazae*) and its potential as a bioindicator of water pollution. *Archives of Environmental Contamination and Toxicology*, 82(3), 367–378.

Ineich, I., X. Bonnet, F. Brischoux, M. Kulbicki, B. Séret, & R. Shine. 2007. Anguilliform fishes and sea kraits: Neglected predators in coral-reef ecosystems. *Marine Biology*, 151(2), 793–802.

Kannan, K., E. Kannapiran, & N. M. Prabhu. 2019. New geographical record of the moray eel *Gymnothorax reticularis*, Bloch, 1795 (*Anguilliformes: Muraenidae*) with taxonomic status and distribution from southwest coast of India. *Thalassas*, 35(2), 567–571.

Kim, I. H., J. Park, H. Y. Suk, H. G. Bae, M. S. Min, T. S. Tsai, & D. Park. 2018. Phylogenetic relationships of three representative sea krait species (*genus Laticauda; Elapidae; Serpentes*) based on 13 mitochondrial genes. *Mitochondrial DNA Part A: DNA Mapping, Sequencing, and Analysis*, 29(5), 772–777.

Gillett, K. 2017. An investigation into the stranding of Australian sea snakes.

Lee, M. S. Y., K. L. Sanders, B. King, & A. Palci. 2016. Diversification rates and phenotypic evolution in venomous snakes (*Elapidae*). *Royal Society Open Science*, 3(1).

Lettoof, D. C., P. W. Bateman, F. Aubret, & M. M. Gagnon. 2020. The broad-scale analysis of metals, trace elements, organochlorine pesticides and polycyclic aromatic hydrocarbons in wetlands along an urban gradient, and the use of a high trophic snake as a bioindicator. *Archives of Environmental Contamination and Toxicology*, 78(4), 631–645.

Lettoof, D. C., V. A. Thomson, J. Cornelis, P. W. Bateman, F. Aubret, M. M. Gagnon, & B. von Takach. 2021. Bioindicator snake shows genomic signatures of natural and anthropogenic barriers to gene flow. *PLoS ONE*, 16(10).

Lillywhite, H. B., & F. Brischoux. 2012. Introduction to the symposium "new frontiers from marine snakes to marine ecosystems." *Integrative and Comparative Biology*, 52(2), 213–216.

Lillywhite, H. B., C. M. Sheehy, F. Brischoux, & J. B. Pfaller. 2015. On the abundance of a pelagic sea snake. *Journal of Herpetology*, 49(2), 184–189.

Lillywhite, H. B., C. M. Sheehy, H. Heatwole, F. Brischoux, & D. W. Steadman. 2018. Why are there no sea snakes in the Atlantic? *BioScience*, 68(1), 15–24.

Littman, R., B. L. Willis, & D. G. Bourne. 2011. Metagenomic analysis of the coral holobiont during a natural bleaching event on the Great Barrier Reef. *Environmental Microbiology Reports*, 3(6), 651–660.

Lorioux, S., X. Bonnet, F. Brischoux, & M. de Crignis. 2008. Is melanism adaptive in sea kraits? *Amphibia-Reptilia*, 29.

Lukoschek, V., & R. Shine. 2012. Sea snakes rarely venture far from home. *Ecology and Evolution*, 2(6), 1113–1121.

Lynch, T. P., R. A. Alford, & R. Shine. 2023. Sex-based divergence in tidal, lunar and seasonal cycles of activity in the olive sea snake, *Aipysurus laevis* (Elapidae, Hydrophiinae). *Coral Reefs*, 42(2), 311–317.

Needleman, R. K., I. P. Neylan, & T. Erickson. 2018. Potential environmental and ecological effects of global climate change on venomous terrestrial species in the wilderness. *Wilderness & Environmental Medicine*, 29.

Rasmussen, A. R., A. Hay-Schmidt, F. Boneka, M. E. Allentoft, K. L. Sanders, & J. Elmberg. 2021. Viviparous sea snakes can be used as bioindicators for diverse marine environments. *Philippine Journal of Systematic Biology*, 19(2 Special Issue 2), 1–16.

Rasmussen, A. R. 2001. Keys to the sea snakes occurring in the area.

Reading, C. J., L. M. Luiselli, G. C. Akani, X. Bonnet, G. Amori, J. M. Ballouard, E. Filippi, G. Naulleau, D. Pearson, & L. Rugiero. 2010. Are snake populations in widespread decline? *Biology Letters*, 6(6), 777–780.

Reed, R. N., R. Shine, & S. Shetty. 2002. Sea kraits (*Squamata: Laticauda* spp.) as a useful bioassay for assessing local diversity of eels (*Muraenidae, Congridae*) in the Western Pacific Ocean. *Copeia*, 2002(4).

Röthig, T., M. A. Ochsenkühn, A. Roik, R. van der Merwe, & C. R. Voolstra. 2016. Long-term salinity tolerance is accompanied by major restructuring of the coral bacterial microbiome. *Molecular Ecology*, 25(6), 1308–1323.

Sanders, K. L., A. R. Rasmussen, Mumpuni, J. Elmberg, A. de Silva, M. L. Guinea, & M. S. Y. Lee. 2013. Recent rapid speciation and ecomorph divergence in Indo-Australian sea snakes. *Molecular Ecology*, 22(10), 2742–2759.

Sevilla, A., & P. Zdunek. 2023. Predation by a yellow-lipped sea krait, *Laticauda colubrina* (Schneider 1799), on a moray eel (*Gymnothorax* sp.) at Balayan Bay, Philippines.

Sherratt, E., & K. L. Sanders. 2020. Patterns of intracolumnar size variation inform the heterochronic mechanisms underlying extreme body shape divergence in microcephalic sea snakes. *Evolution and Development*, 22(3), 283–290.

Shine, R., X. Bonnet, M. J. Elphick, & E. G. Barrott. 2004. A novel foraging mode in snakes: Browsing by the sea snake *Emydocephalus annulatus* (*Serpentes, Hydrophiidae*). *Functional Ecology*, 18(1), 16–24.

Shine, R., T. G. Shine, G. P. Brown, & C. Goiran. 2020. Life history traits of the sea snake *Emydocephalus annulatus*, based on a 17-year study. *Coral Reefs*, 39(5), 1407–1414.

Shine, R., R. N. Reed, S. Shetty, & H. G. Cogger. 2002. Relationships between sexual dimorphism and niche partitioning within a clade of sea-snakes (*Laticaudinae*). *Oecologia*, 133(1), 45–53.

Shine, R., T. Shine, & C. Goiran. 2019. Morphology, reproduction and diet of the greater sea snake, *Hydrophis major* (Elapidae, Hydrophiinae). *Coral Reefs*, 38(5), 1057–1064.

Shine, R., T. G. Shine, G. P. Brown, & V. Udyawer. 2023. Sexual dimorphism in aipysurine sea snakes (Elapidae, Hydrophiinae). *Royal Society Open Science*, 10(12).

Siddig, A. A. H., A. M. Ellison, A. Ochs, C. Villar-Leeman, & M. K. Lau. 2016. How do ecologists select and use indicator species to monitor ecological change? Insights from 14 years of publication in *Ecological Indicators*. *Ecological Indicators*, 60, 223–230.

Somaweera, R., J. C. Wild, S. Indonesia, G. Molchanova, W. Scuba, & I. Article. 2023. Coordinated and communal hunting behaviours by *Erabu* sea krait *Laticauda semifactiata*.

Somaweera, R., V. Udyawer, M. L. Guinea, D. M. Ceccarelli, R. H. Clarke, M. Glover, M. Hourston, J. Keesing, A. R. Rasmussen, K. Sanders, R. Shine, D. P. Thomson, & B. L.

Webber. 2021. Pinpointing drivers of extirpation in sea snakes: A synthesis of evidence from Ashmore Reef. *Frontiers in Marine Science*, 8.

Tandavanitj, N., H. Ota, Y. C. Cheng, & M. Toda. 2013. 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. *Zoological Science*, 30(8), 633–641.

Udyawer, V., M. Read, M. Hamann, C. A. Simpfendorfer, & M. R. Heupel. 2015. Effects of environmental variables on the movement and space use of coastal sea snakes over multiple temporal scales. *Journal of Experimental Marine Biology and Ecology*, 473, 26–34.

Udyawer, V., P. Barnes, X. Bonnet, F. Brischoux, J. M. Crowe-Riddell, B. D'Anastasi, B. G. Fry, A. Gillett, C. Goiran, M. L. Guinea, H. Heatwole, M. R. Heupel, M. Hourston, M. Kangas, A. Kendrick, I. Koefoed, H. B. Lillywhite, A. S. Lobo, V. Lukoschek, ... H. K. Voris. 2018. Future directions in the research and management of marine snakes. *Frontiers in Marine Science*, 9(Nov).

Udyawer, V., C. A. Simpfendorfer, M. Read, M. Hamann, & M. R. Heupel. 2016. Exploring habitat selection in sea snakes using passive acoustic monitoring and Bayesian hierarchical models. *Marine Ecology Progress Series*, 546, 249–262.

Udyawer, V., C. Goiran, O. Chateau, E. Coutures, L. Vigliola, & R. Shine. 2023. Long-distance movements of free-ranging sea snakes (*Hydrophis*, Elapidae). *Coral Reefs*, 42(5), 987–996.

Udyawer, V., C. Goiran, O. Chateau, & R. Shine. 2020. Swim with the tide: Tactics to maximize prey detection by a specialist predator, the greater sea snake (*Hydrophis major*). *PLoS ONE*, 15(10).

Udyawer, V., C. Goiran, & R. Shine. 2021. Peaceful coexistence between people and deadly wildlife: Why are recreational users of the ocean so rarely bitten by sea snakes? *People and Nature*, 3(2), 335–346.

Udyawer, V., M. Cappo, C. A. Simpfendorfer, M. R. Heupel, & V. Lukoschek. 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(3), 777–791.

Ukuwela, K. D. B., M. S. Y. Lee, A. R. Rasmussen, A. de Silva, Mumpuni, B. G. Fry, P. Ghezellou, M. Rezaie-Atagholipour, & K. L. Sanders. 2016. Evaluating the drivers of Indo-Pacific biodiversity: Speciation and dispersal of sea snakes (Elapidae: Hydrophiinae). *Journal of Biogeography*, 43(2), 243–255.

Ukuwela, K. D. B., A. de Silva, Sivaruban, & K. L. Sanders. 2022. Diversity, distribution, and natural history of the marine snakes of Sri Lanka.

van Cao, N., N. Thien Tao, A. Moore, A. Montoya, A. Redsted Rasmussen, K. Broad, H. K. Voris, & Z. Takacs. 2014. Sea snake harvest in the Gulf of Thailand. *Conservation Biology*, 28(6), 1677–1687.

Vidal, N., & S. B. Hedges. 2004. Molecular evidence for a terrestrial origin of snakes. *Proceedings of the Royal Society B: Biological Sciences*, 271(Suppl. 4).

Voris, H. K., & H. H. Voris. 1983. Feeding strategies in marine snakes: An analysis of evolutionary, morphological, behavioral, and ecological relationships. *Contributions in Marine Science*, 23.

Voris, H. K. 1977. A phylogeny of the sea snakes (Hydrophiidae). *Fieldiana: Zoology*, 70(4).

Wassenberg, T. J., D. A. Milton, & C. Y. Burridge. 2000. Survival rates of sea snakes caught by demersal trawlers in northern and eastern Australia.

Wirsing, A. J., & M. R. Heithaus. 2009. Olive-headed sea snakes *Disteria major* shift seagrass microhabitats to avoid shark predation. *Marine Ecology Progress Series*, 387, 287–293.

Yousefkhani, S. S. H., A. Yasser, M. Naser, M. Rezaie-Atagholipour, M. A. Hesni, F. Yousefabadi, & E. R. Pouyani. 2023. Genetic diversity among sea snakes of the genus *Hydrophis* (Elapidae, Reptilia) in the Persian Gulf and Gulf of Oman. *ZooKeys*, 1158, 121–131.

Zheng, H., J. Wang, H. Fan, S. Wang, R. Ye, L. Li, S. Wang, A. Li, & Y. Lu. 2023. Comparative venom multiomics reveal the molecular mechanisms driving adaptation to diverse predator–prey ecosystems in closely related sea snakes. *Molecular Biology and Evolution*, 40(6).

Zhong, J., K. Guo, Z. L. Liao, Y. Du, C. X. Lin, & X. Ji. 2023. Comparative analysis of the skin microbiota between two sea snakes, *Hydrophis cyanocinctus* and *Hydrophis curtus*, with versus without skin ulcer. *Coral Reefs*, 42(3), 743–753.

Figures

Fig. 1. Map of southeastern Asia showing the Coral Triangle (Heatwole et al., 2017).

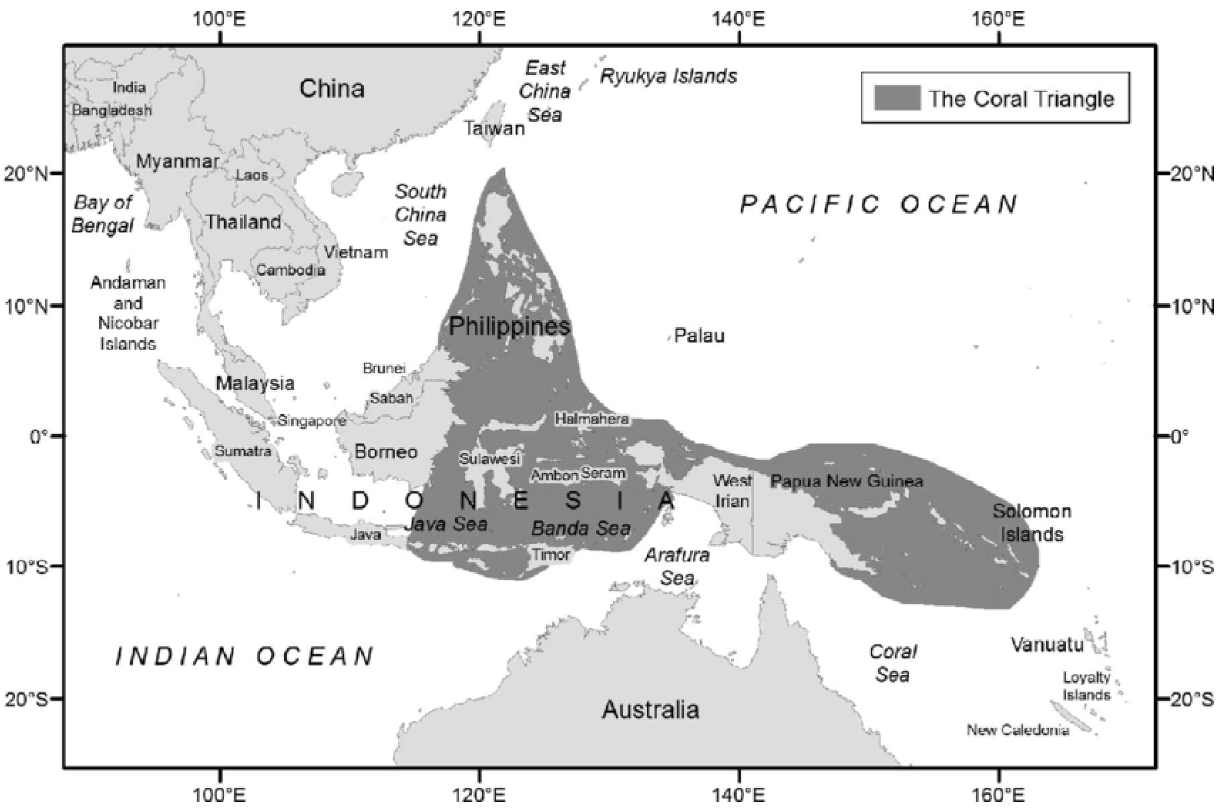
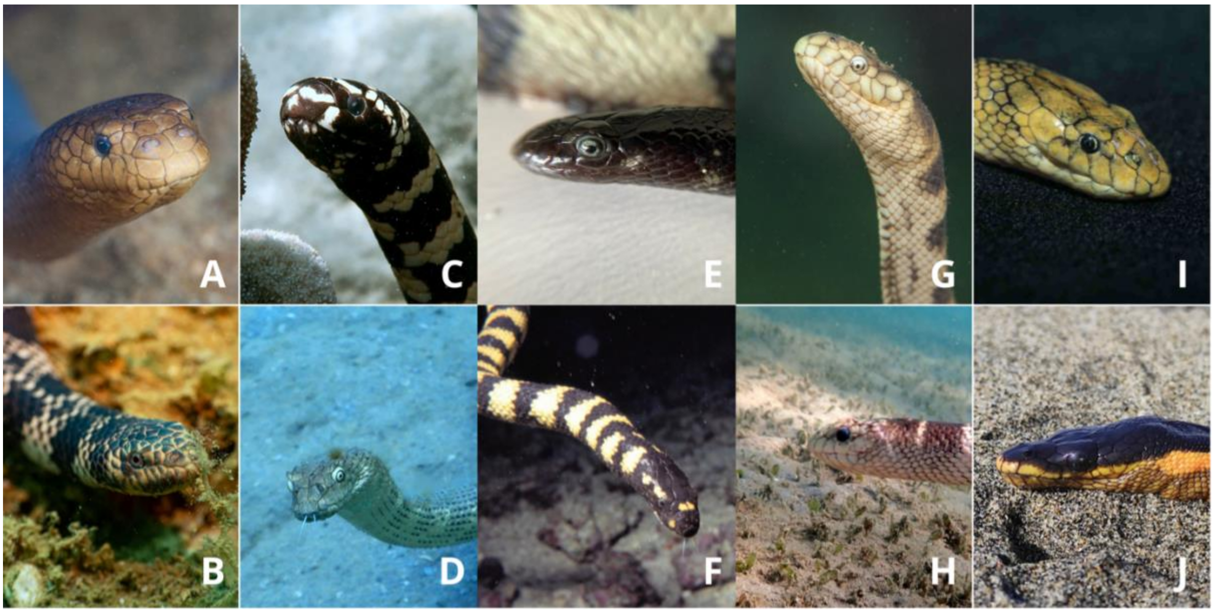


Fig. 2. Photos of the two species of sea kraits mainly found in the New Caledonian lagoon. (A) *Laticauda saintgironsi* and (B) *Laticauda laticaudata*.

Fig. 3. Photos of three species related to the *Aipysurus* group and seven species related to the *Hydrophis* group found in the New Caledonian lagoon. (A) *Aipysurus laevis*, (B) *Aipysurus duboisii*, (C) *Emydocephalus annulatus*, (D) *Hydrophis peronii*, (E) *Hydrophis macdowelli*, (F) *Hydrophis coggeri*, (G) *Hydrophis major*, (H) *Hydrophis ornatus*, (I) *Hydrophis spiralis*, and (J) *Hydrophis platurus*.



Supplementary data

Table S1: The Laticaudines clades

Group	Species	Occurrence in New Caledonia
Laticauda colubrina	*L. frontalis*	*
	L. saintgironsi	*
	L. colubrina	*
	L. guineai	
Laticauda laticaudata	*L. laticaudata*	*
	L. crockery	
Laticauda semifasciata	*L. semifasciata*	
	L. schistorhyncha	

Table S2: The Aipysurines and Hydrophines clades

Group	Species	Occurrence in New Caledonia
Aipysurus	*E. annulatus*	*
	A. mosaicus	*
	A. eydouxii	*
	A. fuscus	
	A. duboisi	*
	A. laevis	
	A. pooleorum	
	A. apraefrontalis	
Hydrophis	*H. obscurus*	
	H. fasciatus	
	H. stricticollis	
	H. pachycercos	
	H. peronii	*
	H. ocellatus	
	H. coggeri	*
	H. lapemoides	
	H. curtus	
	H. belcheri	
	H. parviceps	
	H. macdowelli	*
	H. viperinus	
	H. jerdonii	
	H. major	*
	H. cyanocinctus	
	H. ornatus	*
	H. donaldi	
	H. spiralis	*
	H. platurus	*
	H. elegans	

H. brooki

H. caerulescens

H. schistosus

H. stockesii