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FASCINATING AND FORGOTTEN: THE CONSERVATION STATUS OF MARINE ELAPID SNAKES

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***Abstract.*—An assessment of marine elapid snakes found 9% of marine elapids are threatened with extinction, and an additional 6% are Near Threatened. A large portion (34%) is Data Deficient. An analysis of distributions revealed the greatest species diversity is found in Southeast Asia and northern Australia. Three of the seven threatened species occur at Ashmore and Hibernia Reefs in the Timor Sea, while the remaining threatened taxa occur in the Philippines, Niue, and Solomon Islands. The majority of Data Deficient species are found in Southeast Asia. Threats to marine snakes include loss of coral reefs and coastal habitat, incidental bycatch in fisheries, as well as fisheries that target snakes for leather. The presence of two Critically Endangered and one Endangered species in the Timor Sea suggests the area is of particular conservation concern. More rigorous, long-term monitoring of populations is needed to evaluate the success of "conservation measures" for marine snake species, provide scientifically based guidance for determining harvest quotas, and to assess the populations of many Data Deficient species.**

Key Words.—biodiversity; coastal; endangered species; fishing bycatch; Hydrophiinae; Hydrophiini; Laticaudini; Red List; sea kraits; sea snake

INTRODUCTION

Extant marine snakes evolved multiple times within three independent lineages (Hydrophiinae, Homalopsidae, Acrochordidae), they are ecologically diverse, and demonstrate considerable variation in their specializations for marine habitats (McDowell 1972; Heatwole 1999; Scanlon and Lee 2004; Lukoschek and Keogh 2006; Rasmussen et al. 2011a. Here we focus on the marine elapids in the subfamily Hydrophiinae. Marine elapids are the most speciose and ecologically diverse group of marine reptiles and comprise approximately 90% of extant reptile species living in our world's oceans (Rasmussen et al. 2011a). They are found in tropical and subtropical areas of the Indian and Pacific Oceans, with the greatest diversity in northern Australia, Malaysia and the Indonesian archipelago (Dunson 1975; Heatwole 1999). Marine elapids mostly use benthic habitats including coral reefs, inter-reef soft sediment habitats, and inshore habitats such as river mouths, estuaries and mangrove swamps (Heatwole 1999). Several species have secondarily invaded freshwater lacustrine and riverine habitats; however, the most widely distributed species, *Pelamis platura,* is pelagic and feeds at the water's surface (Dunson and Ehlert 1971; Rasmussen et al. 2001, 2011a; Brischoux and Lillywhite 2011).

All species possess a vertically flattened, paddle-like tail, valved nostrils, and a sublingual salt excreting gland (Heatwole 1999). Many have remarkable diving capabilities and are able to reach depths greater than 100 m and remain submerged for up to 2 h (Heatwole and Seymour 1975a, Rubinoff et al.1986, Brischoux and Lillywhite 2011). Their respiratory morphology is distinct from that of terrestrial snakes and at least one species (*Pelamis platura*) absorbs up to 33% of its oxygen through the skin (Graham 1974), while other species have been reported to obtain 5–21% (Heatwole 1999).

The two clades of marine snakes are in the front-fanged elapid subfamily Hydrophiinae (Fig. 1): the viviparous sea snakes (Hydrophiini), such as *Hydrophis* and *Aipysurus*, and the oviparous sea kraits, *Laticauda* (Laticaudini), which form a close sister lineage to all other hydrophiines (Voris 1977; Keogh 1998; Lukoschek and Keogh 2006). The viviparous sea snakes are by far the most speciose group, with 62 species (excluding *Hydrophis walli*, see Table 1) that occupy diverse marine habitats and typically spend their entire lives at sea, the exceptions being the species that have secondarily moved into freshwater rivers and lakes. The eight *Laticauda* species are amphibious and differ from the sea snakes in that they are tied to the land by their oviparous (egg-laying) reproductive mode (Shetty and Shine 2002). Although they feed exclusively in the water, they spend substantial amounts of time on land where they digest their prey, slough their skins, mate and lay eggs (Shetty and Shine 2002). Both groups are venomous and some species have been studied for the production of anti-venoms and medical research (e.g. Chetty et al. 2004; Li et al. 2004).

Scientific knowledge of sea snakes is limited, with detailed information lacking on species' distributions, abundance, ecology, and physiology. Available data are scattered among published and unpublished sources. Despite being poorly understood, sea snakes are impacted by a number of human activities, including harvesting for food and leather (e.g. Heatwole 1997; Vincent Nijman et al., unpubl. data; Joey Gatus, pers. comm.), incidental mortality in fishing operations (Milton 2001; Courtney et al. 2010) and degradation of coastal habitats (Bonnet et al. 2009). Many species are dependent on very specific habitats. For example, the amphibious sea kraits are strongly associated with coral reefs and are dependent on suitable coastal habitats when on land (Lillywhite et al. 2008; Bonnet et al. 2009). Sea kraits may also show a high degree of philopatry, sometimes returning to within the same 60-meter segment of shoreline (Brischoux et al. 2009a). Several of the marine species are wide spread and dependent on coral reefs and feed exclusively on coral-associated fishes (Su et al. 2005; Brischoux et al. 2009b), and others, such as *Hydrophis semperi* and *Laticauda crockeri*, have geographic ranges restricted to land-locked lakes. These features may make sea snakes particularly susceptible to anthropogenic impacts on the habitats on which they depend.

Identifying centers of high biodiversity and the distribution of threatened species is a fundamental part of prioritization of conservation efforts (Brooks et al. 2006; Hoffman et al. 2008, 2010). Here we present the first comprehensive assessment of the conservation status of marine elapids under the categories and criteria of the International Union for the Conservation of Nature (IUCN) Red List of Threatened Species (IUCN 2001). Our analysis provides not only a list of species with threatened status, but also a review of the major threats, areas of geographic concern, and future needs for research both at global and regional levels.

MATERIALS AND METHODS

Methodology for IUCN Red List assessment.—We applied the IUCN Categories and Criteria of the Red List to all known marine snakes in the family Elapidae: a total of 69 species (Table 1). The IUCN Red List is the most widely accepted system for classifying extinction risk at the species level (Butchart et al. 2005; Rodrigues et al. 2006; de Grammont and Cuarón 2006; Hoffman et al. 2008). Existing literature provided information on

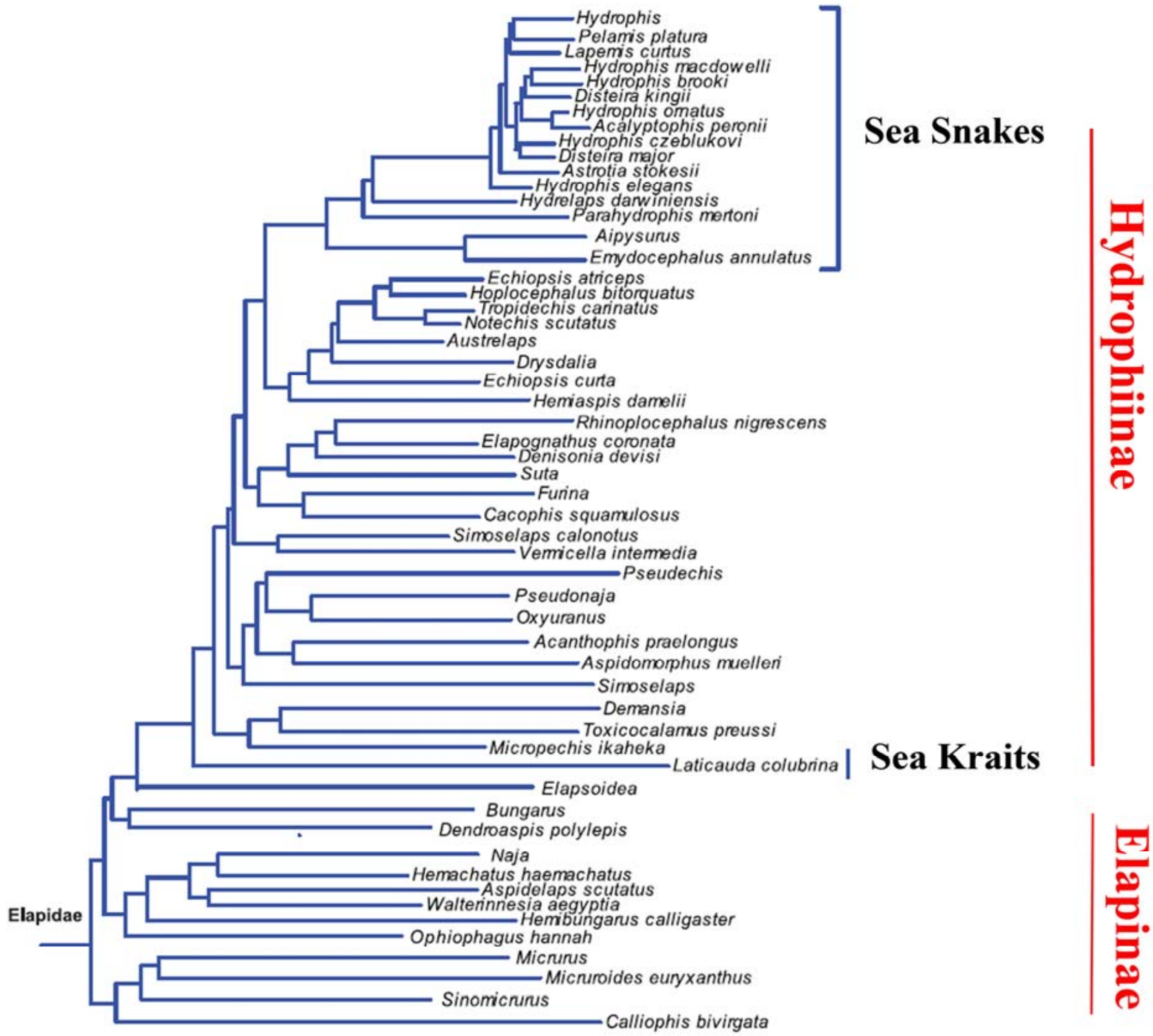

FIGURE 1. The phylogenetic positions of the sea snakes and sea kraits in the family Elapidae, modified from Pyron et al. (2011). The sea snakes (Hydrophiini) are viviparous and the sea kraits (Laticaudini) are oviparous and amphibious.

taxonomy, distribution, population trends, ecology, life history, past and existing threats, and conservation actions for each species. We evaluated each species in a workshop setting with additional input and review from 15 sea snake experts from around the world. Quantitative information determined if a species met the threshold for a threatened category under at least one IUCN Red List Criterion. This process consolidates the most current and highest quality of available data, and ensures peer-reviewed scientific consensus on the probability of extinction for each species. All species' data and the results of Red List assessments, including the names of the contributing scientists, are freely and publicly accessible under each species' account on the IUCN Red List of Threatened Species (www.iucnredlist.org).

The IUCN Red List Categories are comprised of eight different levels of extinction risk: Extinct (EX), Extinct in the Wild (EW), Critically Endangered (CR), Endangered (EN), Vulnerable (VU), Near Threatened (NT), Least Concern (LC) and Data Deficient (DD). A species qualifies for a 'threatened' category (CR, EN, or VU) by meeting a quantitative threshold for that category in one of five available criteria (A-E). These criteria are based on extinction-risk theory (Mace et al. 2008) and provide a standard methodology that can be applied consistently to any species from any taxonomic group (de Grammont and Cuarón 2006; IUCN 2001). Detailed guidelines for the application of the Criteria are described in IUCN (2010).

Sea snakes and sea kraits triggered listings of threat under criteria A, B and D. Criterion A measures extinction risk based on exceeding thresholds of population decline (30% for Vulnerable, 50% for

TABLE 1. Red List category for every species of sea snake assessed in this study, including Criteria used and supporting information. The IUCN Red List Categories used here are: Critically Endangered (CR), Endangered (EN), Vulnerable (VU), Near Threatened (NT), Least Concern (LC) and Data Deficient (DD). References in Supporting Information are abbreviated as: (Br) Branch 1988, (C) Cogger 2000, (CH) Cogger and Heatwole 2006), (G) Guinea et al. 2010, (GV) Glodek and Voris, 1982, (I) Ineich and Laboute 2002, (H) Herre 1942, (HBC) Heatwole et al. 2005, (HKH) Hetch et al. 1974, (Ka) Kanishka et al. 2012, (K) Kunhart et al. 2011, (Kh) Kharin, 1985, (LG) Lane and Guinea 2010, (LGa) Lane and Gatus 2010, (Mc) McDowell, 1974, (ML) Milton et al. 2010, (R) Rasmussen et al. 2001, (R1) Rasmussen 1992, (R2) Rasmussen, 1993, (R3) Rasmussen et al. 2011b, (R4) Rasmussen et al. 2011c, (R5) Rasmussen et al. 2012, (RG) Rasmussen and Guinea 2010, (RLa) Rasmussen and Lobo 2010a, (RLb) Rasmussen and Lobo 2010b, (Sa) Sanders et al. 2012, (Sm) Smith 1974, (S) Steubing and Voris 1990, (To) Torbia 1994, (TS) Tu and Stringer 1973, (T) Tu 1974, (V) Vyas and Patel 2009, (W) Ward 1996, and (Was) Wassenburgh et al. 1994.

ELAPIDAE Species	Red List Category	Criteria Applied	Supporting Information
Acalyptophis peronii	LC		Widespread, taken as bycatch in trawl fisheries (Ku, R3,T).
Aipysurus apraefrontalis	CR	A and B	Restricted range, coral dependent (W).
Aipysurus duboisii	LC		Widespread with some localized declines due to habitat degradation and bycatch (Was).
Aipysurus eydouxii	LC		Widespread, taken as bycatch in trawl fisheries (Ku, S,T).
Aipysurus foliosquama	CR	A and B	Restricted to two reef areas, total area of occupancy < $10km^2$, population, declines of at least 90% over last 15 years (W),
Aipysurus fuscus	EN	A and B	Restricted to a few reef areas, total area of occupancy < $500km^2$, population declines of at least 70% over 15 years (W).
Aipysurus laevis	LC		Common, widespread, taken as bycatch in trawl fisheries (Ku).
Aipysurus mosaicus	*		Recently described, not assessed (Sanders et al. 2012).
Aipysurus tenuis	DD		Rare, known from few specimens in NW Australia and Arafura Sea (W).
Aipysurus pooleorum	*		Not assessed, has been taxonomically confused (Sa, Sm).
Astrotia stokesii	LC		Widespread, taken as bycatch in trawl fisheries (Ku).
Emydocephalus annulatus	LC		Widespread, but patchy distribution, some localized declines (W).
Emydocephalus ijimae	LC		Common in Japan, distribution and threats unknown in other parts of range (TS).
Enhydrina schistosa	LC		Widespread and common, taken as bycatch in trawl fisheries (S,T).
Enhydrina zweifeli	DD		Poorly known, may be conspecific with *E. schistosa* (Kh).
Ephalophis greyae	LC		Endemic to remote area in NW Australia, no known threats, mangrove dependent (Mc).
Hydrelaps darwiniensis	LC		Locally common, no major threats, mangrove dependent (Mc).
Hydrophis atriceps	LC		Widespread, common, no major threats (R3).
Hydrophis belcheri	DD		Poorly known, taxonomy unclear (R3).
Hydrophis bituberculatus	DD		Poorly known, taken as bycatch in fisheries (R1).
Hydrophis brookii	LC		Widespread, taken as bycatch in fisheries (GV).
Hydrophis caerulescens	LC		Widespread, taken as bycatch in fisheries (S).
Hydrophis cantoris	DD		Poorly known, considered rare, probably restricted to Andaman Sea (R3).
Hydrophis coggeri	LC		Widespread, coral dependent, some localized declines (I).
Hydrophis cyanocinctus	LC		Widespread, locally common, taken as bycatch in fisheries (R3, S, T).
Hydrophis czeblukovi	DD		Poorly known, considered rare (C).
Hydrophis donaldi	*		Recently described, not assessed (Ukuwela et al. 2012).
Hydrophis elegans	LC		Locally common, taken as bycatch in trawl fisheries (Ku).
Hydrophis fasciatus	LC		Widespread, locally common, taken as bycatch in trawl fisheries (S).
Hydrophis gracilis	LC		Widespread, locally common, taken as bycatch in trawl fisheries (T).
Hydrophis hendersoni	*		Not assessed, recently resurrected species in the *cyanocinctus* Group (R4).
Hydrophis inornatus	DD		Known only from the holotype, may be invalid (R3).
Hydrophis kingii	LC		Rare, some declines resulting from bycatch in trawl fisheries, currently considered stable (Ku).
Hydrophis klossi	DD		Poorly known, taken as bycatch in trawl fisheries (T).
Hydrophis laboutei	DD		Known from only a few specimens collected in New Caledonia (I).
Hydrophis lamberti	LC		Widespread, locally common, taken as bycatch in trawl fisheries, some harvest for food and skin (R3).
Hydrophis lapemoides	LC		Widespread, taken as bycatch in trawl fisheries (R2).
Hydrophis macdowelli	LC		Uncommon, declines resulting from bycatch in trawl fisheries in parts of its range (Ku).

Hydrophis major	LC		Locally common, taken as bycatch in trawl fisheries (Ku).
Hydrophis mamillaris	DD		Poorly known, considered rare (V).
Hydrophis melanocephalus	DD		Poorly known, taken as bycatch in trawl fisheries (To) (R)
Hydrophis melanosoma	DD		Poorly known (GV).
Hydrophis nigrocinctus	DD		Poorly known, no records since 1943 (R4).
Hydrophis obscurus	LC		Distribution patchy, associated with brackish lagoons, occasionally taken as bycatch in artisanal fisheries (RLa).
Hydrophis ocellatus	LC		Widespread, taken as bycatch in trawl-fisheries (ML).
Hydrophis ornatus	LC		Widespread, taken as bycatch in trawl fisheries (Ku, R3,S,T).
Hydrophis pachycercos	DD		Poorly known, taken as bycatch in trawl fisheries (R3).
Hydrophis pacificus	NT		Rare, restricted range, slow maturing, declines caused by trawl fisheries estimated at 20% over 25 years (Ku).
Hydrophis parviceps	DD		Known only from a few specimens collected in southern Vietnam, taken as bycatch in trawl fisheries (R3, R5).
Hydrophis semperi	VU	B and D	Endemic to a single lake in the Philippines, extent of occurrence ~ 250 km^2, population declines expected due to habitat loss (H).
Hydrophis sibauensis	DD		Known from only three specimens collected in Indonesia (R).
Hydrophis spiralis	LC		Widespread, taken as bycatch in trawl fisheries (S).
Hydrophis stricticollis	DD		Poorly known, may be taken as bycatch in fisheries (RLb).
Hydrophis torquatus	DD		Poorly known, no collections in last 20 years (T).
Hydrophis vorisi	DD		Known only from two specimens collected in southern Papua New Guinea (RG).
Hydrophis walli	DD		Known from a single specimen, taxonomy unclear (This name has now been placed as a junior synonym of *H. nigrocinctus* (R4).
Kerilia jerdoni	LC		Widespread, locally common, taken as bycatch in trawl fisheries, some harvest for skins (R3,T).
Kolpophis annandalei	DD		Poorly known, probably rare, bycatch and coastal development potentially major threats (R3).
Lapemis curtus	LC		Widespread, common, taken as bycatch in trawl fisheries, harvested for skins, food and medicinal purposes (Ku, R3,S, T).
Laticauda colubrina	LC		Widespread, locally abundant, dependent on coral reefs and inter-tidal habitats, rarely taken as bycatch in trawl fisheries (HBC, S).
Laticauda crockeri	VU	D	Endemic to a single freshwater lake in the Solomon Islands, extent of occurrence ~ 155km^2 (HBC).
Laticauda frontalis	NT		Endemic to Vanuatu and New Caledonia's Loyalty Islands, extent of occurrence <15,000km^2, dependent on coral reefs and inter-tidal habitats (HBC).
Laticauda guineai	NT		Restricted to southern Papua New Guinea, extent of occurrence <20,000km^2, dependent on coral reefs and inter-tidal habitats (HBC).
Laticauda laticaudata	LC		Widespread, locally common, dependent on coral reefs and inter-tidal habitats (I).
Laticauda saintgironsi	LC		Restricted to New Caledonia and Loyalty Islands, locally common, dependent on coral reefs and inter-tidal habitats (HBC).
Laticauda schistorhyncha	VU	B and D	Endemic to Niue, extent of occurrence <300km2, dependent on coral reefs and inter-tidal habitats (LG).
Laticauda semifasciata	NT		Significant historical declines in the Philippines due to harvest for skin and food, current population status unknown, dependent on coral reefs and inter-tidal habitats (LGa).
Parahydrophis mertoni	DD		Poorly known, possible localized declines due to coastal development (G).
Pelamis platura	LC		Most widely distributed sea snake, occurs in coastal as well as open ocean habitats, occasionally taken as bycatch in trawl; note two records of this species from the Atlantic coast of Namibia (Br, HKH, T).
Thalassophina viperina	LC		Widespread, rare, occasionally taken as bycatch in trawl fisheries (R3, T).
Thalassophis anomalus	DD		Poorly known, dependent on coral reefs, occasionally taken as bycatch in trawl (T).

Endangered, and 80% for Critically Endangered) over a timeframe of three generation lengths. Criterion B measures extinction risk of species with restricted distributions (extent of occurrence < 20,000 km^2 or area of occupancy < 2,000 km^2 to meet the lowest threshold for Vulnerable) that are also severely fragmented, undergoing a form of continuing decline, or are exhibiting extreme fluctuations. Criterion D is designed to capture the inherent risk of extinction of species with extremely small or restricted populations. Criterion D is applied to species with < 1,000 mature individuals (sub-criterion D1), for which the known area of occupancy is less than 20 km^2, or for which the number of locations is five or fewer (sub-criterion D2).

The category of Near Threatened is assigned to species that come close to, but do not fully meet, all the thresholds or conditions required for a threatened category. A species is listed as Least Concern if it is considered at low risk for extinction. Species are listed as Data Deficient when there is taxonomic uncertainty, lack of key biological information, or inability to quantify the impact of known threats. The Data Deficient category does not indicate that the species is not threatened, only that its risk of extinction cannot be assessed with currently available information (IUCN 2010).

Spatial analyses.—We conducted spatial analyses for all species based on digital distribution maps compiled during the workshop. All digital distribution maps created were convex polygon connecting points of known, inferred or projected presence, excluding cases of vagrancy (IUCN 2001). To improve accuracy and standardize analyses, we cut each of the offshore polygons to a base map of 50 km distance from the shore. This excluded the pelagic species, *Pelamis platura*, which drifts with the currents and does not have a specific home range as do many other snakes. We produced all maps using WGS 1984 as the underlying geodetic datum. For analyses of species richness, including threatened species and those with Data Deficient status, we stacked the polygons of relevant species and converted to a 10 X 10 km raster grid using a geoprocessing script. This script assigns a value for each cell that corresponds to the number of overlapping species distributions at the location of the cell, thus representing species richness per cell. We estimated the presence and percentage of the range of each species within a marine protected area (MPA) by overlaying the range of each species with information from the World Database of Protected Areas (Available at http://www.wdpa.org/ [Accessed 3 January 2012]).

RESULTS AND DISCUSSION

We found six sea snake species (9% of all assessed) at risk of extinction, which we classified in one of the threatened categories of the IUCN Red List: Critically Endangered, Endangered or Vulnerable (Table 1, Fig. 2). An additional four species (6%) we identified as Near Threatened, coming close to, but not meeting the thresholds for classification in a threatened category. One-third (34%) of the species we classified as Data Deficient, and the remainder (53%) as of Least Concern (Fig. 2).

The most threatened species are *Aipysurus apraefrontalis* and *A. foliosquama*, both assessed as Critically Endangered. These species depend on coral reefs and are endemic to Ashmore and Hibernia reefs in northwestern Australia (Smith 1926, Minton and Heatwole 1975, Cogger 2000). Declines are estimated at 90% or more and no individuals of either species have been recorded since 2000 despite extensive surveys (Guinea 2006, 2007; Vimoksalehi Lukoschek unpubl. data). Another coral-reef-dependent species, *A. fuscus,* is listed as Endangered. This species is known from only five reefs in the Timor Sea. Although previously common in areas such as Ashmore Reef, surveys from 2007 suggest that there are severe population declines (> 70%) and possible extirpation in some locations, and 2012 surveys indicated further reduction on most reefs surveyed (Guinea 2007; Michael Guinea, pers. comm.; Vimoksalehi Lukoschek unpubl. data).

Ashmore Reef was once a major "hotspot" of sea snake diversity and abundance, with six species routinely spotted and more than 10 species recorded (Minton and Heatwole 1975; Guinea and Whiting 2005). The two Critically Endangered and one Endangered species are congeners and strongly associated with shallow-water reef flats, suggesting that their declines could be linked to degradation of their preferred habitats. However, species of sea snakes with much broader geographical ranges that occur in a variety of reef habitats have also disappeared from the area. The most recent extensive survey of Ashmore Reef (August 2010) found only one species, the more widely distributed *Aipysurus laevis*, in a restricted area of the massive reef complex (Vimoksalehi Lukoschek, unpubl. data). The reasons for the precipitous decline in the diversity and abundance of sea snake populations on Ashmore Reef are unknown but are being investigated.

Coral reef systems world-wide are threatened by over-fishing, pollution, and impacts associated with the effects of climate change, in particular coral bleaching and diseases (Hoegh-Guldberg 1999; Hughes et al. 2003; Pandolfi et al. 2003; Wilkinson 2008). As such, sea snake declines may be linked to changes in coral reef habitats, including reduced habitat complexity associated with coral bleaching, and declines in the diversity and abundance of small coral reef fishes (Munday et al. 2007, 2009; Pratchett et al. 2008). These effects could reduce the availability of preferred prey (McCosker 1975), as well as limiting access to resting sites for adult and juvenile sea snakes. However, degradation of coral reef habitats is ubiquitous and other Timor Sea Reefs experienced extreme coral bleaching (e.g., Scott Reef in 1998) without concomitant precipitous declines in abundance or diversity of sea snakes. In addition, Ashmore Reef

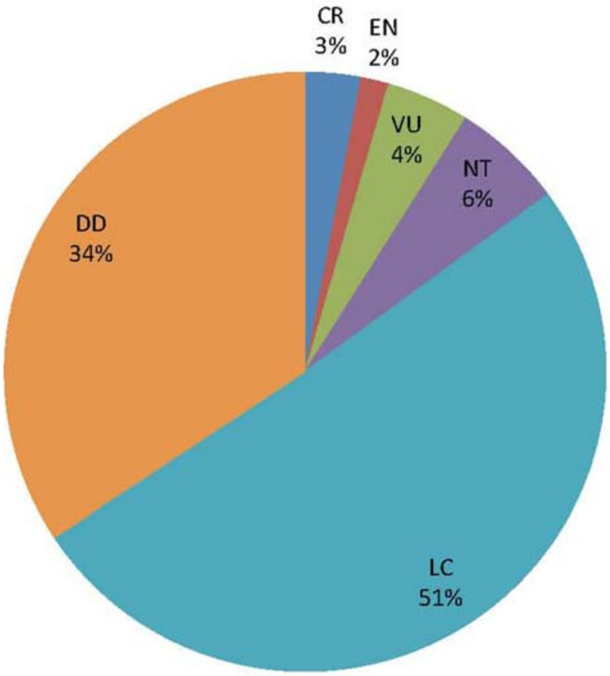

FIGURE 2. Percentage of all sea snakes assessed within each IUCN Red List category. Red List Categories: Critically Endangered (CR), Endangered (EN), Vulnerable (VU), Near Threatened (NT), Least Concern (LC), Data Deficient (DD).

has been an MPA since 1980 and sea snakes are not harvested there. It is not clear why Ashmore Reef, and to a lesser extent Hibernia Reef, show extreme declines, while neighboring reefs have not, and targeted research is needed to investigate this further.

Following the three most threatened species of Ashmore and Hibernia reefs, seven species are assessed as Vulnerable or Near Threatened primarily due to small geographic ranges and continuing degradation of their habitats. Two Vulnerable species are known from a single lake system each. *Laticauda crockeri* is endemic to Lake Te-Nggano on Rennell Island in the Solomon Islands and has an extent of occurrence of approximately 155 km^2, and *Hydrophis semperi* is endemic to Lake Taal, a freshwater lake in the Philippines with an area of 230 km^2. The third Vulnerable species, *Laticauda schistorhyncha*, is endemic to the island of Niue, while the Near Threatened species with restricted ranges include *Laticauda frontalis* (endemic to Vanuatu) and *Laticauda guineai* (endemic to Papua New Guinea).

Five of the eight species in the genus *Laticauda* are classified as Vulnerable or Near Threatened. The sea kraits have unique habitat requirements, being dependent on intact shallow coral reefs, supralittoral nesting sites, and appropriate intertidal and inland resting sites (Heatwole 1999; Shetty and Shine 2002; Lillywhite et al. 2008; Bonnet et al. 2009). Sea kraits play an important role in the functioning of coral reef ecosystems through consumption of predatory fishes, primarily anguilliforms and moray eels (Ineich et al. 2007; Brischoux and Bonnet 2008), and are considered indicator species of coral reef health (Reed et al. 2002; Alcala 2004; Ineich et al. 2007; Brischoux and Bonnet 2008). Due to their frequent alternation between terrestrial and marine habitats, sea kraits are vulnerable to the degradation of either environment. Small, undisturbed (predominantly uninhabited) islands are requisite terrestrial refuge sites for sea kraits. While some species such as *L. saintgironsi* venture quite far inland, others like *L. laticaudata* are restricted to < 4 m of the water's edge (Lane and Shine 2010), where the presence of beach rock in particular is crucial as terrestrial refugia (Bonnet et al. 2009). Even small-scale disturbances to these coastal areas have caused the local extirpation of sea kraits (e.g., *L. saintgironsi* and *L. laticaudata* from Maitre Island in New Caledonia: Brischoux et al. 2009a). Coastal disturbances to sea kraits may be accentuated by the high level of philopatry observed in several species, with individuals returning to their home island, frequently to small stretches of beach (Shetty and Shine 2002; Brischoux et al. 2009a).

Despite the wide distribution and sometimes high density of sea kraits, very few natural nest sites are recorded for the genus (Herre and Rabor 1949; Bacolod 1983). Egg-laying has been documented in *L. semifasciata*, and this species is known to communally deposit eggs in tidal caves on Gato Island in the Philippines and Orchid Island in Taiwan (Bacolod 1983; Tu et al. 1990). Such a reliance on very specific terrestrial habitats for breeding suggests that these areas may require protection. Current harvesting of *L. semifasciata* from their nesting site on Gato Island (discussed below) lends urgency to this concern (Joey Gatus, pers. comm.). A basic understanding of sea kraits' habitat requirements for nesting is needed to inform future conservation assessments.

In addition to threats caused by habitat degradation, sea snakes are vulnerable to impacts of fishing throughout much of their range. In northern Australia, 12 species are commonly taken as by-catch in commercial-scale trawl fisheries. Estimated annual catches of sea snakes in the early 1990s for the northern prawn fishery (NPF) are between 81,000 to 120,000 individuals (Wassenberg et al. 1994; Ward 1996) leading to efforts by the Australian government to monitor and minimize sea snake-trawl interactions. Of the species taken incidentally in the NPF, *Hydrophis pacificus* and *H. kingii* were identified as the most vulnerable due to their apparent rarity and less productive life history (Milton 2001). *Hydrophis kingii*, although rare, is considered to be stable, while *H. pacificus* is classified as Near Threatened based on estimated declines of at least 20% over the past 25 y. Both species are expected to benefit from the reduction in the number of prawn trawlers in the NPF put into effect in 2005. A more recent risk assessment for the NPF suggests that populations of most sea snake species routinely caught in the fishery are stable (Milton et al. 2008). In addition, bycatch measures are implemented in the NPF fishery and appear to be successfully reducing the number of sea snakes caught in trawls (Heales et al. 2008; Milton et al. 2009).

Bycatch in the Queensland east coast trawl fishery is estimated at 105,210 (standard error = 18,828) sea snakes annually, of which 26% died while still in the nets or in the hours and days after trawling (Courtney et al. 2010). One fishery targeting Redspot King Prawns (*Melicertus longistylus*) accounted for 58.9% of all sea snake catches and 84.5% of all deaths (Courtney et al. 2010). Most of the post-trawl mortalities occurred in the first 24 h after trawling and increased amongst larger snakes (Wassenberg et al. 2001; Courtney et al. 2010). An ecological risk assessment has recently been completed for species caught in the Queensland east coast trawl fishery within the Great Barrier Reef Marine Park (Pears et al., unpubl. report). Of the 14 species recorded, only two species, *H. elegans* and *H. ocellatus* (formerly *H. ornatus*), were assessed as "high risk" from this fishery. Based on this assessment, management arrangements will be considered to reduce the risk to these two species (Pears et al., unpubl. report).

Similar studies are needed in Southern and Southeastern Asia, where sea snakes are impacted by densely populated, small-scale coastal fisheries. Surveys in Sri Lanka and Indonesia (Kate Sanders et al., unpubl. data) indicate high levels of bycatch mortality for at least 20 species of true sea snakes and *Acrochordus granulatus*. There is an increasing trend to commercialize, rather than discard bycatch in most artisanal fisheries of tropical Asia (Kelleher 2005). As targeted stocks become further depleted, even low-value "trash fish," including sea snakes, may enter the market as fishmeal for animal feed (Funge-Smith et al. 2005; Lobo et al. 2010). These practices may lead to further declines in sea snake populations. It is crucial that potentially vulnerable species such as sea snakes be included in regular fisheries monitoring programs in these regions.

In addition to being taken in bycatch, sea snakes are directly targeted in some areas for their meat and skin. *Laticauda semifasciata* is classified as Near Threatened due to historical harvests for skins and the trade in smoked sea snake meat in the Philippines and in the Ryukyu Islands of Japan. Harvests plummeted from 450,000 in 1974 to 1,454 individuals by 1981 (Dunson 1975; Bacolod 1983). It is thought that low-level harvesting of this species still supplies Japanese markets; however, no data are available to confirm or quantify this trade (Joey Gatus, pers. comm.). The species is not thought to have recovered from these intensive levels of exploitation and may in fact qualify for higher threat status, although data are lacking to evaluate decline in the global population.

Lapemis curtus is also harvested but currently listed as Least Concern because harvests are localized in peninsular Malaysia and the species is relatively widespread. As with much of the sea-snake trade, the majority of information on levels of exploitation is anecdotal. For example, a single business established in 2004 reportedly exported approximately 6,000 sea snake specimens per month, suggesting high levels of exploitation (Mark Auliya, pers comm.). More detailed surveys are needed to better understand the trade in this species in Southeast Asia, including estimates of trade volumes, value of skins, seasonality and methods of harvest, and identification of major export markets.

No sea snake species are currently listed under the Convention on International Trade in Endangered Species of Flora and Fauna (CITES). For quotas to be established under CITES, non-detrimental findings studies (NDFs) must be carried out to estimate the sustainable off-take for any given species or population. However, NDFs require species-specific information on habitat utilization and population dynamics that is currently unavailable for most species of sea snake. NDFs are urgently needed to determine sustainable harvest and export levels. At present, the lack of relevant information means that off-take quotas are usually based on previous years' trade figures and the demands of traders.

Perhaps the most salient result of this IUCN Red List Assessment is that sea snakes are characterized by a large number of Data Deficient species (23 species or 34%). Despite being primarily near-shore, coastal animals, the proportion of Data Deficient species was similar to that of marine mammals (35%), sharks and rays (47%) and groupers (30%), many of which are wide-ranging and difficult to study (Polidoro et al. 2009). Several species have remaining taxonomic issues, or are known from a limited number of collections that typically occurred decades ago. More information is needed to characterize the threats to sea snakes highlighted here from habitat degradation, fisheries, and direct harvest. More systematic survey data and long-term population monitoring could greatly improve our understanding of anthropogenic impacts on sea snake populations.

Spatial patterns.—Marine elapids are found across the Indo-Pacific region and no species occur in the Atlantic Ocean, Mediterranean, or Caribbean Seas. Our analyses of species richness patterns (Fig. 3) show two broad areas of peak diversity within the inhabited region: Southeast Asia (Gulf of Thailand and Java Sea) and northern Australia (Timor Sea, Arafura Sea and Gulf of

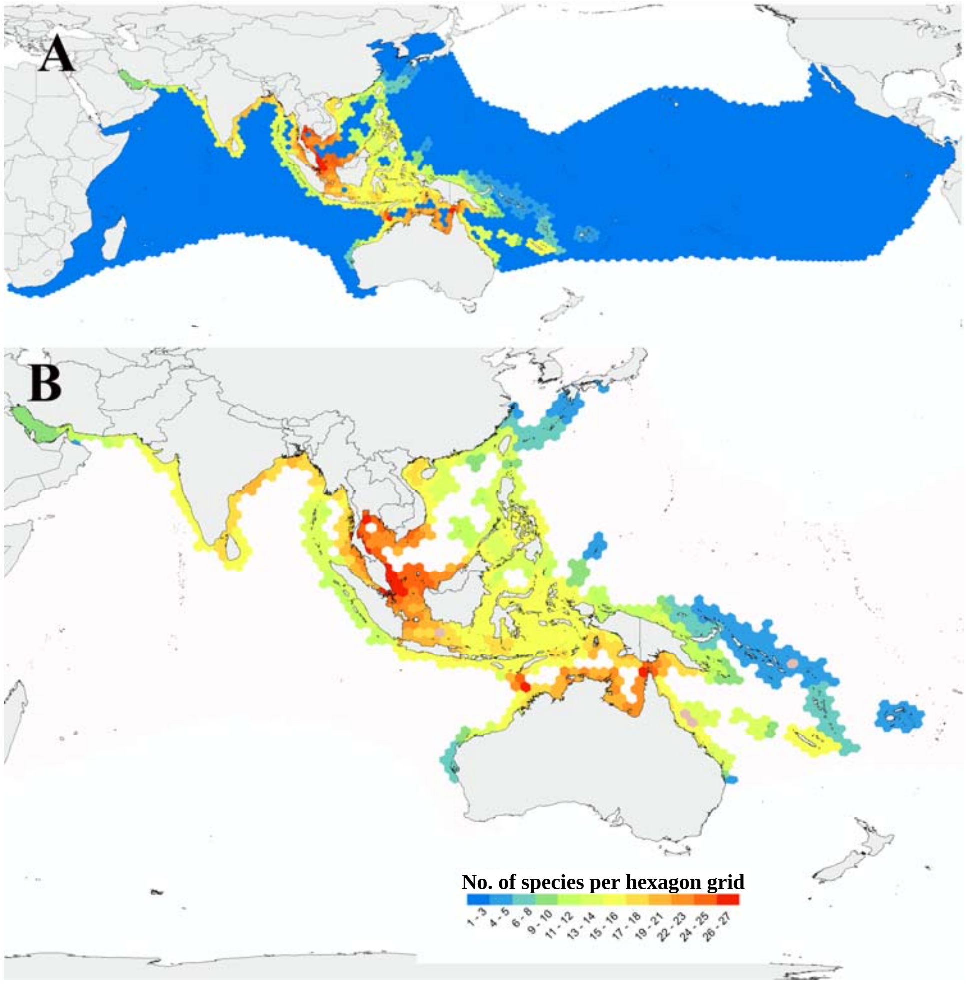

FIGURE 3. Sea snake species richness. A) Distribution including the widespread pelagic species *Pelamis paltura.* B) The distribution of sea snakes and sea kraits without *Pelamis*. Note that since this map was produced, Rasmussen et al (2011b) reported 25 species of marine snakes in Vietnamese waters: slightly more species than this map indicates.

Carpentaria). This pattern of diversity is somewhat different from the "bulls-eye" pattern reported for corals, reef fishes, and other important marine groups in the Coral Triangle (Bellwood and Meyer 2009; Hoeksema 2007), which has its center in eastern Indonesia and the Philippines (Allen 2007; Roberts et al. 2002). The centers of sea snake diversity are found along the western and southern margins of the Coral Triangle hotspot. The comparably low diversity in most of Indonesia and the Philippines is likely to be an artifact of the uneven distribution of survey data. Far fewer field surveys of sea snakes have been carried out in these regions than have been in Australia, Malaysia, Thailand and Vietnam (e.g., Cogger 1975; Stuebing and Voris 1990; Murphy et al. 1999; Rasmussen et al. 2011b).

The two Critically Endangered and one Endangered species are all found at Ashmore and Hibernia reefs in the Timor Sea, making these reefs a "hotspot" for threatened species, with the area of suitable sea snake habitat estimated at only 10 km^2 for both reefs combined. No other overlap areas of threatened species' ranges were found (Fig. 4). However, it is important to note that some species listed as Data Deficient may in fact be threatened and clarification of threat status for Data Deficient species could reveal other important areas requiring conservation.

All sea snakes classified in a threatened category are species with restricted ranges (extent of occurrence less than 2,000 km^2; Fig. 4) and two of the four Near Threatened species are also endemics with small ranges. (*Laticauda guineai* and *L. frontalis*; Table 1). Conservation of these species and mitigation of threats are in some cases facilitated by their limited geographic distribution. For example, the two vulnerable species *Hydrophis semperi* (Philippines) and *L. schistorhyncha* (Niue), experience mostly localized threats such as

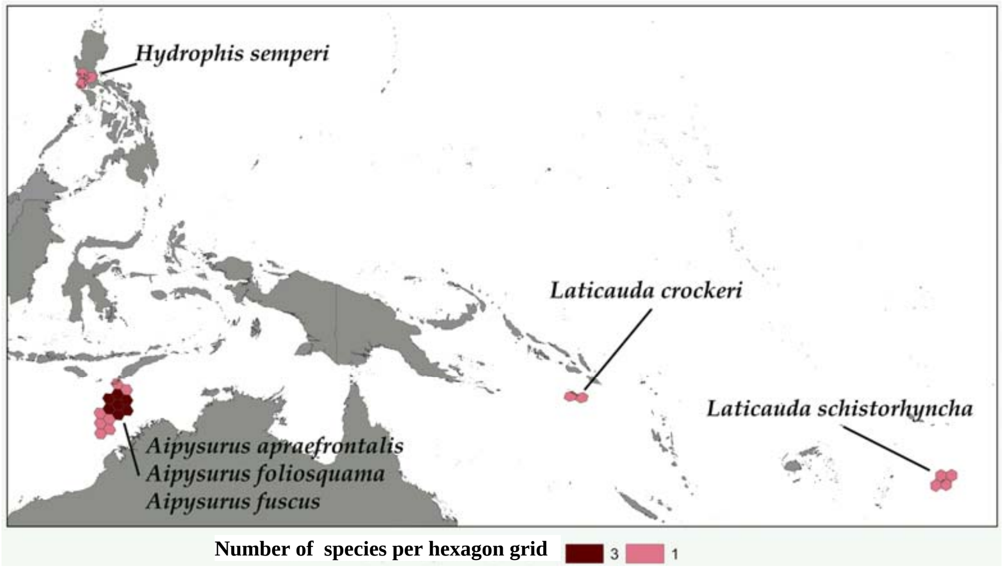

FIGURE 4. Areas and number of threatened species (Critically Endangered, Endangered and Vulnerable) with species for each area labeled.

pollution and are found in areas amenable to regional protection. These species currently receive no protection from MPAs, and conservation efforts targeting their recovery should consider designation of MPAs or Locally Managed Marine Areas as a potential tool.

The majority of species (68%) had < 10% of their range within an MPA. Interestingly, the two Critically Endangered species (*Aipysurus apraefrontalis* and *A. foliosquama*) at Ashmore Reef have the highest MPA coverage of any species (80% of their range protected). Yet, declines have occurred despite the majority of their ranges being found within well-managed MPAs. The endangered *A. fuscus*, also found within the same region, has 50% of its range covered by MPAs. The remaining species with good MPA coverage were those with a portion of their range within the Great Barrier Reef Marine Park on the eastern coast of Queensland, Australia.

Areas identified as having the greatest need for basic research on sea snakes were Southeast Asia and peninsular Malaysia, where the greatest concentration of Data Deficient species was found (Fig. 5). The high number of Data Deficient species probably reflects the higher overall species diversity recorded for these regions. Many Data Deficient species are known only from a few specimens collected as fisheries bycatch. Survey efforts in much of Southern and Southeastern Asia are extremely limited and information is lacking on the taxonomy, abundance, distribution, ecology, and threats in these regions. In particular, Indonesia contains very large areas of suitable sea snake habitat, yet few surveys of sea snakes have been carried out there since that of Smith (1926). Limited recent sampling revealed much higher species diversity than currently recognized, particularly in eastern Indonesia (Kate Sanders et al., unpubl. data). It is important that future surveys for sea snakes include more accurate locality data and that they be standardized by effort so that changes in populations can be monitored over time. In addition, to augment our limited knowledge regarding status and distribution of Data Deficient species, we encourage efforts that integrate known habitat preferences into species' distribution models (e.g., Brischoux et al. 2012).

CONCLUSIONS

Nine percent of the marine elapids are at risk of extinction and an additional 6% are Near Threatened. One-third of all known sea snakes are classified as Data Deficient, indicating that for these species basic biological research is still needed. Given limited knowledge of threats, combined with frequent dependency on very specific types of habitat, it is possible that additional species may be experiencing significant population declines. Our study suggests that immediate conservation efforts should focus on the sea snake "hotspot" in the Timor Sea, where the most threatened species are found, and where the causes of severe population declines remain unknown. The remaining threatened species appear to be impacted by localized threats, and their restricted ranges make them amenable to spatial conservation tools, such as designation of MPAs. More broadly, there is need for basic field research to understand species diversity, abundance, and threats to sea snakes throughout their range, but particularly in Southeast Asia.

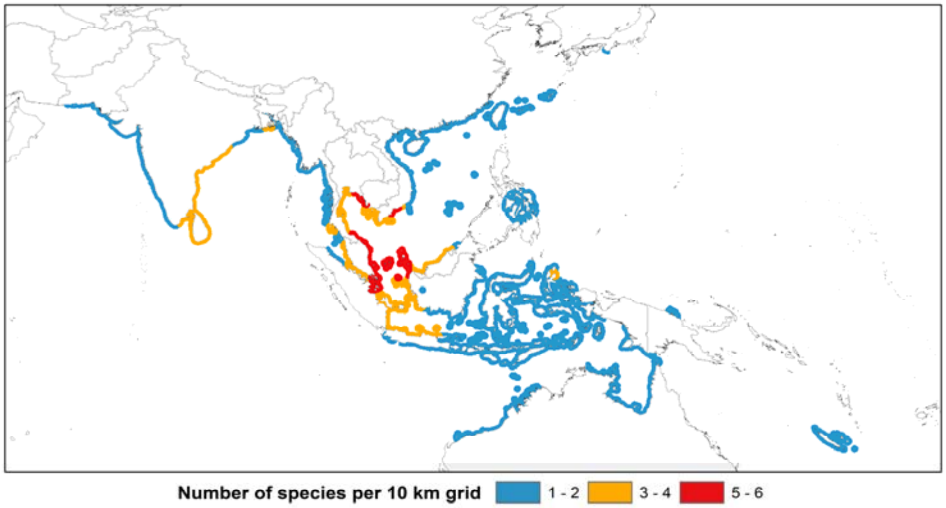

FIGURE 5. Number of Data Deficient species of sea snakes in different geographic regions.

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