Dusky Sea Snake (*Aipysurus fuscus*)

2014-2020

**Bibliography**

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**NCRL subject guide 2020-10**

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Table of Contents

Background & Scope ................................................................................................................................. 3
Sources Reviewed ..................................................................................................................................... 3
Section I: Biology and Life History ............................................................................................................. 4
Section II: Genetics and Population Structure .......................................................................................... 6
Section III: Population Abundance and Trends ............................................................................................ 8
Background & Scope
This bibliography focuses on dusky sea snake literature published since 2014. It is intended as a reference resource for ESA staff of the NOAA Fisheries Office of Protected Resources and the U.S. Fish and Wildlife Service when compiling and summarizing any relevant new (i.e. 2014-present) information for this sea snake. It is organized into three sections: Biology and Life History, Genetics and Population Structure, and Population Abundance and Trends.

Section I – Biology and Life History
Section one is intended to provide an overview of the biology and life history of the dusky sea snake. The research in this area includes a compilation of diet, lifespan, habitat conditions, behavior, feeding, social ecology, and reproduction.

Section II – Genetics and Population Structure
Section two is intended to provide an overview of on genetics, genetic variation, or trends in genetic variation (e.g., loss of genetic variation, genetic drift, inbreeding, etc.) and population structure of the dusky sea snake.

Section III – Population Abundance and Trends
Section three is intended to provide an overview of the latest population estimates and trends for the dusky sea snake.

Sources Reviewed
The following databases were used to identify sources: Clarivate Analytics’ Web of Science: Science Citation Index Expanded and Social Science Index; Science.gov; ProQuest’s Science and Technology including Aquatic Science Fisheries Abstracts; Elsevier’s Science Direct; JSTOR; NOAA’s Institutional Repository; the Biodiversity Heritage Library; BioOneComplete; and Google Scholar.
Section I: Biology and Life History


This compilation of published research, directly related to sea snakes in Western Australia, was produced at the direct request and under contract to Commonwealth of Australia, as represented by Marine Species Conservation, Department of the Environment.


Four specimens of the olive sea snake, Aipysurus laevis, were collected off the coast of Western Australia, and the venom proteome was characterized and quantitatively estimated by RP-HPLC, SDS-PAGE, and MALDI-TOF-TOF analyses. A. laevis venom is remarkably simple and consists of phospholipases A2 (71.2%), three-finger toxins (3FTx; 25.3%), cysteine-rich secretory proteins (CRISP; 2.5%), and traces of a complement control module protein (CCM; 0.2%). Using a Toxicity Score, the most lethal components were determined to be short neurotoxins. Whole venom had an intravenous LD50 of 0.07 mg/kg in mice and showed a high phospholipase A2 activity, but no proteinase activity in vitro. Preclinical assessment of neutralization and ELISA immunoprofiling showed that BioCSL Sea Snake Antivenom was effective in cross-neutralizing A. laevis venom with an ED50 of 821 μg venom per mL antivenom, with a binding preference towards short neurotoxins, due to the high degree of conservation between short neurotoxins from A. laevis and Enhydrina schistosa venom. Our results point towards the possibility of developing recombinant antibodies or synthetic inhibitors against A. laevis venom due to its simplicity.


Sea snakes (Elapidae, subfamilies Hydrophiinae and Laticaudinae) reach high species richness in the South China Sea and in the Australian region; however, most countries in the two regions still lack up-to-
date checklists and identification tools for these snakes. We present an updated reviewed checklist and a new complete identification key to sea snakes in Australian waters. The identification key includes 29 species documented and 4 possibly occurring taxa and is based mostly on easy-to-use external characters. We find no evidence for breeding populations of Laticauda in Australian waters, but include the genus on the list of possibly occurring taxa.


No Abstract


An aquatic animal faces challenges not encountered by its terrestrial counterparts, promoting adaptive responses in multiple traits. For example, a thicker dermis might protect snakes when they are pushed against sharp objects by water currents, and might enable a snake to shed fouling organisms attached to its skin. We thus predicted that marine snakes should have thicker skin than terrestrial species, and that smaller sea snakes should have relatively thicker skin (because absolute, not relative, thickness determines vulnerability to fouling). Measurements of 192 snakes of 44 species supported those predictions. Many (but not all) sea snakes have skins 50% thicker than those of terrestrial and amphibious snake species, representing multiple independent evolutionary origins of thicker skin (in acrochordids, Laticauda sea kraits and both main clades of hydrophiine sea snakes). Marine snakes showed different allometries of skin thickness compared with their terrestrial counterparts; larger snakes had thicker skin within and among species of amphibious and terrestrial snakes, but larger aquatic snake species had thinner skin compared with smaller taxa. Interspecific variation in skin thickness was primarily due to increased collagen in the deep dermis, a physical barrier well suited to protecting against physical injury and to resisting penetration by epibionts.


Viviparus sea snakes are an exceptionally diverse radiation of secondarily marine reptiles that inhabit the shallow tropical and subtropical waters of the Indian and Pacific Oceans with the peak diversity in the Indo-Australian Archipelago (IAA). Although sea snake biology, natural history and diversity are relatively well known, they have a highly unstable taxonomy and poorly understood evolutionary and biogeographic histories. This thesis examined the systematics, species limits, historical biogeography and diversification of Indo-Pacific viviparous sea snakes using molecular phylogenetics and a combination of external and internal morphological characters.
The study of snake venoms has led to the discovery/development of a number of pharmaceutical drugs, diagnostic kits, and research molecular tools in the last 50 years. Furthermore, a deep knowledge of snake venom protein composition is necessary for better understanding the envenomation physiopathology and to contribute to the broadening in the clinical efficacy and range of antivenom therapy. During the past 15 years, several groups have applied proteomic techniques for the determination (to different extents) of peptide and protein compositions of snake venoms from almost 200 species (mostly from Viperidae and Elapidae families). The present review details the different methodological approaches used so far, stressing that none of them has generated a comprehensive snake venom proteopeptidome, ideally defined as the quali-quantitative representation of all proteoforms (including different peptide forms) present in any given snake venom. Due to the technological advancements in high-throughput genomics and transcriptomics allied to state-of-the-art bottom-up proteomics (as well as the possibility of top-down venomics), it is proposed that the time has come to actively pursue the proteopeptidome “dream.” Several issues that should be addressed to achieve this goal are discussed. Finally, it is expected that in the next decade, snake venomics shall surpass the protein family-level-based identification and attain a proteoform-level-based one.

Section II: Genetics and Population Structure


Aim: To investigate phylogeographic patterns among and within co-occurring sea snake species from Australia’s endemic viviparous Aipysurus lineage, which includes critically endangered species, and evaluate the conservation implications of geographically structured patterns of genetic divergence and diversity. Location: Australia’s tropical shallow water marine environments spanning four regions: Great Barrier Reef (GBR), Gulf of Carpentaria (GoC), Timor Sea (TS) and coastal WA (WAC). Methods: Samples from >550 snakes representing all nine nominal Aipysurus group species were obtained from throughout their known Australian ranges. Coalescent phylogenetic analyses and Bayesian molecular dating of mitochondrial DNA, combined with Bayesian and traditional population genetic analyses of 11 microsatellite loci, were used to evaluate genetic divergence and diversity. Results: Mitochondrial DNA revealed highly congruent phylogeographic breaks among co-occurring species, largely supported by nuclear microsatellites. For each species, each region was characterized by a unique suite of haplotypes (phylogroups). Divergences between the TS, GoC and/or GBR were invariably shallow and dated as occurring 50,000-130,000 years ago, coinciding with the cyclic Pleistocene emergence of the Torres Strait land bridge. By contrast, sea snakes from coastal WA were consistently highly divergent from other regions and dated as diverging 178,000-526,000 years ago, which was not associated with any known vicariant events. Main Conclusions: Previously unappreciated highly divergent sea snake lineages in coastal WA potentially represent cryptic species, highlighting this region as a high-priority area for conservation. The cyclic emergence of the Torres Strait land bridge is consistent with observed divergences between the TS, GoC and/or GBR; however, processes involved in the earlier divergences involving the WAC remain to be determined. The observed strong population genetic structures (as
surrogates for dispersal) indicate that sea snakes have limited potential to reverse population declines via replenishment from other sources over time frames relevant to conservation.


Population bottlenecks can result in loss of genetic variation, increased extinction risk, and hybridization with related sympatric species. Many challenges are associated with empirical detection of population declines, thus conservation biologists often use molecular approaches as surrogates. This study explored whether declines in abundances of viviparous sea snakes on Australia's Timor Sea reefs could have been foreshadowed using genetic surveys. Ashmore Reef (the largest Timor Sea reef) once hosted large breeding populations of sea snakes. Abundances have declined precipitously since 1994 and Ashmore Reef has been devoid of snakes since 2012. Moreover, high rates of hybridization between two sympatric species have been documented on Timor Sea reefs, possibly associated with sea snake declines. I analysed mitochondrial DNA and 11 nuclear microsatellites for >250 sea snakes from three species, *Aipysurus laevis*, *Aipysurus fuscus* and *Emdocephalus annulatus*, sampled on four Timor Sea reefs in 2002 and 2010. While there was strong spatial genetic structure among reefs, there was little temporal genetic divergence for *A. laevis* at Ashmore Reef, despite the massive declines in abundance during that temporal window. Positive Tajima's D and Fu's FS values at Ashmore Reef indicated demographic contraction for: *A. laevis* in 2002 and 2010; *E. annulatus* (2002); but not *A. fuscus* (2002). Microsatellites showed inbreeding depression (positive Fis values) and non-random mating (heterozygote deficit) for all three species at Ashmore Reef, consistent with population declines. Bottleneck tests were equivocal, with significant heterozygous excesses at Ashmore Reef, but non-significant M-ratios or mode-shifts in allele frequencies, with the significance of tests differing markedly with microsatellite mutation models. Thus genetic analyses alone would not have been sufficient to provide managers with unequivocal evidence of population declines. There was little evidence for hybridization between *A. laevis* and *A. fuscus*, despite previous research suggesting that the Endangered *A. fuscus* was at risk of reverse speciation secondary to the highly porous reproductive barriers between these species.


The viviparous sea snakes include 62 ecologically diverse species, many of which are of very recent evolutionary origin and have overlapping distributions. Peak sea snake diversity and endemism is recorded from the isolated emergent reefs of the Timor Sea in Northwest Australia. However, nine species have disappeared from Ashmore, the largest of these reefs, over the last 15 years, including two critically endangered *Aipysurus* species that have also disappeared from neighbouring Hibernia Reef. A third Timor Sea endemic, *Aipysurus fuscus*, is now known only from Scott and Hibernia reefs, where it coexists with closely related and locally abundant *Aipysurus laevis*. We analysed microsatellite markers for *A. fuscus* and *A. laevis* sampled across four Timor Sea reefs to assess evidence for recent interspecific gene flow and historical introgression. Our data fit an Isolation–Migration model, which showed significant and asymmetrical levels of gene flow following species divergence, and highest rates of introgression from the large *A. laevis* population into the much smaller *A. fuscus* population. Population
assignment analyses recovered two ancestral clusters that broadly corresponded to morphological
species designations, but revealed high frequencies of hybrids on all four reefs and individuals of pure A.
fuscus ancestry only at Scott and (historically) Ashmore. Most unexpectedly, 95% of snakes sampled at
Hibernia were hybrids that resembled A. laevis in phenotype, revealing a collapse of reproductive
barriers ('reverse speciation') at this reef. These results have dire implications for the conservation
status of A. fuscus, and highlight the fragility of reproductive barriers in a recent marine radiation.

Shaffer, H. B., Gidiş, M., McCartney-Melstad, E., Neal, K. M., Oyamaguchi, H. M., Tellez, M., & Toffelmier,

Amphibians and reptiles as a group are often secretive, reach their greatest diversity often in remote
tropical regions, and contain some of the most endangered groups of organisms on earth. Particularly in
the past decade, genetics and genomics have been instrumental in the conservation biology of these
cryptic vertebrates, enabling work ranging from the identification of populations subject to trade and
exploitation, to the identification of cryptic lineages harboring critical genetic variation, to the analysis of
genes controlling key life history traits. In this review, we highlight some of the most important ways
that genetic analyses have brought new insights to the conservation of amphibians and reptiles.
Although genomics has only recently emerged as part of this conservation tool kit, several large-scale
data sources, including full genomes, expressed sequence tags, and transcriptomes, are providing new
opportunities to identify key genes, quantify landscape effects, and manage captive breeding stocks of
at-risk species.

Section III: Population Abundance and Trends

range and habitat records for threatened Australian sea snakes raise challenges for

Hydrophiine (true) sea snakes are large predatory live-bearing marine reptiles. Australia is a biodiversity
hotspot for true sea snakes with almost half of the ~70 extant species (including 11 endemics). Two
Australian endemics, Aipysurus foliosquama and Aipysurus apraefrontalis, were listed as Critically
Endangered (CR) under IUCN Red List (2010) criteria and Australia's Threatened Species Legislation
(2011) due to their restricted geographic ranges being <10km² (i.e. Ashmore and Hibernia Reefs, Timor
Sea), from where they disappeared between 1998 and 2002. However, museum and anecdotal records
suggested that these species might also occur in coastal locations of Western Australia (WA). We used
intensive field surveys, habitat data, and molecular genetics to document the first unequivocal records
of living A. foliosquama (n=16) and A. apraefrontalis (n=7) since they were listed as Critically
Endangered, in coastal WA. Our data significantly increases the known geographic range and habitats of
A. foliosquama, to include seagrass meadows in subtropical Shark Bay (latitudes 24.5°S to 26.6°S), which
is 500km further south than any previous sighting. Most sea snakes were collected from demersal prawn
trawl by-catch surveys, indicating that these species are vulnerable to demersal trawl gear. Nonetheless,
the disappearance of these two species from Ashmore Reef (which coincided with extirpations of at
least three other sea snake species) could not be attributed to trawling and remain unexplained. Key
threatening processes will need to be identified if effective conservation strategies are to be
implemented to protect these newly discovered coastal populations of two Critically Endangered species.


We, NMFS, have completed comprehensive status reviews under the Endangered Species Act (ESA) for seven foreign marine species in response to a petition to list those species. These seven species are the Eastern Taiwan Strait population of Indo-Pacific humpback dolphin (Sousa chinensis), dusky sea snake (Aipysurus fuscus), Banggai cardinalfish (Pterapogon kauderni), Harrisson’s dogfish (Centrophorus harrissoni), and the corals Cantharellus noumeae, Siderastrea glynni, and Tubastrea floreana. We have determined that the Eastern Taiwan Strait Indo-Pacific humpback dolphin is not a distinct population segment and therefore does not warrant listing. We have determined that, based on the best scientific and commercial data available, and after taking into account efforts being made to protect the species, Pterapogon kauderni, and Centrophorus harrissoni meet the definition of a threatened species; and Aipysurus fuscus, Cantharellus noumeae, Siderastrea glynni, and Tubastrea floreana meet the definition of an endangered species. Therefore, we propose to list these six species under the ESA. We are not proposing to designate critical habitat for any of the species proposed for listing, because the geographical areas occupied by these species are entirely outside U.S. jurisdiction, and we have not identified any unoccupied areas that are currently essential to the conservation of any of these species. We are soliciting comments on our proposals to list the six species. We are also proposing related administrative changes to our lists of threatened and endangered species.


This progress report provides details on fieldwork and analyses conducted for NESP project A8: ‘Exploring the status of Western Australia’s sea snakes’ between the period of May 2017 – December 2017. Snorkel, research trawl and baited remote underwater video station (BRUVS) surveys were conducted by Hub researchers and collaborators between May and October 2017 that were combined with existing datasets to update occurrence records and conduct spatial and time-series analyses. Data from BRUVS were used to assess sea snake assemblages in multiple locations within Australian Marine Parks (AMPs) and in locations where repeated sampling was conducted to construct species distribution models (SDMs) for all sea snake sightings and three priority species (Aipysurus apraefrontalis, A. foliosquama and A. fuscus).

Declines in the abundance of marine vertebrates are of considerable concern, especially when they occur in isolated locations relatively protected from most major anthropogenic disturbances. This paper reports on sustained declines in the abundance and diversity of sea snakes at Ashmore Reef, a renowned biodiversity hotspot in Australia’s Timor Sea. Surveys conducted in eight years between 1973 and 2010 recorded the highest abundances (average 42–46 snakes day$^{-1}$) and species richness (nine species) in 1973 and 1994. In 2002 abundance had declined by more than 50% (21 snakes day$^{-1}$) and only five species were recorded. Since 2005 abundances have been consistently low (1–7 snakes day$^{-1}$), with just two species, Aipysurus laevis and Emydocephalus annulatus, recorded in significant numbers. Despite extensive searches since 2005 (especially in 2010) five species of sea snake historically abundant at Ashmore Reef have not been sighted and are presumed to have become locally extinct. These species include three Timor Sea endemics Aipysurus apraefrontalis, Aipysurus foliosquama, Aipysurus fuscus, and one Australasian endemic Aipysurus duboisii. Declines in the abundance and diversity of sea snakes at Ashmore Reef cannot be attributed to differences in survey methods among years. Ashmore Reef was declared a National Nature Reserve (IUCN Category 1a) in 1983 and, although the causes for the declines are not known, this protection has not prevented their occurrence. We discuss possible causes for these enigmatic declines however, in order to implement effective management strategies, studies are needed to determine why sea snakes have disappeared from Ashmore Reef.


This draft report was produced in response to a petition received from WildEarth Guardians on July 15, 2013, to list 81 marine species as endangered or threatened under the Endangered Species Act (ESA). Three of the petitioned species were sea snakes. The National Marine Fisheries Service (NMFS) evaluated the petition to determine whether the petitioner provided substantial information as required by the ESA to list these species. On November 6, 2013, NMFS announced in the Federal Register that the petition did present substantial information that listing may be warranted for one of the three sea snakes, Aipysurus fuscus, commonly referred to as the dusky sea snake; and NMFS requested information on this species from the public (78 FR 66675). Subsequently, NMFS initiated a status review of this species, which I document in this report. This draft report summarizes available data and information on the dusky sea snake and presents an evaluation of the species’ status and extinction risk.


Offshore reefs of the North West Shelf of Australia support the most diverse and abundant sea snake communities in the world. Ashmore Reef (12° 17′S, 123° 02′E) is the regional centre of diversity hosting 17 species, including two endemics (Rasmussen et al. 2011; Elfes et al. 2013). However, over the last decade the diversity and abundance of sea snakes at Ashmore Reef have declined drastically. In 2010, only two species (Aipysurus laevis, Astrotia stokesii) were observed and at least five species are now presumed locally extinct (Lukoschek et al. 2013). Here we report on a 2013 survey of Ashmore Reef where, despite extensive boatbased searches over nine days and SCUBA-surveys encompassing 12 ha of reef and lagoonal habitat, no sea snakes were encountered.
We, NMFS, issue a final rule to list three foreign corals and the dusky sea snake under the Endangered Species Act (ESA). We considered comments submitted on the proposed listing rule and have determined that the three foreign corals (Cantharellus noumeae, Siderastrea glynni, and Tubastraea floreana) and the dusky sea snake (Aipysurus fuscus) should be listed as endangered species. We will not designate critical habitat for any of the species because the geographical areas occupied by these species are entirely outside U.S. jurisdiction, and we have not identified any unoccupied areas within U.S. jurisdiction that are currently essential to the conservation of any of these species.


All sea snakes are listed marine species under the EPBC Act and three Australian endemic species are listed as Critically Endangered or Endangered, and as such are a national conservation priority. Recent findings of two Critically Endangered sea snake species (Aipysurus apraefrontalis and Aipysurus foliosquama) in locations outside of their previously defined ranges have highlighted the lack of information on species distributions along the North West coast of Australia. Data on sea snake sightings on previously collected baited remote underwater video surveys (BRUVS) and fisheries independent trawl surveys were used to assess the utility of these methodologies to accurately define relative abundance and distribution patterns of sea snakes in the North West Marine Region (NWMR), including within Commonwealth Marine Reserves (CMRs), to refine species’ status. Presence/absence data from BRUVS were used to predict locations that are likely important habitats for sea snake populations within the NWMR, which included mid-shelf and oceanic shoals along the Kimberley and Pilbara coasts. Limited fisheries-independent trawl sampling data collected in Shark Bay and Exmouth Gulf highlighted patterns of interaction between sea snakes and trawl fishing, with survivorship curves indicating that most sea snake species encountered within these regions may be able to sustain low to moderate levels of trawl fishing. Trawl survey data also highlighted the need for additional fisheries interaction data to accurately assess the species-specific influence of fishing activities (e.g. trawl and trap fishing) on different life stages of sea snakes susceptible to incidental capture (bycatch). This project highlights the need for more data on sea snakes in regions lacking information (e.g. mid-shelf shoals of Kimberley coast, Pilbara coast and Rowley Shoals). In addition, further research is also required to assess the degree of connectivity between sea snake populations from offshore reefs that have seen recent declines, and those on adjacent mid-shelf and oceanic shoals.


Strategies aimed to conserve and manage rare species are often hindered by the lack of data needed for their effective design. Incomplete and inaccurate data on habitat associations and current species distributions pose a barrier to effective conservation and management for several species of endemic
sea snakes in Western Australia that are thought to be in decline. Here we used a correlative modelling approach to understand habitat associations and identify suitable habitats for five of these species (Aipysurus apraefrontalis, A. foliosquama, A. fuscus, A. l. pooleorum and A. tenuis). We modelled species-specific habitat suitability across 804,244 km² of coastal waters along the North-west Shelf of Western Australia, to prioritise future survey regions to locate unknown populations of these rare species. Model projections were also used to quantify the effectiveness of current spatial management strategies (Marine Protected Areas) in conserving important habitats for these species. Species-specific models matched well with the records on which they were trained, and identified additional regions of suitability without records. Subsequent field validation of the model projections uncovered a previously unknown locality for A. fuscus within the mid-shelf shoal region, outside its currently recognised global range. Defining accurate geographic distributions for rare species is a vital first step in defining more robust extent of species occurrence and range overlap with threatening processes.