Original Research Article

Prioritising search effort to locate previously unknown populations of endangered marine reptiles

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ABSTRACT

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 km^2 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.

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1. Introduction

The biological diversity of our planet is facing unprecedented threats from changes in land and sea use, the direct exploitation of organisms, climate change, pollution and invasive alien species (Díaz et al., 2019). Ambitious conservation solutions to address the decline in species presence and abundance are urgently required for terrestrial, fresh water and marine environments (O'Leary et al., 2016). However, the implementation of effective conservation actions for threatened species depends significantly on: (a) knowing where species are (their distribution), (b) understanding the characteristics and availability of habitats suitable for the persistence of viable populations, and (c) quantifying the level of exposure to threatening processes within these habitats (Hoffmann et al., 2008). However, for rare (or rarely sighted) species, this information is often unavailable or lacking in adequate detail. For rare (or rarely sighted) species, spatial conservation and management advice is typically based on species' extent of occurrence (EOO) models (Syfert et al., 2014). Yet the effectiveness of these models is significantly compromised when occurrence data are limited or incomplete (Rondinini et al., 2006).

Data deficiency is a significant hindrance to conservation and management programs aimed to address ongoing global declines in reptile populations (Bland and Böhm, 2016). Some of the most severely data-deficient species are the 'true' (i.e. viviparous) sea snakes (Elapidae: Hydrophiinae; Elfes et al., 2013). The Hydrophiinae are an ecologically diverse clade of more than 60 species that represent the only truly marine reptiles (comprising ca. 90% of extant marine reptile species; Rasmussen et al., 2014). Dramatic declines in the abundance and diversity of hydrophiine sea snakes in places known for their global conservation value (e.g. New Caledonia; Goiran and Shine, 2013; Ashmore and Hibernia Reefs; Lukoschek et al., 2013; Southern Great Barrier Reef; Lukoschek et al., 2007) have resulted in the recognition of sea snakes as a conservation priority within Australian waters (DoEE, 2010a, b).

Of particular concern are sea snakes in the genus *Aipysurus*, with current evidence suggesting low reproductive rates and low levels of connectivity among populations (Burns and Heatwole, 1998). The waters off north-western Australia have the most biodiverse assemblage of *Aipysurus* species and the highest proportion of endemic sea snakes in the world, including the short-nosed sea snake (*Aipysurus apraefrontalis*), leaf-scaled sea snake (*Aipysurus foliosquama*), dusky sea snake (*Aipysurus fuscus*), brown-lined sea snake (*Aipysurus tenuis*) and the Shark Bay sea snake (*Aipysurus laevis pooleorum*) (d'Anastasi et al., 2016b; Elfes et al., 2013; Lukoschek, 2018; Sanders et al., 2015; Smith, 1974). Against a backdrop of the significant deficiency in data regarding the biology of these species, these species have experienced recent declines and extirpations (e.g. Sanders et al., 2015), as well as being recently documented in new areas (e.g. d'Anastasi et al., 2016b).

Systematic surveying of new locations is the most reliable way of filling knowledge gaps relating to the spatial distribution of species. However, achieving adequate spatiotemporal replication over large geographical areas or in difficult to survey habitats is impractical and inefficient. Correlative models linking species presence records to a set of environmental characteristics of those locations (hereafter species distribution models; SDMs; Peterson et al., 2011) are a practical and efficient tool that can be used to inform data collection strategies (Jackson and Robertson, 2011), improving estimates of species distributions (Gherghel et al., 2018) and identifying suitable habitats (Guisan et al., 2006). When applied to understanding the distributions of rare or information-deficient species, SDMs can identify geographic regions that have similar habitats to those known to be occupied, but that have no known records (Maycock et al., 2012). These areas represent high priority targets for future survey efforts and for consideration when planning for conservation management.

In this study, we sought to address severe shortfalls in knowledge relating to the distribution of sea snakes in the genus *Aipysurus* to improve outcomes for conservation. First, we constructed SDMs for five species (*Aipysurus apraefrontalis*, *A. foliosquama*, *A. fuscus*, *A. tenuis* and *A. l. pooleorum*) endemic to north-west Australia to: (a) understand key environmental covariates that are associated with known species occurrences, and (b) identify locations with similar habitats to known areas of presence to support prioritisation of search efforts for cryptic populations. Second, to contextualize our findings in current policies for spatial conservation, and assess the effectiveness of the network of Marine Protected Areas (MPAs) in north-west Australia for sea snake conservation, we assessed how much suitable habitat predicted by the model was available within current MPAs. Last, to test the ability of our models to identify new populations, we undertook field validation surveys in areas of high projected suitability that had no previous records.

1.1. Study species and current conservation status

Of the five short-range endemic focal species, two (*A. apraefrontalis* and *A. foliosquama*) are currently listed as Critically Endangered under the International Union for the Conservation of Nature (IUCN) Red List criteria (Elfes et al., 2013). Until 2001, breeding populations of these two species were only known from Ashmore and Hibernia Reefs in the Timor Sea (Cogger, 1975). However, neither species has been detected at those two reefs since 2001, and both species were presumed extirpated, coinciding with a drastic decline in the overall sea snake assemblage in the area (Guinea, 2013; Lukoschek et al., 2013; Sanders et al., 2015). Subsequently, breeding populations of both *A. apraefrontalis* and *A. foliosquama* were recently discovered in coastal Western Australia up to 800 km away from their previously known range in the Timor Sea (d'Anastasi et al., 2016b; Sanders et al., 2015). The third species, *A. fuscus*, listed by IUCN as Endangered (Elfes et al., 2013), is historically recorded only from the Ashmore and Scott Reef complexes in the Timor Sea and has declined throughout that restricted range (Lukoschek et al., 2013). The last two species, *A. tenuis* and *A. l. pooleorum*, are among the least-studied *Aipysurus* species, and are currently categorised as Data- Deficient and unassessed respectively by IUCN, due to the lack of information on their geographic ranges and population trends (Elfes et al., 2013). Although *A. l. pooleorum* forms a closely related subpopulation of the more widely

studied *A. l. laevis*, very little is known about this highly localised subspecies, currently only recognised from Shark Bay in Western Australia (d'Anastasi et al., 2016a).

2. Methods

2.1. Species records

We compiled occurrence records for the five species of interest (*Aipysurus apraefrontalis*, *A. foliosquama*, *A. fuscus*, *A. tenuis* and *A. l. pooleorum*) from four sources: (a) museum records stored in the Atlas of Living Australia (ALA; www.ala.org.au), (b) snorkel, SCUBA and boat-based day and night-time surveys conducted by the authors (collected between 2014 and 2017), (c) sightings on baited remote underwater video stations (BRUVs; collected between 1999 and 2016), and (d) research trawl-bycatch data collected between 2016 and 2017 by the Western Australian Department of Fisheries (Appendix A). Each occurrence record was quality controlled to remove or correct duplicate records, suspect or imprecise data, and verify the identification of species where voucher specimen, photographic or video records were available (i.e. State museum collections, BRUVs and fisheries data). Together, we assembled a total of 470 records for the five species prior to processing, ranging from 48 records for *A. fuscus* to 127 records for *A. l. pooleorum* (Appendix A). After the quality control process, the final occurrence dataset included 28 records of *A. apraefrontalis*, 50 records of *A. foliosquama*, 17 records of *A. fuscus*, 34 records of *A. l. pooleorum* and 11 records of *A. tenuis* (Fig. 1).

2.2. Environmental covariates

Although species within the *Aipysurus* genus are most often observed on coral reefs, individuals of the study species have been recorded in other habitat types within northwest Australia (d'Anastasi et al., 2016a, b; Sanders et al., 2015), therefore a wide array of climatic and habitat factors were initially considered as environmental covariates. As the selection of covariates have a significant influence on resulting SDMs (Fourcade et al., 2017), expert opinion and knowledge of *Aipysurus* ecology was used to make an *a priori* selection of 17 candidate variables relating to oceanic climate, geophysical and habitat conditions (Table 1). We assessed multicollinearity between pairs of environmental covariates using Pearson correlation coefficients, and removed highly correlated variables (coefficients > |0.7|; Appendix B). The final set of 14 environmental covariates included four oceanic climate variables, one oceanic productivity variable, three topographic variables, two geomorphological
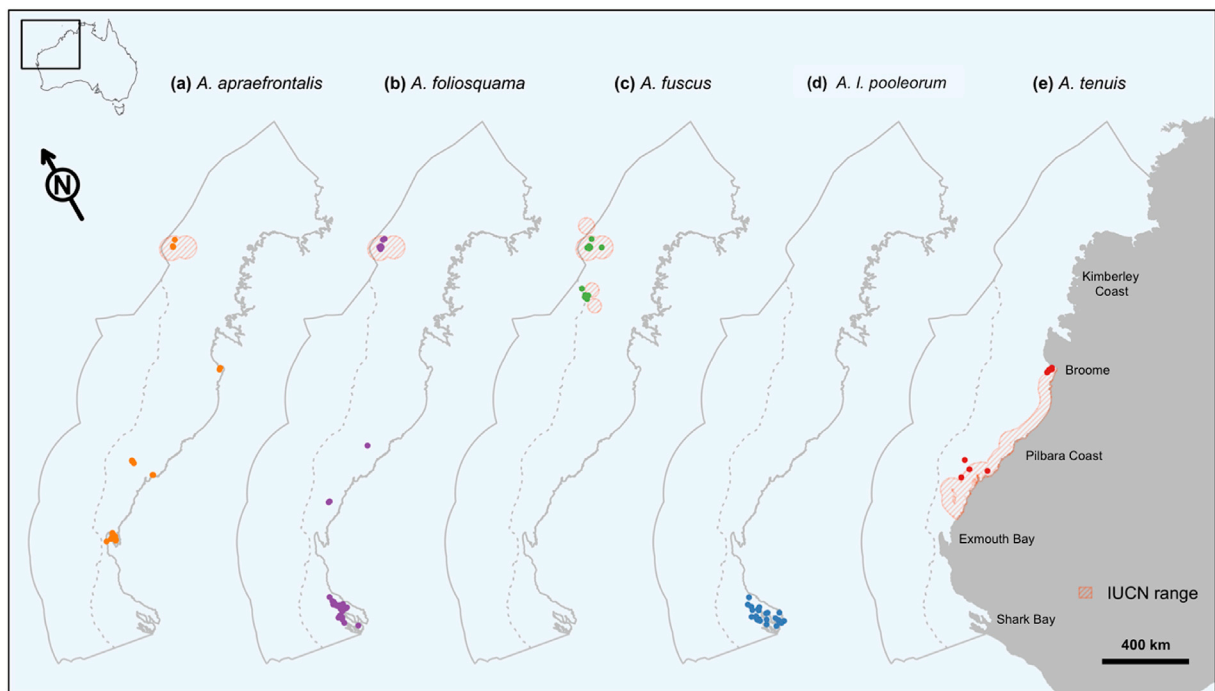
Fig. 1. Occurrence data used to construct MaxEnt models for five sea snake species endemic to north-west Australia: (a) *Aipysurus apraefrontalis*, (b) *A. foliosquama*, (c) *A. fuscus*, (d) *A. l. pooleorum* and (e) *A. tenuis*. Red shaded areas represent currently recognised IUCN Redlist species ranges. Due to the recent description of *A. l. pooleorum*, a range is currently not recognised by the IUCN redlist, and it is currently grouped with the widely ranging *A. l. laevis*. The grey polygon represents the North-West Bioregion, with the broken line indicating the 1000m contour line and the edge of the continental shelf (i.e. the model background and region of projection). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 1

Summary table of all biologically relevant environmental, biophysical and habitat parameters considered as covariates for MaxEnt models. Covariates in bold were retained in final models after removing collinear variables (see Appendices B & C).

Environmental/Physical Parameters	Variable name	Range	Mean ± SD
Oceanic climate variables: (Source: AODN)			
Mean annual sea surface temperature (C)	**sst_mean**	**14.71−25.98**	**20.93 ± 0.97**
Annual amplitude of sea surface temperature (C)	**sst_amp**	**0−3.51**	**1.98 ± 0.48**
Mean annual sea surface salinity (psu)	**sal_mean**	**34.23−35.82**	**34.89 ± 0.31**
Annual amplitude of sea surface salinity (psu)	**sal_amp**	**0.05−0.45**	**0.22 ± 0.07**
Oceanic productivity: (Source: AODN)			
Mean annual Chlorophyll *a* concentration (mg m^{-2} day^{-1})	**chlor_mean**	**0−4.07**	**0.31 ± 0.35**
Seabed topography: (Source: GA)			
Depth (m)	**bathymetry**	**3.70−120**	**38.24 ± 20.34**
Aspect of bathymetry (degrees)	**aspect**	**0−360**	**225.82 ± 112.76**
Slope of bathymetry	**slope**	**0−16.4**	**0.30 ± 0.57**
Seabed geomorphology: (Source GA)			
Proportion of mud substate(%)	mud	14.71−25.99	20.94 ± 0.97
Proportion of gravel substate(%)	**gravel**	**0−88.02**	**14.93 ± 11.85**
Proportion of sand substate(%)	**sand**	**2.76−99.79**	**61.57 ± 15.96**
Habitat variables: (Calculated)			
Relative distance alongshore (South → North)	along	0−1	0.58 ± 0.26
Proximity to the coast (km)	**DistToLand**	**0−248.60**	**66.47 ± 62.61**
Proximity to reef systems (km)	**DistToReef**	**0−246.90**	**45.98 ± 67.36**
Proximity to seagrass habitats (km)	**DistToSeagrass**	**0−351.40**	**124.20 ± 106.81**
Proximity to mangrove habitats (km)	DistToMang	2.34−295.20	172.90 ± 79.03
Proximity to fresh water source (km)	**DistToFW**	**4.61−365.60**	**213.50 ± 98.41**

Note: Data were sourced at 20 arc-second resolutions from the Australian Ocean Data Network (AODN; http://portal.aodn.org.au/), Geosciences Australia (GA; https://www.ga.gov.au/data-pubs) or calculated using habitat distribution spatial layers from Seamap Australia (https://seamapaustralia.org).

variables and four habitat variables (Table 1, Appendix C). Further model iterations to remove the least influential covariates (i.e. to avoid over-fitting) did not result in any significant improvement to the models, nor did it result in any meaningful difference in areas projected to have high habitat suitability (data not shown).

2.3. Model construction and parameterisation

We used a correlative modelling approach to identify suitable habitats for each species using maximum entropy modelling (MaxEnt [version 3.4.1]; Phillips et al., 2006). For all five models, we used default settings, with the exception that we conducted a bootstrap tuning process to optimise hyperparameter settings prior to fitting final models. Correlative modelling is subject to biases from 'ad hoc' sampling (e.g. some museum records or opportunistic sightings), and variable detectability of target species during surveys (Yackulic et al., 2013). Sampling bias in geographic space was addressed in two ways. First, we regularised occurrence records through consolidation of multiple records within each grid cell of the raster resolution used for model projection (30 arc second). Second, we created a bias grid (as per Clements et al., 2012), which was a Gaussian probability distribution function based on all known records of sea snakes from the region (genera *Aipysurus, Emydocephalus, Hydrophis* and *Parahydrophis*), with the standard deviation for the probability distribution defined by the known home-range of reef-associated sea snakes (1500–1800 m^2; Burns and Heatwole, 1998). This bias grid was used for selecting pseudoabsence points from within the model space.

The background used to generate pseudo-absences for all models was defined spatially but with the goal to provide optimal 'buffering' in covariate space beyond the covariate range occupied by occurrence records (Appendix D; Webber et al., 2011). Such an approach ensures that the models are better able to discriminate between presence and pseudoabsence points on one hand, but are not informed by covariates that are driven by differences of minor relevance to the study region (e.g. if a global background was used). Extending the background was also limited by the spatial extent of covariates under consideration, in particular the high-resolution bathymetry and seabed cover. We decided on a single background for all models that was restricted to the North-west Marine Bioregion of Australia, and within the continental shelf (i.e. depths shallower than the 1000 m bathymetry contour), reflecting the known ranges and depth preferences of the species of interest (Cogger, 1975). 10,000 background points were randomly selected at the same spatial density as the bias grid for each species model.

We restricted model projections to the same region as the training domain (background), to avoid the dangers of extrapolating correlative models (Elith and Leathwick, 2009) either outside the univariate range of covariates (Type 1 novelty; Mesgaran et al., 2014) or into novel covariate combinations (correlations) still within the univariate range of covariates (Type 2 novelty). Mapped projections and response functions were visually assessed for features that might indicate causes for concern or that may produce model outputs with questionable ecological plausibility.

Given the small sample sizes of occurrence data for most focal species, we developed models using a 'n-1 jackknife' approach as recommended by Pearson et al. (2007). This approach is a special form of k-fold cross validation, where k is equal to the number of occurrence records (Peterson et al., 2011). With small samples sizes, model tuning is essential to identify optimal model settings and prevent over fitting of models (Morales et al., 2017). We conducted model tuning by testing a range of model setting combinations specific to MaxEnt models. These include the regularization multiplier (rm); a parameter that adds constraints to the model to avoid model over fitting, and feature class selection (fc); parameters that determine the shape of environmental correlations in the model.

We conducted all data pre-processing and spatial modelling in the R statistical environment (R Development Core Team, 2019). Model tuning was undertaken using the 'ENMeval' R package (Muscarella et al., 2014), which constructed a series of MaxEnt models across a range of rm (between 0.5 and 4 in 0.5 steps) and tested all combinations of fc (i.e. linear, quadratic, hinge, product and threshold features). In total, 48 setting combinations were tested for each species, resulting in 48 x n models for each; where n is the number of occurrence records. We selected the optimal model settings using an Akaike Information Criterion adjusted for small sample sizes (AICc; Burnham and Anderson, 2002). We used the average model output across the jackknife iteration with the optimal model settings for the final chosen projection for each species.

2.4. Model evaluation

The area under the receiver operating curve (henceforth AUC; Fourcade et al., 2017), and true skill statistic (TSS) were used to assess the ability of the model to discriminate between presence and background points. An AUC score ranges between 0 and 1, where a score of 0 represents a complete mismatch between the model projection and actual occurrence data, while a score of 1 represents a perfect alignment between the projection and occurrence data. The true skill statistic (TSS) accounts for both model omission and commission errors, and ranges from -1 to $+1$, where $+1$ indicates perfect agreement and values of zero or less indicate a performance no better than random (Fourcade et al., 2017). Mean AUC and TSS scores across the jackknife iteration with optimal model settings were calculated and reported for each species.

2.5. Identifying suitable habitats

To quantify 'suitable' and 'unsuitable' habitats, thresholds are often applied to model outputs to simplify continuous outputs into binary maps, which often aids in validating and interpreting SDMs (Peterson et al., 2011). We defined the threshold level as the lowest predicted value associated with any of the occurrence records, also known as the 'lowest presence threshold' (LPT; Pearson et al., 2007). This threshold is considered a conservative estimate of a species' tolerance to each environmental variable and can provide an ecological basis to habitat suitability (Peterson et al., 2011). We created binary maps to identify suitable habitat based on this threshold value.

2.6. Spatial conservation assessment

Marine protected areas provide varying levels of human access, and consequently provides varying levels of protection for threatened marine organisms. No-take areas provide high-level protection (i.e. IUCN protected area categories IA, IB and II), while multi-use zones (i.e. IUCN categories IV $-$ VI) provide limited protection (see Day et al., 2012). We identified what proportions of suitable habitats were present within no-take zones, multi-use zones and outside MPAs for each focal species. This enabled quantification of the potential interactions with anthropogenic threats outside protected areas and how much suitable habitat is available within different levels of protection within MPAs. Estimated area values excluding the Ashmore Reef complex were also calculated to assess the remaining suitable habitats available given the recent disappearance of sea snakes from that particular reef system (Guinea, 2013; Lukoschek et al., 2013).

### 2.7. Field validation of models

We conducted field validation surveys along nearshore habitats and mid-shelf shoals of the Pilbara and Kimberley regions in Western Australia, targeting areas that our models identified as having high habitat suitability for *A. apraefrontalis, A. foliosquama* and *A. fuscus*. To increase encounter rates, we used a combination of survey methodologies including research trawls, night-time spotlight surveys and baited-trap fishing. A total of 436 h of survey effort was expended over a 24-day expedition on the R.V. Naturaliste (Department of Fisheries, Western Australia) at 139 locations.

3. Results

3.1. Model projections

All model projections matched well with the occurrence records for species on which they were trained (AUC ranging from 0.86 to 0.99; TSS ranging from 0.90 to 0.99, Fig. 2). Areas of high projected habitat suitability fit well with the currently known distribution ranges recognised by the IUCN for *A. apraefrontalis, A. foliosquama, A. fuscus* and *A. tenuis*; however, areas with high habitat suitability were also identified in regions without species occurrence records (Fig. 2). Model projections for *A. l.*
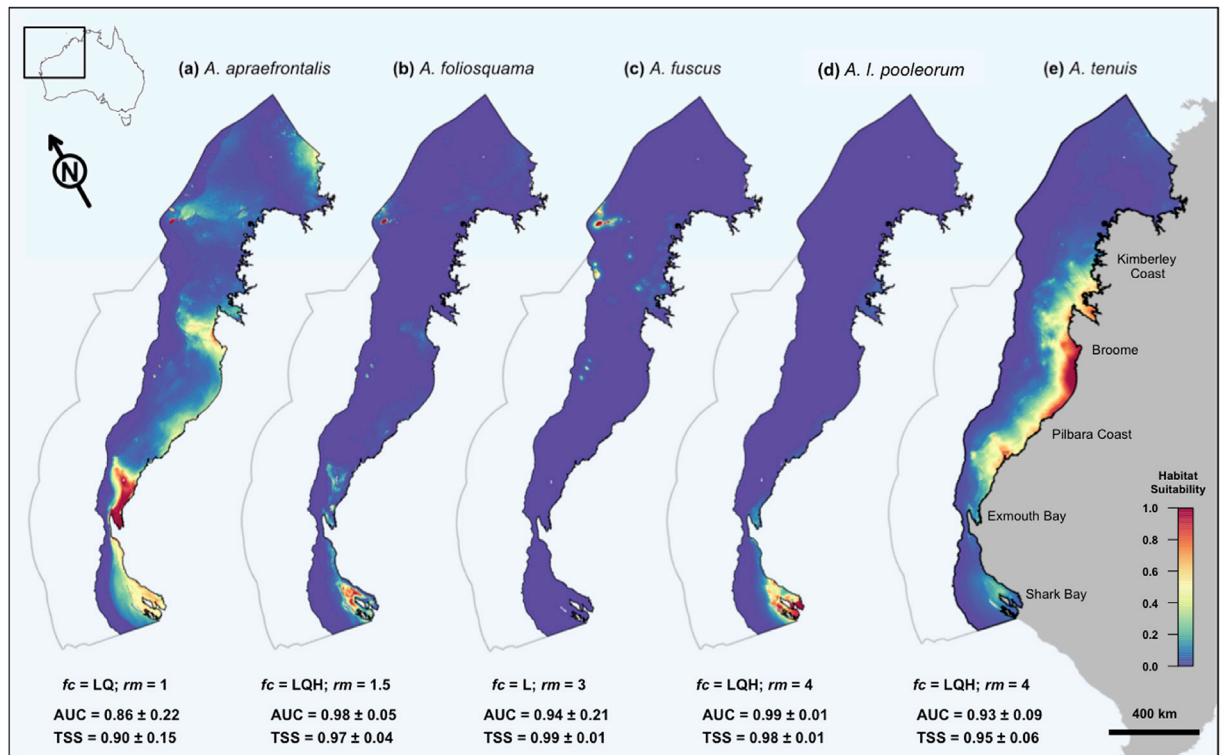
Fig. 2. MaxEnt model projections of modelled habitat suitability from jackknife iteration with optimal model settings for (a) *Aipysurus apraefrontalis*, (b) *A. foliosquama*, (c) *A. fuscus*, (d) *A. l. pooleorum* and (e) *A. tenuis*. Optimal model settings (feature classes; *fc*: L = linear, Q = quadratic, H = hinge, and regularization multiplier; *rm*) for each model presented. Mean ± SD of AUC and TSS score across optimal jackknife iterations presented. The grey polygon represents the North-West Bioregion. Scalable versions of models can be found here: https://goo.gl/emRMy5. Model outputs are provided in Appendix G.

pooleorum fit well with verified occurrence records, and provided the first distribution range for the recently described species within Shark Bay (AUC = 0.99; Fig. 2d). Model predictions also highlighted areas in coastal and mid-shelf regions north of Broome as areas suitable for *A. apraefrontalis* and *A. fuscus,* with Exmouth Gulf and regions adjacent to Barrow and Montebello Islands suitable for *A. foliosquama*. Model predictions for *A. apraefrontalis, A. foliosquama* and *A. fuscus* also highlighted regions around the Rowley Shoals with suitable habitats for their presence despite the lack of records of any sea snakes in that region historically (Fig. 2a–c).

3.2. Influential environmental covariates

Models were assessed to identify key environmental covariates that influence species-specific habitat suitability. Proximity to fresh water sources, seagrass and reef habitats contributed significantly to all five species models (Fig. 3), with response curves identifying environmental parameters in close proximity to seagrass and reef habitats as important for most species (Fig. 4). In addition, sea surface temperature was an influential climatic variable in determining suitable habitats for *A. l. pooleorum* and *A. foliosquama*; however, played a less significant role in determining suitable habitats for *A. apraefrontalis* and *A. fuscus* (Fig. 3). Similarly, the percent of gravel in seabed cover was a significant correlate for identifying suitable habitat for *A. fuscus* (Figs. 3 and 4); however, was not important for any other species model.

3.3. Suitable habitats and level of protection afforded by current spatial management

Models thresholded using the LPT identified regions within Ashmore Reef Marine Park as suitable habitat for *A. apraefrontalis, A. foliosquama* and *A. fuscus.* These are based on occurrence data in these regions prior to the declines recorded between 2010 and 2012. The thresholded models identified new distributions for *A. apraefrontalis* extending from Exmouth Gulf and around the Murion Islands to the Montebellow Islands Marine Park (Fig. 5a, Appendix E1, Table 2). Similarly, model projections for *A. foliosquama* highlighted additional coastal regions within Shark Bay and around Barrow Island as suitable habitat for this species (Fig. 5b, Appendix E2, Table 2). Models extended the distribution of *A. fuscus* to reef systems within the Northwest shoals, and highlighted the patchy distribution of this species on mid-shelf and outer reef systems (Fig. 5c,
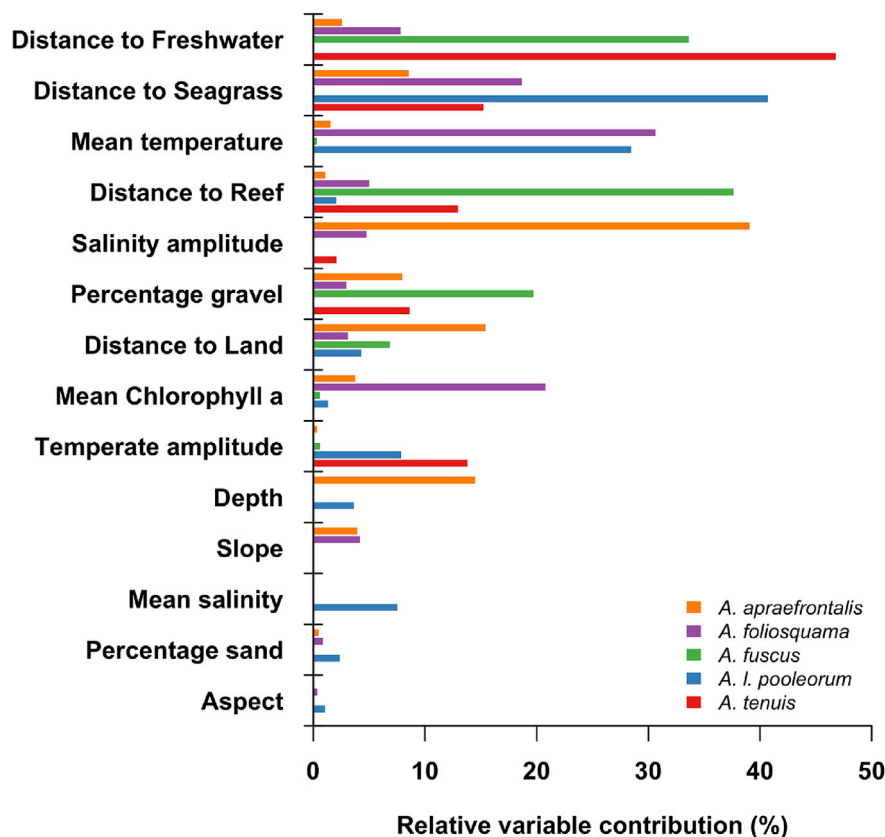
Fig. 3. Summary of the relative variable contribution for each environmental variable used in optimal MaxEnt model for each species. Variable contribution was calculated across each jackknife iteration of the tuned model, identifying the gain in model performance in the presence of absence of each environmental variable. Variable on the y-axis are ranked in decreasing order based on average overall variable influence across all species models.

Appendix E3, Table 2). Models defined the new range for *A. l. pooleorum* within Shark Bay (Fig. 5d, Appendix E4, Table 2), and highlighted the Pilbara coast as suitable habitat for *A. tenuis* (Fig. 5e, Appendix E5, Table 2).

Models highlighted that only a limited proportion of suitable habitats for all the five species overlapped with current spatial management zones within the West coast of Australia (Fig. 6, Appendix E, Table 2). A large proportion of protections for *A. apraefrontalis, A. foliosquama* and *A. fuscus* were within suitable habitats predicted within the Ashmore Reef Marine Park. However, as these species have not been recorded in this region for the last decade, it is likely that this region provides limited protection for this species. Most influentially, if these regions are discounted as areas that provide protection for *A. fuscus*, the total amount of suitable habitat protected by MPAs significantly reduces from 618.63 km^2 to 11.44 km^2 (Fig. 6, Table 2).

3.4. Field validation surveys

Field-validation surveys resulted in the record of 81 sea snakes from 10 species (including *A. l. laevis, Emydocephalus annulatus, Hydrophis peronii* and *H. ocellatus*; Fig. 7, Appendix F). Additionally, a new record of *A. fuscus* was made from a location where this species has not previously been know from (Fig. 7). The new occurrence record for this species was at Heywood Shoal, a location outside any MPA; however, identified as suitable for this species with the model predicting a 0.63 likelihood of presence (Fig. 7). Genetic material collected from the surveyed individual was used to verify species identification (Appendix F).

4. Discussion

Two key challenges in conserving rare species are delineating suitable habitat types for species, and delimiting the location of suitable habitat patches in an area of management interest (Marcer et al., 2013). In our study, SDMs provided a strong predictive framework for locating potential additional populations, providing guidance for future surveys (Guisan et al., 2006), and prioritising conservation and management practices (Oh et al., 2017; Syfert et al., 2014).
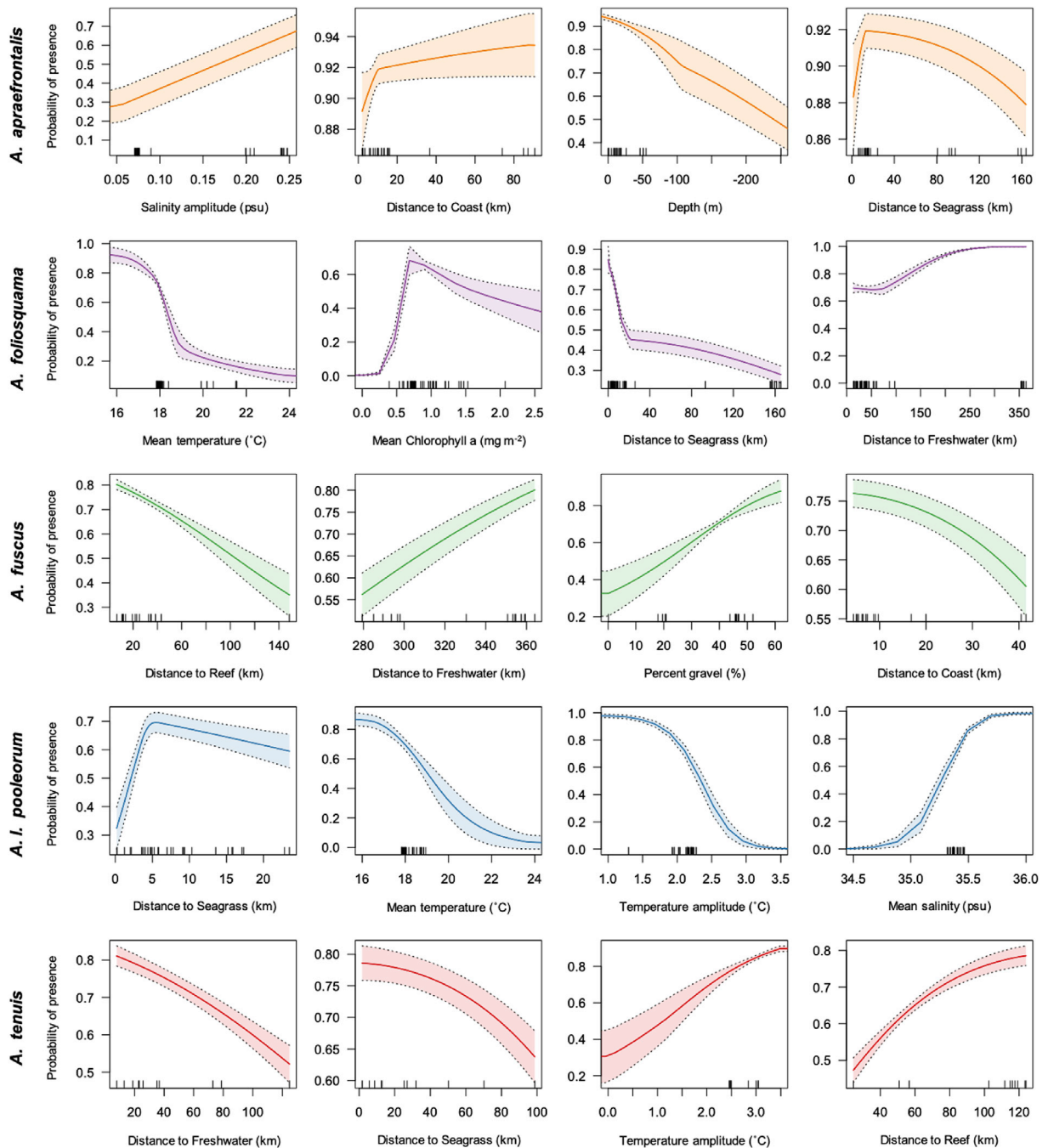
Fig. 4. Response curves for the top four influential environmental covariates as determined by relative variable contribution to optimal model (see Fig. 3). Environmental covariates ranked from left to right with each row representing each species; (row 1, orange) *Aipysurus apraefrontalis*, (row 2, purple) *A. foliosquama*, (row 3, green) *A. fuscus*, (row 4, blue) *A. l. pooleorum* and (row 5, red) *A. tenuis*. Mean response curve averaged from jackknife iteration of optimal model setting represented by solid line, with standard deviation band presented in each plot. Rug plots along the x-axis represent environmental variable at each occurrence record. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

4.1. Environmental and habitat associations

The use of SDMs proved valuable for identifying additional areas that share similarities to those currently occupied, and for elucidating the species-environment relationships that are correlated with spatial patterns in sea snake occurrence along the north-west coast of Australia. At the landscape level, our models identified that critical habitats required for persistence of sea snake populations were consistently associated with seagrass and coral reef habitats, which is corroborated by regional
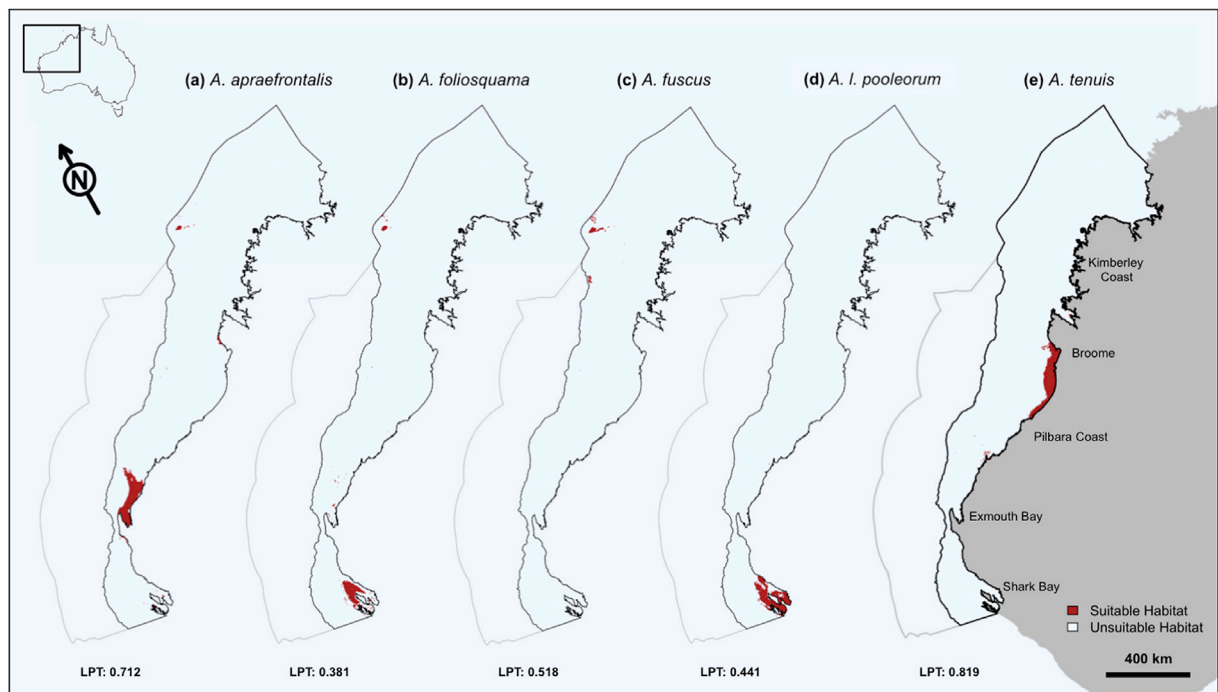
Fig. 5. Habitat suitability maps for (a) *Aipysurus apraefrontalis*, (b) *A. foliosquama*, (c) *A. fuscus*, (d) *A. l. pooleorum* and (e) *A. tenuis* within north-west Australia. Suitable habitats were determined by applying the lowest presence threshold approach (LPT) to model projections. The grey polygon represents the North-West Bioregion, with the model background and projection domain represented as the black polygon.
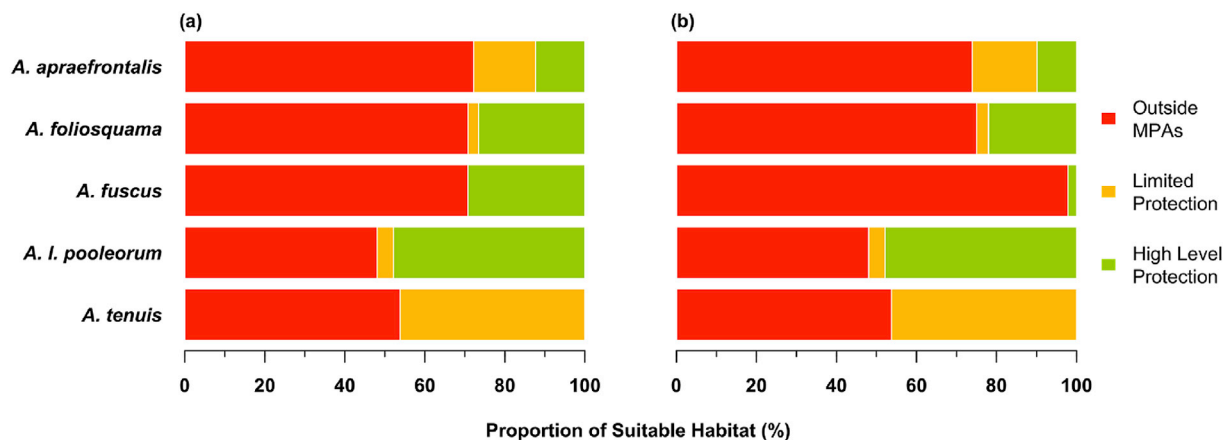
Table 2
Summary of key locations and area of suitable habitat within and outside spatial management zones estimated from model outputs. Spatial management zones with IUCN protected areas categories of IA, IB and II were defined as high-level protection areas (no-take zones), and categories IV-VI were defined as providing limited protection (multi-use zones).

| Species	Key locations of suitable habitat	Total suitable habitat (km²)	Area of suitable habitat (km²)		
			No-take zones	Multi-use zones	Outside MPAs
A. apraefrontalis	Ashmore Reef[a], Exmouth Gulf, Murion and Montebello Islands	14,365.95 [13,763.27]	1771.04 [1356.31]	2226.26 [2226.26]	10,368.65 [10,180.70]
A. foliosquama	Ashmore Reef[a], Shark Bay, Exmouth Gulf, Barrow and Montebello Islands	7456.79 [6739.43]	1980.08 [1481.16]	199.04 [199.04]	5277.67 [5059.22]
A. fuscus	Ashmore Reef[a], Scott Reef, mid-shelf Shoals	2114.82 [540.49]	618.63 [11.44]	—	1496.19 [529.05]
A. l. pooleorum	Shark Bay	11,284.15	5399.97	460.20	5423.97
A. tenuis	Pilbara coastline between Broome and Port Headland	16,606.59	—	7676.60	8929.99

[a] Estimated areas of total suitable habitats include those predicted around the Ashmore Reef complex. Severe declines in sea snake abundance has been recorded at this location in recent years (Lukoschek et al., 2013; Guinea, 2013). Estimated area values excluding this region have been provided in parentheses for species that were previously found at Ashmore Reef.

studies (e.g. d'Anastasi et al., 2016a). Additionally, water temperature and salinity within these habitats strongly influenced modelled habitat suitability. High modelled suitability was associated with locations with mean annual sea surface temperatures between $18° - 22\,°C$ and seasonally stable salinity (Brischoux et al., 2012; Heatwole et al., 2012). Another key aspect of species-environment relationships identified by models was the close association of some species with sources of fresh water. Access to fresh water has been a significant factor in distributions and habitat use in other regional populations of sea snakes (Liu et al., 2012) and is required to maintain osmotic balance (Lillywhite et al., 2015).

Although our models identified key landscape-level environmental correlates to sea snake occurrence along the north-west coast of Australia, insights on regional, fine-scale habitat associations are beyond the scope of the modelling techniques applied. It is likely that fine-scale differences in habitats and biotic interactions influence the distributions of sea snakes, and patterns of their abundance. For example, previous surveys within Shark Bay have identified that subtle differences in structural complexity between seagrass habitats, coral reefs and stromatolite reefs drive the abundance of *A. l.*

Fig. 6. Proportion of suitable habitat within spatial management zones that provide high-level protection, limited protection and no protection (i.e. outside marine protected areas) along the coast of northwest Australia a) including and b) excluding the Ashmore Reef complex where severe declines in sea snake abundance has been recorded in recent years. Spatial management zones with IUCN protected areas categories of IA, IB and II were defined as high-level protection areas (no-take zones), and categories IV–VI were defined as providing limited protection (multi-use zones).
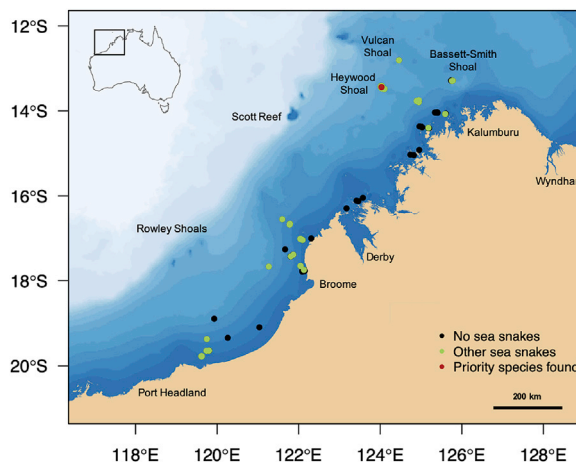
Fig. 7. Survey locations for field validation focused on areas of high habitat suitability identified by the modelling for *A. apraefrontalis, A. foliosquama* and *A. fuscus*. Sites where no sea snakes were recorded are marked in black, sites where other species of sea snakes were recorded (i.e. *Aipysurus* spp., *Hydrophis* spp., *Emydocephalus* sp.) are in green, and the site at Heywood Shoal where an *A. fuscus* was recorded is marked in red. The *A. fuscus* record is the first outside of its currently recognised range of Scott and Ashmore Reefs. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

pooleorum and *A. foliosquama* (d'Anastasi et al., 2016a). Similarly, predator avoidance behaviours and tidally mediated access to resources greatly influenced the assemblage and abundance of two species of sea snake (Hydrophis elegans, Kerford et al., 2008; Hydrophis major, Wirsing and Heithaus, 2009) that occupy seagrass habitats within the same bay. Additionally, a significant marine heatwave in the region during 2010–2011 caused a severe decline in seagrass habitats, by up to 40% within Shark Bay (Thomson et al., 2015), and widespread coral mortality within the wider region (Moore et al., 2012), which was associated with a significant decline in the sea snake assemblage in Shark Bay (Nowicki et al., 2019). Our models provide a first step to generating an understanding of environmental drivers and landscape-level habitat associations of sea snake distribution. Ultimately, our models are merely putting forward hypotheses on putative environmental drivers and habitat associations. A process-based investigation of these ideas would be needed to test their validity and thereby understand the capacity of sea snakes for long-term persistence and recovery in the face of global environmental change.

4.2. Model limitations

As our aim was to model the distribution of rarely encountered and short-ranged species, the number of records on which the models were built is low. It is important to realise that models developed using small sample sizes should be cautiously interpreted, and in no way do they reflect the full potential distribution of the species in question (Gherghel et al., 2018;

Marcer et al., 2013; Peterson et al., 2011). Limitations in available occurrence datasets and environmental covariate coverage means that open-ended response curves were unavoidable and as such, require careful interpretation. Similarly, small sample sizes within and across seasons limited the assessment of seasonal influences on species distribution. We were deliberately conservative by not using the models to extrapolate into non-analogous climates, and would urge caution for interpreting our findings in areas outside the study region. Even so, our modelling produced ecologically plausible results using an array of environmental parameters that are known to be meaningful to the ecology of sea snakes.

Additional factors not considered in the modelling (i.e. predator-prey interactions, inter- and intra-specific competition, evolutionary history, changes in habitat cover or resource availability) mean that species rarely occupy all areas with suitable conditions, and moreover, may be present in habitats identified here as unsuitable. The associations to environmental and habitat variables highlighted in the present study are likely mediated by ecological traits of the species (i.e. diet, predators, etc.). The likely incongruence between modelled projections and actual ranges does not necessarily mean that the models are wrong, but simply that they are incomplete (Pearson et al., 2007). An example of this is the identification of the Rowley Shoals as suitable habitats for *A. praefrontalis, A. foliosquama* and *A. fuscus* (Fig. 5a–c). The models identified these areas as ideal habitats for these species; however, historic biodiversity surveys (e.g. Berry, 1986; Bryce, 2009) and ongoing monitoring programs (i.e. Reef Life Survey, Australian Institute of Marine Science Long Term Monitoring) have not recorded sea snakes at these localities. It is likely that other factors not considered in this modelling (e.g. oceanographic processes, predator or prey density) may prevent sea snakes from establishing populations in these locations (Berry, 1986).

4.3. Protection from current spatial management

MPAs are considered an effective tool for ecosystem-based marine conservation and management, especially for restricted range species (McCook et al., 2010). Suitability projections from SDMs can provide an effective means by which to assess current spatial management practices and identify new regions that may require prioritised survey efforts or protection to maintain populations of rare or threatened species (Abecasis et al., 2014; Oh et al., 2017). Current MPA networks encompass only a small proportion of suitable habitats for the three species of conservation priority examined in the present study, with more than 50% of suitable habitats for *A. praefrontalis, A. foliosquama,* and *A. fuscus* occurring outside of MPAs (Fig. 6a). The majority of suitable habitats with high-level protection for these three species are confined within the Ashmore Reef Marine Park, a location where these species have not been sighted in over a decade (Guinea, 2013). Exclusion of the Ashmore Reef Marine Park drastically reduces this protection, which is especially significant for *A. fuscus* (reduced from 29.3 to 2.1% of suitable habitat within MPAs; Fig. 6). Nevertheless, HSMs identified additional suitable habitats for the other species within Exmouth Gulf and Shark Bay, which have some level of protection within no-take and multi-use zones respectively (Appendices. E1-3).

4.4. Prioritising future surveys

The current distribution patterns recognised by the IUCN Red List and local management agencies are based on incomplete occurrence records and are restricted to the Ashmore Reef complex for *A. praefrontalis* and *A. foliosquama,* where they have not been detected since 2001 (Guinea, 2013); and the Ashmore and Scott Reef Complexes for *A. fuscus* (Fig. 1). Our model outputs predicted additional localities for *A. praefrontalis* and *A. fuscus* in coastal and mid-shelf regions north of Broome, and for *A. foliosquama,* regions within Exmouth Gulf and around Barrow and the Montebello Islands, approximately >800 km away from the range used in currently available conservation assessments. Field validation of these models have already yielded an additional locality for *A. fuscus* in the mid-shelf Shoals. In the case of *A. tenuis*, there is little information about geographic range; but model results identified potential key habitats along the Pilbara coast, Roebuck Bay and coastal habitats north of Broome, which represent candidate locations for further field validation efforts.

Future survey work to inform conservation management should build on our model outputs and target surveys in coastal and mid-shelf sites identified north of Broome, and around Barrow and the Montebello Islands, to clarify sea snake assemblages and abundances in these areas. Additionally, long-term monitoring and detailed regional assessments of key threatening processes, such as trawl and trap fishing, coastal development, offshore mining, needs to be conducted within known habitats and newly identified locations, to quantify the risk and impacts caused by these activities to regional populations of sea snakes.

4.5. Management and conservation implications

Typically, conservation and management planning are based around extent of occurrence (EOO) maps created using simplistic minimum convex polygon or buffering techniques (Syfert et al., 2014). In a marine setting where specific bathymetry or structure is relevant, these maps cover large tracts of open ocean where the likelihood of species presence is low for species such as sea snakes (Gherghel et al., 2018; Marcer et al., 2013). This approach can therefore incorrectly suggest a species is wide-ranging and does not capture the reality of the often patchy and fragmented distribution of sea snakes. Here the use of SDMs to understand EOO has highlighted the fragmented nature of suitable habitats and likely distribution of priority species, and consequently the varying exposure to threatening processes across their regional distributions (Appendix F). Considering the restricted movements (Lukoschek et al., 2007) and limited genetic connectivity (Lukoschek,

2018; Nitschke et al., 2018; Sanders et al., 2015) between fragmented populations of sea snakes in the *Aipysurus* genus, identifying and managing threatening processes at appropriate scales is a critical step in conserving species.

Further survey effort and ecological insight is required to better understand the true abundance and diversity of assemblages of sea snakes in newly identified locations, across seasons, and quantify their risk from threatening processes (i.e. anthropogenic activities, climate change, extreme weather events) across their full distribution (Udyawer et al., 2018). The present study is a key starting point that identifies potential new locations along the coast of northwest Australia that should be prioritised for further work. These findings refine and update the known distribution patterns of species of conservation concern and should be used as the basis for additional sampling in conjunction with reassessment of their status and risk of extinction. Reassessments should take into consideration the effectiveness of current spatial management practices, and recognise the fragmented nature of distributions among short-range species that have limited movement and genetic connectivity between sub-populations. The high degree of habitat specialisation of these species also needs to be considered in the context of potential impacts from extractive activities (i.e. mining and exploration, trawl and trap fishing, coastal development), and exposure to extreme weather events (i.e. cyclones, marine heatwaves). Addressing conservation and management policy at regional and indeed sub-population levels is recommended to ensure overall species persistence in the face of increased global environmental change in the region.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2020.e01013.

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