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Long-distance movements of free-ranging sea snakes (*Hydrophis*, Elapidae)

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Abstract :

The capacity for individuals to move long distances can profoundly influence how species are affected by localised threatening processes. Previous studies on the movement patterns of sea snakes have highlighted the highly site-attached nature of some species, but constraints on collecting data at large spatial and temporal scales have underestimated the snakes' capacities for dispersal. Here we used acoustic tags implanted in four species of free-ranging sea snakes to provide the first records of long-distance movements by these large marine predators. Although most movements recorded were within 2 km of the snake's release site, some individuals moved farther than has previously been recorded for any sea snakes. We recorded displacements from capture-release sites of up to 13 km in Hydrophis coggeri and 15 km for Hydrophis major. Thus, although some sea snakes are highly philopatric to small areas, others travel over larger areas and hence may be less vulnerable to localised threats.

Résumé

La capacité des individus à se déplacer sur de longues distances peut profondément influencer la façon dont les espèces sont affectées par des processus menaçants localisés. Des études antérieures sur les schémas de déplacement des serpents de mer ont mis en évidence la nature fortement attachée au site de certaines espèces, mais les contraintes de collecte de données à grande échelle spatiale et temporelle ont sous-estimé les capacités de dispersion des serpents. Ici, nous avons utilisé des étiquettes acoustiques implantées dans quatre espèces de serpents de mer en liberté pour fournir les premiers enregistrements des déplacements à longue distance de ces grands prédateurs marins. Bien que la plupart des mouvements enregistrés se soient déroulés à moins de 2 km du site de libération du serpent, certains individus se sont déplacés plus loin que ce qui avait été enregistré auparavant pour tous les serpents de mer. Nous avons enregistré des déplacements depuis les sites de capture-relâchement jusqu'à 13 km pour Hydrophis coggeri et 15 km pour Hydrophis major. Ainsi, bien que certains serpents de mer soient très philopatriques dans de petites zones, d'autres se déplacent sur de plus grandes zones et peuvent donc être moins vulnérables aux menaces localisées.

Keywords : Serpentes, Elapidae, Hydrophiinae, Home range, Spatial ecology

Introduction

Despite the diversity and abundance of sea snakes in the tropical Indo-Pacific, fundamental ecological knowledge on these animals remains scarce (Udyawer et al. 2018a). Ecological data relevant to the management of sea snakes have been obtained primarily through fishing bycatch (e.g., Voris and Voris 1983; Fry et al. 2001), a method with limitations and biases associated with destructive sampling. Detailed ecological research has been conducted on only a few species, and for logistical reasons these have been mostly philopatric taxa studied in shallow-water habitats (e.g., Shetty and Shine 2002; Lukoschek and Shine 2012; Bonnet et al. 2015). Genetic studies reveal considerable interspecific diversity in population structure among sea snakes, suggesting that individuals of some species range widely (e.g., Nitschke et al. 2018; Garcia et al 2022) whereas others exhibit metapopulation structure and have restricted ranges around specific reef sites (e.g., Lukoschek and Shine 2012).

Variability in space use and the ability to disperse have profound consequences for the fate of populations, because species capable of travelling long distances may display greater population connectivity and reverse local extirpations. However, due to the paucity of data on movements of sea snakes, little is known about the dispersal capacities of these animals, with most information derived from species in confined embayments (Udyawer et al. 2015) or from species that are highly site-attached or philopatric (Shetty & Shine 2002). The collection of movement data from free-swimming sea snakes is challenging, with limited mark-recapture or telemetry studies defining movement capacities for this group. Longterm mark-recapture studies on Turtle-headed sea snakes (*Emydocephalus annulatus*) in inshore coral reefs of New Caledonia reported that individuals were consistently recaptured <10 – 20 m from their capture locations in the previous year, suggesting a highly site-attached nature (Shine et al. 2020). In contrast, telemetry of larger Spine-bellied sea snakes (*Hydrophis curtus*) inhabiting soft sediment coastal embayments of Australia showed that individuals regularly disperse to distances of 5 – 7 km (Udyawer et al. 2015).

Here we surveyed the movement of four species of sea snakes in southern New Caledonia using an array of acoustic receivers deployed across coastal embayments, mid-shelf patch reefs and offshore islands. This study used acoustic telemetry to explore the spatial ecology of free-swimming sea snakes within and beyond nearshore habitats, quantify species-specific dispersal capacities and obtain the first direct evidence of long-range movements in telemetered animals.

Methods

Acoustic telemetry

In southern New Caledonia, we surgically implanted acoustic transmitters (V9P-2H, Innovasea Ltd.; 3 g) into the peritoneal cavities of sea snakes across four species (Fig 1; *Hydrophis major*, *H. coggeri*, *Aipysurus laevis* and *A. duboisii*) that had been hand-captured in shallow bays beside the city of Noumea (Anse Vata and Baie des Citrons: see Udyawer et al. 2021 for details). The snakes were released at their points of capture within a day of surgery, and 18 underwater listening stations in the area provided information on subsequent movements (total of 51,076 location records; Udyawer et al. 2021). Our original listening stations were within the bays where the snakes were released (Fig. 2b), and were not designed to provide data on long-distance movements. Fortuitously, some of our snakes were also detected at listening stations deployed at a wider spatial scale (N = 64,608 records for 10 sea snakes at 41 stations; Fig. 2c), for research on sharks (Bonnin et al. 2019, 2021, 2022), providing an array of 62 receivers deployed over a 20 x 20 km area.

Study species

Among the four tagged species, two are large-bodied species that visit the shallow bays only intermittently (Goiran and Shine 2019). The heavy-bodied Greater Sea Snake (*Hydrophis* *major*) grows to around 1.5 m in length, and specimens in the Noumea area feed exclusively on catfish (*Plotosus lineatus*) that occur in coral-reef habitats (Shine et al. 2019; see Fig. 1). In contrast, the Slender-necked Sea Snake (*Hydrophis coggeri:* to 1.2 m) has an elongate forebody and small head, and feeds primarily on small eels in seagrass and sandy-bottom substrates (Sanders et al. 2013; Sherratt et al. 2018; see Fig. 1). A third species, the Reef Shallows Sea Snake (*Aipysurus duboisii*, to 1.1 m) inhabits shallow-water habitats year-round and eats a wide range of small fish species (Ineich and Laboute 2002; see Fig. 1). The fourth species, the Olive Sea Snake (*Aipysurus laevis,* 1.4 m) is a generalist taxon that feeds on a range of fish and benthic invertebrates, has been observed infrequently within the shallow bay and is known to move between these habitats and deeper waters across southern New Caledonia.

Analysis of movements

Detection data from both the original coastal array and wide-ranging array were combined to assess broadscale movements and activity spaces of individuals for which sufficient data were available. Individual dispersal metrics were calculated using the 'VTrack' R package (Udyawer et al. 2018b), based on distances between the release location of the animal and each subsequent detection. The distances between release location and each detection were then summarised to understand the average distance from release location recorded of each individual, and the maximum distance from release location. The 'VTrack' package was also used to examine activity space for each individual using a Utilisation Distribution (UD) calculated using a Brownian Bridge movement model (Horne et al. 2007). We estimated the area of core activity space (50% UD) and extent (95% UD). Data for individuals showing large dispersal distances were identified, mapped and examined further.

Results

In total, 33 individuals across four species were tagged (22 *Hydrophis major*, 3 *H. coggeri*, 2 *Aipysurus laevis* and 6 *A. duboisii*). Sufficient detections were recorded from *Hydrophis major, H. coggeri* and *Aipysurus duboisii* to conduct movement and space use analysis. Only two individuals of *Aipysurus laevis* were tagged, and these provided very little information, with only three detections from one of the individuals recorded (all on the coastal array). As insufficient detections were obtained for this species to inform long-distance movements, we have omitted this species from further analysis. Overall, no snakes were detected on listening stations north of Ile Freycinet and near Dumbea, with some individuals recorded on the offshore islands (Ilot Larégnère and Ilot Signal) (Fig. 3). The maximum distances between release points and recorded locations are shown in Table 1, based on the minimum distance that a snake would need to swim to move between those sites. Detection data from the three other individuals highlighted species-specific differences in the use of coastal habitats and long-distance movement capacities.

Aipysurus duboisii – Detection data from this species highlighted primarily coastal movements, restricted primarily to within Baie des Citrons where most individuals were tagged. One of the tagged *Aipysurus duboisii* also moved further than our initial coastal array had documented, moving to the mouth of Baie de Sainte-Marie, and across to Ile aux Canards (Fig. 3a). The maximum displacement recorded for this species was 3.4 km (Anse Vata to Baie de Sainte-Marie; Table 1), with most individuals remaining within 1 km of their release sites (Fig. 4).

Hydrophis coggeri – Of the three individuals of this species that were monitored, two were primarily detected within 2 km of their release site within Baie des Citrons (Fig 3b, Fig 4). The third individual (Zahra; Fig 4) displayed longer movements, regularly travelling between Baie de Sainte-Marie in the west to the Port of Noumea in the east. The maximum displacement for this individual was recorded at 12.6 km (Baie des Citrons to Ilot Larégnère), which is also reflected in the expanded core and extent of activity space for this species (Table 1). The limited detections on offshore islands recorded from this species suggest that the individual was moving from coastal habitats into offshore habitats outside the range of the wider acoustic array (Fig 5).

Hydrophis major – Detection data from this species highlighted frequent long-distance movements outside the coastal habitats where they were released (Fig 3c). Like the widely dispersing individual of *Hydrophis coggeri*, individuals of this species were frequently detected on receivers near offshore islands and across to the mouth of Baie de Sainte-Marie in the east. As with the other species, most movements recorded were within 2 km of the release sites (Fig 4), but four individuals (Magali, Oscar, Salyne and Riley) regularly dispersed over longer distances. The maximum displacement for this species was 15.3 km (Baie des Citrons to Ilot Signal), reflecting larger activity spaces for this species (Table 1). Further examination of the larger dispersal events highlighted that one individual (Riley) undertook regular movements to and from the offshore Ilot Signal and across to Ilot Uere in the west (Fig 5). The detection patterns show that individuals conducted repeated movements offshore before returning to shallow waters. All but one individual of *Hydrophis major* that displayed these largescale dispersals were adult females, with the long-distance movements recorded between July and September during the monitoring period.

Discussion

Our data provide the first direct evidence of regular long-distance movements by large hydrophiine sea snakes. Most terrestrial snakes travel over far smaller distances (see review by Macartney et al. 1988), but with long migrations from overwintering sites to feeding habitats in a few species such as Red-sided Gartersnakes (*Thamnophis sirtalis parietalis*) in Manitoba, Canada (to 18 km: Gregory and Stewart 1975). The marine environment may facilitate long-distance travel by allowing pelagic snake species to utilise ocean currents (e.g., Graham et al. 1987; Cook et al. 2016), and coastal species to exploit tidal flow (e.g., Udyawer et al. 2020, Goiran et al. 2020). Also, swimming is less energetically expensive than terrestrial crawling (Heatwole 1999; Lillywhite 2014).

Mark-recapture studies on amphibious Sea Kraits (Laticaudinae) in Fiji have reported movement (homing after translocation) between two islands 5.3 km apart (for *Laticauda colubrina*: Shetty and Shine 2002). In the New Caledonian Lagoon, sea kraits not only move occasionally among islands, but adult female Sea Kraits from outlying islands migrate tens of kilometres back to the main island to lay their eggs (for *L. saintgironsi*: Bonnet et al. 2015). The patterns in long-distance movements highlighted in this study showed increased dispersal distances of adult females during the breeding season. This contrasts with patterns of occurrence and activity observed in other sea snake species (*Aipysurus laevis*, Lynch et al. 2023). The limited numbers of long-distance movements recorded here, with the fragmented coverage of the wider acoustic array, makes the interpretation of the seasonal pattern difficult. Additional telemetry data on these species need to be collected to identify if this pattern of increased female movements still holds with a larger sample size, and broader spatial and temporal coverage.

The spatial scale of movements by individual snakes bears on important management issues, because sea snake populations have undergone dramatic and enigmatic declines in many areas (e.g., Goiran and Shine 2013; Somaweera et al. 2021). A capacity for long-distance movements by individual snakes suggests that any locally-acting processes (such as habitat destruction via development or coral bleaching) may have impacts over a wide scale; and that local extirpation of populations may be reversed by colonisation over ecologically relevant time periods (Lukoschek at al. 2007). On the other hand, long-distance movements and the consequent expanded activity spaces can also increase the risk of species interacting with threatening processes (e.g., fisheries, boat strike; Hays et al. 2016). Specifically with sea snakes, movements outside protected shallow habitats can increase exposure to trawling and net-fishing that can impact population persistence (Udyawer et al. 2016). In contrast, extreme philopatry (as in some sea snakes: Lukoschek and Shine 2012) renders impacts more local, and recolonisation less likely. Historic declines in sea snake populations have largely been recorded in remote locations, and in species for which dispersal capacities are presumed to be limited (Somaweera et al. 2021).

The paucity in our understanding of dispersal capacities of sea snakes has primarily been due to methodological constraints in the ability to monitor movements across seasonal timescales, and across wider spatial extents (Udyawer et al. 2018a). The growing use of acoustic telemetry – and collaboration between researchers on different types of marine organisms – provides an exciting opportunity to expand the taxonomic range, spatial scale and duration of monitoring, in order to clarify the extent and timing of movement of sea snakes in tropical oceans.

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Data availability Data will be deposited in Dryad on acceptance.

Declarations

Conflict of interest All authors declare no conflict of interest.

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Table 1 Sea snakes studied with acoustic tags in the Noumea region of New Caledonia, showing sexes, body sizes, date of release and duration of monitoring (battery life of transmitters), and maximum displacement distances, core and extent of activity spaces documented. F = female; M = male; SVL = snout-vent length; BdC – Baie des Citrons; AV = Anse Vata

Species	Name	Sex	SVL (mm)	Mass (g)	Location of release	Date of release	Date of final location	Number of days detected	Duration of monitoring (days)	Average distance from release point (km)	Farthest distance from release point (km)	Core activity space area [50% UD] (km^2)	Extent of activity space area [95% UD] (km^2)
Aipysurus duboisii	AD1	F	850	240	BdC south	10 Jan 2017	31 Dec 2017	162	350	0.279	0.655	0.005	0.0625
	AD3	M	880	320	BdC north	10 Jan 2017	30 Dec 2017	218	350	0.287	0.655	0.019	0.099
	AD2	F	805	350	BdC south	10 Jan 2017	3 Jan 2018	42	350	0.192	0.192	-	-
	AD4	F	900	580	AV north	20 Jan 2017	25 Jan 2017	6	350	0.527	0.638	0.007	0.169
	Suzanne	F	780	264	BdC north	24 Jan 2020	-	0	509	-	-	-	-
	Valentine	F	940	518	AV north	27 Feb 2020	10 May 2020	16	374	1.439	3.422	3.689	17.718
Aipysurus laevis	AL1	F	870	710	AV north	10 Jan 2017	22 Feb 2017	3	350	0.728	1.002	-	-
	AL2	F	870	990	BdC south	10 Jan 2017	-	0	350	-	-	-	-
Hydrophis coggeri	Zahra	F	1090	319	BdC north	27 Feb 2020	22 Sep 2020	129	374	2.536	12.607	2.574	52.595
	Sidonie	F	1410	753	BdC south	23 Mar 2020	21 Apr 2020	6	374	0.741	2.101	0.098	0.504
	Aglaé	F	910	153	BdC middle	23 Mar 2020	23 Mar 2020	1	374	-	-	-	-
Hydrophis major	Hal	M	110	780	BdC north	10 Jan 2017	-	0	350	-	-	-	-
	Hedonia	F	121	1250	BdC north	10 Jan 2017	-	0	350	-	-	-	-
	Henriette	F	106	980	BdC north	20 Jan 2017	25 Jul 2017	12	350	0.728	1.718	0.116	0.528
	Enzo	M	63	130	BdC north	6 Oct 2017	26 Jan 2018	39	349	0.577	0.881	0.058	0.452
	Axel	M	123	950	BdC north	6 Oct 2017	1 Sep 2018	107	349	0.670	1.695	0.138	1.639
	Matthew	M	109	560	BdC north	6 Oct 2017	18 Sep 2018	60	349	0.541	1.510	0.069	0.667
	Harvey	M	105	560	BdC north	6 Oct 2017	12 Mar 2018	20	349	0.811	0.856	0.009	0.066
	Cassandre	F	115	580	BdC north	16 Oct 2017	10 Dec 2017	5	349	0.431	0.881	0.133	0.499
	Jeremy	M	125	780	BdC north	16 Oct 2017	3 Oct 2018	90	349	0.573	1.510	0.038	0.492
	Hector	M	102	660	BdC north	16 Oct 2017	3 Apr 2018	34	349	0.585	2.115	0.072	0.066

	Robin	M	118	930	BdC north	16 Oct 2017	28 Sep 2018	78	349	0.595	1.510	0.187	0.902
	Nathan	M	103	540	BdC north	16 Oct 2017	21 Nov 2017	16	349	1.126	2.115	0.905	3.587
	Rick	M	108	790	BdC north	16 Oct 2017	30 Jul 2018	6	349	0.958	1.510	1.133	4.077
	Kaya	M	105	740	BdC north	25 Oct 2017	29 Sep 2018	159	349	0.482	1.510	0.007	0.168
	Maya	F	110	1140	BdC north	25 Oct 2017	21 Sep 2018	69	349	0.882	1.695	0.301	1.409
	Lili	F	67	160	BdC north	16 Oct 2017	15 Oct 2017	1	349	0.759	1.718	-	-
	Oscar	M	960	350	AV north	24 Jan 2020	4 Feb 2021	53	374	3.079	11.881	7.739	22.318
	Magali	F	1130	364	BdC south	24 Jan 2020	2 Feb 2020	8	374	7.001	7.715	1.272	6.073
	Riley	F	123	574	BdC south	24 Jan 2020	29 Jul 2020	108	374	0.827	15.292	3.093	78.423
	Salyne	F	1240	743	BdC north	24 Jan 2020	6 Oct 2020	49	374	1.827	11.881	6.125	50.172
	Emma	F	1260	802	BdC south	27 Feb 2020	19 Apr 2020	17	374	0.672	1.845	0.234	1.676
	Blanche	F	1300	1150	AV north	27 Feb 2020	-	0	374	-	-	-	-

Figures

Fig. 1 | Photographs of the three sea snake species whose movements were studied by acoustic telemetry, and for which sample sizes were sufficient for analysis. (a) *Aipysurus duboisii*; (b) *Hydrophis coggeri*; (c) *Hydrophis major*. Photographs by Claire Goiran

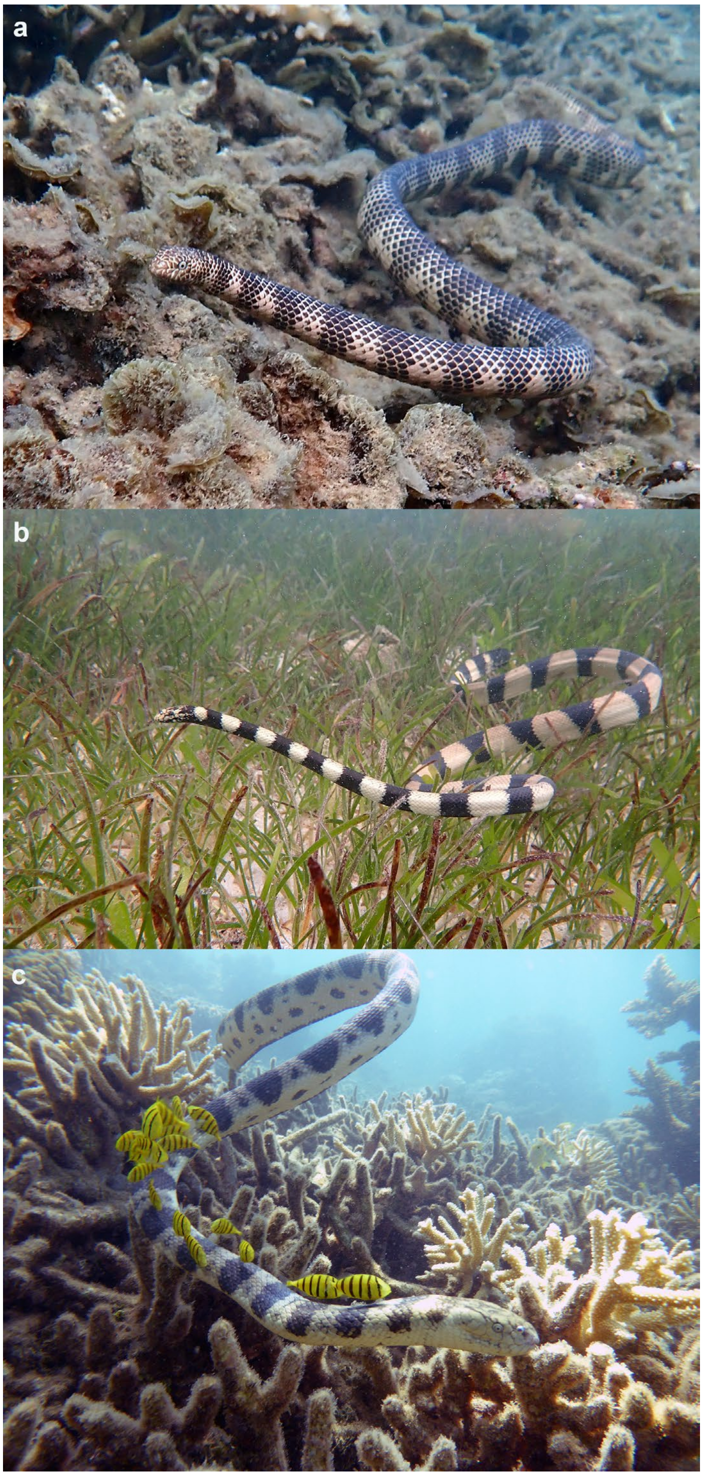

Fig. 2 | Study site and configuration of the original and expanded arrays used to track movements of sea snakes. The study was conducted in Nouméa, New Caledonia (a). The original array (b) was deployed within Baie des Citrons, Anse Vata and Ie aux Canards, whereas the expanded array (c) extended from Ilot Signal in the west to Baie de Magenta in the east

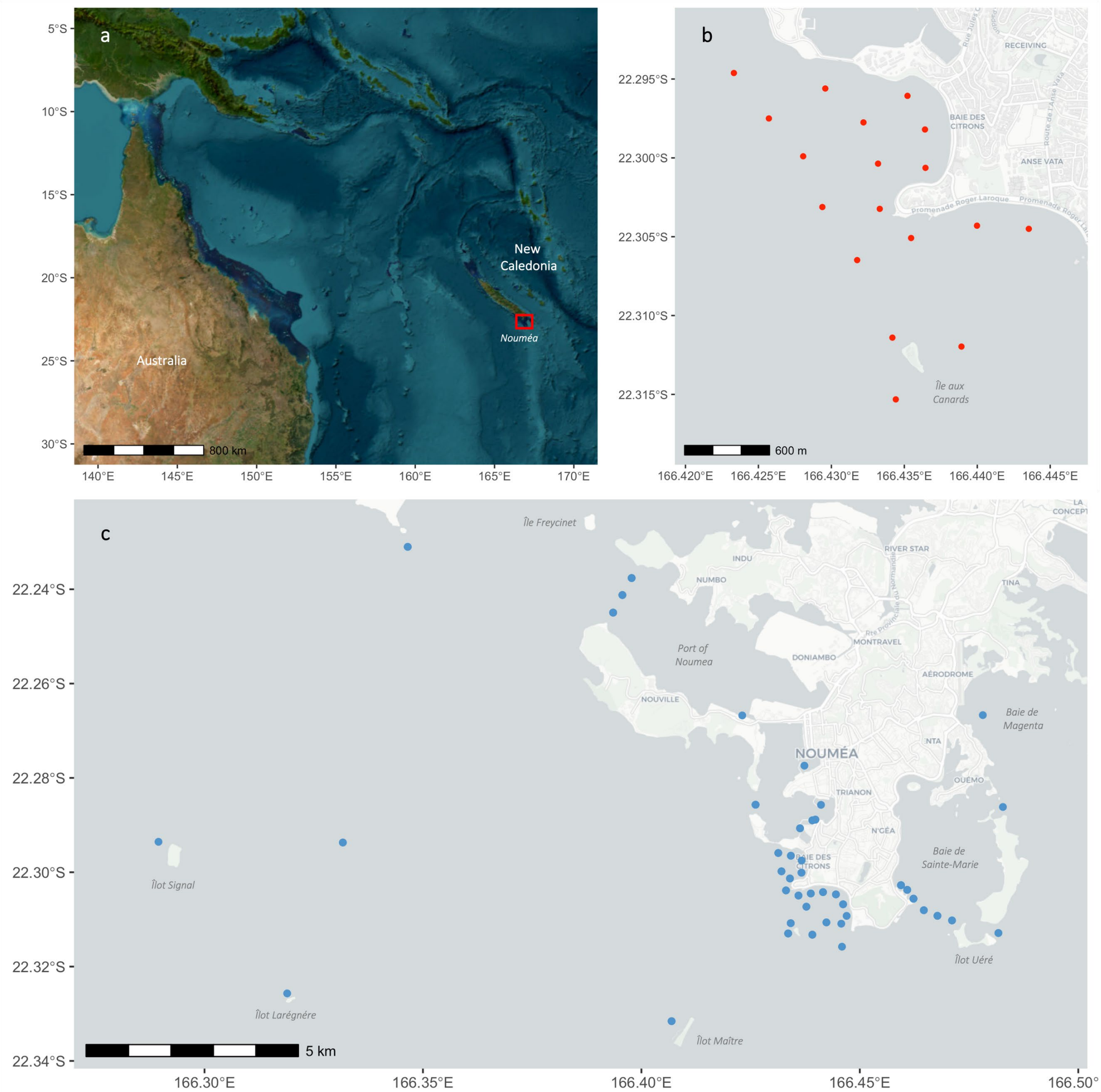

Fig. 3 | Patterns in detection of acoustically-tagged sea snakes in the Noumea region of New Caledonia. Grey points represent the acoustic array deployed to monitor animal movements, with coloured points representing the listening stations at which each species was detected. The size of coloured points represent the total detections recorded for that species on each acoustic receiver. Release locations of tagged individuals indicated by ‘x’ points.

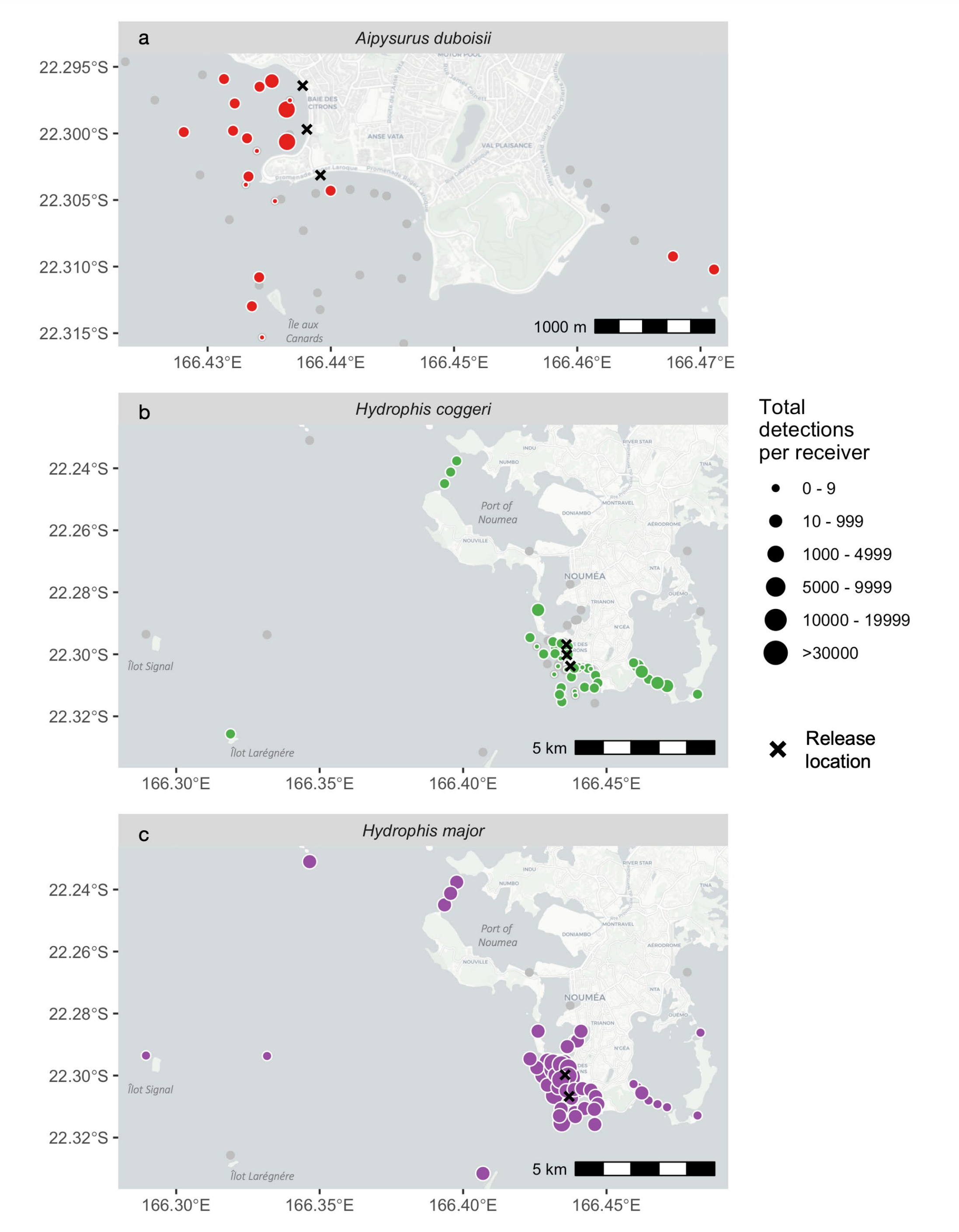

Fig. 4 | Summary of distances of each detection from release location for 27 individuals within 3 species monitored using acoustic telemetry in Noumea, New Caledonia. Grey points represent the raw displacement data, with coloured points and error bars representing mean and standard error of individual distance metrics. Vertical lines at each row represent the maximum distances recorded for each individual across the full monitoring period.

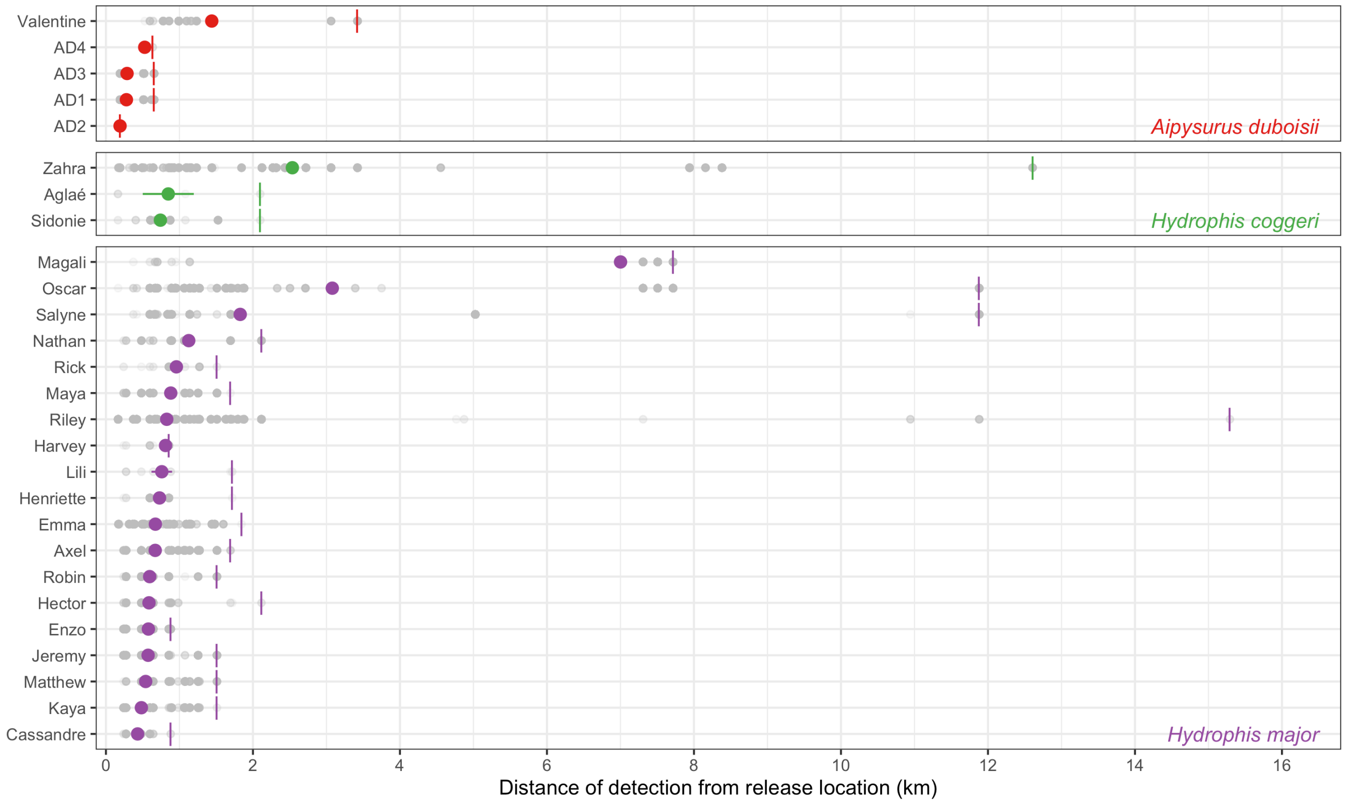

Fig. 5 | Movements and activity space of the sea snakes (a) Riley (*Hydrophis major*) and (b) Zahra (*H. coggeri*) highlighting the long-distance movements recorded using acoustic telemetry across the southern part of the New Caledonioan Lagoon. Green squares represent the release locations of each individual and red triangles represent the last detection locations. Black lines represent movement patterns within the acoustic array, with white points representing positions of acoustic receivers within the array.