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ABSTRACT

Viviparous sea snakes (Elapidae: Hydrophiinae) are fully-marine reptiles distributed in the tropical and subtropical waters of the Indian and Pacific Oceans. Their known maximum diving depths range between 50 and 100 metres, which is thought to limit their ecological ranges to shallow habitats. We report two observations, from industry-owned remotely operated vehicles (ROVs), of hydrophiine sea snakes diving and foraging at depths of approximately 250 metres in the Browse Basin on Australia's Northwest Shelf, in 2014 and 2017. These observations show that sea snakes are capable of diving to the dim-light, cold-water (14.5^{o}C) mesopelagic zone, also known as the 'twilight' zone. These record-setting dives raise new questions about the thermal tolerances, diving behaviour and ecological requirements of sea snakes. In addition to significantly extending previous diving records for sea snakes, these observations highlight the importance of university-industry collaboration in monitoring understudied deep-sea habitats.

KEYWORDS: sea snakes, , depth, Northwest Shelf, remotely operated vehicles (ROVs), , industry collaboration

MAIN TEXT

Viviparous sea snakes (Elapidae: Hydrophiinae) are a recent, secondarily marine radiation of venomous snakes that have many physiological and anatomical adaptations to marine life, including valvular nostrils, paddle-shaped tails, sublingual salt glands and cutaneous gas exchange (Dunson & Stokes 1983; Dunson 1975; Rasmussen et al. 2011). Of the 62 recognised sea snake species, only the pelagic *Hydrophis platurus* is known to hunt at the sea surface; all other sea snakes are benthic foragers that hunt close to the sea floor, typically by probing crevices and burrows (Rasmussen *et al.* 2011). Sea snakes are thought to supplement up to 23% of their oxygen requirements while submerged by using cutaneous gas exchange, but must also periodically swim to the sea surface to breath air (pulmonary oxygen uptake), which limits the duration and depth of dives (Seymour 1974; Heatwole and Seymour 1975; Udyawer *et al.* 2016). The known depth distributions of most species are shallower than 40–50 m depth (Heatwole and Seymour 1975; Cook *et al.* 2016) and there are only a few records of sea snakes at depths greater than 100 m. A snake identified by a diver as *Aipysurus laevis* (B. Sheils pers. comm.) was observed at 133 m at the Goodwin oil platform on the Northwest Shelf off Karratha, Western Australia (Greer 1997). In 2006, the Galathea III expedition collected a *Hydrophis elegans* at the sea surface above depths of 145 m offshore from Broome, Western Australia; immediately after capture the snake regurgitated a benthic eel species indicating that it had been foraging near the sea floor (A.R. Rasmussen, pers. obs.). The deepest record from a demersal trawl vessel, at 93-103 m, is also from Western Australia and the specimen was identified as *Hydrophis czeblukovi* (formerly *H. geometricus*) (Smith 1986).

The maximum depths and diving limits have been difficult to determine for sea snakes because underwater observations are typically limited to shallow water habitats that are easily surveyed (*e.g.* coral reefs, seagrass beds, coastal bays), and the logistical challenges of tagging individual snakes means that remote tracking efforts have been restricted to a few

50 species in coastal localities (Udyawer *et al.* 2018; Cook *et al.* 2016). However, remotely
51 operated vehicles (ROVs) and baited remote underwater video stations (BRUVS) provide an
52 effective way to observe diving behaviour at greater depths (Udyawer *et al.* 2014; Macreadie
53 *et al.* 2018).

54 Here, we report the deepest dives ever recorded for sea snakes, substantially
55 extending current knowledge of the diving capabilities and ecological requirements of these
56 marine reptiles. The two observations were video-recorded on ROVs in 2014 and 2017 in the
57 Browse Basin on Australia's Northwest Shelf. On the 16th of November 2014, a sea snake
58 was filmed swimming at 245 m depth (Figure 1A). The second snake was filmed on the 18th
59 of July 2017 at 239 m and appeared to be foraging by swimming close to the sandy sea floor
60 and stopping in several places to briefly probe the substrate with its head (Figure 1B); the
61 ROVs' temperature probe recorded 26.5^{o}C (degrees Celsius) at the sea surface and 14.5^{o}C at
62 the time the snake was video-recorded. Oceanic depths between 200 and 1000 m encompass
63 the mesopelagic ('twilight') zone characterised by low-light penetration and a cold-water
64 thermocline. The mesopelagic zone of the Browse Basin ranges from approximately 14^{o}C
65 and 21 atmospheric pressure (atm) at 200 m to 8^{o}C and 51 atm at 500 m (Rayson 2011).

66 The two snakes were provisionally identified as *Hydrophis* species due to their
67 distinctive head and body proportions; both have small heads and narrow fore-body relative
68 to hind-body girths that are typical of the many *Hydrophis* species that specialise on
69 burrowing prey (Sherratt *et al.* 2018). The snakes appear to belong to the same species
70 because of their very similar head-body proportions and colour patterns (between 40 and 45
71 dark bands in both specimens). However, based on the images available, it was not possible
72 to identify these snakes to species level or exclude the possibility that they belong to a
73 presently unrecognised species.

The new records of sea snake activity at depths of up to 245 m significantly extend the known depth range for sea snakes, prompting questions about the physiological mechanisms that allow them to function at cooler waters and higher pressures. Extended dives to deep-sea habitats are likely achieved by a bimodal gas exchange: an increased level of cutaneous gas exchange might relieve the higher pressures of internal gases (i.e. 'the bends'), and cooler temperatures might decrease total oxygen consumption– reducing the frequency of trips to the sea surface to breathe and thus extending total submergence times (Udyawer *et al.* 2016; Seymour 1974). However, further studies are needed to understand the interaction between metabolism, bimodal oxygen uptake and activity levels across temperature gradients for deep-diving sea snakes (Udyawer *et al.* 2016). Thermal tolerance estimates for sea snakes are predominately based on laboratory studies of *H. platurus* that indicate an ideal thermal range of 20-37^{o}C, cessation of feeding, locomotion and orientation at temperatures below 18^{o}C, and lower lethal limits of 14-17^{o}C (Dunson and Ehlert 1971; Graham *et al.* 1971). The present study reports two records of sea snakes at 14.5^{o}C and describes foraging behaviour at this temperature (Figure 1B), indicating a higher range for thermal tolerance than previously recorded for sea snakes. Sea surface temperatures are a major determinant of the current geographic distribution of sea snakes (Heatwole *et al.* 2012; Lillywhite *et al.* 2017), but how oceanic temperatures affect the vertical distribution (i.e. diving ranges) is a comparatively understudied aspect of the spatial ecology of sea snakes (Udyawer *et al.* 2018). Finally, these observations raise questions about sensory adaptations of deep-diving sea snakes, such as how they might orient and navigate in this light-reduced habitat.

The record-setting dives reported here challenge widely held assumptions of the limits to sea snake behaviour, physiology and ecology. Further observations (using *e.g.* animal tracking, ROV surveys) are needed to determine whether such deep dives are an unusual or

typical behaviour of the species recorded in the present paper, and other sea snakes more generally. Finally, these new dive records emphasise the importance of collaborations between research and industry organisations to survey previously overlooked deep-sea habitats for sea snakes.

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FIGURE LEGEND

Figure 1. New depth records for sea snakes, observed from video-recordings from remotely operated underwater vehicles (ROVs), on Australia's Northwest Shelf. A) Image of an unidentified sea snake species swimming at a depth of approximately 245 m on 16th of November, 2014. B) Image of an unidentified sea snake foraging at a depth of approximately 239 m on 18th of July, 2017. The snakes appear to belong to the same species because of their very similar head-body proportions and colour patterns of between 40 and45 dark bands in both the 2014 and 2017 specimens.