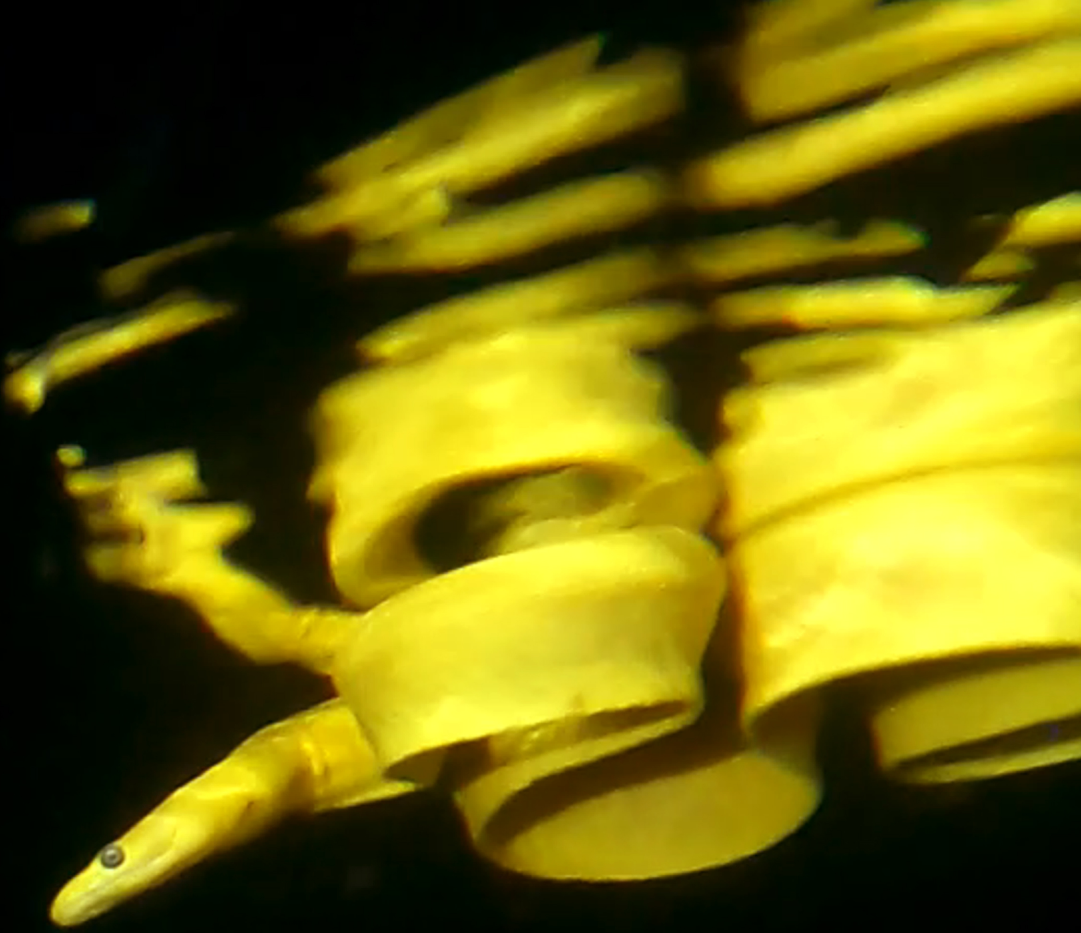

THE UNIQUE ECOLOGY OF AN ENDEMIC SEA SNAKE

Hydrophis platurus xanthos

BROOKE L. BESSESEN

The unique ecology of an endemic sea snake *Hydrophis platurus xanthos*

A thesis submitted in fulfillment of
the requirements for the degree of
Doctor of Philosophy

University of Reading

In the discipline of
Ecology and Evolutionary Biology

Brooke L. Bessesen

July 2022

Declaration

I confirm that this is my own work and the use of all material from other sources has been properly and fully acknowledged.

Brooke L. Bessesen

Acknowledgments

Many fine people directly or indirectly influenced this work and deserve recognition for their vital contributions.

My first and deepest thanks go to Manuela González Suárez for offering this late-blooming doctoral student the opportunity to fulfil a life-long dream. Finding her biography, I sensed she would be the perfect supervisor for my studies, and how right I was! Manuela's expertise and early advocacy brought me to the University of Reading, and her generous investment of time and knowledge, steady guidance, and genuine concern saw me though every turn that followed. Happily, graduation is not a goodbye as we are already immersed in a new collaboration, with hopes for more ahead. I am sincerely grateful to Brian Pickles, too, for the safety net of his support as my backup supervisor. Though we only met in person once and exchanged a handful of email updates, I was fortunate to have him in my corner and truly hope we will stay in touch.

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This final paragraph is reserved for my best friend, greatest collaborator, and tireless champion. I dedicate this thesis to my husband, Kevin Steiner, who sacrificed so much to see this wild endeavor to fruition. He listened patiently as I nattered on (and on and on) about sea snakes. He stayed the course through every new idea and insight. Every moment of uncertainty. Every stumbling failure and rebounding success. I feel so much love and gratitude. Thank you for sharing the journey.

Impact Statement

The author's research has resulted in numerous published peer-review articles, including two of the four thesis chapters†, plus a Spanish translation of an associated 2021 interview study to help ensure community access to those results (see also *Brooke L. Bessesen* https://orcid.org/0000-0003-0272-3889):

†**Bessesen BL**, Oedekoven CS, Galbreath GJ, González-Suárez M. 2022. Population abundance and density estimates for Costa Rica's endemic sea snake, *Hydrophis platurus xanthos*. Frontiers in Marine Science 9: 924966.

†**Bessesen BL**, González-Suárez M. 2022. Safe from sunburn: The divergent diel pattern of a *Hydrophis* sea snake. Ecology and Evolution 12(1): e8436

Bessesen BL, González-Suárez M, Herra-Miranda D, Oviedo L. 2021. *Hydrophis platurus xanthos* (Golfo Dulce Yellow Seasnake): Harassment by dolphins. Natural History Note. Herpetological Review 52(2): 425–426.

Bessesen BL, González-Suárez M. 2021a. The value and limitations of local ecological knowledge: Longitudinal and retrospective assessment of flagship species in Golfo Dulce, Costa Rica. People and Nature 3:627–638.

Bessesen BL, González-Suárez M (traducido por Daniel Colgan). 2021b. El valor y limitaciones del conocimiento ecológico local: Una evaluación longitudinal y retrospectiva de especies bandera en Golfo Dulce, Costa Rica. Universidad de Reading CentAUR DOI: 10.48683/1926.00100401, https://centaur.reading.ac.uk/100401/.

Bessesen BL, Galbreath GJ. 2017. A new subspecies of sea snake, *Hydrophis platurus xanthos,* from Golfo Dulce, Costa Rica. ZooKeys 686: 109–123.

Bessesen BL. 2015. Occurrence and distribution patterns of several marine vertebrates in Golfo Dulce, Costa Rica. Revista de Biología Tropical 63 (Supl.1): 261–272.

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Bessesen BL, Saborío-R G. 2012. Tropical fiord habitat as a year-round resting, breeding, and feeding ground for East Pacific green sea turtles (*Chelonia mydas*) off Costa Rica. Herpetological Review 43: 539–541.

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The two unpublished thesis chapters are in review:

Bessesen BL, Garrido-Cayul C, González-Suárez M. (In review). Habitat suitability and area of occupancy defined for rare New World sea snake. Conservation Science and Practice.

Bessesen BL, González-Suárez M. (In review). The effect of bathymetry on sea snakes in Golfo Dulce, Costa Rica. Herpetological Conservation and Biology.

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Chapter 6: Coalescing new knowledge

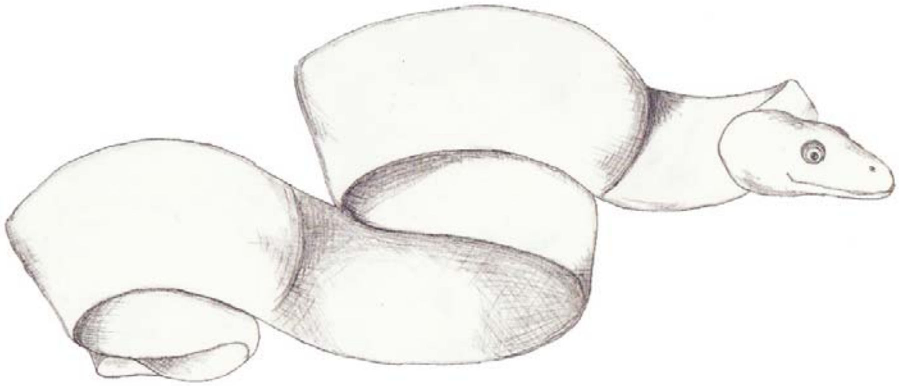
A.1 Bessesen BL, González-Suárez M. 2021. The value and limitations of local ecological knowledge: Longitudinal and retrospective assessment of flagship species in Golfo Dulce, Costa Rica. People and Nature 3:627–638.

A.2 Bessesen BL, González-Suárez M, Herra-Miranda D, Oviedo L. 2021. *Hydrophis platurus xanthos* (Golfo Dulce Yellow Seasnake): Harassment by dolphins. Natural History Note. Herpetological Review 52(2): 425–426.

Abstract

As we, humans, charge through the twenty-first century with our pioneering technology and global interests, we threaten to destabilize Earth's natural processes and destroy biodiversity before fully understanding what is being lost. New species are still discovered, even as thousands go extinct, and science is in a race to deliver crucial knowledge that can inspire conservation. This thesis explores ecological aspects of a recently described sea snake *Hydrophis platurus xanthos.* Given its vibrant canary coloring and unusual behavior, xanthos, as it's come to be called, is sure to spark curiosity and wonder in readers. Chapter 1 of this thesis provides an introduction that chases the evolutionary trail from the emergence of reptiles in the Carboniferous to the first diving elapids of the Miocene before detailing the physiological and ecological characters of *H. platurus* and its journey across the vast Pacific Ocean, eventually giving rise to a xanthic (all-yellow) population in Golfo Dulce, Costa Rica. Chapter 2 combines survey sightings with bathymetric data to investigate the geographic partitioning of xanthos from its pelagic relatives. Chapter 3 considers several hydrographic conditions that govern habitat suitability for xanthos and measures its range. Chapter 4 looks at the taxon's behavioral patterns and activity cycle, revealing yet another remarkable example of divergence. Chapter 5 applies distance-sampling techniques to compute the first total population abundance estimate for xanthos from which future trends can be assessed. Finally, Chapter 6 explains the comprehensive value of our findings, which confirm the Golfo Dulce yellow sea snake to be a unique evolutionary organism. This work provides evidence to promote protection of Costa Rica's endemic marine reptile as a biological treasure, and going forward, has set us on course to examine whether xanthos is a separate species.

Chapter 1



CHAPTER 1: On the making of a yellow sea snake

1.1 | INTRODUCTION

The true sea snakes (Hydrophiinae: Hydrophiini) represent a specialized group of venomous squamates adapted to aquatic life. These are the world's most successful marine reptiles (Sanders et al. 2010). Viviparity, valvular nostrils, sublingual salt-excretion glands, and partial cutaneous respiration represent but a few of the fascinating adaptations that allow survival in the ocean realm (Greene 1997, Heatwole 1999). Sixty-four species (Uetz et al. 2022) are currently known to range across the Indo-Pacific region (Lillywhite et al. 2018), including *Hydrophis platurus* Linnaeus, 1766 (as *Anguis platura*). There is also a unique canary-yellow sea snake endemic to the warm inner-basin waters of a fiord-like inlet in Costa Rica: *Hydrophis platurus xanthos* Bessesen & Galbreath, 2017.Locally called 'xanthos' (Greek for 'yellow'), it may be undergoing allopatric speciation as it is geographically separated from black and yellow conspecifics inhabiting the broader Pacific Ocean (Bessesen 2012, Sheehy et al. 2012, Bessesen & Galbreath 2017; Fig. 1.1). Carl von Linné is credited with developing the taxonomic nomenclature still in use today in which a rank lower to the binomial may be used to describe a geographical variety, or subspecies (Greene 1997), yet as an evolutionarily distinct organism, with unusual morphology and behavior, *H. p. xanthos* is expected to someday be elevated to species. The four research chapters that follow strive to illuminate key aspects of xanthos ecology, including suitable habitat, surfacing behavior, and abundance. Before proceeding forward, however, we must first travel back. Evolutionary biology examines organisms through the lens of time and the mechanisms of natural selection (Greene 1997). To establish a framework for the findings presented here, we must trace the lineage of xanthos from its earliest reptilian roots, through the rise and radiation of snakes and the transition of some terrestrial species to the marine environment, then pursuing the world's most widely distributed squamate. Much of this introduction will focus on key adaptations of *H. platurus* before fully introducing its evolutionary relative and our principal subject, *H. p. xanthos.*

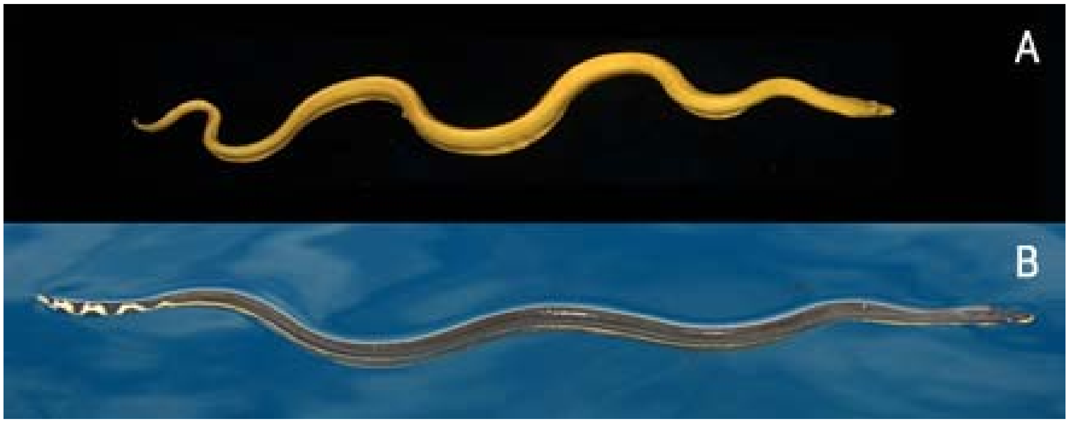


Figure 1.1. Color patterns and typical surfacing periods for A) *Hydrophis platurus xanthos* (nocturnal); B) *Hydrophis platurus platurus* (diurnal); photo credit: B. Bessesen.

1.2 | SNAKE EVOLUTION

1.2.1 The origins debate

The fossil record suggests life on Earth began some 3.5 billion years ago (Mooers & Redfield 1996), yet it was not until the swampy Carboniferous Period ~350 mya that the earliest chordates adapted to terrestrial living (Rowe 2004). The first egg-laying amniotes divided into the mammal-bound synapsids and the diapsid reptiles, the latter forging the bird-inclusive monophyletic clade Reptilia (Lee et al. 2004). Two stem reptiles were discovered in fossilized tree hollows in Joggins, Nova Scotia: the incomplete and disarticulated skeleton of the 200-mm *Hylonomus,* which dates to 310 mya (Carroll 1964) and the more intact *Paleothyris* from 300 mya (Carroll 1969). It is clear these lizard-like creatures are basal to a diverse array of reptilian descendants, but myriad twists and turns of paleontological discovery have generated heated debate over the details of their divergence. Sues (2019) addresses many conflicting hypotheses, which frequently originate from clashes between morphological and molecular analyses. It is currently accepted that the scaled lepidosaurs, excluding the tuataras of New Zealand, form the order Squamata (Latin *squama* for 'scale') to encompass lizards, snakes, and amphisbaenians. Although phylogenetic studies retain snakes within this 'lizard' clade (Gauthier et al. 2012), modern taxonomy simplifies them into the suborder Serpentes (from Latin) or Ophidia (from Greek). Whereas modern-day ophidians lack any trace of forelimbs or shoulder girdle, basal ophidians may have had two or four small legs and so are diagnosed by derived skull features that allow increased mobility during feeding (Sues 2019). Today we recognize many characteristic serpent traits, such as a forked tongue used in conjunction with a chemoreceptive vomeronasal (Jacobson's) organ, translucent ocular scales called spectacles or brilles that replace protective eyelids, the loss of the tympanic membranes called eardrums (Underwood 1967, Lillywhite 2014), a long attenuate body supported by 140–600 vertebrae, and the absence of any distinct limbs (Lee et al. 2004).

Snakes are asserted to have radiated from the continental mass known as Gondwanaland, the southern region of a disbanding Pangea (Caldwell et al. 2015, Hsiang et al. 2015), yet much about their origins remains unknown. There is a dearth of early ophidian specimens and delicate bones in those recovered are often missing or poorly preserved. The confoundingly scant fossil record even fails to elucidate the habitat from which the crown group emerged, inciting two main competing camps of thought (Benton 2005, Sues 2019). One is focused primarily on morphology and asserts

Figure 1.2. Crown-group snake reconstruction based on the findings of Hsiang et al. 2015; artwork: Julius Csotonyi (published with the artist's permission).

that snakes evolved in the marine habitat and are related to predatory anguimorphs like mosasaurs (Lee et al. 2004, Simões et al. 2018). The other references molecular studies to show burrowing tetrapods underwent body elongation and limb reduction to favor a fossorial existence (Conrad 2008, Conrad et al. 2011). While it is conceivable that two lineages could have played out in parallel, extant snakes have a monophyletic origin (Lillywhite 2014), so the question remains: did modern ophidians arise by land or sea? A mid-Cretaceous (~95 mya) stem-snake was proposed in support of each theory: the land-dwelling *Najash* (Caldwell et al. 2015, Garberoglio et al. 2019) and the aquatic *Pachyrhachis* (Caldwell & Lee 1997). More recent studies support the burrowing theory (Fig. 1.2), yet the evidence is sufficiently confutable for discord to persist (Hsiang et al. 2015, Miralles et al. 2018, Sues 2019). Caldwell and colleagues (2015) recently described four new fossil species from the Jurassic Period and suggested they were secondarily aquatic invaders, but those specimens have failed to gain consensus as stem ophidians because they are fragmentary and combine disassociated skull and post-cranial bones (Sues 2019). Should the oldest among them, *Parviraptor,* from 167 mya, ever be accepted, it would supplant all other basal snakes and revise the evolutionary record by tens of millions of years (from 128.5 mya per Hsiang et al. 2015).

1.2.2 Ophidian radiation

Wherever and whenever the first snakes appeared, they were morphologically and phylogenetically diverse by the late Cretaceous (Caldwell et al. 2015). While dinosaurs, pterosaurs, and plesiosaurs were annihilated at the K-Pg boundary, also known as the KT Mass Extinction, it was long thought that the squamates fared relatively well (Benton 2005). That assumption has since been reversed. It is now understood that only about 17% of squamate families survived into the Cenozoic (Longrich et al. 2012), including as few as six lineages of ophidian (Klein et al. 2021). Of those that persisted, boa-like macrostomatans (from Greek *makros* 'large' + *stoma* 'mouth' per Sues 2019) grew into sizeable constriction predators. Indeed, *Titanoboa,* the largest serpent in Earth's history, came and went around 60 mya and reached up to 14.3 m with an estimated mass of 1,135 kg (Head et al. 2009, Head et al. 2013). Within the 'advanced snakes' called caenophidians (Greene 1997), the superfamily Colubroidea emerged and diversified sometime around 50–65 mya, presumably filling niches emptied by the KT extinction event (Hsiang et al. 2015). An explosive radiation occurred during the Miocene Epoch, sometimes referred to as the Age of Snakes (Holman 1987). Of the almost 4000 extant snake species (Uetz et al. 2022), 80% are colubroids and they inhabit every continent except Antarctica (Sues 2019).

Although the precise interrelationships between snake lineages are yet unresolved (Lee et al. 2004), there have been four traditionally recognized taxonomic families within Colubroidea. Two of those comprise highly venomous species. Viperidae encompasses the long-fanged ophidians like rattlesnakes and other pit vipers, while Elapidae, a clade of more than 395 species (Uetz et al 2022), shares the derived character of proteroglyphous dentition: short, fixed and permanently erect fangs on the anterior maxilla (Greene 1997, Lillywhite 2014). Among the elapids, the subfamily Elapinae, cobras, mambas, coral snakes, and the like, retained their terrestrial ecology while other elapid ancestors made their way to the sea (Sues 2019). Two modern lineages independently evolved for marine life (Sanders et al. 2008): the oviparous subfamily Laticaudinae, called sea kraits, and the viviparous 'true' sea snakes of Hydrophiinae: Hydrophiini (Smith 1926, Lukoschek & Keogh 2006, Sanders et al. 2013).

1.2.3 Hydrophis clade

Sometime after 18 million years ago the hydrophiines were radiating from Australasia (Lee et al. 2016), with most speciation events occurring within the past 2.5 million years as fluctuations in sea level created or closed marine basins, imposing adaptive pressure (Lukoschek & Keogh 2006, Ukuwela et al. 2016). Two main clades are now recognized: 'Aipysurus', strongly associated to coral reefs, and the young 'Hydrophis'. More than ten genera were recently combined into the genus *Hydrophis* (Sanders et al. 2013), which now encompasses up to 49 species (IUCN 2022, Uetz et al. 2022). The clade is taxonomically unstable, however, given the inadequate molecular resolution caused by rapid radiation, and numerous taxonomic revisions have been proposed over the last 90 years (Lukoschek & Keogh 2006, Rasmussen 2011). Even when employing cutting-edge methods, low variability in nuclear markers make the mitochondrial tree challenging to resolve. Nevertheless, significant strides in hydrophiine phylogeny are being made. When Sanders and colleagues (2013) reclassified the only planktonic reptile, *Pelamis platura,* from its monotypic genus into the speciose *Hydrophis*, a long adjustment period was required (Lillywhite 2014). *Hydrophis platurus,* the specific epithet now accepted, is the closest living relative and sister taxon to our study subject, *H. p. xanthos* (Bessesen & Galbreath 2017); hence, its morphology, ecology, and behavior are germane to our investigations.

1.3 | *HYDROPHIS PLATURUS*

1.3.1 Dispersal of a pelagic sea snake

Hydrophis platurus, known as the pelagic sea snake, originated in the Indo-Australian region five to seven million years ago (Lee et al. 2016, Fig. 1.3). Its scientific binomial derives from Greek *hydor* + *ophis*, meaning 'water-serpent' and *platys* + *oura* for 'flat-tail'. Its laterally compressed body has prominent dorsal and ventral keels well-designed for underwater undulations (Pickwell & Culotta 1980, Sues 2019). Whereas most sea snakes spend their entire lives in relatively warm shallow coastal waters (Tu 2011), *H. platurus* can transverse deeper realms and has expanded across the Indian and Pacific Oceans to become the most widely ranging serpent in the world (Pickwell 1972). This true pelagic species is a surprisingly weak swimmer. It is commonly associated with drift lines, also called 'slicks' for their smooth glassy aesthetic, where floating debris and small fish concentrate (Kropach 1971a, Dunson and Ehlert 1971, Tu 1976, Lillywhite et al. 2010; Fig. 1.4). Surfacing may be used to facilitate positional changes (Rubinoff et al 1988), and planktonic exploitation of ocean currents through waif dispersal has led to a sizeable pan-oceanic population of pelagic sea snakes (Brischoux et al. 2016). However, with a critical thermal minimum of <18 °C (Dunson and Ehlert 1971, Graham et al. 1971), colonization is restricted at approximately 40 degrees north and south by the oceanic isotherms of February and August (Fig. 1.3). Expanding from their site of origin, west across the Indian Ocean, pelagic sea snakes reached the African Continent, but unable to endure the cold currents that converge at the southern cape, could not enter the Atlantic Ocean. While members of the extinct lineage Palaeophidae once inhabited the Atlantic Ocean, no modern marine serpents have managed to populate those waters (Hecht et al. 1974, Lillywhite et al. 2018), though intriguingly, two sightings of *H. platurus* off Namibia (Branch 1998) suggest the possibility of an expanding range (Ukuwela 2013). In the opposite direction, after crossing the Pacific Ocean, eastbound progress of the waif population was halted by the Americas, which extend north and south toward both polar caps. Having arrived at the New World after the Central American Seaway was closed by the Isthmus of Panama there was no longer a thruway (Lillywhite et al. 2018), the land bridge having reached completion 2.8–6 mya (Bacon et al. 2015, O'Dea et al. 2016). A few curious sightings of *H. platurus* have been reported on the Caribbean side of Columbia but are presumed to be isolated individuals who somehow crossed through the Panama Canal or were carried in the ballast of ships or otherwise introduced by anthropogenic activity (Hernández-Camacho et al. 2006).

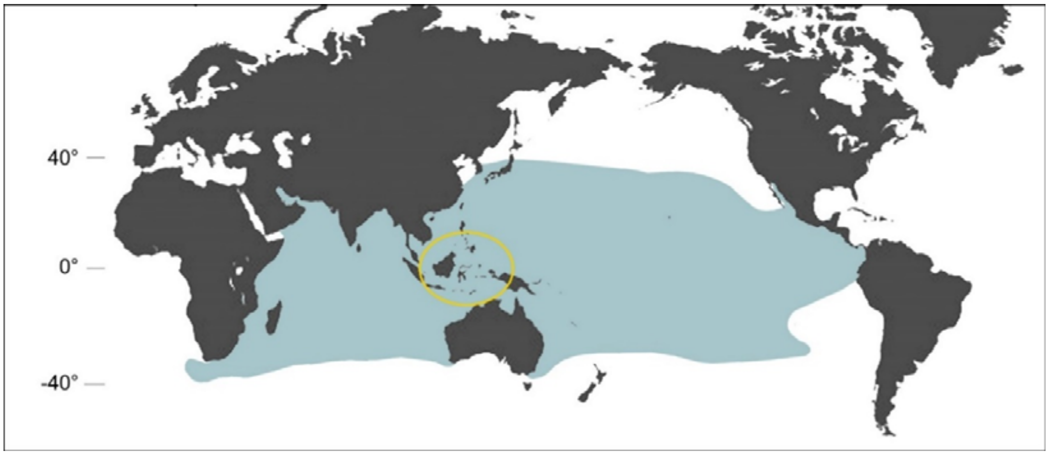


Figure 1.3. Global map in Mercator projection; blue area describes the general distribution of *Hydrophis platurus* (based on Brischoux et al. 2016), while the yellow circle represents the area of origin for the species (based on Ukuwela et al. 2016); map created in PhotoShop (Adobe 2010).

1.3.2 Aposematic coloration

Chronicled by human mariners in the Eastern Tropical Pacific (ETP) off Central America since as early as 1519 (Taylor 1953), *H. platurus* is the only sea snake to successfully colonize the New World (Hecht et al. 1974). In addition to the common name of pelagic sea snake, it is also sometimes called the 'yellow-bellied sea snake' because the color pattern essentially describes a black dorsum with yellowish ventral surfaces, always with black spots or bands on the tail paddle (Smith 1926). Two of those color forms represent ≥79% of specimens in the ETP: the characteristic bicolor (black above, bright yellow below) and a tricolored pattern of black dorsal coloring with lateral yellow stripes and a brownish venter (Bolaños et at. 1974, Tu 1976). The brownish underside apparently darkens between sheds and may be related to age (Kropach 1973, Hecht et al. 1974). Countershading presumably offers some degree of camouflage (Graham et al. 1971) and conspicuous coloration is considered aposematic in snakes, including *H. platurus* (Kropach 1975; Fig. 1.4). While other hydrophiines may fall prey to eagles, crocodiles, sharks, and other large fishes, the pelagic sea snake has few if any natural predators. In addition to being venomous, it is presumably noxious or at least distasteful (Heatwole et al. 1974, Heatwole 1999). A partially digested snake was once regurgitated by an ailing leopard seal, although it was unclear whether the ingestion contributed to the animal's poor condition (Heatwole & Finnie 1980). Sailfish have been reported attacking the snakes, but consumption was never confirmed (Pickwell et al. 1983). No *H. platurus* was recovered from the stomach contents of 25 species of predatory fish or two dolphin species from the ETP (Kropach 1975). In the laboratory, starved fish and one hawksbill sea turtle from the Pacific Ocean outright rejected offerings of pelagic sea snake or expelled pieces that had been hidden in squid. Conversely, fish from the Atlantic Ocean attacked the unfamiliar snakes, sometimes dying from their venomous bites (Rubinoff & Kropach 1970). Kropach (1975) also noted that seabirds in the ETP do not readily descend upon *H. platurus,* and disturbances at the sea surface do not prompt the snakes to dive. Heron species native to Panama that were presented with several serpentine-shaped potential prey items displayed a dramatic flight response to the pelagic sea snake (Caldwell & Rubinoff 1983). Hence, it may be that no population-limiting predation pressure occurs from above (Rubinoff et al. 1988). Despite this apparent aposematism, individual *H. platurus* sometimes do evince scars and scratches indicating previous if unsuccessful threats to their life (Heatwole 1999, Weldon & Vallarino 1988). There are reports of *H. platurus* being seized, injured, or killed by octopus (van Bruggen 1961), magnificent frigates (Wetmore 1965, Sheehy et al. 2011), pufferfish (Pickwell et al. 1983), lava gull (Reynolds & Pickwell 1984), pelican (Álvarez-León & Hernández-Camacho 1998), wood stork (Solórzano & Kastiel 2015), black hawk (Solórzano & Sasa 2017), tiger heron (Nuñez Escalante & `Calvo Benavides) and even

Figure 1.4. *Hydrophis platurus* feeds in a drift line surrounded by flotsam; note the snake's countershading and aposematic bright yellow undersides; photo credit: B. Bessesen.

bottlenose dolphins (Durso 2015), which suggest it is vulnerable to harm by a variety of organisms. Moreover, aposematism is powerless against biofouling. Algae, decapods, and barnacles are generally removed by the pelagic sea snake through ecdysis, using a unique 'knotting' behavior (Pickwell 1971). This shedding of the skin is undertaken relatively frequently, every 5–65 days (optimal interval=19–23; Kropach 1973), and illness or injury may lead to a pathological presence of epibiota and/or parasites (Gillett et al. 2017). Humans pose additional risks to *H. platurus*. Thousands of snakes aggregating in drift lines in the ETP have been collected for science (e.g., n=>500: Dunson & Ehlert 1971; n=~2000: Rubinoff & Kropach 1970; n=102: Bolaños et at. 1974; n =>125: Graham 1974a-b; n=3077: Tu 1976; n=635: Vallarino & Weldon 1996), though efforts to mitigate destructive sampling are now promoted (Udyawer et al. 2018). The species also suffers incidental capture in fishing nets and is particularly susceptible as bycatch in trawls (Fry et al. 2015). On a positive note, the pelagic sea snake does not play a significant role in the sea-snake-skin trade that is decimating other species (Tu 2011, Van Cao et al. 2014).

1.3.3 Adaptive physiology and behavior

For *H. platurus,* life begins and ends at sea. Reproductive behaviors, including mating and parturition, thus take place in the water and potentially occur year-round (Kropach 1975). During copulation, the male and female intertwine their tails (Solórzano & Sasa 2011) and may remain attached at their cloacal openings, also called vents, for more than an hour (Vallarino & Weldon 1996). Sperm is released through a hemipenis (males have paired hemipenes but only one is used at a time), which is everted from a pocket in the tail and inserted into the female's vagina by way of her cloaca. The cloaca is a common chamber through which reproductive products pass and feces and urates are evacuated. In paired oviducts higher up, sperm can be stored, and fertilized eggs develop (Lillywhite 2014). As a viviparous species, a gravid mother retains placental connections with her embryonic young during a six- to eight-month gestation period (Savage 2002), giving live birth to a litter of one to six snakelets (Visser 1967). Each neonate is expelled through the cloaca either head- or tail-first following rhythmic contractions by the mother. It immediately surfaces to breathe and removes any residual fetal membrane by knotting its body (Vallarino & Weldon 1996). Like many ophidians, *H. platurus* exhibits sexual dimorphism with females larger than males, a quality almost certainly related to fecundity given larger litters and neonate size (Rivas & Burghardt 2001). Adult total length (TL) averages 70–80 cm (Cogger 1975, Savage 2002, Leviton et al. 2003), though the largest known individual stretched to 113 cm (Pickwell & Culotta 1980). Tail length is estimated to account for 11.2% of TL (Cook & Brischoux 2014) with a norm of 8–9 cm (Leviton et al. 2003). Average weight has been reported as 91 g by Graham et al. (1971) and as 140 g by Rubinoff et al. (1986). Five mothers documented by Vallarino & Weldon (1996) measured 60–74 cm and weighed 88–159 g post-parturition, and their 26 neonates averaged 23 cm in length and 8.4 g in weight. The natural lifespan of the species is yet unknown but conjectured at less than 10 years (Brischoux et al. 2016). In captivity, individuals have lived 3.5 years (Snider & Bowler 1992), and more than six to nine months housed in fresh water (Dunson & Ehlert 1971, Kropach 1973).

Several physiological adaptations are essential for the success of *H. platurus,* including those related to locomotion, diving, and protection from the elements. Using lateral undulation, the pelagic sea snake has the ability to swim both forward and backward (Kropach 1975, Heatwole 1999) with its flattened morphology increasing surface area for propulsion (Brischoux & Shine 2011). Still, *H. platurus* is not a robust swimmer. It actively avoids turbulent waters (Dunson & Ehlert 1971, Tu 1976, Rubinoff et al. 1986, Cook & Brischoux 2014) and horizontal movements are driven largely by currents (Rubinoff et al. 1988). It can sprint up to 20 cm/s at the ocean surface, but its submerged velocity is only 2–4 cm/s (Graham et al. 1987). Rubinoff et al. (1986) tracked 15 pelagic sea snakes in the Gulf of Panama for up to 31.2 hours and found the animals spent 51–99% (mean=87%) of their time submerged, surfacing briefly to breath, longer to forage. Dive depth averaged 15 m, with one unusual dive reaching 50 m. The longest dive time was 213 minutes (however, laboratory specimens have survived forced submersion for up to 5.5 hours: Dunson & Ehlert 1971). Which brings us to perhaps the most interesting ability of this seafaring squamate: cutaneous respiration. Amphibians, numerous fish, and certain aquatic turtles and snakes rely significantly on 'skin breathing', but the pelagic sea snake is the most robust example among the reptiles (Feder & Burggren 1985). *Hydrophis platurus* can absorb 12–33% of its oxygen requirements through its skin and excrete 55–94% of carbon dioxide to prevent CO_2 build-up leading to respiratory acidosis. This process is so reflexive that the snake continues to uptake oxygen even at the surface (Graham 1974a). It also ventilates through its nostrils, called nares (narial valves open only above the water). Many vertebrates employ paired lungs to extract oxygen from the air but in snakes one lung is typically reduced or missing while the other is modified to accommodate a narrow body cavity (Heatwole 1999, Lillywhite 2014). In the pelagic sea snake, the left lung has completely disappeared. The right lung, which runs neck to vent, can be divided into three anatomical sections: the tracheal section (ending just posterior to the caudally positioned heart), the large alveoli-rich bronchial section (this and the former make up the vascular lung responsible for pulmonary gas exchange) and the most caudal section, the small bulbous saccular lung, which acts as a reservoir for air storage (Graham et al. 1975, Gillett et al. 2017). Such voluminous capacity not only supports positive buoyancy at the surface where the snake feeds but also facilitates neutral buoyancy at greater depths and allows for longer submersions. Intracardiac shunting is used to manage both oxygen reserves and buoyancy changes during dives, and skin breathing augments vital requirements. The serpent offsets pulmonary deflation by slowly ascending from depth along a gradual incline that accounts for 82% of its total down time, always maintaining energy-efficient buoyancy control (Graham et al. 1987). The flattened morphology of *H. platurus* may further aid transcutaneous gas exchange as dorsoventral elongation increases the dermal surface area (Brischoux & Shine 2011). Another factor in the diffusion of oxygen from seawater into the bloodstream is skin thickness (Feder & Burggren 1985) as the outer β-keratin layer of the pelagic sea snake's epidermis is notably thin over an immature lipid-rich mesos layer. This specialized integument permits gases to permeate while effectively retaining moisture and blocking sodium from entering the tissues (Dunson 1975). When the snake basks or feeds at the surface, it is adapted to endure the intense solar radiation impinging the ocean (Lomonte et al. 2014). Unlike most ophidians with overlapping scales, *H. platurus* has knobby polygonal-shaped scales that lay side-by-side. The interscale trenches called hinge regions entrap water to form a protective layer of moisture that prevents dehydration in the open air (Lillywhite & Menon 2019). Dense melanin pigment in the snake's dorsum presumably shields the integument and internal organs from sun damage and may reduce the exposure of ultraviolet light on the venom glands (Pough et al. 1978, Greene 1997).

Hydrophis platurus is an opportunistic piscivore that employs a float-and-wait strategy (Klauber 1935, Kropach 1975, Brischoux & Lillywhite 2011). Passively floating in drift lines with an elongate body posture, the snake attracts a variety of tiny fishes that gather beneath it, much as they would under a stick or flotsam (Fig. 1.4, 1.5). Prey is seized with a sideways strike of the head (Brischoux & Lillywhite 2011). The species is a generalist, known to consume at least 34 species of fish from 27 families (Klawe 1964, Visser 1967, Kropach 1975, Voris & Voris 1983, Brischoux & Lillywhite 2013) with mostly mullet- and rabbitfish-shaped bodies (Voris & Voris 1983). Interestingly, no shifts in prey size occur during ontogeny. Second to prey availability, suitable prey size is the driving factor in food selection (Klawe 1964, Kropach 1975; Fig. 1.5) with the size of consumed fish (primarily larval and juvenile <60 mm) remaining consistent throughout life. Larger snakes simply eat a greater quantity. The hypothesized advantage of this foraging strategy is to avoid the extensive body swelling associated with consuming large prey that could hinder lateral compression and thus prevent effective swimming. Over-

Figure 1.5. The diurnal *Hydrophis platurus* at the water surface with a prey-size fish (juvenile golden trevally, *Gnathanodon speciosus*); photo credit: B. Bessesen.

stretched skin could also reduce capacity for cutaneous respiration or sodium resistance (Brischoux & Lillywhite 2013). Captured prey is swallowed whole and headfirst (Kropach 1973, Voris & Voris 1983), usually after being subdued by a venom composed of potent neurotoxins excreted through a pair of small (1–2 mm) hollow fangs (Greene 1997). Additional solid and recurved dentary and maxillary teeth along with two rows of palatine teeth aid prey transport toward the esophagus (Pickwell & Culotta 1980). *Hydrophis platurus* is an extremely venomous species with a lethal dose of 0.06–0.44 *µ*g/g per the traditional scale of LD50 in mice; however, yield is quite low (Tu 2011). The venom protein composition is relatively simple as seen in other sea snakes (Lomonte et al. 2014) and it appears similar between pelagic sea snake populations around the globe (Tu 1976). Such small fangs and low venom yield may render humans relatively safe from mortal envenomation. Cases of death by this species are mostly anecdotal and documented bites have been described as either symptomless or causing localized pain and stiffness in adjacent joints. A myth persists that the mouth of *H. platurus* is too small to bite a human (Solórzano 1995), which is untrue: its gape is sufficiently wide owing to an exceptionally long jaw (Lillywhite 2014, pers. obs.). A defensive strike *can* cause injury. And yet, given all the snakebite envenomation events historically reported in Costa Rica, about 500 cases per year (predominantly by the terrestrial viperid *Bothrops asper*: Sasa & Vazquez 2002), including 48 mortalities from snakebite recorded over a 13-year period ending in 2006, none were from *H. platurus* (Fernández & Gutiérrez 2008).

An array of discriminating senses informs the pelagic sea snake as it navigates its aquatic world. Although it has been suggested that vision does not aid marine serpents in the capture of prey (Heatwole 1999), Brischoux & Lillywhite (2011) demonstrated a preference for high light levels in *H. platurus* that suggests some reliance on visual cues, and its genetically derived spectral characteristics indicate diurnality (Simões et al. 2020). Many nocturnal snakes have elliptical pupils that contract to slits in bright light, whereas all sea snakes have circular pupils more characteristic of diurnal foraging (Greene 1997, Lillywhite 2014). They do, however, have highly contractive function (Gillett et al. 2017) and can reduce to pinholes. The retinas of the pelagic sea snake have uncommonly extensive development of horizontal cell fibers associated with the perception of shape and movement, and overall eye structure promotes visual acuity above the water as well as below (Hibbard & Lavergne 1972). When it comes to sound, water is an excellent conductor, and sea snakes have well-developed inner ears, similar in structure to other vertebrates, despite lacking ear holes or eardrums (Lillywhite 2014). They are particularly sensitive to low frequencies. *Hydrophis platurus* is likely able to hear underwater auditory stimuli between 40–600 Hz, with peak sensitivity at 100 Hz (Chapuis et al. 2019). Environmental vibrations are sensed tactility through the whole body and into the quadrate bone near the jaw, stimulating the delicate ossicle called the columella (Lillywhite 2014). Local movements in the water may be detected by small tactile mechanoreceptors called scale sensilla, which are microscopic filamentous protrusions from the skin (Crowe-Riddell et al. 2016). Even though olfactory receptors are greatly reduced in sea snakes (Kishida & Hikida 2010), air-borne scents are detected via dorsally directed nares (Lillywhite 2014). The tines of the tongue, which are flicked out to collect chemical molecules, activate the vomeronasal organs above the palate. Somewhat surprisingly, sea snakes also possess taste buds (Greene 1997, Lillywhite 2014).

Ocean salinity averages 3.5%, and since a hydrophiid may ingest seawater during feeding, it has developed a salt gland under the tongue to aid osmoregulation (Greene 1997). This secretory organ effectively offsets salt loading (Dunson 1968). It was long presumed that *H. platurus* survived by drinking saltwater and employing its specialized gland to concentrate and excrete excess sodium (Greene 1997). Instead, it drinks from fresh-water lenses on the ocean surface produced by rainfall (Heatwole 1999, Lillywhite et al. 2019) and may endure long periods of chronic dehydration, especially in regions of severe drought (Lillywhite et al. 2012, 2014). The pelagic sea snake is sometimes mistaken as a strictly deep-sea species, when, in fact, it occupies areas of various depths, including waters ≤10 m (Kropach 1975). It is most often spotted 1–20 km from land (Savage 2002). When close to shore, beaching is a grave risk. Lacking the robust musculature and broad ventral scutes (the bony, plated scales used by terrestrial snakes for locomotion; Greene 1997) and with a circulatory system poorly adapted for gradients of gravitational or hydrostatic pressure (Lillywhite 1987, 1988, 2014), a pelagic sea snake is as helpless as a sea jelly on land. Individuals washed ashore by high wind or waves find themselves victims to exposure, predation, and circulatory collapse with no means of returning to the sea. Beaching appears to be a relatively common occurrence and a major cause of mortality (Dunson & Ehlert 1971, Kropach 1973, 1975).

Snakes are ectothermic, body temperature being primarily governed by external conditions (Greene 1997). The debated thermal melanism hypothesis posits that darkly colored individuals gain advantage in low temperature habitats owing to their ability to warm more rapidly through solar exposure (Trullas et al. 2007), but even if true, capricious seas and strong currents can carry a pelagic sea snake beyond the 18 °C isotherm and into waters too cold for reproduction or long-term survival (Hecht et al. 1974). The snakes do not even dive into thermoclines cooler than 19 °C (Rubinoff et al. 1986). If cold is a limiting factor for *H. platurus,* so is heat. Dark dorsal pigment naturally collects solar radiation during periods of feeding and basking, and while appropriate levels of heat can aid metabolic processes (Greene 1997), extreme thermal increases are hazardous. Dunson and Ehlert (1971) reported a critical thermal maximum of 33 °C. Graham et al. (1971) reported a higher lethal limit of 36 °C and demonstrated that the snakes dive to cooler thermoclines when temperatures are elevated. Diving, however, does not appear to be a direct function of thermoregulation (Graham 1974b) and is more likely used for positional purposes, allowing the animal to slow or change its lateral movement relative to surface velocity (Rubinoff et al. 1988). Waif records account for the wide range of *H. platurus* throughout the tropical and subtropical Indo-Pacific, but only a select number of locations meet the requirements for resident populations. Within the 26 °C isotherm and 100 m isobath where the prevailing currents, weather patterns and water depth are conducive, permanent breeding colonies of pelagic sea snakes may establish (Hecht et al. 1974). With average sea surface temperatures of ~28 °C (Wellington and Dunbar 1995, Rasmussen et al. 2011), the western coast of Central America is suitable habitat (Hecht et al. 1974).

1.4 | *HYDROPHIS PLATURUS XANTHOS*

1.4.1 An endemic emerges

Unicolor snakes were not in Smith's (1926) original seven forms, but because pelagic sea snakes have long been recognized as polymorphic, when Voris et al. (1970) and Kropach (1971b) collected all-yellow individuals in the ETP, they reported them as another color variety. Early studies conducted off northern Costa Rica showed the presence of all-yellow snakes to be extremely rare, from about 0.1% (4 of 3077 specimens: Tu 1976) to 1% (1 of 102 specimens: Bolaños et al. 1974). Farther south, however, near the mouth of Golfo Dulce, 3% of recorded snakes were of the yellow variety (9 of 278 specimens: Kropach 1971b). Nothing more followed in the literature until around 30 years later when a whole population of all-yellow sea snakes was discovered *inside* Golfo Dulce (Solórzano 2011, Bessesen 2012). When taxonomically described, the xanthic (Greek adjective for 'yellow') endemic was given the scientific name *Hydrophis platurus xanthos* (Bessesen & Galbreath 2017). Its original common name of yellow sea snake requires referencing Golfo Dulce to differentiate it from the Asiatic eel-eater, *Hydrophis spiralis,* which earned the same epithet for its golden hues marked by thin black bands (Ganesh et al 2019). In recent years *H. p. xanthos* has simply come to be called 'xanthos' by the local community—a shorter and perhaps more memorable common name.

Golfo Dulce is a curved embayment situated between the Osa Peninsula and Costa Rican mainland just above Panama (Wolff et al. 1996; Fig. 1.6). Several tectonic blocks make up the Central American landmass and Costa Rica is within the Chorotega Block, which forms the 'backbone' of the isthmus over which land mammals, including fossil horses, elephants, and mastodonts began migrating some 2.7 mya. The closure of the seaway between the ETP and the Caribbean was driven in large part by the subduction of the Cocos Ridge, which now extends from the Osa region southwest to the Galapagos Islands (Malzer & Fiebig 2008). Golfo Dulce opened approximately one to two million years ago when Panama's Burraca peninsula moved south, creating a pull-apart basin (Berrangé and Thorpe 1988, Hebbeln et al. 1996). The inlet measures 50 km long and 10–15 km wide (Hebbeln & Cortés 2001) and is characterized by a 215-m deep inner basin protected by an effective 60-m sill and shallow outer basin that restrict free exchange with the coastal masses. Due to its unusual bathymetry, currents in the upper gulf are weak and the deepest waters are occasionally anoxic, earning the term 'tropical fiord' (Svendsen et al. 2006). The regional climate is bimodal (Morales-Ramírez et al. 2015) and as the Golfo Dulce marine environment receives freshwater from four large rivers, saline measurements are low compared with the ocean, with fluctuations pursuant to seasonal rainfall. Sea surface temperatures also vary but remain relatively warm (Rincon-Alejos & Ballestero-Sakson 2015). Much like the proximal islands of Cocos and Galapagos, Golfo Dulce is rich in biodiversity. It hosts more than 1,028 residential and visiting species (Morales-Ramírez 2011), including conservation 'flagships': a variety of sea turtles (Bessesen & Saborío-R. 2012, Chacón-Chaverri et al. 2015a, Chacón-Chaverri et al. 2015b, Viejobueno Muñoz & Arauz 2015) and cetaceans (Cubero-Pardo 2007, Oviedo et al. 2015), as well as whale sharks (Toft & Larsen 2009, Pacheco-Polanco et al. 2015) and scalloped hammerhead sharks (Zanella et al. 2019).

During a 2010 pilot sighting survey we found typical pelagic sea snakes, *H. p. platurus,* near the mouth of Golfo Dulce and in the waters outside, and a seemingly evolutionarily distinct xanthic population inhabiting the inner basin (Fig. 1.6). Preliminary distribution maps suggested xanthos to be restricted to an extremely limited range with the entire allopatric clade contained above the sill, geographically separated from the pelagic sea snakes by a gap of about 22 km. Dozens of local fishermen and tour boat guides who participated in interviews during the same survey period confirmed seeing only xanthic snakes in that region (Bessesen 2012). It is yet undetermined when or how the endemism occurred. Perhaps a historically established resident population of pelagic sea snakes became sequestered by a rising seafloor or dropping sea levels, or perhaps waif individuals were washed into the quiet upper-gulf waters by shifting currents and formed a colony. Either way, a morphologically and behaviorally unique organism emerged.

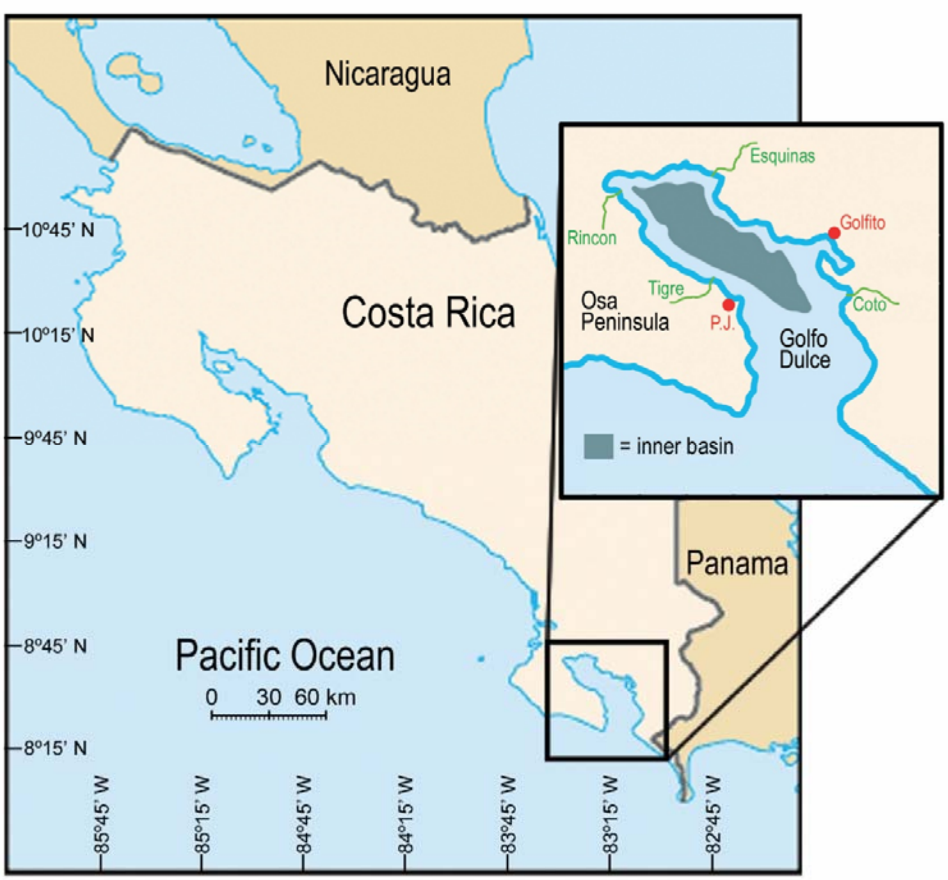


Figure 1.6. Costa Rica with insert of Golfo Dulce showing the four main rivers (green), two largest townships, Golfito and Puerto Jiménez (PJ; red), and inner basin area; map created in in PhotoShop (Adobe 2010).

1.4.2 Divergent morphology and behavior

A nonspecialized diet and ability to thrive in lower saline conditions likely allowed the original colonizers to inhabit the fiord-like habitat (Bessesen 2012). However, elevated temperatures presumably pushed the snakes toward their upper critical thermal threshold and could have resulted in the adaptive loss of black-producing dermal melanophores in favor of yellow-producing xanthophores (Fig. 1.1, 1.7) to reduce overheating at the water surface (Solórzano 2011, Bessesen 2012). The role of developmental plasticity in phenotypic expression is not fully understood but may also contribute to thermal optimization (Little & Seebacher 2017). *Hydrophis platurus xanthos* appears entirely yellow at first glance, prompting early postulation that such animals lacked the genetic material needed to produce black pigment (Tu 1976). Such speculation is unsubstantiated, though, as most specimens evince one or more tiny black dots or spots on the body and/or head, often near the supraocular scales. This vestigial melanin rarely generates marks larger than 5 mm (Bessesen 2012), and lacking dark skin around the eyes, xanthos' irises are usually pale with a greenish hue. I have examined the dermal tissues of live snakes under black light, and they do not appear to fluoresce (unpubl. data).

Whether the display of a yellow dorsum has any bearing on rates of predation is unknown, but *H. p. xanthos* appears timider than *H. p. platurus*. Every pelagic sea snake I have documented (n=10) was easily approached and most remained at the surface during the full observation period. When two pelagic specimens were touched on the tail, they both quickly turned and struck the boat hull. In contrast, xanthos is prone to dive when rapidly approached, especially during the day, and when touched on the tail has never struck but instead always dove (Bessesen 2012). Xanthos are occasionally found with scars that indicate traumatic injury, including one with a missing eye (unpubl. data). The fact that several known avian predators are present in Golfo Dulce (pelicans, wood storks, black hawks, and magnificent frigates) allows for some possibility of top-down predation, and dolphins are known to occasionally harass the yellow sea snakes (Bessesen et al. 2021). Of relevance here, Lamonte et al. (2014) found the yellow snakes to have the same venom protein profile as their black-and-yellow conspecifics.

While monochromatism is the most conspicuous diagnostic character of *H. p. xanthos,* the subspecies is also ≥30% shorter than *H. p. platurus* (Bessesen & Galbreath 2017). Measuring 69 adult specimens (43 free-ranging and 31 museum-held), we found TL averaged 49.1 cm (range: 40–59 cm), and none reached the reported minimum reproductive length for female pelagic sea snakes (60 cm: Vallarino & Weldon 1996; 65

cm: Kropach 1975). The mean tail length for xanthos was 5.4 cm (range: 4.3–7 cm; Bessesen & Galbreath 2017); this is shorter than the 8–9 cm reported for the sister group (Leviton et al. 2003) but consistent with the 11.2% of TL described by Cook and Brischoux (2014). At an average weight of only 46.6 g (range: 22–95 g), *H. p. xanthos* is also substantially lighter than *H. p. platurus* (Graham et al. 1971, Rubinoff et al. 1986, Bessesen & Galbreath 2017). Although no xanthic neonates have been systematically measured, the smallest specimens observed in Golfo Dulce appear to be around 15 cm in length (unpubl. data), which is significantly shorter than the 23 cm length described for neonate *H. p. platurus* (Vallarino & Weldon 1996) but consistent with the estimate of ≥30% shorter than adult TL. Physical size reduction at a population level suggests adaptive advantage. Snakes generally grow larger in warmer climates where there is less demand on ectothermic metabolism; however, small body size increases the surface-area-to-mass ratio and therefore promotes rapid thermal exchange, which could prove advantageous for snakes living in persistently elevated temperatures (Ashton & Feldman 2003).

In addition to morphological differences, xanthos exhibits modified behavior. Unlike *H. p. platurus,* which hunts diurnally in quiet waters, xanthos appears more nocturnal and is regularly seen in moderately turbulent seas, often assuming a sinusoidal, head-down feeding posture never reported for the species (Fig. 1.7). Xanthos is sometimes tumbled by larger waves when floating elongate (pers. obs.) and its bunched-up hunting position appears to be stabilizing (Bessesen & Galbreath 2017).

1.4.3 Taxonomic ranking

Within the systematic used to identify phylogenetic lineages, called taxonomy, the rank of subspecies is often contested as lacking meaning because characters based on overlapping geographic variation, especially coloration, might have no evolutionary bearing (Greene 1997, Burbrink et al. 2000, Phillimore & Owens 2016). That is clearly not the case with *H. p xanthos.* Indeed, our description of a subspecies was conservative (Bessesen & Galbreath 2017). Although the diagnosis lacked a few traditional components such as scale counts and hemipenis measurements, there is ample evidence of distinct genetic heritage: a singular population inhabiting an insulated marine habitat, evincing major morphological changes with associated phenotypic

Figure 1.7. Nocturnal ambush posture of *Hydrophis platurus xanthos:* floating at the sea surface, head down, mouth slightly agape (nearby a golden trevally, *Gnathanodon speciosus*); the slight distortion was caused by the camera flash through the water; photo credit: B Bessesen.

behavioral traits of adaptive significance (Dingemanse et al. 2007, Bessesen 2012, Bessesen & Galbreath 2017), as well as preliminary biochemical differences (Sheehy et al. 2012). Sea snake physiology and behavior can quickly evolve under selective pressure (Lukoschek & Keogh 2006), and the genus *Hydrophis* appears to be one of the most rapidly speciating clades of reptiles (Lee et al. 2016, Sanders et al. 2020). When Sheehy and colleagues (2012) compared mitochondrial DNA between xanthos and *H. p. platurus* from a gulf in northern Costa Rica near Nicaragua, they found significant difference ($p<0.05$) in two of four tests (Ks* and Z*, but not X^2 and Hs*). Notably, no cytochrome-b haplotypes were shared. Because shallow genetic divergence is expected (Lukoschek & Keogh 2006), *H. p. xanthos* may, in fact, be a rapidly evolved species deserving elevation to *Hydrophis xanthos*. This thesis forms the grounds for our efforts in that direction.

With the entire population of xanthic sea snakes bound to a single habitat, our primary goal in naming the subspecies was to provide a substantive, if preliminary, foundation for protection (Lenin 2017). Any geographically isolated endemic with a narrow range is rare and at risk (Rabinowitz 1981). Snake populations are facing precipitous declines worldwide (Reading et al. 2010) with losses among marine snakes prompting an urgent call for action (Udyawer et al. 2018). As *H. p. xanthos* resides in a habitat with increasing anthropogenic impacts, every effort to establish this organism in the faunal record and promote its protection is judicious (Bessesen & Galbreath 2017).

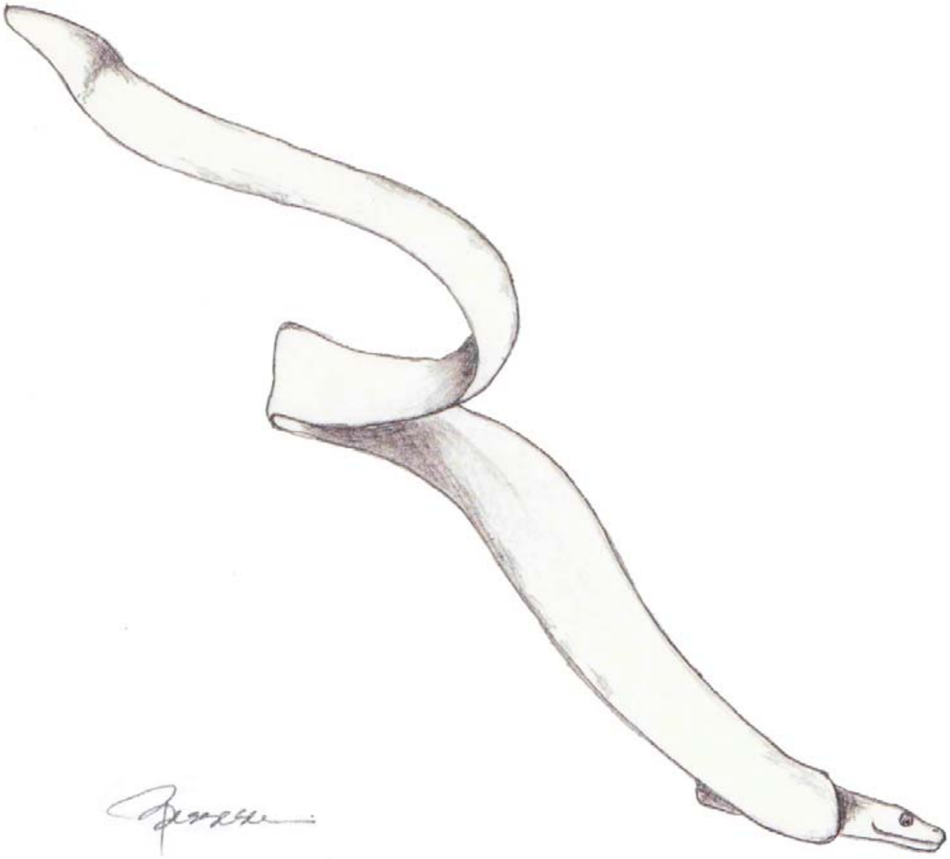
1.5 | AIMS AND STRUCTURE OF THIS THESIS

Driven by continuous curiosity about the natural history of xanthos, I proposed a doctoral research project under the supervision of Dr. Manuela González-Suárez in the Department of Ecology and Evolutionary Biology at the University of Reading School of Biological Sciences to build on the findings of my earlier work. I thereafter undertook six field studies in Golfo Dulce, Costa Rica, between January 2020 and May 2021. My research results are presented in this thesis as a collection of papers. Chapters and 3 have been submitted for publication at peer-reviewed journals and Chapters 4 and 5 have been published in *Ecology and Evolution* (Bessesen & González-Suárez 2022) and *Frontiers in Marine Science* (Bessesen et al. 2022), respectively. Another research article, published in *People and Nature,* can be found as an Appendix. It is based on local ecological knowledge (LEK) obtained through longitudinal interviews with fishermen and tour boat guides (Bessesen & González-Suárez 2021) and although it relates community perspectives about sea snakes in Golfo Dulce it also reports on other marine fauna and thus felt too tangential to the core theme of this thesis to include as a chapter. A short note about xanthos being harassed by dolphins, published in *Herpetological Review* (Bessesen et al. 2021), is also presented as an Appendix.

Each chapter following this introduction builds upon the previous. In Chapter 2 we combine published bathymetry data and sea snake sighting records collected during three survey periods over the course of a decade to investigate correlations between depth and presence of xanthos (observed in the inner basin) and the pelagic sea snakes (observed nearer the mouth of Golfo Dulce). In Chapter 3, we add to our understanding of depth as a predictor of xanthos presence by collecting hydrography data and using Maxent modelling to assess habitat suitability, plus we determine the taxon's area of occupancy. In Chapter 4, we investigate the snakes' activity cycle, which contrasts that of its ancestors. In Chapter 5, we use distance-sampling to model total population abundance and density estimates for *H. p. xanthos*. The concluding discussion in Chapter 6 draws upon key elements from each of the four research chapters to examine the comprehensive contribution of this thesis and the future work it inspires.

Expanded knowledge of *H. p. xanthos* not only has implications for the conservation of the snake itself (Elfes et al. 2013) but also for other flagship species dependent on Golfo Dulce, including whales, dolphins, sea turtles, sharks, and coral reefs (Bessesen 2015, Vargas-Zamora at al. 2021). A recent report by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services indicates that more than one million species of animals and plants are currently at risk of extinction—some within mere decades (IPBES 2019). According to Pimm et al. (1995), endemics are disappearing at the fastest rates. Such news emphasizes the need to improve our basic knowledge of ecology and population biology for many species worldwide with added urgency for protecting rare unique organisms like *Hydrophis platurus xanthos.* Consequently, this research focuses on the Golfo Dulce yellow sea snake with aims to serve both science and conservation.

Chapter 2



Author contributions: BLB conceived and designed the study, collected, and analyzed the data, and led the writing. MGS contributed to data analysis and manuscript review.

CHAPTER 2: The effect of bathymetry on sea snakes in Golfo Dulce, Costa Rica

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2.0 | ABSTRACT

Costa Rica is a biodiversity hotspot with its own endemic sea snake, *Hydrophis platurus xanthos*. Three reported aspects of xanthos ecology stem from a pilot study conducted in 2010: (1) the population inhabits the inner basin of Golfo Dulce (per basic delineations from nautical maps); (2) the population is allopatric (distribution maps showed a gap between *H. p. xanthos* and the related pelagic sea snake *H. p. platurus*); and (3) individuals do not aggregate in smooth water drift lines (as is common in the nominate taxon). As all these ecological aspects are likely to be influenced by bathymetry, we examine correlations between depth and sea snake presence in Golfo Dulce and its potential effect on distribution, partitioning, and drift-line use. We used data from three surveys conducted in 2010, 2011 and 2020 representing a combined effort of 85 days (25–30 days per 2-month study period) and >650 observation hours to analyze a total of 134 sighting records: *H. p. xanthos* (n=124) in the mid to upper gulf and *H. p. platurus* (n=10) nearer the entrance. Spatial distribution between surveys confirmed the xanthic population is isolated to the deep inner basin of Golfo Dulce, protected by shallow waters. Drift lines are not used by xanthos so they must not have the same ecological value observed for the pelagic sea snakes. We are cautiously encouraged in that encounters of *H. p. xanthos* progressively increased throughout the years, though overall counts remained relatively low.

Key words: distribution, drift lines, marine reptiles, New World sea snakes, sighting data, taxa partitioning, topography, water depth

2.1 | INTRODUCTION

The true sea snakes (Elapidae: Hydrophiinae) are an at-risk clade, facing a range of anthropogenic threats, from bycatch to human harvests to climate change (Hamann et al. 2007, Van Cao et al. 2014 Fry et al. 2015, Lillywhite et al. 2019). As many of the species are listed as Data Deficient by the International Union for Conservation of Nature (Elfes et al. 2013, IUCN 2021), there is a certain urgency for research focused on the natural history and ecology of these under-studied reptiles (Udyawer et al. 2018). Our main subject, the Golfo Dulce yellow sea snake, *Hydrophis platurus xanthos,* locally called xanthos, is a recently described endemic (Bessesen & Galbreath 2017; Fig 2.1B) bound to the inner basin of Golfo Dulce (Bessesen 2012, 2015). It is related to the pelagic sea snake, *Hydrophis platurus platurus* (previously *Pelamis platurus* or *platura*; Fig 2.1C), the only hydrophiine ever to cross the Pacific Ocean and arrive in the New World (Lillywhite et al. 2018).

The sister taxon, *H. p. platurus,* leads a planktonic lifestyle, passively transported by ocean flow (Cook & Brischoux 2014), although permanent breeding colonies may establish given suitable habitat ("demarked by the 26 C isotherm correlated with the 100 meter [sic] isobath"; Hecht et al. 1974). As air-breathing reptiles, all sea snakes must surface to ventilate, but the pelagic species spends approximately 87% of its time submerged (Rubinoff et al. 1986). Unlike congeners that actively hunt, pelagic sea snakes opportunistically capture small fish using a float-and-wait strategy (Klauber 1935, Brischoux & Lillywhite 2011), swimming slowly if at all at the water surface (Kropach 1975). Carried on ocean currents*, H. p. platurus* reached the American coastline sometime after the Central American Seaway closed (Bacon et al. 2015, O'Dea et al. 2016, Lillywhite et al. 2018). Easily recognized by their iconic two-tone coloring: black back with bright yellow undersides (Smith 1926), these venomous serpents were recorded by mariners in Costa Rican waters as early as 1519 (Taylor 1953). Some number presumably entered the narrow fiord-like inlet of Golfo Dulce and became separated from the wider population by a shallow shelf though precise understanding of the bathymetric partition has to date been absent. Unable to escape, the isolated group was obligated to adapt to its new environment.

Hydrophis platurus xanthos developed conspicuous all-yellow coloring and significantly smaller body size (Bessesen & Galbreath 2017), traits likely connected to thermal tolerance. While sea surface temperatures in the Eastern Tropical Pacific average ~28.5 °C (Wellington & Dunbar 1995, Rasmussen et al. 2011), well below the critical thermal maximum of ≥33 °C for *H. p. platurus* (Dunson & Ehlert 1971, Graham et al. 1971), sea surface temperatures in Golfo Dulce can reach 32.5 °C (Bessesen 2015, Rincon-Alejos & Ballestero-Sakson 2015). Lighter skin may help xanthos avoid overheating (Solórzano 2011, Bessesen 2012) and greater surface-area-to-volume ratio allows more rapid dispersal of heat. Dramatic behavioral differences may also increase survival. For example, pelagic sea snakes are considered diurnal across their transoceanic range (Brischoux & Lillywhite 2011, Simões et al. 2020), while xanthos are predominantly nocturnal (Bessesen & González-Suárez 2022). Pelagic sea snakes actively avoid rough seas (Dunson & Ehlert 1971, Tu 1976, Rubinoff et al. 1986; Cook & Brischoux 2014), but xanthos are commonly found among the waves, which they accommodate with an unusual sinusoidal ambush posture (Bessesen & Galbreath 2017). Of substance here, pelagic sea snakes are known to aggregate and feed in smooth water drift lines, or 'slicks' (Fig 2.1A), created by converging currents (Dunson & Ehlert 1971, Tu 1976, Lillywhite et al. 2010); they sometimes form sizable enclaves with possible reproductive value (Kropach 1971a, 1975). Early observations of xanthos, however, suggested minimal if any association with drift lines (Bessesen 2012, Lillywhite et al. 2015); thus, a departure from the usage of those marine features, if confirmed, could have important implications for feeding and reproduction.

Despite its common name, the pelagic sea snake is not exclusive to deep water. These serpents are frequently found in coastal regions (Hecht et al. 1974) and even in areas with waters <10 m deep (Kropach 1975). Xanthos, by contrast, are rarely encountered near the shallow coastal shorelines that surround Golfo Dulce's inner basin. We therefore expected the lateral distribution of *H. p. xanthos* to be highly determined by water depth. By comparing its spatial presence to that of *H. p. platurus* and systematically investigating the bathymetry associated with their divide, we contribute to the understanding of sea snake ecology in the Eastern Tropical Pacific, especially the tropical fiord of Golfo Dulce where increasing anthropogenic impacts of tourism, water contaminants, and fishery conflicts (Spongberg & Davis 1998, Spongberg 2004, Fargier et al. 2014, Fournier et al. 2019; Bessesen & González-Suárez 2021) highlight the need for stronger protective measures.

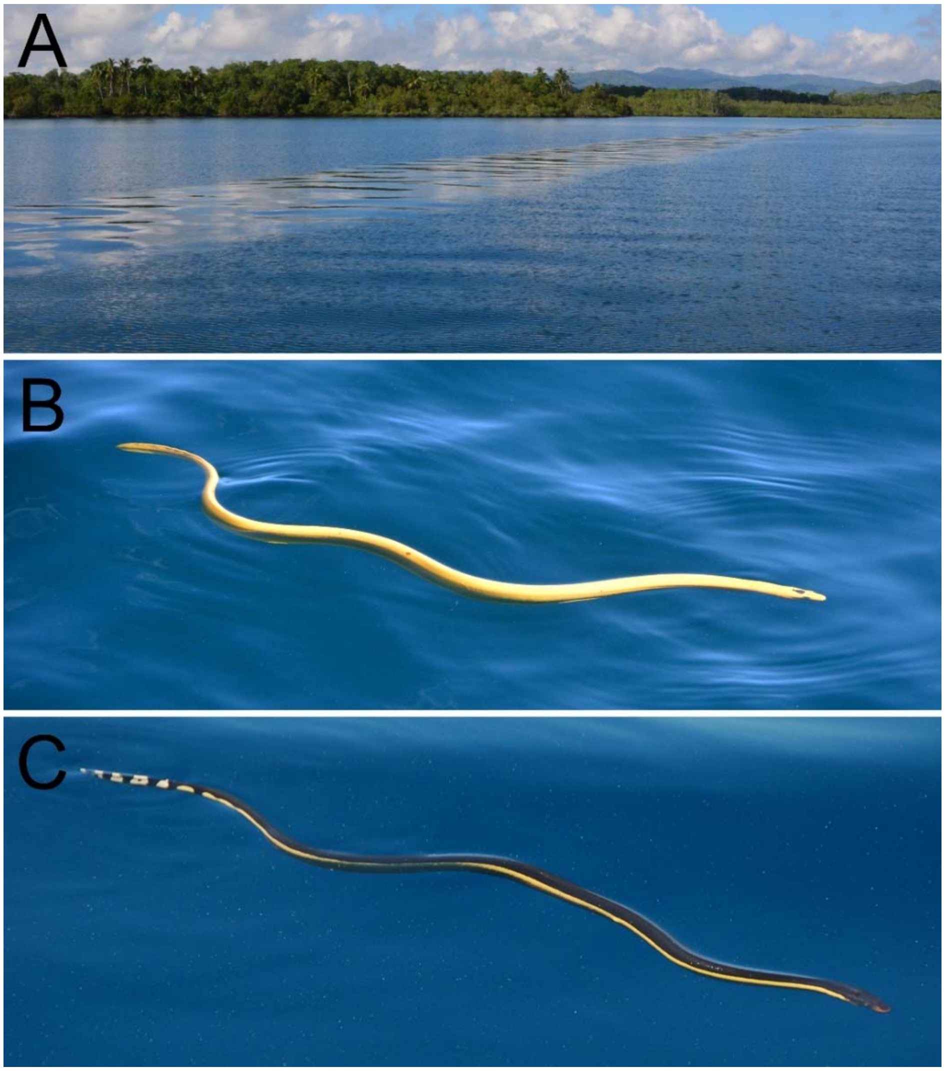

Figure 2.1. Photos of **(A)** a drift line (stripe of smooth water) in the inner basin of Golfo Dulce; **(B)** a xanthos, *Hydrophis platurus xanthos,* floating in the inner basin (not in a drift line); and **(C)** a Pelagic Sea Snake, *H. p. platurus,* floating in a drift line near the entrance of the embayment; photo credit: Brooke Bessesen.

2.2 | MATERIALS AND METHODS

2.2.1 Study site

Golfo Dulce is a dynamic marine environment (Quesada & Cortés 2006, Vargas-Zamora et al. 2021) positioned in the tropical zone between 8°22’N and 8°45’N and 83°06’N and 83°29’W (Fig. 2.2). This semi-enclosed embayment formed 1–2 mya through tectonic shifts (Berrangé 1989, Wolff et al. 1996). At approximately 50 km long and 10–15 km wide (Svendsen et al. 2006), its surface area measures about 725 km2 (Bessesen 2012).

A steeply sloped inner basin >200 m deep dominates the upper gulf, defined by an effective sill at 60 m and a shallow outer basin extending south toward the entrance that limit free exchange between the deep interior waters and broader coastal masses (Hebbeln et al 1996; Hebbeln & Cortés 2001). The average water depth above the sill line is 112.7 m (range: 0.1–215 m per GEBCO 2014). Such fiord-like features are rare to the tropics (Richards et al. 1971). Drift lines, seen as bands of smooth water, may develop wherever currents converge (Fig. 2.1A). Golfo Dulce has a generally clockwise pattern of circulation throughout the central waters with increased irregularity in the littoral zones. The current structure is stratified: the deep inner basin maintains a slow-moving, two-layer estuarian circulation (out-flowing surface layer and deep in-flow), while the outer basin is marked by a three-layer current structure (flowing outward at the surface and at depth, with an in-flowing middle layer), creating disorderly currents in the transition area between (Svendsen et al. 2006). There is significantly stronger circulation in the outer basin (Morales-Ramírez et al. 2015), subject to complex forces, including tides, wind stress, and freshwater runoff (Svendsen et al. 2006). Several rivers feed the marine and mangroves are common to those riparian zones, while skerries, coral reefs, sandy beaches, montane rainforest, and deforested slopes are featured along the coastal periphery (Wolff et al. 1996).

2.2.2 Field surveys

Between 2010 and 2020, we conducted 85 daily onboard sighting surveys across all waters of Golfo Dulce. Effort was divided into three 2-month study periods: January–February 2010 (dry season), July–August 2011 (rainy season) and January–February 2020 (dry season). Data were collected from a small (3-6 m) boat, always replicating the same methods (Bessesen 2012, 2015) with the same observers (BLB and research assistant/ boat captain Jorge Largaespada). The gulf was divided into four Geographical Areas labelled GA1–4 (Fig. 2.2). Because Puerto Jiménez served as our base of operations, GA2 and GA3 were designed larger to account for additional time spent passing through them as corridors to GA1 and GA4. Each day we traversed one Geographical Area in a variable pattern, generally employing a rotation of GA1, GA3, GA2, GA4, and every effort was made between years to ensure similar coverage near the coast and in the midwaters. We did not actively survey waters outside the gulf, marked GA5, although sightings did occasionally occur there while we worked along the border of GA4/5. Nearly all surveys were completed during daylight hours, with three nighttime outings in 2010, one in 2011, and two in 2020. Sea snake sightings were registered using Global Positioning System (GPS), along with observation time, initial distance from our boat, and closest approach. We identified drift lines as bands of obviously smoother water than the surrounding sea, often slick in appearance and/or marked by flotsam (Fig. 2.1A). Taxa were recorded as X (for xanthos, *H. p. xanthos*) or P (for pelagic sea snakes, *H. p. platurus*), and photographs and/or video were collected for documentation whenever possible (Fig. 2.1B–C). Daily solar and tidal charts were kept, and we recorded environmental conditions near the marina of Puerto Jiménez at the start and end of each observation period, including time, Beaufort Wind Force (BWF), air temperature, sea surface temperature (SST), visibility, and prevailing weather. Approximate survey coverage of the study area divided by Geographic Area is presented in Table 2.1.

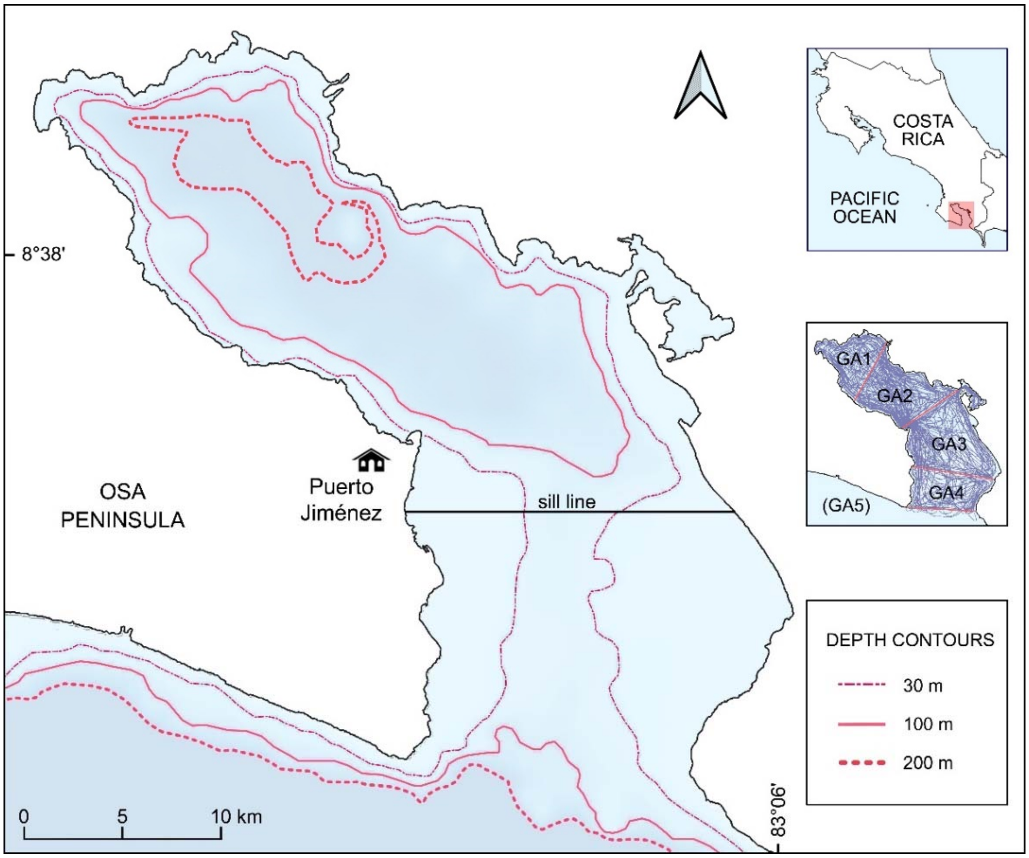

Figure 2.2. Map of the study area (Golfo Dulce, Costa Rica), showing location, bathymetry, 60-m sill line (per Hebbeln and Cortez 2001), and Geographic Areas (GA1–4) with survey coverage

as track lines; maps created with QGIS (QGIS Development Team 2020).

2.2.3 Data analysis

To ensure a robust analysis of our dataset, we compared sighting frequencies in Geographical Areas between taxa using a chi-square test with p-value calculated using Monte Carlo simulation with 5000 replicates fitted using the function chisq.test in base R (R Development Core Team 2020). All sea snake sightings were mapped, and spatial analyses were conducted using QGIS (QGIS Development Team 2020). A water depth raster at a resolution of 60x60 m pixels was acquired from the General Bathymetric Chart of the Oceans (GEBCO 2014) Grid from the Global Multi-Resolution Topography Synthesis (Ryan et al. 2009). To establish depths for the entire embayment, we first created 6152 systemized random sampling points in Distance 7.3 (Thomas et al. 2010) covering all waters of Golfo Dulce and then extracted raster-to-point values for depth in QGIS and examined them using R. Due to anomalies in the GEBCO data showing two tiny areas of extreme depth, possibly stitching errors, we capped maximum depth at 215 m as described by Svendsen et al. (2004). Next, we extracted raster-to-point depth values for all snake sightings. For depth comparisons, we analyzed presence-absence: presence was defined as ≥1 sightings per 60x60 depth pixel (we note that nearly all records fell in separate pixels). Shapiro tests (shapiro.test in R) indicated depth data were not normally distributed, so we compared depth data between taxa and with systemized random points using non-parametric Mann-Whitney U tests (function wilcox.test in R). To compare sightings with systemized random sampling points, we first used the sample function in R (without replacement) to generate 1000 random datasets, each with sample size equal to that of the sighting data for each taxon. Each of those random datasets were then compared to the sighting data, generating 1000 Mann-Whitney U test results. We used the percentage of significant results and the differences in medians from these 1000 tests as evidence of deviations in sighting depths from the expected (the systemized random). For association with drift lines, we compared taxa using a Pearson's Chi-squared test (chisq.test in R), based on whether individuals were observed inside a drift line (*yes* or *no*). We conservatively used Yates' continuity correction given the 2x2 contingency table and low numbers of observations for pelagic sea snakes. In all tests we use alpha=0.05. Descriptive statistics are provided as mean, SD and range for normally distributed variables and as median, interquartile range (IQ), and range for non-normally distributed data.

2.3 | RESULTS

On-water observation periods typically began after sunrise and were completed by late afternoon. Near the shores of Puerto Jiménez where we recorded environmental conditions at the start and end of each day, dry season air temperature averaged 29.7 ± 2.8 °C (mean ± SD; range, 24.5–35.2 °C), as compared with the rainy season at 27.5 ± 2.2 °C (range, 23.5–31.0 °C). Sea surface temperature in the dry season averaged 30.3 ± 1.0 °C (range, 28.0–32.5 °C) and 29.0 ± 1.2 °C (range, 26.5–31.5 °C) in the rainy season. Waters in the marina were most frequently recorded as BWF2 (smooth wavelets, <0.1m), rarely reaching BWF4 (slight, small wave caps, 0.5–1.2 m). Clouds prevailed throughout all three study periods and visibility was generally greater than 15km.

Over the course of three survey periods (85 survey days; 656.25 observation hours) covering both dry and rainy seasons, we encountered 134 sea snakes. More than three quarters were photographically documented. Xanthos accounted for 124 sightings, and our counts increased in every subsequent survey period (n=30→38→56), nearly doubling between 2010 and 2020 despite a consistent sampling effort. In contrast, only one Pelagic Sea Snake was encountered in 2020, which, when compared with 9 in 2010, marked an 89% decline in counts of that taxon between the dry-season surveys (none were seen in the rainy season). We found a significant difference in taxa distribution by Geographic Area (χ^2=134, p=0.0002). In all three study periods, *H. p. xanthos* encounters were limited to GA1 or GA2, with the exception of a single individual found in GA3 during the rainy season and at an unusual depth (9 m). On the other hand, pelagic sea snakes were never observed above GA4. The estimated distance between populations, based on sightings, remained similar between 2010 (21.6 km) and 2020 (22.9 km).

Table 2.1. Approximate surface area (km^2) for four Geographical Areas: GA1 (innermost gulf), GA2 (mid-upper gulf), GA3 (mid-lower gulf), GA4 (closest to entrance) with GA5 representing waters just outside the gulf; estimated survey effort for each survey period by days and hours

with sighting counts of sea snakes by taxa: X (Xanthic Sea Snakes, *Hydrophis platurus xanthos*) and P (pelagic sea snakes, *H. p. platurus*).

GA		**2010**			**2011**			**2020**		
Location	km^2	Days of rotation	Survey hours	X|P	Days of rotation	Survey hours	X|P	Days of rotation	Survey hours	X|P
GA1	130	7.25	55.50	7|0	6.50	42.25	3|0	7.50	55.25	14|0
GA2	192	8.25	65.75	23|0	6.00	51.00	34|0	8.00	65.25	42|0
GA3	256	7.25	63.25	0|0	6.50	55.25	1|0	7.25	63.25	0|0
GA4	147	7.25	47.50	0|4	6.00	41.50	0|0	7.25	47.00	0|0
GA5	-	-	1.00	0|5	-	0.75	0|0	-	1.75	0|1
Totals	**725**	**30**	**233.00**	**30|9**	**25**	**190.75**	**38|0**	**30**	**232.50**	**56|1**

Xanthos was dependably recorded in the inner basin at water depths considerably deeper than the gulf average (100% of tests returned $p<0.001$) and deeper than areas used by pelagic sea snakes ($W=1086$, $df=10$, $p<0.0001$; Fig. 2.3). Xanthos' median depth (from 118 unique presences by depth) was 197.9 m (IQ 184.3–203.3; range, 9.3–215.0), while the pelagic sea snake's median depth was 101 m (IQ 79.3–110.7; range, 22.8–194.4), and the median depth of the entire gulf was 74.5 m (IQ 15.9–160.4; range, 0.1–215.0). Depths utilized by pelagic sea snakes were less clearly different from the expected based on average gulf depths (39% of tests had $p<0.05$). We additionally note that xanthos were quite rare in waters of 30–99 m depth (2.4% of 118 locations) while pelagic sea snakes were seen fairly frequently in those depths (40% of 10 locations; Table 2.2).

Drift lines were commonly seen in Golfo Dulce and appeared to occur in all four Geographic Areas (Fig. 2.1A), but association to slicks was significantly different between the two sea snake taxa ($\chi^2=202.4$, $df=4$, $p=0.0002$; Fig. 2.1B–C). For *H. p. platurus*, 80% (8 of 10 snakes) were seen inside drift lines compared with 3% (4 of 124 snakes) for *H. p. xanthos.* Moreover, three of those xanthic individuals were found on a morning after heavy overnight rains along with five other xanthic snakes that were recorded *outside* the drift line.

Table 2.2. Surface sightings by taxa (X=xanthos, *Hydrophis platurus xanthos*; P=pelagic sea snakes, *H. p. platurus*) and water depth (in meters).

Depth	X	P
<30	1	1
30-99	3	4
100-149	10	4
150-199	54	1
≥200	50	0
Totals	**118**	**10**

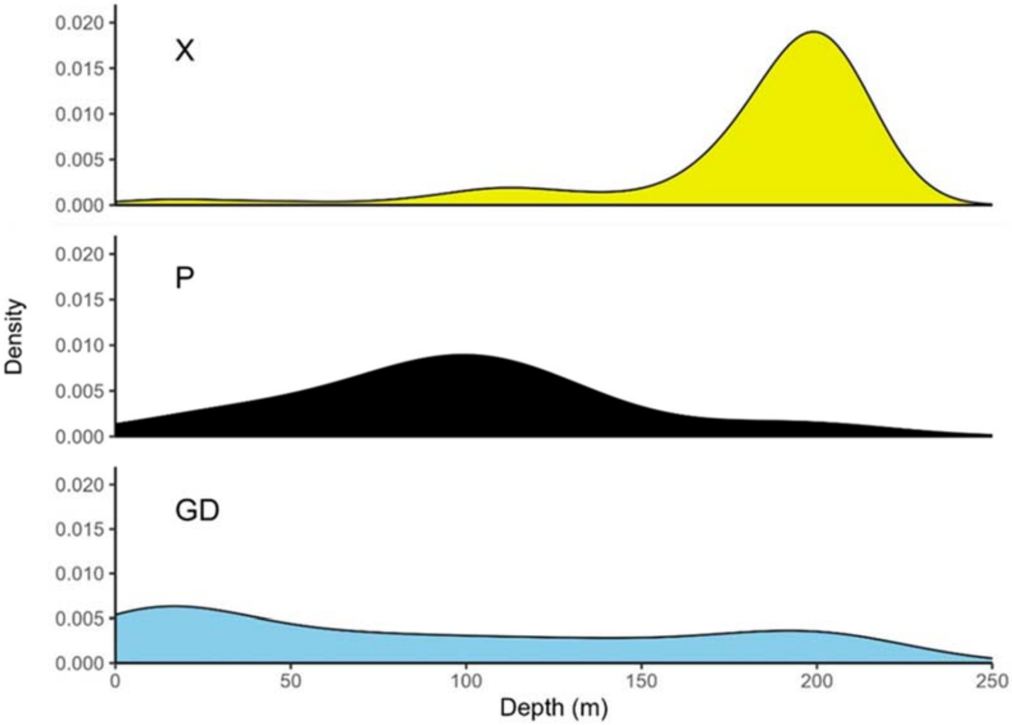

Figure 2.3. Density plots of water depth (in meters) for sightings of xanthos, *Hydrophis platurus xanthos* (X; n=118), sightings of pelagic sea snakes, *Hydrophis platurus platurus* (P; n=10), and systemized random waypoints across Golfo Dulce (GD; n=6152).

2.4 | DISCUSSION

This study improves our understanding of the ecology of Costa Rica's endemic sea snake, *H. p. xanthos,* by describing how bathymetric features correlate with sea snake distribution and population isolation. Sea snake encounter data accrued over more than a decade confirmed site fidelity of the xanthic population to the deep inner basin of Golfo Dulce. During our surveys we only made a few nighttime outings and found xanthos at the surface more commonly after dark, though day or night they remain in areas of deep water (Bessesen 2012, 2015); an investigation of the population's diel cycle confirmed nocturnal activity (Bessesen & González-Suárez 2022; Chapter 4). Our findings show a preference for the deepest sectors. North of the 60-m sill line described by Hebbeln et al. (1996) water depths average 112 m (GEBCO 2014), yet the endemic sea snakes were consistently found in depths closer to 200 m and rarely entered depths <100. We hypothesize that prey availability plays a role in xanthos selecting for deeper zones, and those areas may provide more suitable water conditions. The snakes may also seek to avoid disruptive circulation patterns closer to shore. Although pelagic sea snakes were found in the relatively deep waters near the entrance, they also evidently venture into shallower areas. Our ability to infer details about *H. p. platurus* is limited given our small sample size (n=10) and the fact that all waters surveyed below the sill line were <200 m. The seafloor outside Golfo Dulce drops to >500 m (GEBCO 2014), but since we did not actively search the deep Pacific Ocean where the largest proportion of the Indo-Pacific population of pelagic sea snakes resides, observed depths for that taxon are likely not representative of the species overall.

The geographical gap between populations of *H. p. xanthos* and *H. p. platurus* is expected to prevent genetic flow and maintain two allopatric populations. The basis of the partitioning appears predominantly to be bathymetric. Depths in the inner basin and the open Pacific Ocean reach >200 m, but the shallow outer basin measures ≤30 m. That Kropach (1975) reported seeing pelagic sea snakes off Panama in waters <10 m deep suggests profundity alone is an insufficient barrier. Therefore, other factors likely contribute. For example, the depth disparity between the inner and outer gulf have led to complex hydrographic patterns, and the disorganized currents near the sill line and more-intense circulation in the southern gulf (Svendsen et al. 2006, Morales-Ramírez et al. 2015) may prevent the regular passage of sea snakes, evinced by a dearth of easily recognized black-and-yellow snakes in GA1–GA3. Temperature and/or other environmental conditions could also influence sea snake distribution. Elevated thermal conditions inside Golfo Dulce, which may have led to adaptive coloring (Solórzano 2011) and a nocturnal activity pattern in xanthos (Bessesen and Gonzalez-Suarez 2022), could potentially limit survival of pelagic sea snakes above the sill. Sea surface temperatures in Golfo Dulce reach >32 °C (Bessesen 2015, Rincon-Alejos & Ballestero-Sakson 2015) and the critical thermal limit of *H. p. platurus* is 33–36 °C (Dunson & Ehlert 1971, Graham et al. 1971). Only two adult *H. p. platurus* have ever been documented above the sill line: one presumably swept in by Hurricane Otto (Bessesen & Galbreath 2017), and the other almost certainly carried to port in a ship's ballast (Phoebe Edge, pers. comm.). Both appeared ailing and likely to die. Similarly, if xanthos is stenotopic, it may not thrive outside the gulf. A few all-yellow sea snakes have been recorded in the Eastern Tropical Pacific (Kropach 1971b, Bolaños et at. 1974, Tu 1976) and are therefore thought to sometimes exit the gulf. Within our dataset, only one *H. p. xanthos* was logged in GA3 during the rainy season survey, perhaps swept from the inner basin by weather-induced wind and waves (Bessesen 2015). The animal appeared healthy at the time of sighting but whether it eventually entered the Pacific Ocean and/or thrived outside the inner basin remains unknown.

We were encouraged by increasing encounters of *H. p. xanthos.* This positive relative abundance trend was also described by fishermen and tour boat guides systematically interviewed in 2010 and again in 2020 (Bessesen & González-Suárez 2021; Appendix). If that taxon's numbers are indeed rising, there are three possible explanations: (1) the xanthic population is newly established and still expanding toward the inner basin's carrying capacity; (2) the xanthic population naturally experiences stochastic fluctuations in size; or (3) the xanthic population is long established but suffered a decline from which it is now recovering. While the first supposition cannot be ruled out, particularly when considering storms, it seems implausible that a few reproductive individuals of *H. p. platurus* recently washed into Golfo Dulce from the Pacific Ocean, survived the heat, and quickly proliferated. We consider it is more feasible that colonization occurred when the waters were cooler. Perhaps a residential colony of *H. platurus* was trapped by shifting sea levels and/or currents. A longer timeline would have allowed the serpents to successfully adapt through rising temperatures to a monochromatic state, reduced body size, and nocturnal foraging strategy, emerging as a different organism. Shallow but distinct genetic differences between the pelagic and xanthic populations support this theory (Sheehy et al. 2012). A recovery from a past decline or fluctuating dynamics are more likely explanations for the recent increase. Pelagic sea snakes are bycatch in trawl fisheries in other parts of the world (Fry et al. 2015), and semi-industrial shrimp trawlers did historically ply the waters of Golfo Dulce. Those trawlers were bought out in 2010 (Fargier et al. 2014), the same year as the pilot study for this work (Bessesen 2012), which could explain the increase in xanthos seen since that time.

Concerningly, we note an apparent decline in pelagic sea snakes near the gulf entrance. Although our sample is too small to provide strong evidence, and natural fluctuations in presence may be at play, a fisherman we interviewed in 2020 also described seeing fewer pelagic sea snakes in recent years (Bessesen & González-Suárez 2021; Appendix). *Hydrophis platurus platurus* is the world's most widely ranging snake (Pickwell & Culotta 1980; Smith 1926), and Kropach (1973) recorded thousands of them in Panama Bay, yet it remains possible that the regional population is now declining (Lillywhite et al. 2015), and an assessment of the pelagic sea snakes in the Eastern Tropical Pacific is strongly suggested.

We unfortunately did not collect quantitative data for drift line counts in Golfo Dulce, although they were commonly seen throughout the embayment. Pelagic sea snakes were almost always seen floating in drift lines, corroborating a study by Lillywhite et al. (2015) that found 99% of observed pelagic sea snakes off the shores of northwestern Costa Rica to be in drift lines. Meanwhile, only a few xanthos showed any association, and even then, most individuals remained outside the slick. Two hypotheses are proposed for *H. p. xanthos'* divergent disassociation with drift lines. The first addresses a potential lack of utility for passive transport and/or reproduction. If drift lines fail to carry snakes out of the embayment, perhaps they prove of little use: adapted to the inner basin environment, the xanthic snakes have nowhere else to go. Unlike in the vast ocean, reproduction within a narrow distribution area may not require aggregation; still, there seems no reason why the snakes would not continue to forage in drift line unless other factors are at play. Our second hypothesis, which may work in combination with the first, has to do with *H. p. xanthos* feeding at night. It has been proposed that given good visual acuity (Hibbard & Lavergne 1972) and a preference for high light levels (Brischoux & Lillywhite 2011), pelagic sea snakes may identify drift lines by sight (Rubinoff et al. 1988). That possibility that would not exist for the nocturnal xanthos. Whatever influenced the xanthic population to disassociate with drift lines, it would be worth examining whether rates of feeding and/or reproduction have been affected.

Confirming that *H. p. xanthos* is a bathymetrically isolated endemic sparks curiosity in numerous other ecological aspects that could be explored to gain insight into the population's natural history. For example, we would be interested to understand how environmental conditions, such as temperature, dissolved oxygen, and salinity influence habitat suitability for the xanthos and limit its potential geographic range. Most importantly, given that several taxa of sea snakes are apparently disappearing due to unknown causes (Goiran & Shine 2013, Lukoschek et al. 2013, Udyawer et al. 2018), and that the xanthic population occupies a relatively small area of habitat, a systematically derived abundance estimate of the *H. p. xanthos* population could prove critical for future assessment of trends and ideally guide conservation policy and marine management in Golfo Dulce.

2.5 ACKNOWLEDGMENTS

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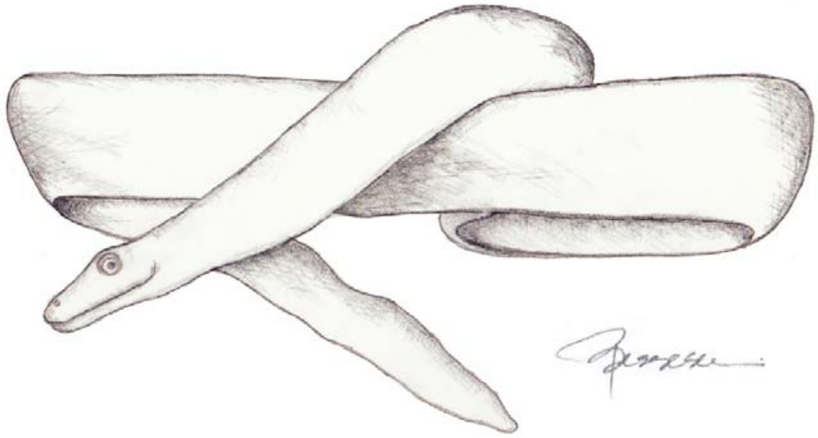
Chapter 3



Author contributions: BLB conceived and designed the study, collected the data, undertook most of the analyses, including distance weighted interpolations, and drafted the manuscript. CGC created exploratory Kriging interpolations and reviewed the manuscript. MGS contributed to the statistical methods, data analysis and manuscript revisions.

CHAPTER 3: Habitat suitability and area of occupancy defined for rare New World sea snake

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3.0 | ABSTRACT

Xanthos (*Hydrophis platurus xanthos*) is a marine reptile endemic to the inner basin of Golfo Dulce, Costa Rica, and one of only two sea snake taxa found in the New World. In this study we assessed several marine conditions that describe its habitat, and we define its geographical distribution range. We used 423 occurrence records of xanthos collected during multiple studies to model habitat suitability in Maxent considering water depth and 12 interpolated hydrographic variables: Beaufort wind force, sea surface temperature, and probe readings at 0.5 m and 10 m for temperature, salinity, dissolved oxygen, turbidity, and pH collected in 2020 and 2021 at 68 sampling locations. We used area under the curve (AUC) to evaluate our Maxent models and the cloglog minimum training presence threshold to render our suitable habitat maps. The most influential environmental predictor was depth, but occurrences were also affected by hydrographic conditions. Indeed, a model excluding depth consistently identified only areas in and around the inner basin area as suitable, suggesting the sea snakes are not only restricted by depth but likely have adapted to water conditions that differ from those farther to the south and outside the gulf in the broader Pacific Ocean. Anthropogenic and climate-induced changes may already be impacting the marine environment of this single, isolated population. Our study offers the first quantitative evaluation of habitat suitability and estimates of its extent of occurrence (282 km^2) and current area of occupancy (260 km^2) that can inform conservation assessments and guide protection measures.

Key words: area of occupancy, Costa Rica, extent of occurrence, Golfo Dulce, habitat suitability, Hydrophis platurus xanthos, species distribution modelling

3.1 | INTRODUCTION

Understanding and protecting biodiversity require information about where taxa occur and their habitat preferences. Species distribution models (SDM) combine occurrence data and environmental information to delineate potential distribution ranges and identify natural conditions within an animal's habitat (intuitively deemed 'suitable') and can aid assessments of conservation status for potentially vulnerable taxa. Xanthos (*Hydrophis platurus xanthos* Bessesen & Galbreath, 2017) is the yellow sea snake confined to the inner basin of Golfo Dulce, Costa Rica, inhabiting an extremely narrow range. The semi-enclosed embayment where the population resides is considered a rare tropical fiord where relatively warm waters prevail, freshwater discharge creates brackish conditions around several large river outlets, and reduced circulation causes periodic anoxia in the deepest regions (Svendsen et al. 2006). These conditions contrast the habitat of the pelagic sea snake, *H. p. platurus,* xanthos' closest relative and sister group, which has a wide distribution ranging across the Indo-Pacific. The pelagic sea snake inhabits cooler waters with a thermal tolerance of 18–33 °C (Dunson & Ehlert 1971), and oceanic salinity (35 ppt) is managed through dermal osmoregulation (Dunson 1975) and sublingual salt-excretion glands (Dunson 1968). The species, which spends most of its time in long slow dive cycles to an average max depth of 15 m (Rubinoff et al. 1986), also depends on dissolved oxygen in the marine environment as it respires up to 33% of its oxygen requirements through its skin (Graham 1974a). How the early colonizers of Golfo Dulce adapted to the embayment's distinct conditions is unclear, but it has been hypothesized that elevated thermal conditions have resulted in morphological and behavioral adaptations, including lighter coloration (Solórzano, 2011), smaller body size (Bessesen & Galbreath 2017) and a nocturnal diel cycle (Bessesen & González-Suárez 2022; Chapter 4). Although xanthos appears to be restricted to the deepest, presumably coolest, waters of Golfo Dulce (Bessesen 2015, Bessesen & González-Suárez, in review; Chapter 1), habitat suitability has remained largely undefined.

Among available tools for SDM, MaxEnt, machine learning maximum entropy modelling, is one of the most widely used (Phillips et al. 2004, Phillips et al. 2006, Franklin & Miller 2010). While SDMs can be utilized with presence-only data (Elith et al. 2011, Merow et al. 2013), defining pseudo-absences as records of other taxa in the same ecological zone appears to improve performance (Phillips et al. 2009, Barbet-Massin et al. 2012). Careful data selection and model settings (Warren & Seifert 2011, Halvorsen 2012, Merow et al. 2013, Phillips et al. 2017), mitigation of sampling bias (Kramer-Schadt et al. 2013, Syfert et al. 2013, Fourcade et al. 2014), and model tuning (Radosavljevic & Anderson 2014, Kalinski 2019) also support reliable results, and there has been a judicious call for the mapping of SDM model uncertainty (Jansen et al. 2022). In this study we use MaxEnt to define the range of suitable habitat for xanthos considering 13 variables and greater than 400 sea snake sightings accrued through multiple surveys in Golfo Dulce over more than a decade. Our work fills a sizeable knowledge gap about the potential effect of near-surface water conditions on a geographically isolated sea snake.

3.2 | MATERIALS AND METHODS

3.2.1 Study area

Golfo Dulce is a semi-enclosed embayment located along the southwestern shoreline of Costa Rica just above Panama (Fig. 3.1). It measures about 50 km long and 10–15 km wide, curving toward the northwest, with fiord-like features marked by the proximity of neritic and mesopelagic zones (Wolff et al. 1996). A deep (215 m) inner basin with a slow-moving two-layer estuarine circulation is held by an effective 60-m sill (Svendsen et al. 2006). Stratification is dynamic and influenced by the El Niño–Southern Oscillation (ENSO; Quesada-Alpízar & Morales-Ramírez 2004). Dalsgaard et al. (2003) found the pycnocline at a depth of 40–55 m. Dissolved oxygen rapidly declines in the vertical column (Richards et al. 1971, Quesada-Alpízar & Morales-Ramírez 2004); anoxic conditions periodically affect the deeper realms due to limited water circulation (Hebbeln et al. 1996). A more-shallow outer basin extends from the sill line south to the mouth of the gulf. Currents in that area show substantially greater speed and strength due to a three-layer current structure: a surface and deep layer flowing outward and a middle layer flowing inward (Svendsen et al. 2006, Morales-Ramírez et al. 2015).

The regional climate is bimodal with a dry season from December through April (<300 mm/mo rainfall) and rainy season May through November (>500 mm/mo rainfall; Acuña-González et al. 2006, Morales-Ramírez et al. 2015). February is the driest month (<100 mm rainfall; Lobo et al. 2008). Freshwater drainage from multiple rivers feeds the marine environment (Umaña-V 1998) and relative to the ocean's average salinity of 35 ppt, measurements in Golfo Dulce are low at <32 ppt, sometimes dropping to <21 ppt near large river outlets during the rainy season (Acuña-González et al. 2006, Rincón-Alejos & Ballestero-Sakson 2015). Sea surface temperatures (SST) in Golfo Dulce vary but remain relatively warm, averaging approximately 30 °C and occasionally reach 32.5 °C (Rincón-Alejos & Ballestero-Sakson 2015) as compared with SST of 28.3–28.6 °C in the adjacent Pacific (Wellington & Dunbar 1995, Rasmussen et al. 2011, Lillywhite et al. 2015). Dissolved oxygen levels in the inner basin are generally higher near the surface, decreasing with depth, and are considered anoxic below about 100 m depth (Dalsgaard et al. 2003). Oxygen concentrations reach $\simeq 0$ in waters 150–180 m deep (Richards et al. 1971, Acuña-González et al. 2006, Morales-Ramírez et al. 2015). Turbidity has historically been assessed with a Secchi disc and measurements in Golfo Dulce have suggested temporal variance: during the dry season, lower turbidity readings are obtained in the deeper midwaters with higher readings nearest the shoreline, especially at rivermouths, while in the rainy season river output increases turbidity throughout the embayment (Rincon-Alejos & Ballestero-Sakson 2015).

3.2.2 Hydrographic and bathymetric data

We used the program Distance version 7.3 (Thomas et al. 2010) to create a systematic survey design with 68 sampling locations, or waypoints (WPs), across the study area: 42 WPs in the Upper Gulf (an area known from previous studies to support more sea snakes) and 26 WPs in the Lower Gulf (Fig. 3.1). Sampling was conducted in shallower depths (0–10 m) where sea snakes breathe, rest, and feed, when they are not deep-diving. During 7 days in 2020 (between 12–29 January) and 3 days in 2021 (from 15–17 March), we used a lab-calibrated YSI ProDSS multiparameter probe to collect hydrographic data. Readings of temperature (°C), salinity (ppt), dissolved oxygen (optic; mg/L), turbidity (NTUs), and pH (scaled 0–14) were taken at depths of 0.5 m and 10 m. We also used a Traceable ISO 17025 calibrated water thermometer to take additional temperature readings at the sea surface. Date, time, prevailing weather, and Beaufort wind force (BWF; Fig. 3.2) were also recorded. Readings were repeated on two or more days at 30 WPs and 2–4 times per day at 6 WPs. Visits to WPs took place during daylight hours, except for one visit to U1, U2, and U22 after dark (1800–2030 h; these sites were also sampled multiple times during the day). For comparison, we also report 88 SST readings and 709 BWF records at actual xanthos sightings collected over approximately 11 years (not always during daylight hours). At 10:21 on 14 March 2020, a 29-min tank-assisted scuba dive was carried out to a depth of 31.4 m at 8°40' N, 83°22' W and thermal readings were recorded on a Suunto Vyper dive computer.

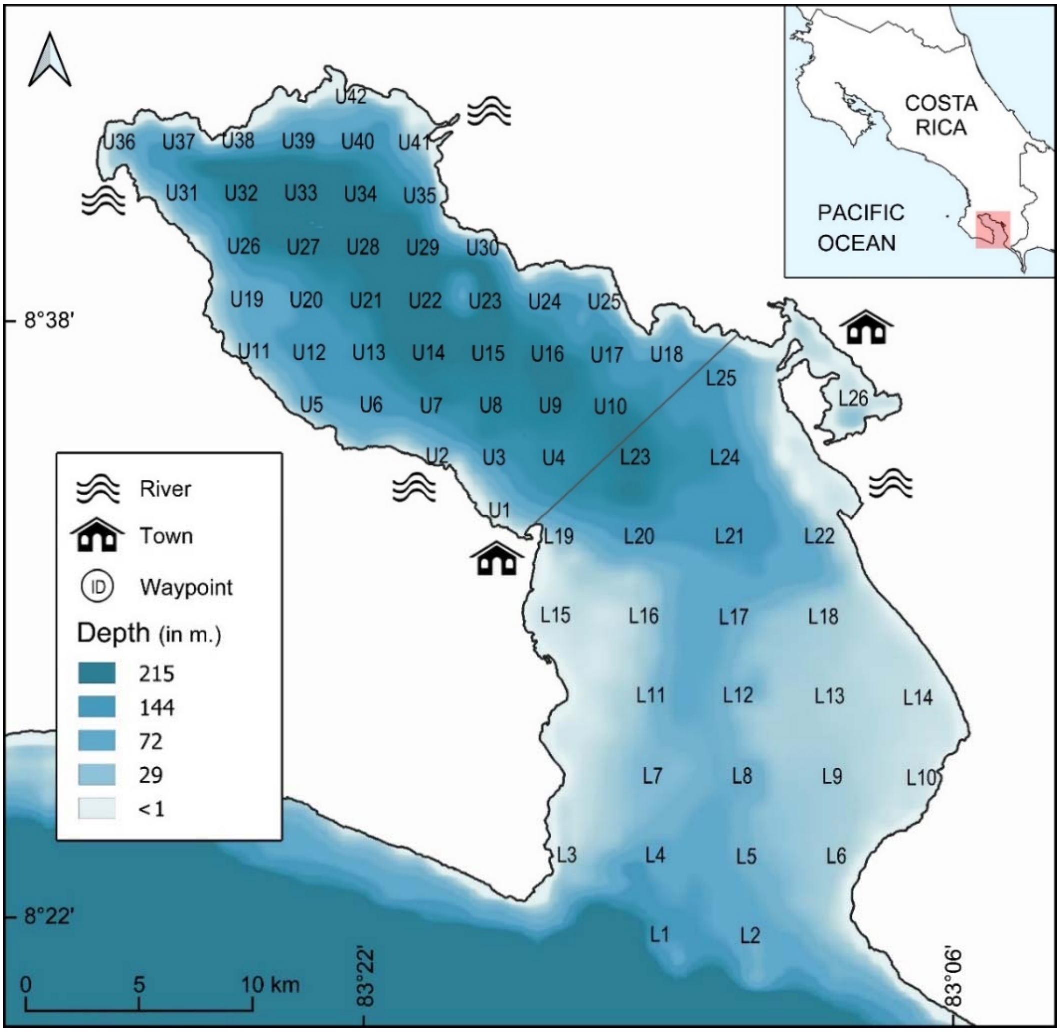

Figure 3.1. Bathymetric map of study area (Golfo Dulce, Costa Rica) with 68 water-testing waypoints divided by zone (grey line): Upper Gulf (n=42) and Lower Gulf (n=26); the lighter area near U23 is an underwater pinnacle; map rendered in QGIS (QGIS Development Team 2020) with features added in PhotoShop CS5 (Adobe Inc. 2010).

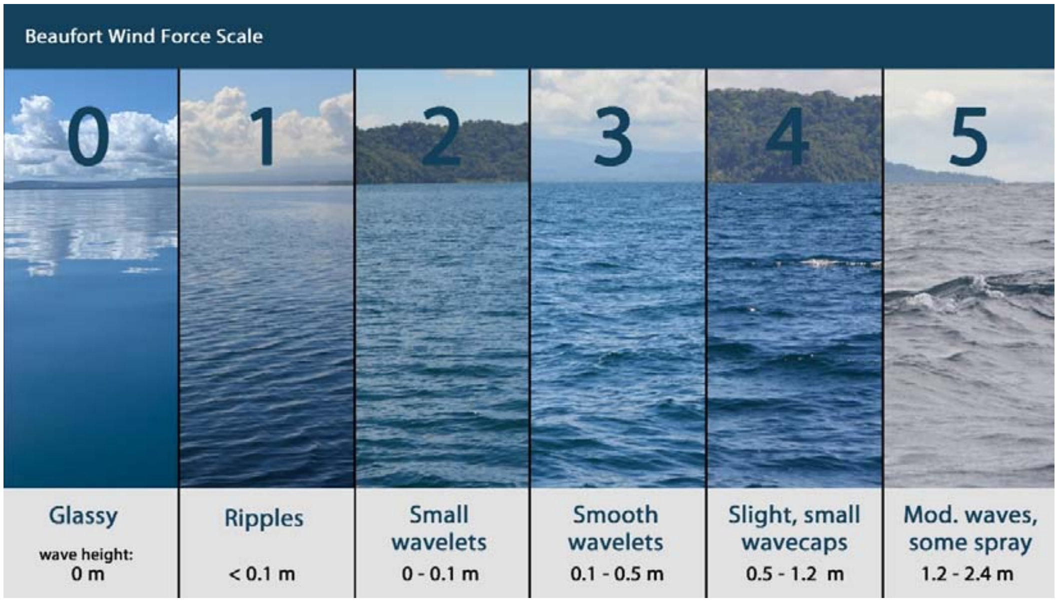

Figure 3.2. Beaufort wind force (BWF) scale showing sea states in the study area of Golfo Dulce, Costa Rica; photo credit: B. Bessesen.

To create environmental layers from waypoint readings, we calculated a combined mean of all readings (minimum 2) taken for each variable at each WP and depth. WPs were only sampled once in 2021, but if a site was sampled more than once in 2020, then all readings from that year were averaged before averaging between years. To generate interpolated maps in the exploratory phase, we used inverse distance weighted (IDW), as well as ordinary and simple kriging (Oliver & Webster 2007), creating one layer per hydrographic variable. IDW layers were created in QGIS version 3.10 (QGIS Development Team 2020) with a distance coefficient setting of 3.0. To define the Kriging layers, we used empirical semivariograms and the Kriging tool in the Geostatistical Analyst toolbar in ArcMap version 10.8 (ESRI 2019). All layers were converted to ascii raster files in QGIS. We explored both methods because while IDW rasters are commonly used in Maxent; IDW is sensitive to the number and location of data points (Babak & Deutsch 2008) and can display a bulls-eye effect. On the other hand, kriging methods use statistical modelling for interpolation and can result in high correlations among mapped variables as well as a prism-like effect in the visual output. We experienced all these artefacts with our data and despite the bulls-eye effect, we decided to maximize the number of predictors in the models, proceeding with IDW. In addition, because bathymetry appeared a delineating factor in sighting distribution maps of xanthos (Bessesen 2012, 2015, Bessesen & González-Suárez, in review; Chapter 1), depth was also included in our study. A raster of the General Bathymetric Chart of the Oceans (GEBCO 2014) was downloaded from the Global Multi-Resolution Topography (GMRT) Synthesis (Ryan et al. 2009). To eliminate two possible artefacts seen as tiny areas of unconfirmed extreme depth, we capped depth maximum at 215 m as reported for the study area (per Svendsen et al. 2006). Finally, the environmental layers were projected in WGS 84, trimmed to match the extent of Golfo Dulce and prepared at a resolution of 0.000545 degrees (grid cell size ~60 m^2), which was the finest scale available for our corresponding depth data. Traditional bioclimatic variables were downloaded from WorldClim version 2.1 (Fick & Hijmans 2017) but were not used as the resolutions of those projections were too broad to spatially divide our small area of study.

3.2.3 Presence-absence data

Between 2010–2021, a total of 765 occurrence records of xanthos were collected during multiple studies: three large multi-species surveys covering all waters of Golfo Dulce (n=125; Bessesen 2012, 2015, Bessesen & González-Suárez, in review; Chapter 1), a sampling survey with 46 shore-to-shore transect lines above the sill (n=203; Bessesen et al. 2022; Chapter 5), a diel study (n=358; Bessesen & González-Suárez 2022; Chapter 4), and two exploratory studies (n=79; including Bessesen & Galbreath 2017). To mitigate spatial autocorrelation from data in the diel study, in which a few short transect lines were rerun continuously for periods of 12 hours, we removed the majority (n=341) of sightings, retaining only a few random points near the start, middle, and end of our transects. Following Liu et al. (2017), we also removed one extreme outlier: a single xanthic snake apparently swept from its natural range by currents and found in the Lower Gulf (Bessesen 2015). This effort resulted in 423 occurrence records for the analyses. No true absence points of xanthos were recorded in the field but from data collected during the multi-species surveys (85 days, 657 observation hours), we were able to extract 318 occurrences of other marine taxa identified at the ocean surface and within the minimal-distance range of sea snake detectability (≤20 m) to serve as ‘pseudo-absences’ (Phillips et al. 2009, Stephenson et al. 2021).

3.2.4 Maxent modelling

We used Maxent version 2.4.4 (Phillips et al. 2006) to infer habitat suitability based on environmental variables of depth, BWF and SST, as well as temperature, salinity, dissolved oxygen, turbidity, and pH taken at 0.5 and 10 meters (temp05, temp10, sal05, sal10, do05, do10, turb05, turb10, ph05, ph10). We also fitted a model excluding depth to explore in more detail the role of hydrographic variables. For reliable results in Maxent, it is critical to remove highly (Pearson R>0.70) correlated variables, so we used the aster.cor.matrix function in the R package 'ENMTools' (Warren et al., 2011) to test for correlations among predictors. A correlation of 0.72 was detected between SST and temp05. We ran exploratory models and found that SST provided a lower percent contribution and permutation importance than temp05 and so SST was removed in the final models. To address sampling bias, we created an ascii bias file with our environmental layers, occurrence records (presence data), and pseudo-absences in the R packages 'MASS' (Ripley et al. 2021) and 'raster' (Hijmans et al. 2021).

Following the recommendations of Radosavljevic and Anderson (2014) and Kalinski (2019), we used the R package 'ENMeval' (Muscarella et al., 2014) to conduct model tuning prior to Maxent modelling. To run ENMeval, we used the selected environmental rasters, the 423 occurrence records and the bias file and applied a random 10-fold partitioning scheme for cross-validation. ENMeval compares many potential model configurations to determine the one with greatest goodness of fit (lowest AIC as delta.AICc=0), and outlines the best Maxent settings for feature classes (linear, quadratic, hinge, product, and/or threshold, referred to as L, Q, H, P, T) and the regularization multiplier (rm 1–5). We used the identified settings and ran 100 replicates with jackknife testing to determine variable contributions. Because the bias file only addresses relative sampling effort (Kramer-Schadt et al. 2013), it is still necessary to select the number of background points to be used in the Maxent model. The ENMeval process consistently returned >200,000 potential background points, which justified a model setting value of 10,000 background points as recommended by Phillips and Dudík (2008). We retained the default cloglog output for two reasons: (1) probability of presence is estimated between 0 and 1, considered the most conceptually intuitive (Phillips et al. 2017), and (2) improved performance when target-group background data are used (Phillips et al. 2009). We considered a ≥0.8 AUC (area under the curve) score as good (per Araújo et al. 2005, Franklin & Miller 2010). When evaluating the results, we considered relative contribution of the environmental variables based on percent contribution (the regularized gain/loss attributed to a variable during iterations of the training algorithm) and permutation importance (which uses random permutation to examine the values of the variable against training presence and background data for a decrease in training AUC; normalized to a percentage); however, we focused on the latter because it is independent of a particular model path. Maxent also generates response curves from individual models for each variable, and those were used to identify and describe the most suitable conditions for xanthos.

When mapping model output, the minimum training presence threshold demonstrates the lowest predicted suitability for each occurrence point, allowing the broadest range extent for the population, but can only be applied with strict confidence in the presence localities (Escalante et al. 2013). Since the occurrence data were collected by us, we trusted the coordinates as reliable and mapped the minimum training presence output (mean of the 100 replicates) as an ascii raster in QGIS. Grid cells were classified as non-suitable (any value below the minimum training presence clog-log threshold) or suitable (classified as low suitability <0.33, medium suitability 0.33–0.66, or high suitability >0.66). To represent uncertainty in suitability estimates we also mapped the standard deviation among the 100 replicates in predicted suitability for each grid cell. Finally, we used all available sighting records of the taxon to determine its extent of occurrence (EOO; minimum convex polygon encompassing all known occurrences, excluding vagrancies) and area of occupancy (AOO; tally of 2-km^2 grid cells identified with sighting records or with suitable habitat encircled by grids with sighting records within the EOO; IUCN 2022).

3.3 | RESULTS

3.3.1 Water conditions

During our designated water-testing periods, we recorded 1795 probe readings, 149 SST thermometer readings, and 183 BWF records. The resulting environmental layers showed variation across the study area and at different depths (Table 3.1, Fig. 3.3, 3.4). Both BWF (Fig. 3.2) and salinity tended to be lower in the Upper Gulf relative to the

Lower Gulf, though the opposite was true for dissolved oxygen and pH. Turbidity, which was generally low in the midwaters, became marginally elevated along the shorelines, peaking near river outlets and areas of high wave activity. All recorded temperatures throughout the embayment averaged 30.2 °C (raw data: 28.80–32.37 °C), though waters were consistently cooler and more stable at 10 m depth than near the surface. Measurements of pH were also lower at depth. Conversely, dissolved oxygen and salinity were higher at 10 m than at 0.5m. During our tank-assisted scuba dive, temperatures dropped from 31.60 °C at the water surface to 17.8 °C at 31.4 m depth.

Table 3.1. Environmental conditions in Golfo Dulce (Costa Rica), including depth and 12 hydrographic variables describing the entire area (EA) and suitable habitat for *H. p. xanthos* (SH) from interpolated data, and the Upper Gulf (UG) and Lower Gulf (LG) from raw data taken at 68 waypoints in 2020 and 2021 for Beaufort wind force (BWF), sea surface temperature (SST), and temperature, salinity, dissolved oxygen, turbidity, and pH at depths of 0.5 and 10 m (temp05, temp 10, sal05, sal10, do05, do10, turb05, turb10, ph05, ph10); values are reported as means and standard deviations; depth obtained from GEBCO (2014).

Variable	EA	SH	UG	LG
Depth (m)	82.83 ± 70.65	154.37 ± 42.15	129.21 ± 68.16	54.62 ± 54.06
BWF (1-5)	2.90 ± 0.65	2.64 ± 0.67	2.39 ± 0.91	3.25 ± 1.11
SST (°C)	30.76 ± 0.29	30.76 ± 0.30	30.75 ± 0.73	30.66 ± 0.69
temp05 (°C)	30.60 ± 0.25	30.59 ± 0.25	30.51 ± 0.63	30.54 ± 0.61
temp10 (°C)	29.69 ± 0.22	29.60 ± 0.17	29.54 ± 0.33	29.78 ± 0.42
sal05 (ppt)	29.49 ± 0.42	30.99 ± 0.28	30.97 ± 0.54	31.47 ± 0.70
sal10 (ppt)	31.91 ± 0.17	32.84 ± 0.15	31.77 ± 0.53	31.96 ± 0.63
do05 (mg/L)	6.46 ± 0.09	6.50 ± 0.07	6.51 ± 0.12	6.42 ± 0.12
do10 (mg/L)	6.58 ± 0.12	6.64 ± 0.10	6.62 ± 0.2	6.54 ± 0.17
turb05 (NTU)	0.61 ± 0.63	0.62 ± 0.52	0.62 ± 1.14	0.55 ± 0.52
turb10 (NTU)	0.59 ± 0.89	0.29 ± 0.09	0.26 ± 0.13	0.75 ± 1.63
pH05	8.20 ± 0.02	8.21 ± 0.02	8.21 ± 0.06	8.19 ± 0.06
pH10	8.18 ± 0.02	8.19 ± 0.02	8.19 ± 0.08	8.18 ± 0.06

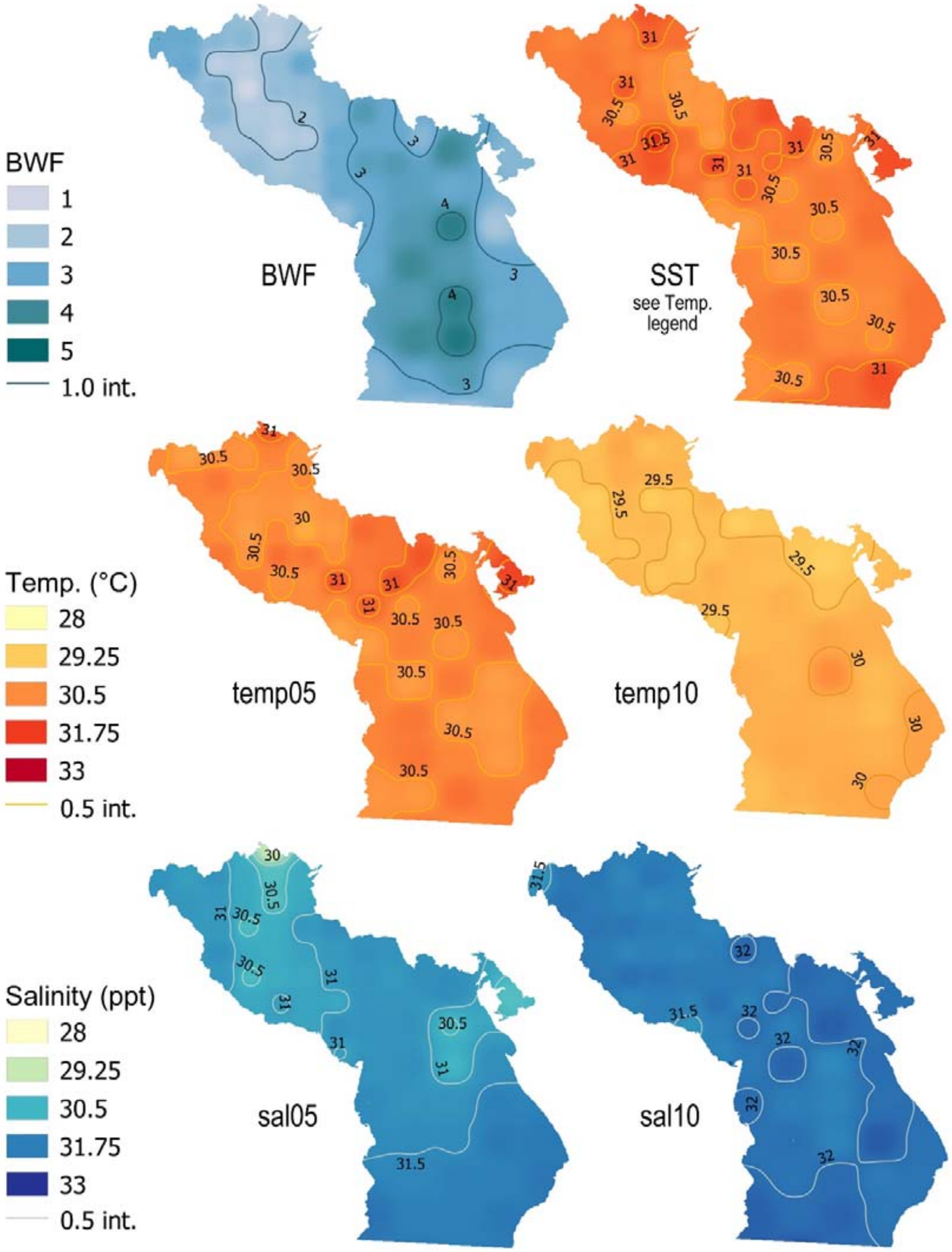

Figure 3.3. Distance-weighted interpolated maps reflecting hydrographic conditions in Golfo Dulce for averaged Beaufort wind force (BWF), sea surface temperature (SST), and temperature and salinity at depths of 0.5 and 10 m (temp05, temp 10, sal05, sal10); interpolations rendered with QGIS (QGIS Development Team 2020); see Fig. 3.1 for depths.

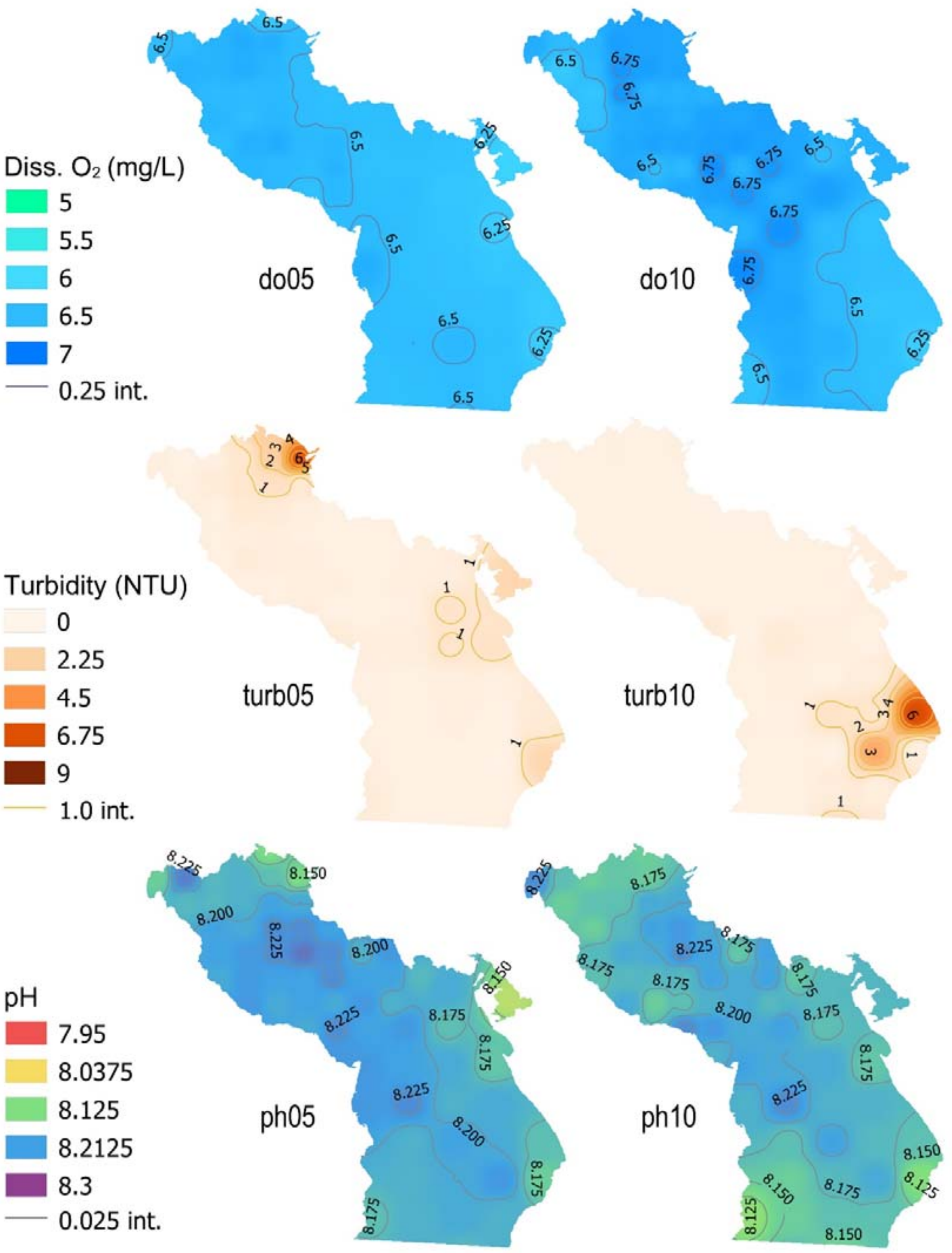

Figure 3.4. Distance-weighted interpolated maps reflecting hydrographic conditions in Golfo Dulce for dissolved oxygen, turbidity, and pH at depths of 0.5 and 10 m (do05, do10, turb05, turb10, ph05, ph10); interpolations rendered with QGIS (QGIS Development Team 2020).

3.3.2 Habitat suitability and range

The optimal full model (including depth) as identified in ENMeval included four feature classes (LQHP) with a regularization multiplier of 1 and had a good AUC (across 100 replicates mean and SD: 0.897 ± 0.044). Depth was the most influential predictor with permutation importance of 64.3% (Table 3.2). When depth was excluded as a predictor, the optimal model (as identified with ENMeval) included one feature class (H) with a regularization multiplier of 1. It also had a good AUC (across 100 replicates mean and SD: 0.868 ± 0.057). Variable importance partly differed from the full model, as salinity at 0.5 m became the strongest predictor given a permutation importance of 46.8%. In both models, ph10 was the second most influential predictor, and a few other variables were consistently at PI ≥3.5, including do05, temp05, and turb05, suggesting that measurements collected at 0.5 m depth generally had more influence than those at 10 m. In the model without bathymetric data, turb10 was also important, indicating some influence of that variable at both depths (Table 3.2). The individual response curves for the most important variables suggest a higher probability of presence in areas where the water is deeper (>100 m), salinity is <32 ppt, pH is close to 8.2, dissolved oxygen is higher, temperatures are cooler, and turbidity is lower (Fig. 3.5).

Suitable habitat for xanthos was primarily restricted to the Upper Gulf in the full model (Fig. 3.6A) but also when depth was excluded as a predictor (Fig. 3.6B). In both, suitability rapidly diminished below the sill line. Waters near the central mouth of Golfo Dulce were identified by the full model as minimally suitable with moderate levels of uncertainty (Fig. 3.6A, C); this appears solely as an effect of depth because when considering only hydrographic variables the area is deemed unsuitable with high certainty (Fig 6B, D). Thus, we consider waters near the mouth unlikely to be truly suitable. Similarly, despite almost 900 active observation hours in Golfo Dulce since 2010, we have never recorded sea snakes in the most southerly sector of the inner basin where suitability is low and ‘disorderly’ surface circulation patterns occur (Svendsen et al. 2006) that may be disadvantageous for sea snakes. All sightings of xanthos documented by the lead author (765 observations, excluding one clear vagrant) delineate a contiguous extent of occurrence (EOO=282 km2) with a slightly more-narrow area of occupancy (AOO=260 km2). Ninety-nine percent of all sightings occurred in medium- or high-suitability habitat.

We also report two important findings not directly related to our models that suggest selection by xanthos within its range and therefore provide additional insight into habitat use. First, although SST readings averaged 30.75 °C in the Upper Gulf (Table 3.1), readings at 88 xanthos sightings in the same zone averaged 29.7 °C, suggesting the snakes prefer cooler conditions when surfacing. Second, BWF records averaged 2.39 in the Upper Gulf (Table 3.1), but records from 709 xanthos sightings in the same zone averaged 2.87, indicating a preference for rougher conditions within its territory.

Table 3.2. Environmental variables related to the presence of *H. p. xanthos* in Golfo Dulce as identified in two Maxent models (full model and one based solely on hydrographic variables, without depth); we show variable contributions as percent contribution (% C) and permutation importance (PI) for Beaufort wind force (bwf), and temperature, salinity, dissolved oxygen, turbidity, and pH at depths of 0.5 and 10 m (temp05, temp 10, sal05, sal10, do05, do10, turb05, turb10, ph05, ph10); ordered by highest-to-lowest PI for the full model.

Variables	Full model		Without depth	
	% C	PI	% C	PI
depth	74.2	64.3	--	--
ph10	2.6	8.3	11.8	16.9
sal05	1.7	7.5	51.4	46.8
temp05	2.1	5.2	1.9	6.6
do05	3.4	3.6	9.1	10.5
turb05	2.3	3.6	3.9	3.5
do10	3.6	3.0	0.9	1.7
temp10	4.2	2.3	2.0	1.5
bwf	3.2	1.7	6.7	0.8
sal10	1.3	0.2	2.4	2.1
turb10	0.2	0.2	6.3	7.8
ph05	1.2	0.0	3.7	1.9

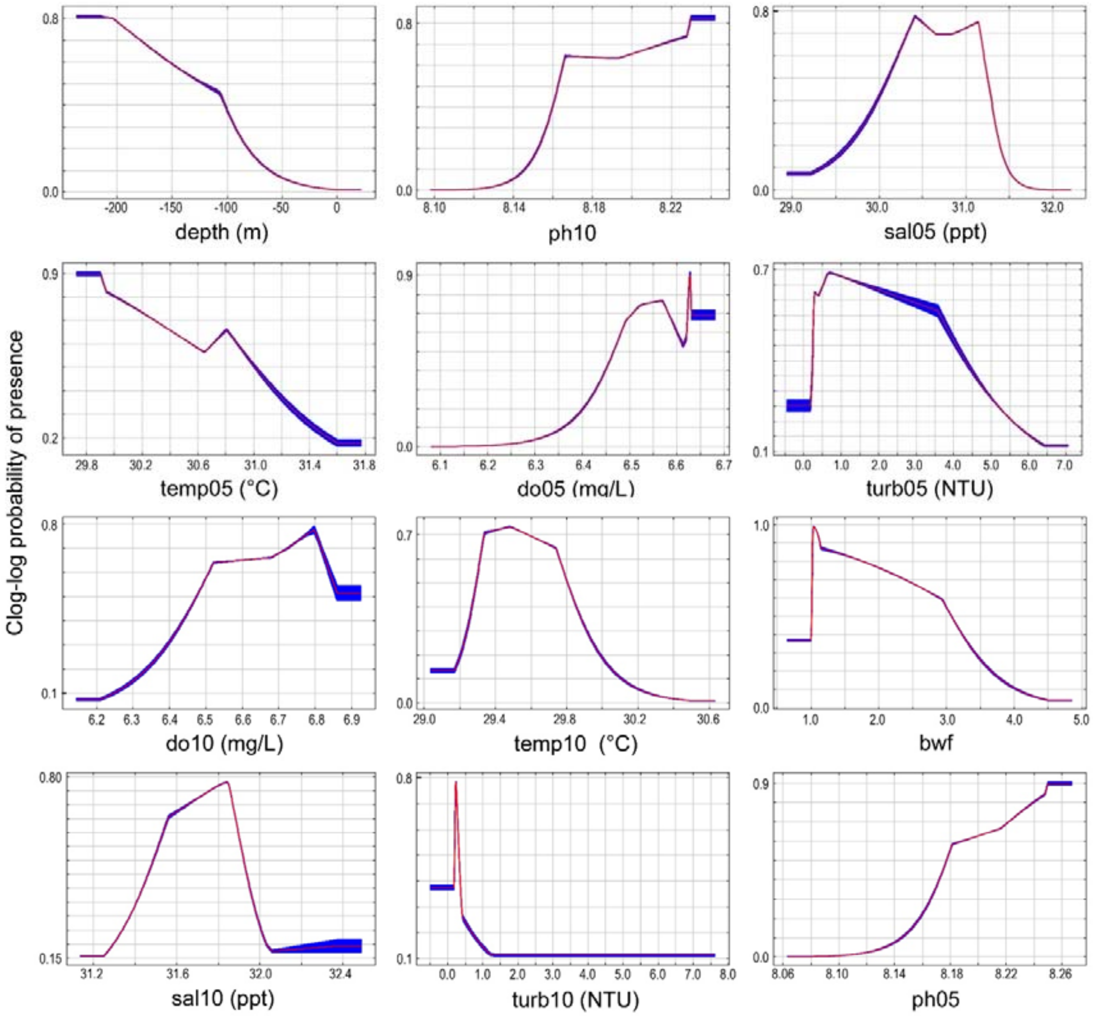

Figure 3.5. Response curves in order of permutation importance showing probability of presence for *H. p. xanthos* in Golfo Dulce (Costa Rica) across values of 12 environmental variables: depth, Beaufort wind force (bwf; 1–5 scale), and temperature, salinity, dissolved oxygen, turbidity, and pH (0–14 scale) at depths of 0.5 and 10 m (temp05, temp 10, sal05, sal10, do05, do10, turb05, turb10, ph05, ph10). Curves were defined by the full model: four feature class parameters (linear, quadratic, hinge, product; LQHP) and regularization multiplier of 1; averaged from 100 replicates showing mean (red) +/- one standard deviation (blue).

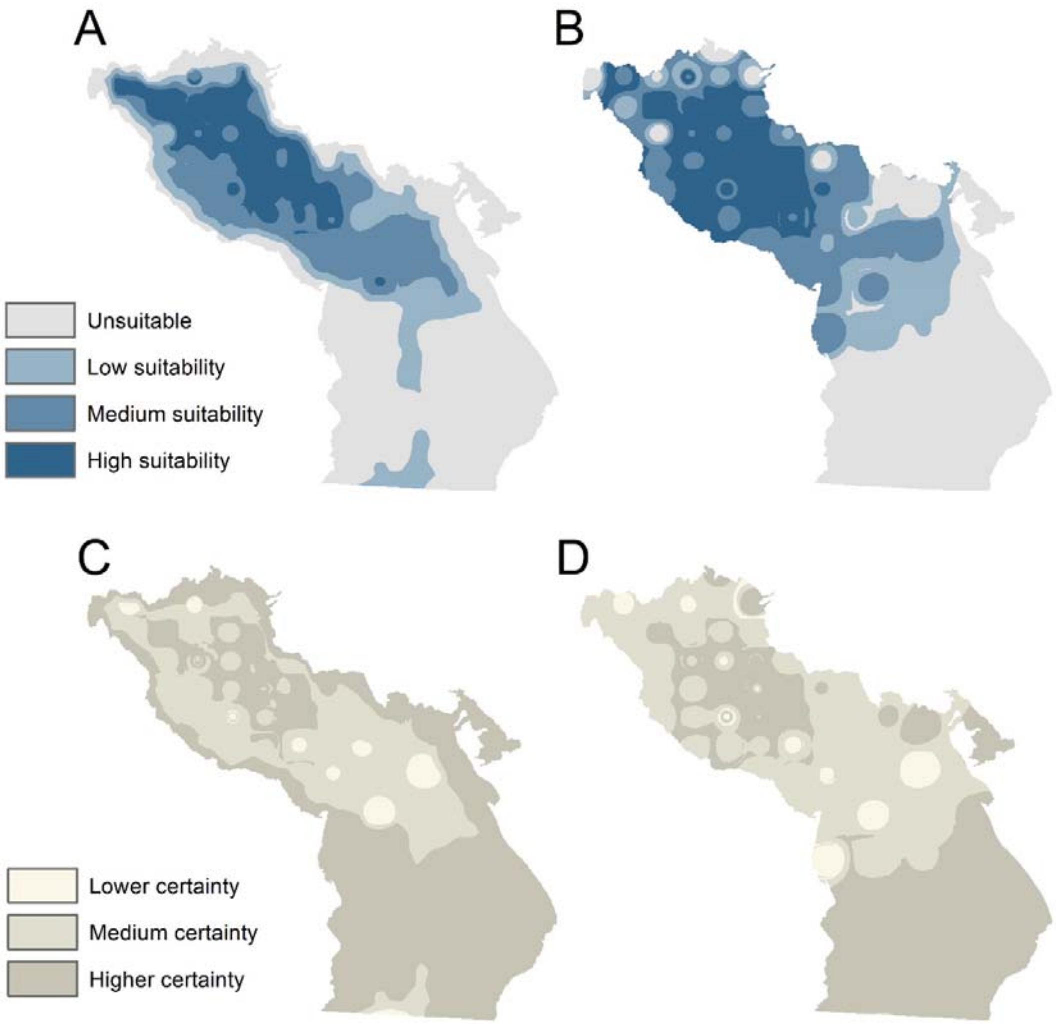

Figure 3.6. Habitat suitability maps (blue; A–B) with associated model uncertainty (tan; C–D) for *Hydrophis platurus xanthos* in Golfo Dulce, Costa Rica, based on Maxent cloglog thresholds of minimal training presence (mtp) and maximum probability (maxP) from 100 replicates; **(A)** mean suitability from 100 replicates of the full model (including depth) and 11 hydrographic variables as predictors (mtp=0.065; suitability classified as low [0.065–0.33], medium [0.33–0.66] and high [>0.66]; maxP=0.973); **(B)** mean suitability from 100 replicates of based on a model using only the 11 hydrographic variables as predictors (mtp=0.164; suitability classified as low [0.164–0.33], medium [0.33–0.66] and high [>0.66]; maxP=0.990); see Table 3.2 for predictor importance; **(C)** standard deviation in estimated suitability from 100 replicates of uncertainty for the full model (ranges: lower certainty=0.020–0.054, medium certainty=0.061–0.019, higher certainty=0.00002–0.060; mean shown in panel A); and **(D)** standard deviation in estimated suitability from 100 replicates of uncertainty for the model without depth (ranges: lower certainty=0.020–0.049, medium certainty=0.061–0.019, higher certainty=0.000002–0.060; mean shown in panel B).

3.4 | DISCUSSION

Our results identified environmental conditions suitable for the yellow sea snake, *H. p. xanthos*, and we also delineated its extent of occurrence (EOO=282 km^2) and area of occupancy (AOO=260 km^2), which can be used in assessing risk of extinction. Suitable conditions were based on depth, along with 11 hydrographic variables, among which salinity, pH, dissolved oxygen, temperature, and turbidity showed importance. Our analyses provided quantitative evidence to confirm the importance of depth in the distribution of xanthos (Bessesen & González-Suárez, in review; Chapter 1), as found for several sea snake species (Udyawer et al. 2020). Preference for deeper waters may be related to xanthos' pelagic roots and studies pertaining to dive depth and duration should be further explored. Depth alone, however, does not explain xanthos' presence and even excluding this variable suitability was still limited to the Upper Gulf.

Surface salinity was another key predictor of suitability, becoming the most influential variable when depth was excluded (with depth it was third most important following pH at 10 m). Surface salinity in the suitable range for xanthos was 30.5 to 31.25 ppt. The salt concentration of seawater is typically 35 ppt (Dunson & Ehlert 1971) but owing to freshwater discharge from several rivers entering Golfo Dulce (Umaña-V 1998), levels are naturally lower. Salinity increases and is more stable at depth and may reach 35 ppt between 100–150 m inside the embayment (Acuña-González et al. 2006, Morales-Ramírez et al. 2015), a halocline considerably deeper than the sea snakes are likely to dive (Rubinoff et al. 1986). For marine animals, environmental salinity can affect hydration and drinking behavior and potentially lead to evolutionary adaptation (Rash & Lillywhite 2019). As an endemic population, it is possible that xanthos has physiologically adapted to low-saline conditions, which presumably require less salt excretion and/or dermal protection from sodium osmosis. Several species of sea snakes including *H. p. platurus* can endure low-saline conditions (Dunson & Ehlert 1971, Rasmussen et al. 2001, Ukuwela et al. 2012, Voris 2015), but it is unclear whether the opposite is true for xanthos. Infrequently, all-yellow individuals have been found in the broader Pacific Ocean (Kropach 1971b, Bolaños et al. 1974, Tu 1976), presumably carried out of Golfo Dulce by rogue currents (Bessesen 2015), but whether those animals survive long-term in cooler, higher-saline waters remain unclear. Salinity may also influence xanthos' diet. The pelagic sea snake consumes >30 species of fish

(Brischoux & Lillywhite 2013); however, the warmer more-brackish conditions of the inner basin may not be suitable for all of them, potentially limiting prey selection. Somewhat surprisingly, both of our models showed pH (at 10 m) as the second highest predictor of suitability. In Golfo Dulce pH ranges from 7.9 to 8.5 mg/ L (Richards et al. 1971; our raw data 7.98–8.29 mg/ L). Xanthos appeared to prefer higher values (>8.16 mg/ L at 10 m depth). Climate change is causing ocean acidification due to the absorption of anthropogenic CO^2 emissions (Raven et al. 2005, Jiang et al. 2019) and over time could diminish habitat suitability.

Dissolved oxygen and temperature were consistently in the top five most influential variables for our SDM models, and xanthos presence was greater in areas of higher oxygen concentrations and cooler thermal readings. Dissolved oxygen levels averaged 6.5 mg/L across the entire study area with slightly higher values in the Upper Gulf, especially at 10-m depth. In a biseasonal study, Morales-Ramírez et al. (2015) reported an average of 5.5 mg/L at the surface. Low concentrations of dissolved oxygen define Golfo Dulce as a tropical fiord, and levels decline precipitously as the water deepens (Richards et al. 1971), at times dropping to <4 mg/L within 0–20 m of depth in the inner basin (Quesada-Alpízar & Morales-Ramírez 2004, Acuña-González et al. 2006). Concentrations below 4 mg/L can alter behavior in marine vertebrates (Carson & Parsons 2001, Burke et al. 2021) and likely affect the vertical range of xanthos in the water column. Dissolved oxygen levels are declining in seas worldwide, and fauna that utilize both shallow and deep strata, like xanthos, may suffer habitat compression (Global Ocean Oxygen Network 2018). In addition, if oxygen levels are lower at depth, cutaneous respiration may be affected and snakes may need to reduce dive times, surfacing more frequently to ventilate through their nares.

Warmer temperatures can also reduce dive times by increasing metabolism (Cook & Brischoux 2016, Udyawer et al. 2016). Sea snakes are sensitive to thermal shifts (Heatwole et al. 2012) and water temperature can define their range (Lillywhite et al. 2018). Matching the biseasonal data of Rincón-Alejos & Ballestero-Sakson (2015), our thermal readings throughout Golfo Dulce averaged about 30 °C with SST occasionally exceeding 32 °C, which approaches the maximum thermal tolerance of 33–36 °C for the pelagic sea snake, *H. p. platurus* (Dunson and Ehlert 1971, Graham et al. 1971); thermal tolerance for xanthos is unknown. In the Pacific, Lillywhite et al. (2015) found no effect of temperature (or salinity) on the surfacing patterns of the pelagic sea snake; however, we found xanthos surfacing to be associated to cooler temperatures. In fact, high temperature has been proposed as a driver of morphological and behavioral adaptations in xanthos, including light coloring and a nocturnal feeding cycle that may also help protect pale skin and eyes from solar sensitivity (Bessesen & González-Suárez 2022; Chapter 4). We found cooler thermal conditions at depth. Several studies report a 50-m thermocline averaging 20–25 °C (Acuña-González et al. 2006, Svendsen et al. 2006; Morales-Ramírez et al. 2015, Rincón-Alejos & Ballestero-Sakson 2015). Richards et al. (1971) reported cooler temperatures at that depth, closer to 17 °C, which we also found during a tank-assisted dive (17.8 °C at 30 m depth). Since pelagic sea snakes expire in temperatures below 18 °C (Dunson & Ehlert 1971, Graham et al. 1971), xanthos may occasionally be sandwiched between very warm surface waters and very cold thermoclines, limiting their inhabitable vertical space. The issue may be compounded by global warming, as the area is already experiencing increased temperatures (Morales-Ramírez et al. 2015; Murayama et al. 2018), a trend likely to continue.

Turbidity also played a role in our models, and xanthos was overall more likely to occur in areas with lower turbidity, especially at 10 m depth. During our study, low turbidity generally prevailed across most of the gulf (except near rivers or beaches), but it is known to increase during the rainy season, considerably reducing water transparency in the Upper Gulf (Rincon-Alejos & Ballestero-Sakson 2015). While pelagic sea snakes favor calmer, clearer waters (Kropach 1973, Brischoux & Lillywhite 2011), xanthos may be more like sea snake species residing in tidal zones where some level of turbidity is inherent in the habitat (Voris 2015). Golfo Dulce has near-constant wave activity and xanthos demonstrated greater tolerance for turbidity near the surface. Perhaps relatedly, we found BWF to be reduced in the Upper Gulf (as did Morales-Ramírez et al. 2015), yet within that 'calmer' environment the snakes surfaced in rougher-than-normal conditions.

This study offers valuable insight into the role of hydrographic conditions in the distribution of xanthos. There are some limitations, however. Water testing took place during a small temporal window in the dry season; still, our readings were generally in accord with other year-round studies (see review by Vargas-Zamora et al. 2021).

Additional factors, including tides, currents, wind, and weather, plus hydrographic conditions at greater depths likely influence xanthos directly and indirectly. Occurrence data were accurate and recorded consistently by the same observers, reducing errors, but were predominantly collected during the dry season. While seasonal sampling could introduce bias, a comparison of xanthos distribution between rainy and dry season surveys found no temporal differences in spatial range (Bessesen 2015). Finally, our analyses are based on presence-only data, but we used a careful protocol to reduce biases, tune models and explore model uncertainty.

Golfo Dulce is a national biodiversity hotspot (Quesada & Cortés 2006) hosting up to 23% of Costa Rica's marine diversity (Morales-Ramírez 2011), including a sea snake found nowhere else on Earth. Given its small area of occupancy, *H. p. xanthos* is an inherently rare taxon (Rabinowitz 1981) that could be negatively affected by changes to its marine habitat. Indeed, the population's risk of extinction should be assessed as soon as possible given that an IUCN status of endangered may be warranted (IUCN 2022). Sea snakes appear in global decline (Rasmussen et al. 2011, Elfes et al. 2013, Somaweera et al., 2021), and sensitive to environmental changes they are valuable bioindicators for other marine species (Rasmussen et al. 2021). It is critical to appreciate the gradual yet substantial effects of climate change (McGill et al. 2015, Poloczanska et al. 2016). Possibly stenotypic and unable to migrate away from the inner basin of Golfo Dulce to escape warming sea temperatures, ocean deoxygenation and acidification, as well as the more direct anthropogenic impacts of boat traffic and habitat contamination, xanthos faces an uncertain future. Taking a long view of conservation, we recommend Costa Rican officials readily sponsor environmental policies that protect the unique habitat of their country's only endemic marine reptile.

3.5 ACKNOWLEDGMENTS

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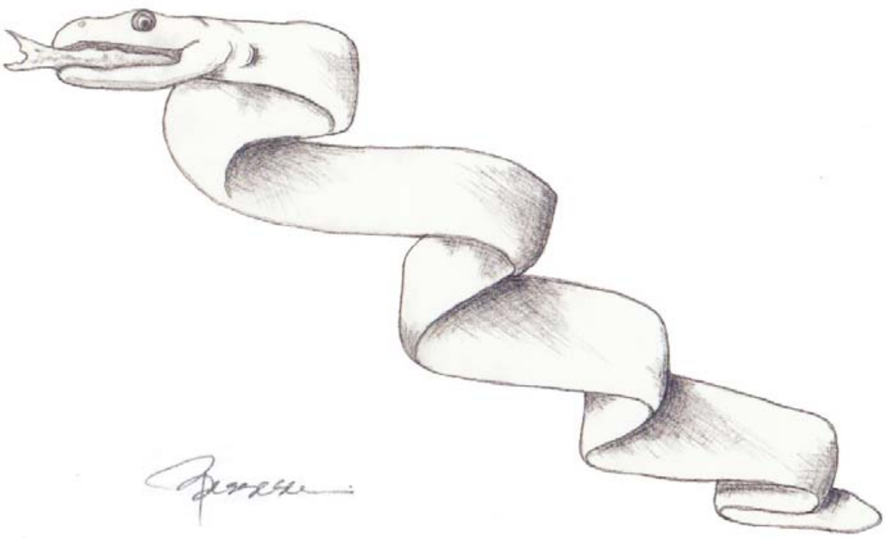
Chapter 4



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CHAPTER 4: Safe from Sunburn: The divergent diel pattern of a *Hydrophis* sea snake

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4.0 | ABSTRACT

Diel activity patterns are an important aspect of wildlife ecology and evolution and provide valuable information for conservation and monitoring, yet for many species, activity patterns remain unstudied and may be presumed to mirror related taxa. Here, we describe the distinct diel patterns of an endemic population of venomous sea snakes *Hydrophis platurus xanthos* inhabiting a narrow range in Golfo Dulce, Costa Rica. To investigate, we conducted a systematic visual survey over five 24-h cycles and evaluated 339 h of previously obtained sighting data from different studies spanning a decade. While sporadic diurnal surfacing does occur, mostly for respiration, our observations revealed marked crepuscular peaks with regular surfacing through the night. We also report on observed surface behaviors that were also found to vary in frequency at different phases of the photoperiodic cycle. In particular, we show feeding as more common at night. *Hydrophis platurus xanthos* has developed a circadian rhythm that differs noticeably from its sister group (*H. p. platurus* is reported as diurnal across its Indo-Pacific range), and no congeners have been categorized as crepuscular. Our work thus contributes to the ecological knowledge of this evolutionarily distinct marine elapid and offers insights into the potential role of environmental conditions in shaping animal activity.

Key words: activity levels, circadian rhythms, Costa Rica, endemic, ethology, marine snakes

4.1 | INTRODUCTION

Animal activity patterns are an important aspect of ecology and evolutionary biology, yet they are an understudied facet of behavioral ecology due to the challenges of recording and quantifying the behaviors of free-ranging populations over time-specific periods (Bridges & Noss 2011). Four biological clocks are triggered by changing environmental conditions that predictably repeat at regular intervals: circadian, tidal, lunar, and seasonal. These clocks influence animal activity patterns, the most obvious of which may be seen on the diel scale (Pittendrigh 1981, Aschoff 1984). It has been suggested that an internal timer, often referred to as a "circadian clock," syncs with changes in the animal brain and/or other parts of the central nervous system that effect a variety of physiological functions and behaviors. The most ubiquitous zeitgeber, or cue, for these circadian rhythms is the daily light-dark cycle, which includes both the principal periodic states (day: light, night: dark) and the transitions between those states (twilight; Aschoff 1954, 1984). Temperature is another primary driver (Edery 2000), and thermoregulation through exposure to or protection from solar radiation is a well-studied aspect of circadian rhythmicity (Angilletta 2009). Selection pressure favors organisms that conform to the most beneficial periodicities allowed by their environment (Cloudsley-Thompson 1960), and wild populations are generally adapted to diurnality (active during the day), nocturnality (active at night), crepuscularity (active during twilight), or cathemerality (active at irregular hours; Vazquez et al. 2019), although such categories do not account for more subtle shifts in activity levels through the 24-hour cycle.

Activity is usually meant to denote movement (Aschoff 1954), observed as periods of foraging, traveling, or reproductive behaviors juxtaposed to periods of stillness (resting or sleeping). Certain fauna, however, such as air-breathing marine snakes that must regularly surface to ventilate, may not present such defined periods. The wide-ranging pelagic sea snake, *Hydrophis platurus platurus,* spends 87% of its time submerged, either descending or ascending in the water column (Rubinoff et al. 1986). Subsurface swimming occurs at a slow rate of 2–4 cm/ s (Graham et al. 1987), and long dive cycles keep the animal in a near-constant state of movement. Meanwhile, many vital behaviors take place at the ocean surface with minimal physical activity, including feeding (opportunistically capturing small fish from a floating position; Klauber 1935, Brischoux & Lillywhite 2011), hydration (drinking from freshwater lenses after rainfall;

Lillywhite et al. 2012, 2019); parturition (live birth: true sea snakes are viviparous; Greene 1997), pulmonary ventilation (every 37 minutes on average; Rubinoff et al. 1986), and possibly resting in the conventional sense (episodes of relative stillness; pers. obs.). Therefore, 'diel surfacing patterns' rather than 'diel activity patterns' may be more appropriate for interpreting the behavioral ecology of this species and for monitoring purposes. Across its entire Indo-Pacific range, *H. p. platurus* is described as diurnal, spending more time at the ocean surface (often in drift lines: Kropach 1971a, Tu 1976, Lillywhite et al. 2010) during daylight hours, a deduction based upon field observations (Kropach 1975, Rubinoff et al. 1986, Brischoux & Lillywhite 2011, Lillywhite et al. 2015), ocular structure (Lillywhite 2014), and optical genetics (Simões et al. 2020). Other *Hydrophis* species were categorized by Simões et al. (2020) as diurnal, nocturnal, or cathemeral, but none as crepuscular.

In opposition to the diurnality of *H. p. platurus*, its closest evolutionary relative and the subject of our research, *Hydrophis platurus xanthos*, has been suggested to exhibit nocturnal surfacing (Bessesen 2012, Bessesen 2015, Lillywhite et al. 2015), although no systematic diel studies had been conducted, and those preliminary data were hindered by low or no sampling efforts for certain times. *Hydrophis platurus xanthos* is endemic to the inner-basin waters of Golfo Dulce, Costa Rica, an area with higher sea surface temperatures (SST) and lower salinity than those found in the neighboring Eastern Tropical Pacific Ocean (Wellington & Dunbar 1995, Rasmussen et al. 2011, Rincon-Alejos & Ballestero-Sakson 2015). This allopatric population has transitioned from a black-backed, yellow-bellied phenotype to monochromatic xanthic (yellow) coloration and smaller body size (Bessesen & Galbreath 2017), presumably to avoid overheating under solar exposure (Solórzano 2011, Bessesen 2012). Though, with numerous avian predators in Golfo Dulce (pers. obs.), such conspicuous coloration and lost countershading could negate certain survival advantages. Phenotypic adaptations are often associated with behavioral shifts (Shetty & Shine 2002, Lukoschek & Keogh 2006), and a change in circadian rhythm may be another consequence of occupying a warmer habitat and any related morphological changes.

Diel studies of wild animals were historically conducted via direct observations (Belovsky & Slade 1986) and often bore challenges such as concealing observer presence to avoid disruption of natural behaviors and ensuring sufficient visibility at night. For land-based studies, the development of tracking collars and then camera traps that could autonomously detect and capture animals in action without the disturbance of human presence (Bridges & Noss 2011) provided new opportunities for the statistical modelling of animal activity patterns and increased contributions to this growing field of study (Rowcliffe et al. 2014, Zhang et al. 2017, Lashley et al. 2018, Distiller et al. 2020). Camera trap studies with terrestrial snakes suggest adequate performance for faunal detection (Neuharth et al. 2020) but may be less effective for specific ethological investigations (Welbourne et al. 2017). Camera traps in marine environments are even more problematic. Baited remote underwater video stations (BRUVS) attached to the sea floor have been used to assess sea snake presence in the Great Barrier Reef (although diel patterns were not described; Udyawer et al. 2014). However, securing cameras at the ocean surface in waters <200 m deep, to sample a small, rarely seen marine snake that produces minimal lateral movement across a study area of several hundred square kilometers, impaired by waves, weather, and low light conditions is logistically untenable. Other sea snake studies have employed transmitters (Burns & Heatwole 1998, Shetty & Shine 2002), including Udyawer et al. (2015, 2017), who used surgically implanted transmitters in two different *Hydrophis spp.* off Australia to study their fine-scale diel patterns, even applying accelerometry to decipher behavioral activities (Brown et al. 2013). Rubinoff et al. (1986, 1988) worked specifically with *H. p. platurus*, suturing dive tags to the outer skin of 15 individuals off Panama and following them with a hydrophone to trace their movements. Transmitter studies have substantial scientific value, but small sample size may limit inference about the population (Lindberg & Walker 2007), unnatural behavior can bias data (Fitch & Shirer 1971), and the methods may negatively impact captured and tagged individuals (Rudolph et al. 1998, Weatherhead & Blouin-Demers 2004, Wilson & McMahon 2006, Riley et al. 2017). Thus, to systematically examine the diel surfacing patterns of *H. p. xanthos,* we opted for real-time around-the-clock visual observations analyzed with circular statistics. During our observations we also classified various surface behaviors that allowed us to consider other behavioral rhythms. Our results help fill several knowledge gaps, adding to the literature on behavioral ecology in sea snakes and the adaptive evolution of geographically isolated organisms, while demonstrating the potential for dynamic diel patterns to be recorded on a population scale.

4.2 | MATERIALS AND METHODS

4.2.1 Study subject

Hydrophis platurus xanthos (Bessesen & Galbreath 2017) is currently listed as a subspecies of the venomous pelagic sea snake *H. p. platurus.* Apparently allopatric and geographically bound to the Costa Rican embayment known as Golfo Dulce, with an estimated range of occurrence around 280 km^2 (Chapter 3), *H. p. xanthos* is an inherently rare and vulnerable taxon (Rabinowitz 1981, Drever et al. 2012). Xanthic coloration and small body size (average 49 cm long and 47 g in weight) presumably increase fitness in its relatively warm environment (Bessesen & Galbreath 2017), but in addition to morphological adaptations, *H. p. xanthos* exhibits distinct behavioral differences (Bessesen 2012, Lillywhite et al. 2015). Like its conspecifics, *H. p. xanthos* eats small fish that gather at the surface; prey is secured with a sideways strike of the head, envenomated and swallowed whole. However, by and large, feeding appears to occur at night, when the snake frequently assumes a unique sinusoidal ambush posture with its head directed downward (Bessesen & Galbreath 2017). Despite the ability to swim both forward and backward, this sea snake never travels more than a meter or two across the sea surface except through passive drift (pers. obs.). Unlike its sister group, this taxon shows no association with drift lines (Bessesen 2012, Lillywhite et al. 2015; Chapter 2).

4.2.2 Study site

Our diel survey took place in the inner basin of Golfo Dulce, Costa Rica (centered at 8°37' N, 83°19' W). In this northern sector of the 50-km long embayment, waters up to 215 m deep are held by steep coastal slopes and a 60-m sill. In addition to the protective bathymetry, the inner basin is sheltered by the geographic shape of Golfo Dulce, which hooks strongly to the left, further limiting the effects of oceanic currents and hydrographic exchange (Svendsen et al. 2006). As a tropical region, the climate is bimodal, with seasonality based on monthly precipitation: dry (<300 mm rainfall, December–April) and rainy (>500 mm rainfall, May–November; Morales-Ramírez et al. 2015). Air temperatures are generally warm, averaging 21–33.5 °C (Lobo et al. 2008). Combining dry and rainy season data, SST in Golfo Dulce can average ~30 °C (Rincon-

Alejos & Ballestero-Sakson 2015), compared with an average of ~28 °C in the neighboring Eastern Tropical Pacific (Wellington and Dunbar 1995, Rasmussen et al. 2011). Conversely, salinity in Golfo Dulce is lower at ≤31.9 ppt (Rincon-Alejos & Ballestero-Sakson 2015) compared with the oceanic standard of 35 ppt, probably due to the influx of freshwater from four large rivers and numerous tributaries (Wolff et al. 1996). Annual day-length variation in Costa Rica is minimal (~1 h; Rivera & Borchert 2001), and during the diel survey, the photoperiod only changed by 15 min, with sunrise shifting from 0539 h to 0524 h and sunset remaining constant at 1750 h.

4.2.3 Field protocols

In a camera trap study, the sensor (camera) remains stationary, and the animal makes lateral movements past the lens, but because *H. p. xanthos* does not swim notable distances at the surface, we were required to construct the opposite scenario: the animal was considered fixed, and the sensor (human observer) made lateral movements. On consecutive weekends in March and April 2021, we undertook five 24-hour cycles of boat-based survey effort for a total of 120 observation hours (OH) with homogenous by-hour coverage of 5 hours per clock-hour. Travelling along five 6-km long transect lines, we recorded observations of *H. p. xanthos* at or within 3 m of the water surface. Each cycle was completed over two 12-hour sessions: one from ~0545 h to ~1745 h Saturday, followed by an overnight from ~1745 h Sunday evening to ~0545 h Monday morning. During each 24-hour cycle, we repeatedly traversed one transect, generally traveling at 6 kph (equating to about one hour of travel time per pass) with tight 180-degree turns at each end. The observer remained at the prow scanning the water while the boat driver navigated using a handheld Garmin GPSMAP 64. As both crewmates were experienced at detecting snakes and accustomed to working extensive hours, we were able to sustain continuous observational effort through the sessions. During breaks for personal or logistical needs, which were infrequent (2–5 per 24-hour cycle) and short (average=7.2 minutes), at least one crewmate maintained visual contact with the water. For the overnight sessions, LED lamps were attached to the bow, illuminating waters between 60 degrees port and starboard and to approximately 20 m distance; headlamps and flashlights provided supplemental light. If a snake was seen near the end of a transect line, we took care to ensure a duplicate recording was not logged at the start of the next pass; although we could not confirm that individual snakes were never resighted in the middle of the transect line, the likelihood was extremely low because surface drift was never directly in line with the transect, so floating snakes were steadily carried away from our observation area. All snake sightings were marked in a handheld Garmin GPSMAP 64 and documented in a field log with date, time, and distance from boat. Every 30 minutes we recorded environmental variables, including Beaufort Wind Force (BWF), prevailing weather (clear, cloudy, overcast, or raining), and SST measured to 0.01 °C using a traceable standards thermometer.

Recorded surface behaviors for *H. p. xanthos* were coded using a pictorial ethogram (Fig. 4.1). We recorded all distinct behaviors detected during each observation, but because observation periods were usually 15–90 seconds, in most cases only a single behavior occurred. Feeding can occur when a snake is in its tight ambush posture, *FS* (feeding-foraging sinusoidal), but also while swimming backward or from an open posture with the head held low and/or mouth open. For our purposes, any floating body position other than the ambush posture was considered “resting” with one of two categories of contraction registered: *RO* (resting open: floating in a looser or elongated posture) or *RS* (resting serpentine: contracted into a pronounced “S” shape). Other behaviors were *A* (arriving-avoidance: seen <3 m depth while arriving to the ocean surface or diving away), *K* (knotting: looping or coiling of the body), *N* (swimming [*nadando* in Spanish]: forward or backward movement across the sea surface via lateral undulation), or *P* (procreation: breeding or birthing). Snakes found dead were classified as *D*.

4.2.4 Datasets and analyses

We analyzed two datasets: diel data (DD) represented hourly sightings collected during the 2021 diel survey, and non-diel data (NDD) comprised hourly effort and counts for 406 sightings of *H. p. xanthos* recorded outside the diel survey. The NDD came from other studies conducted between 2010 and 2021 and comprised both dry- and rainy-

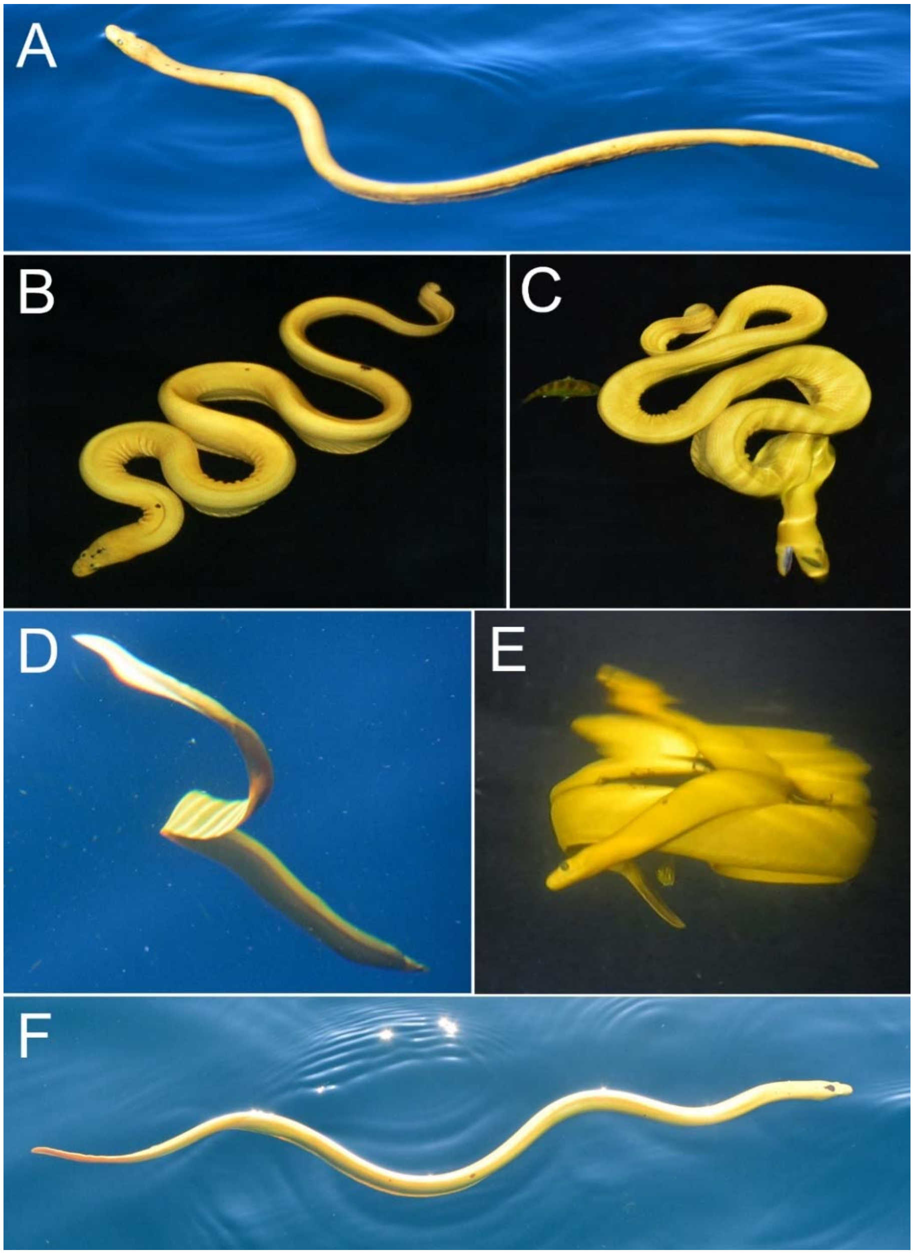

Figure 4.1. Ethogram of surface behaviors for *Hydrophis platurus xanthos*: **(A)** RO, resting open: floating loosely at the surface (the snake is also breathing here with nares above water); **(B)** RS, resting serpentine: floating in pronounced S-shape; **(C)** FS, feeding sinusoidal: tight ambush posture, head pointing down; **(D)** A, avoidance: diving down (or arriving to the sea surface); **(E)** K, knotting: looping or coiling (seen here from below the surface with a light-induced reflection); **(F)** N, *nadando*: swimming forward or backward; procreation: breeding/birthing, not shown; photo credit: B. Bessesen.

season encounters in the inner basin of Golfo Dulce (Bessesen 2012, Bessesen 2015, unpubl. data). Using R version 4.0.3 (R Core Team 2020), we employed circular statistics to analyze the datasets, with sightings binned into clock hours (24 bins) and day-night boundaries set at 0600 h and 1800 h. Encounter rates were computed as sightings (counts) divided by observation hours (OH) within the snake's distribution area (effort) for each bin. We compared encounter rates for the DD and NDD to test if both supported the same patterns with the Watson's Two-Sample Test of Homogeneity using the watson.two.test function in the R library 'circular' (Agostinelli & Lund 2017).

Focusing on the DD dataset, we tested the null hypothesis that observations were uniformly distributed across 24 hours using the Rayleigh test of uniformity (rayleigh.test function in the R library 'circular') and the Hermans-Rasson test (Hermans & Rasson 1985), which has been found more reliable for data that follow a multimodal distribution (Landler et al. 2019). The Hermans-Rasson test was completed using code provided by Landler et al. (2019) with p-values defined based on comparison with 1000 simulated uniform distributions. To identify times at which observations departed from the values expected given a uniform/random surfacing activity, we simulated 10,000 diel studies (using the rcircularuniform function in R) in which the total number of detected snakes and sampling effort (5 hours per hour bin) were equal those of the DD, but with observations randomly allocated to each hour. We then calculated simulated encounter rates and compared those values with observed rates in the DD and NDD. Observed values outside the 95% CI of the simulated rates were used to identify times at which snake sightings were significantly more or less frequent than expected if surfacing activity was similar over all hours of the day. Finally, we used the R package 'activity' (Rowcliffe 2021) to estimate activity rates for both DD and NDD using a kernel bandwidth multiplier of 1.5 as suggested by Rowcliffe et al. (2014).

For each recorded ethogram behavior, we computed hourly frequencies and ran a Herman-Rasson test in R to investigate non-uniformity in the diel pattern (as above, p-values were defined comparing with 1000 simulated uniform distributions). We then investigated differences in behavior by assigning records into day and night periods (day was from 0600 h and 1800 h). Using these counts we first compared behavior percentages for each period (counts of the behavior / total records for the periodic state). This helped us determine what snakes are more likely to do during the day or night. To test whether particular behaviors were significantly more or less likely to occur at night, we fitted a generalized linear mixed-effects model (using the glmer function in R, with a binomial error structure) with day vs. night as the binary response and the observed surface behavior categories as a predictor. To control for temporal and spatial non-independence of records obtained in the same transect and sampling period we included transect line as an intercept random factor. We report model coefficients as odds ratios.

4.3 | RESULTS

4.3.1 Field survey

During the diel survey, we logged a total of 358 sightings of *H. p. xanthos*. The skies above were most often cloudy but frequently became overcast with occasional rain. Mean SST across all hours of observation was measured at 29.2 °C (Table 4.1; daytime=29.4 °C, night-time=28.9 °C). The BWF ranged from 0 (glassy) to 5 (moderate waves, some spray), and snakes were recorded in all except BWF0. Because data were collected over multiple weekends and times, environmental conditions and solar exposure varied (Fig. 4.2) but we found *H. p. xanthos* to be consistently detectable at or near the sea surface. Approximately 200 sightings of the NDD had been previously modelled in the multi-covariate distance sampling engine of Distance 7.3 (Thomas et al. 2010) to test the effect of time of day and/or BWF on detection by distance and no effect was found (p=0.20–0.48). Sometimes two or more detections of *H. p. xanthos* occurred close to each other (<50 m) and in a matter of minutes, although individuals did not interact with one another and were rarely closer than 15 m. With the boat moving slowly and at a consistent speed, the animals showed no reaction to our presence. All sightings occurred within 20 meters of the boat, even during the day when overall visibility could be >25 km, mitigating concerns of perception bias between day and night.

Table 4.1. Survey data information for each transect line, including the survey date, observation hours, total sighting counts for day and night, prevailing weather, minutes of rainfall, and average sea surface temperature.

Transect	Dates	Hours	Total day	Total night	Weather	Rain	SST
TL3	Mar 27-29	24	8	33	C, X	0	30.48
TL2	Apr 3-5	24	19	74	C, O, R	120	28.62
TL1	Apr 10-12	24	16	114	O, C, R	45	28.59
TL4	Apr 17-19	24	6	57	O, C, R	165	28.43
TL5	Apr 24-26	24	9	22	C, O, R	195	29.71
All		120	58	300		525	29.16

Day: 0600–1800 h; Night: 1800–600 h

X: clear/no clouds, C: clouds, O: overcast, R: rain; listed in order of recorded frequency

Bottom line (All) calculates column tallies, except for SST shown as mean

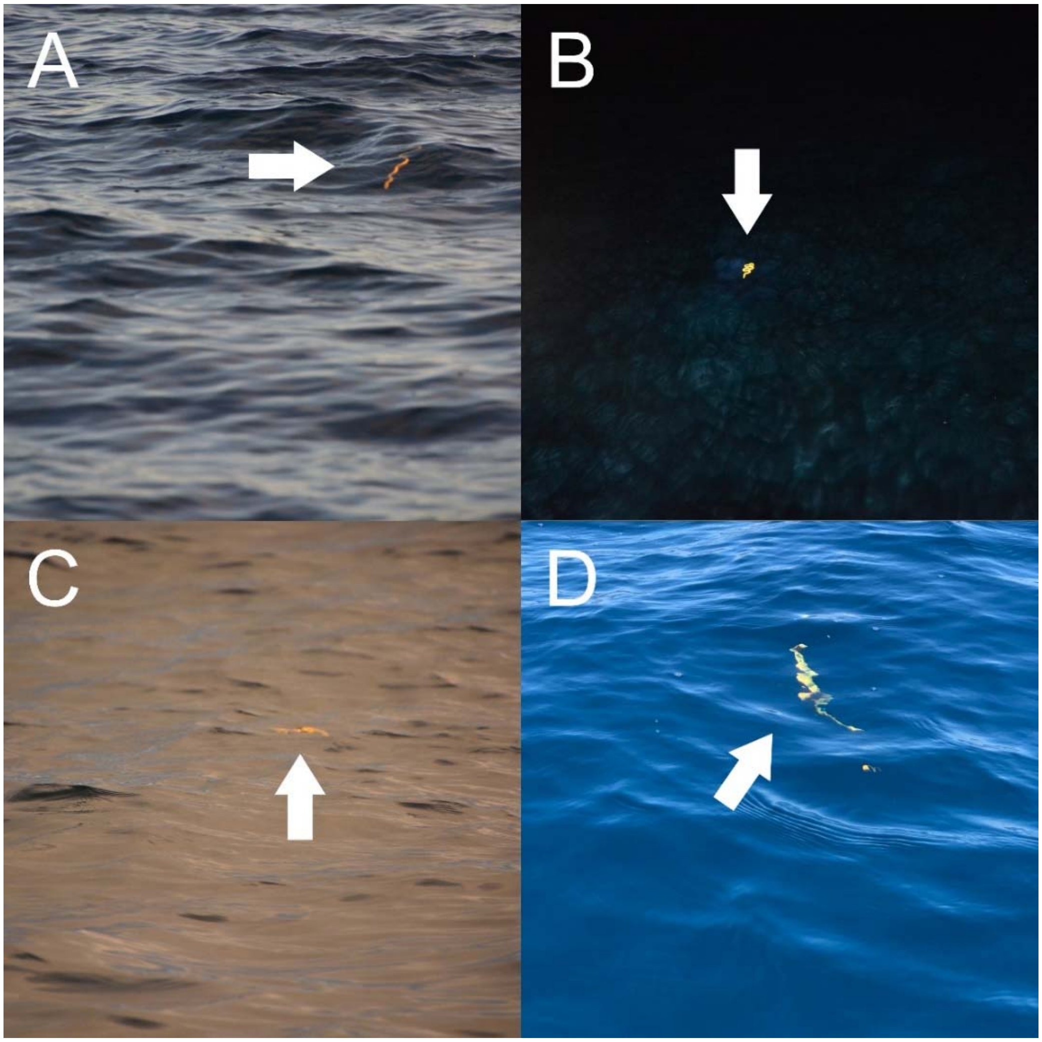

Figure 4.2. Detectability of *Hydrophis platurus xanthos* (pointed by white arrows) in various periodic states: **(A)** lifted by a late-afternoon wave; **(B)** in spotlight at night (sinusoidal ambush posture); **(C)** in first sunrays of morning; and **(D)** diving midday (at <3 m depth).

4.3.2 Diel surfacing pattern

During the diel survey, only 16% (n=58) of *H. p. xanthos* sightings occurred during the day (0600–1800 h) with a significant departure from uniform surfacing activity (Rayleigh test statistic=0.46, p<0.001; Hermans-Rasson test statistic=-649.47, p<0.001). Compared to simulated uniform observations, snakes were significantly less often found at or within 3 m of the sea surface between 0800 h and 1600 h but were more frequent than expected between 0400 h and 0500 h and from 1800 h to 2100 h (Fig 4.3). This pattern corresponds to crepuscular-nocturnal activity, with the highest level of surfacing detected post sunset. Noticeably during the diel survey, no sightings were logged between the daytime hours of 1100 and 1400 (15 hours of observation with no sightings). Hourly survey effort was estimated for the NDD and varied: no surveys were conducted from 0300 h to 0400 h, for other times effort ranged from 1 to 23.5 OH (average=14). Despite the variable sampling effort, encounter rates from the 406 sightings of the NDD had a similar pattern to those of the DD data (Watson's Two-Sample Test of Homogeneity statistic=0.15, p>0.10) supporting crepuscular-nocturnality, although rates were overall lower (Fig. 4.3).

We estimated the mean activity rate (proportion of time at surface) from the DD for *H. p. xanthos* to be 0.330 (SE=0.0337), and hourly probability rates varied with the observed crepuscular-nocturnal pattern (Fig 4.3). The NDD rendered a lower mean activity rate of 0.177 (SE=0.0140), reflecting fewer sightings overall during the studies from which the NDD were compiled, as well as gaps in survey effort with scant night-time coverage, especially between 2300 h and 0600 h. Although diurnal sightings were sporadic, more were present in the NDD owing to much greater daytime sampling effort (up to 23.5 OH per clock hour). We note that these activity rates could be overestimated because the model assumes all snakes are at the surface during the peak hour (Rowcliffe et al. 2014, Rowcliffe 2021), which might not be true. Foraging would be unlikely to draw all numbers to the surface at once since snakes do not normally eat every day (Greene 1997, Lillywhite 2014). Yet, it is still possible that most or all *H. p. xanthos* surface when the sun goes down, if for the sole purpose of resting after a day of dive cycles, reducing energy expenditure through positive buoyancy (Graham et al. 1975). Sighting surveys across both seasons suggested higher encounter rates around dusk and dawn, although we did find differences in surface activity patterns between the dry season (2010 and 2020; n=87 records) and rainy season (2011; n=37; Watson's Two-Sample Test of Homogeneity statistic=0.31, p<0.01). This may reflect true temporal variation or the relatively small size of the rainy-season sample and discrepancies in hourly survey effort between years (for example, when considering the period between 1300–2400 h, in the dry season we logged 2–19 OH per clock hour but ≤1 OH per clock hour in the rainy season).

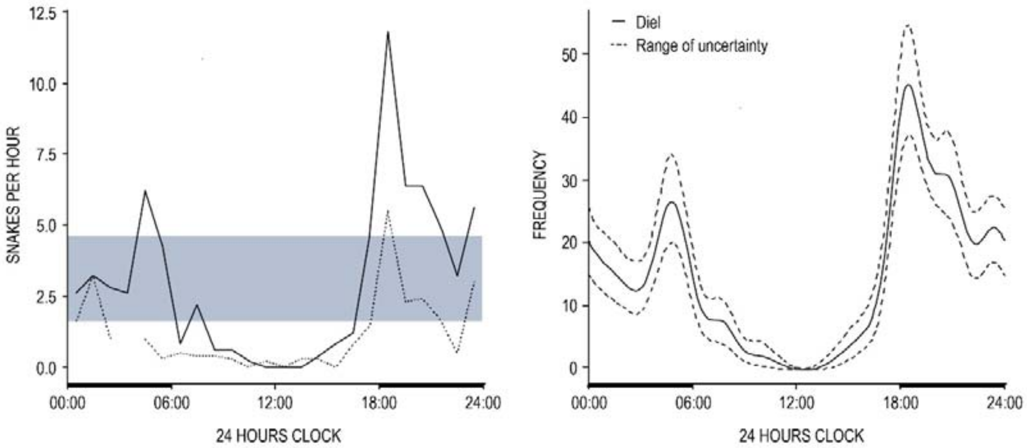

Figure 4.3. Diel data on 24-h clock (bold x-axis line: night between 18:00 h and 06:00 h); LEFT: Observed by-hour encounter rates of diel data (solid line; consistent effort with five 24-h cycles) and non-diel data (dashed line; opportunistic records with variable effort and no surveys from 03:00–04:00 h); gray ribbon shows 95% confidence intervals of simulated uniform encounter rates; RIGHT: Estimated by-hour surfacing probability rates (mean and 95% CI) of *Hydrophis platurus xanthos.*

4.3.3 Surface behaviors

For the ethogram-coded behaviors (Fig 4.1), we recorded a total of 470 data points in order of frequency: *RO* (n=213), *RS* (n=126), *A* (n=47), *FS* (n=38), *N* (n=38), and *K* (n=8); no procreative behavior or dead snakes were observed. For most snakes we observed a single behavior, but for about a quarter of individuals (n=92) we recorded 2–4 different behaviors within the brief period of observation allowed as we passed. Snakes were equally likely to exhibit multiple behaviors by day or night (26% of sightings in both periods). All six behaviors were significantly nonuniform (Herman-Rasson tests: A statistic=-78.57, p=0.024; FS statistic=-73.01, p=0.011; K statistic=-25.94, p=0.013; N statistic=-86.78, p=0.002; RO statistic=-377.43, p<0.001; A statistic=-295.08, p<0.001).

Sea snake behavior varied between night and day (Fig 4.4, Table 4.2). For example, nearly a quarter of sea snakes found during the day were diving and surfacing (*A*) compared to only 11% of those found at night. Floating in an open or loose body posture (*RO*) also appeared a more common daytime behavior. Conversely, resting in a serpentine shape (*RS*) and feeding sinusoidal (*FS*) were far more common at night, when snakes fluidly shifted between *RO* and *RS,* and sometimes in and out of *FS*. As previously reported by Bessesen & Galbreath (2017), we only saw *H. p. xanthos* in its ambush posture (*FS*) between sunset and sunrise (3 sightings of *FS* occurred post-sunset but within 9 min of 1800 h). Snakes were found swimming (*N*) and knotting (*K*) in similar percentages during day and night (Fig 4.4).

Odds ratios provided an intuitive way to interpret our model results (Table 4.2). For all 470 records, behavior was 4.7 times (SE=1.23) more likely to occur at night than during the day. This value provides a reference for comparison with OR estimates for different behaviors and shows *FS* and *RS* to be primarily nocturnal behaviors. *FS* was 10.78 times more likely to occur at night, more than twice the average likelihood, and *RS* was nearly three times the average (OR=12.62). Because we considered all observed behaviors and sometimes more than one behavior was observed in the same snake, our model results could have been influenced by pseudo-replication, and because we recorded a single behavior for most snakes, using snake ID as a random factor (to control for non-independence) resulted in convergence issues. Confidence was gained, however, when a model that considered only the first recorded behavior for each snake showed the same qualitative results.

TABLE 4.2. Odds ratios for nighttime observation of surface behaviors of *Hydrophis platurus xanthos* based on a generalized linear mixed-effects model (glmer function in R, family binomial, day and night as binary responses, observed surface behaviors as predictors, transect line as random factor modifying the intercept).

	OR	CI		
Diving-surfacing (A)	2.43	1.212	–	4.888
Feeding sinusoidal (FS)	10.78	3.188	–	36.458

Knotting (K)	6.26	0.746	–	52.482
Swimming (N)	3.86	1.664	–	8.949
Resting open (RO)	3.63	2.314	–	5.684
Resting serpentine (RS)	12.62	5.994	–	26.588

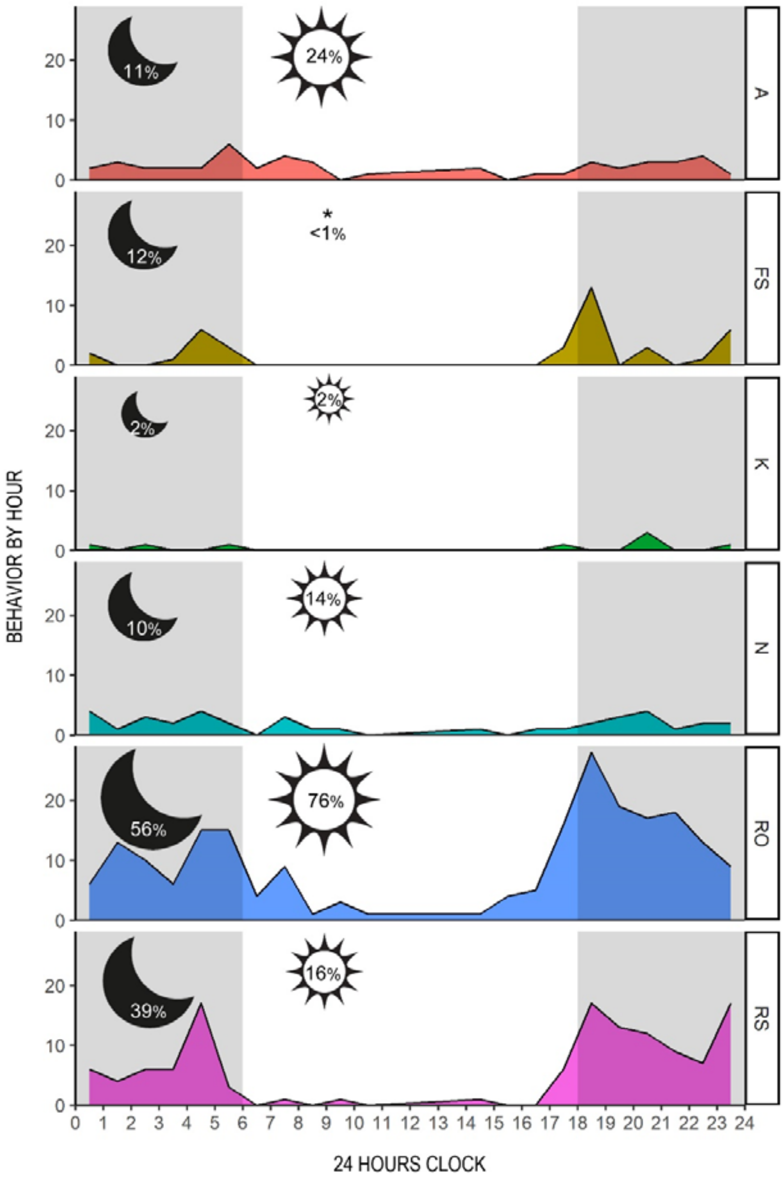

FIGURE 4.4. Area graphs for by-hour frequencies of surface behaviors of *Hydrophis platurus xanthos*: A (diving or surfacing), FS (feeding sinusoidal), K (knotting), N (swimming), RO (resting open), and RS (resting serpentine); percentages of total recorded behaviors by period are shown inside moons (night) and suns (day), scaled for quick reference (larger icons for higher percentages).

4.4 | DISCUSSION

Confined to the deep inner-basin waters of Golfo Dulce, *H. p. xanthos* appears to have developed a defined multimodal circadian rhythm. Its surfacing pattern is one of crepuscular-nocturnality, described by more observable surfacing at night with conspicuous peaks in the twilight hours. Nocturnality was patterned by some surface behaviors too. Notably, the taxon's unique ambush posture and seemingly associated position of resting serpentine are almost exclusively seen at night, when individuals fluidly transition between resting, foraging, swimming, and knotting. While daytime sightings of *H. p. xanthos* are rarer, they do occur. In fact, the reported diel surfacing pattern is more likely to reflect duration of time at the surface than number of surfacing events. Given the need to breathe, sea snakes undoubtedly surface repeatedly throughout the day (diving and surfacing actually represented a higher percentage of behavior records during the day than at night), but because they can take 1–2 breaths and resubmerge in a matter of seconds (Myers 1945, Rubinoff et al. 1986, pers. obs.), the chance of detection is greatly reduced. Every observed dive required active propulsion, but surfacing did not always occur through lateral undulation. Some snakes rose up through the water column while seemingly motionless and horizontally positioned, the maneuver ostensibly managed through buoyancy. The most common surface behavior in both principal periodic states was resting open; it accounted for more than half of the nighttime and three-quarters of the daytime records. Two behaviors appeared equally common in daylight or darkness: swimming and knotting, granting the sample size of the latter was too small for confidence.

Because all *H. p. xanthos* reside in one small and relatively sheltered marine habitat, we were able to identify patterns for the entire population, although it is worth noting that we did occasionally find snakes floating at the surface during atypical hours. That two or more snakes sometimes surfaced in the same general area within a narrow time frame, even during the day, suggests that common factors drive surfacing, and pockets of conducive underwater conditions may help explain proximal groupings. Even in peak hours, multiple factors likely influence behavior and length of time at the surface, including environmental conditions, physiological needs, and prey availability (Helfman 1986, Daltry et al. 1998), which could be explored in future studies. Whereas we focused on the diel scale, other biological clocks besides circadian (tidal, lunar, and seasonal) may also affect behavioral patterns (Udyawer et al. 2017, 2020). Seasonal comparisons in the NDD suggested some temporal difference, but the reliability of that finding is uncertain due to small sample size and limited survey effort. It is possible that cloud cover during the rainy season and a slightly shorter photoperiod allows *H. p. xanthos* to extend its surfacing hours into early post-sunrise morning and/or late afternoon. Still, the basic pattern appeared to hold year-round and over a decade of observations, and we would not expect it to change significantly given that tropical regions are relatively stable, and the snakes are obligated to regularly breathe, eat, and drink at the water surface in the periodic state most suitable for their survival.

Temperature plays a prominent role in snake biology (Greene 1997, Weatherhead & Madsen 2009), and while rainfall appears to have little effect on the activity of tropical snakes (Brown & Shine 2002), overcast skies and rain bring cooler temperatures. Our survey ended in April, the last month of the dry season in Costa Rica, and precipitation became progressively heavier and more frequent through the study period. Although SST does not fully describe the thermal environment, we measured an average of 29.2 °C, with the daytime average only 0.3 °C higher than at night. Importantly, at the height of the dry season, SST in Golfo Dulce can surpass 32 °C (Bessesen 2015, Rincon-Alejos & Ballestero-Sakson 2015), and while the critical thermal maximum for *H. p. xanthos* is unknown, its sister taxon, *H. p. platurus,* has a reported maximum of 33–36 °C (Dunson & Ehlert 1971, Graham et al. 1971). A black dorsum collects heat when exposed to sunlight (Graham 1974b) and diurnal foraging naturally increases that exposure. It was almost certainly temperature that drove *H. p. xanthos* to evolve its nearly all-yellow coloring. It has already been suggested that cooling in xanthic sea snakes is promoted by lighter skin color (Solórzano 2011, Bessesen 2012), and a smaller body size (Bessesen & Galbreath 2017) increases the surface-area-to-mass ratio for more rapid thermal exchange (Ashton and Feldman 2003). We hypothesize that *H. p. xanthos* could also have functionally transitioned to warmer waters by reducing its surfacing time during the day, shifting from diurnality to nocturnality to avoid overheating. If despite these morphological and behavioral adaptations, *H. p. xanthos* is surviving near the top of its thermal limit, the trend of warming SST in Golfo Dulce, as recently reported by Murayama et al. (2018), could threaten long-term survival of the population.

Temperature, however, might not be the only, or even the main, driver of night-time surfacing by *H. p. xanthos*. Melanin protects a squamate's integument and internal organs against the damaging effects of ultraviolet radiation (Porter & Norris 1969, Greene 1997, Lillywhite 2014). Dark skin over venom glands may specifically protect venom from degradation (Pough et al. 1978). Thus, lacking the protective melanin of *H. p. platurus*, *H. p. xanthos* may be photosensitive, and if so, nocturnality could mitigate tissue damage from solar radiation and preserve venom potency for successful feeding. We further hypothesize that the observed post-sunset peak in surfacing could be caused by energetic needs. Tiny fish are frequently seen in association with *H. p. xanthos* at sightings around the clock and snakes do sometimes feed when the sun is above the horizon (from an RO posture; pers. obs.), but if solar radiation and/or other factors limit the duration of daytime surfacing events, snakes could become increasingly hungry while waiting until the sun sets before floating for prolonged foraging periods. While fish also evince diel patterns (Helfman 1986), *H. p. xanthos'* prey may be regularly present: one of more fish are commonly observed alongside, ascending, and descending in the water column (unpubl. data), though the snakes never feed at depth. The snake's sinusoidal ambush posture likely developed to accommodate for ocean turbulence, which commonly increases in Golfo Dulce in the late afternoon and evening (pers. obs.).

A potentially important benefit of nocturnal surfacing could be predator avoidance. The nominate taxon, *H. p. platurus* is advantaged by both countershading (Graham et al. 1971) and aposematism, with no known natural predators (Kropach 1975). Whether transitioning to a yellow dorsum in *H. p. xanthos* has bearing on rates of predation is unknown; however, these snakes do appear timider than their black-backed conspecifics (Bessesen 2012). Xanthic snakes are known to be harassed by dolphins (Bessesen et al. 2021; Appendix). They are also occasionally found with scars that indicate traumatic injury, including one with a missing eye (unpubl. data). Since several known avian predators are present in Golfo Dulce (pelicans, ospreys, black hawks, and magnificent frigates), nocturnal surfacing could mitigate risk of incidental attack. Avoidance of boat traffic in the embayment might be another added benefit of night-time activity, though regular daytime surfacing for ventilation could still put snakes at risk. Xanthic sea snakes rarely if ever dive when a boat drives near or even over them, apparently ignorant to the mortal danger of propeller strikes (pers. obs.), but we have noticed that during the day, snakes are more likely to react to loud, sudden noises nearby such as a boat motor starting or thumps inside the hull, and will sometimes swim forward with the head lifted well above the water to presumably make observations before quickly diving away (the retinal structure of *H. p. platurus* suggests visual acuity below and above the water; Hibbard & Lavergne 1972).

Crepuscularity is rare among sea snakes (Simões et al. 2020). As previously stated, *H. p. platurus* is considered diurnal (Kropach 1975, Rubinoff et al. 1986, Brischoux & Lillywhite 2011, Simões et al. 2020), though Lillywhite et al. (2015) noticed a more nuanced pattern that emphasized morning surfacing (between 0700–1100 h; also see Tu 1976). While Udyawer et al. (2015) found free-ranging congener species, *H. curtus* and *H. elegans*, to be more active at the water surface at night, Heatwole and Seymour (1975) studied *H. elegans*, *H. peronii*, and *H. belcheri* in the laboratory and found all three to be less active at night. Simões et al. (2020) inferred diel activity patterns for several sea snakes using genetic variation in spectral sites, trawl bycatch data and previous literature. They identified *H. elegans* as cathemeral (which might explain the contradictive findings between field and lab) and confirmed *H. curtus* and *H. peronii* as diurnal; *H. belcheri* was not categorized. Of the 17 species from the genus *Hydrophis* for which a diel pattern was included, similar numbers were reported as cathemeral (n=5), nocturnal (n=5), and diurnal (n=7), yet even with an explicit fourth category, none were reported as crepuscular. That *H. p. xanthos* breaks from the patterns of its closest relatives poses an interesting evolutionary question and calls attention to the limits of inferring the behavior of understudied taxa.

Garnering behavioral and activity data is not easy (Bridges & Noss 2011), especially on a population level and under natural conditions. However, such studies are needed. Transmitters are a common tool for securing activity and spatial data. These devices are typically attached to or implanted in the bodies of anesthetized snakes through surgical methods (as in Rubinoff 1986, Shetty & Shine 2002, Udyawer et al. 2015) or swallowed (as in Burns & Heatwole 1998, Weatherhead & Blouin-Demers 2004), but can have negative impacts on immunity, fecundity, and lifespan (see Riley et al. 2017 for a review). Tag studies are also expensive and sample sizes tend to be small (Lashley et al. 2018), plus resulting changes in behavior can bias results (Fitch & Shirer

1971). Camera trapping is slowly gaining ground as a method for detecting terrestrial snakes, but diel patterns have yet to be published, and the potential for use in the marine environment is yet undetermined (Welbourne et al. 2017, Neuharth et al. 2020). Unmanned underwater object tracking devices show real potential for collecting movements and behavioral data, but currently require a transponder attached to the animal (Dodge et al.2018; such equipment is easily suction-cupped to a sea turtle shell but less applicable for a sea snake). New marine research tools continue to emerge, from passive acoustic monitoring to side-scan sonar to remote-sensor satellites, and with collaborative pioneering between ecologists and engineers, improved techniques for recording the behavior and activity patterns of sea snakes are likely to be developed. In the meantime, the value of non-invasive if arduously collected observational data should not be underestimated and can be particularly useful in taxa that, like *H. p. xanthos,* are observable and inhabit narrow, navigable ranges. Real-time visual diel surveys are especially advantageous when dealing with small, endemic, or otherwise vulnerable populations, which could suffer from invasive or potentially detrimental methods.

There is an intensifying need to facilitate the research and monitoring of sea snakes around the world. The International Union for Conservation of Nature identifies approximately a third of species as Data Deficient (Elfes et al. 2013, IUCN 2021), and of those studied, many are reported in inexplicable decline (Goiran & Shine 2013, Lukoschek et al. 2013, Udyawer et al. 2018). Among the fundamental ecological data required to inform protection strategies, established diel patterns not only enable improved survey designs, but may also serve as indicators since altered or declining activity can reveal negative trends (Barrueto et al. 2014). Our work therefore supports the conservation of *H. p. xanthos*. It also contributes to the overall understanding of this endemic subspecies, which given genetic isolation and the accumulative evidence of morphological and behavioral distinctiveness, may warrant recognition as a new species.

4.5 ACKNOWLEDGMENTS

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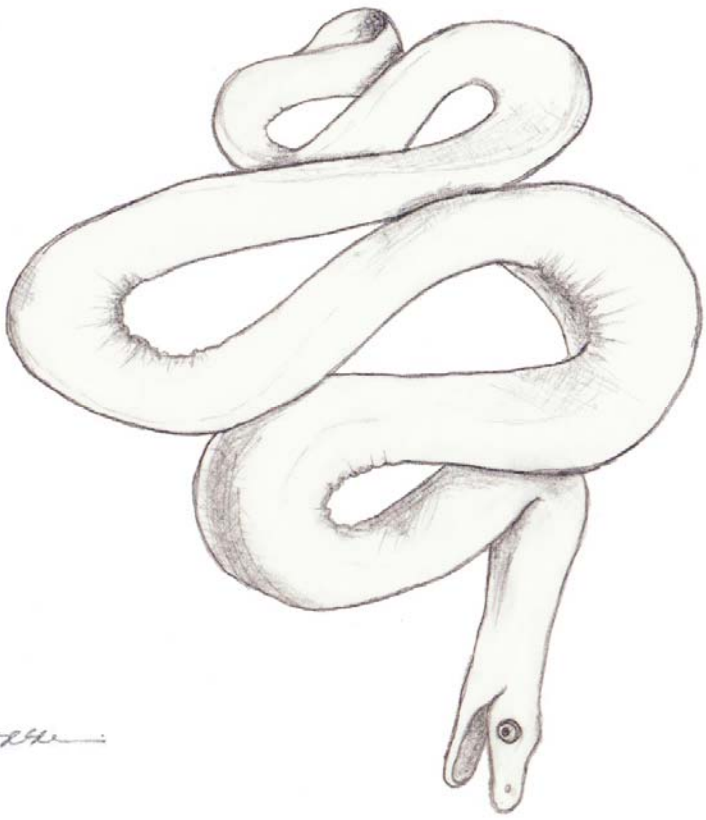
Chapter 5



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Author contributions: BLB conceived and designed the study, collected, and analyzed the data, and led the writing of the manuscript. CSO guided and inspected the statistical analyses and reviewed the manuscript. GJG contributed to interpretation of the results and preparation of the manuscript. MGS participated in methodology, data analyses, and manuscript writing.

CHAPTER 5: Population abundance and density estimates for Costa Rica's endemic sea snake, *Hydrophis platurus xanthos*

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5.0 | ABSTRACT

Population abundance and density estimates provide key information for conservation assessment and prioritization of efforts and management. However, data are still largely unavailable for many taxa, including sea snakes, which appear to be facing global declines. Here, we present the first quantitative abundance and density estimates for the geographically isolated sea snake *Hydrophis platurus xanthos* endemic to the inner basin of Golfo Dulce, Costa Rica. Using systematic distance sampling methods, we obtained and analyzed 199 snake detections from 46 transect lines covering the entire known distribution (totaling nine days and 469 km of effort). Our modeling methods accounted for (i) the probability of detecting a snake given it was available to be detected (ii) the average availability of snakes at the water surface during a 24-hr cycle, and (iii) the by-hour variance in the taxon's activity pattern. The best estimate of population abundance was 29781 individuals (95% CI=20104–44115) with an estimated density of 76 snakes/ km^2. Without historical abundance estimates or minimum viable population size, it is unknown whether this number represents a healthy population. However, with all individuals inhabiting a relatively small inlet increasingly exposed to anthropogenic impacts, the long-term persistence of *H. p. xanthos* may be threatened by ongoing impacts (boat propeller strikes, agricultural runoff, and climate change), as well as unforeseen events in the future.

Key words: abundance estimation models, activity bias, availability bias, distance sampling, Golfo Dulce yellow sea snake, *Hydrophis platurus xanthos,* line transect survey, marine reptile

5.1 | INTRODUCTION

The late Holocene, frequently referred to as the Anthropocene, is marked by destabilizing changes in nature (Steffen et al. 2007), eliciting concern for ecosystem functioning and the future of biodiversity (Dulvy et al. 2003, Hector and Bagchi 2007, Cardinale et al. 2012). Supporting and protecting biodiversity requires ecological knowledge including reliable population estimates from which abundance trends can be measured (Dornales et al. 2018). Securing abundance data, however, is exceedingly difficult. Accurate estimates are available for few species and filling the gaps presents challenges associated with the diversity of habitats and natural histories that need to be studied with limited resources. To date, only 5% of all described species worldwide have been evaluated for risk of extinction (IUCN, 2022) even as thousands are disappearing, often without ever being identified (Pimm et al. 1995, IPBES 2019, WWF 2020).

Among at-risk fauna, a fifth of all reptile species may be threatened with extinction (Böhm et al. 2013), and snakes are declining at an alarming rate (Gibbons et al. 2000, Reading et al. 2010). Marine populations may be increasingly susceptible to pathogens, predators, boat strikes, environmental changes (Somaweera et al. 2021), and trawlers (Fry et al. 2001), but numbers may also be reduced by inexplicable causes (Goiran & Shine 2013, Elfes et al. 2013, Lukoschek et al. 2013, Udyawer et al. 2018). Reading et al. (2010) identified three general characteristics among snake species experiencing sharp decreases: they inhabit narrow ranges, tend to be sedentary (minimal travel), and display ambush-style foraging. It is hypothesized that these traits make them more vulnerable to anthropogenic impacts and/or habitat degradation. All three of these traits occur in a recently described sea snake: *Hydrophis platurus xanthos* (Bessesen & Galbreath 2017). This taxon exhibits geographic rarity occupying a relatively small area of aquatic habitat within the semi-closed embayment of Golfo Dulce, Costa Rica (Bessesen 2012), it rarely swims across the ocean surface, and uses a floating ambush posture to opportunistically capture tiny fish (Kropach 1973, Brischoux & Lillywhite 2011, Bessesen & Galbreath 2017). Moreover, confined to an area of active human use, there are already several potential threats to the population, including boat traffic (Bessesen & González-Suárez 2021; Appendix) and water pollutants (Spongberg 2004, Fournier et al. 2019). Climate change poses additional risks (Lillywhite et al. 2018, Udyawer et al. 2018). Sensitive to thermal shifts (Heatwole et al. 2012) already reported in the region (Morales-Ramírez et al. 2015; Murayama et al. 2018) and bound by rainforest and mountains to the north, *H. p. xanthos* is unable to migrate into higher latitudes to escape warming waters (Poloczanska et al. 2016). Despite its likely vulnerability and ongoing threats in its habitat, quantitative data on population abundance and density have to date been unavailable. Such data are key to assessing this taxon's conservation status and detecting potential declines in the future.

Distance sampling is a long-established method that uses line transect data to model population abundance and density (Eberhardt 1978, Buckland et al. 1993, Williams et al. 2017). This method has been used with a variety of cetaceans (Jaramillo-Legorreta et al. 1999, Miller et al. 2013, Doniol-Valcroze et al. 2015, Kreb et al. 2020), but has not been applied to sea snakes. Distance sampling has been considered for terrestrial snakes (Dorcas & Willson 2009) but often failed to return reliable results (Rodda & Campbell 2002, Stellati et al. 2019), largely because of difficulties in achieving the required minimal number of detections (60–80 per Buckland et al. 2001, 2015). For terrestrial snakes, abundance studies have historically used mark-recapture techniques when possible; otherwise, occupancy monitoring or relative abundancy indices have been employed (Dorcas & Willson 2009). Abundance estimates for sea snakes are exceedingly rare (IUCN 2022) and usually provide single-site data for broader-ranging species (Saint Girons 1964, Voris 1985, Lading et al. 1991, Shine et al. 2021). Mark-recapture was attempted with the related pelagic sea snake, *H. p. platurus*, but proved unsuccessful (Kropach 1973). Because *H. p. xanthos* is limited to a narrow range, however, and much like a cetacean is detectable at the ocean surface between dives, distance sampling is a viable approach for this taxon.

Baseline occupancy and relative abundance data for *H. p. xanthos* have been previously published (Bessesen 2012, Bessesen 2015), and two questionnaire surveys with local fishermen and tour boat guides offered insight into perceived abundance and trends (Bessesen & González-Suárez, 2021; Appendix). Lillywhite et al. (2015) reported an encounter rate of 21.4 ± 4.4 snakes/h (mean ± SD) based on two-nights of data. By completing 45.9 survey hours and applying robust statistical methods we offer the first total abundance and density estimates for this rare, likely vulnerable marine snake. We hope this work can serve to inform stakeholders in the conservation of *H. p. xanthos,* and more broadly contribute to the knowledge base for marine reptiles and biodiversity in the American tropics. Our methods may prove informative to those working to estimate sea snake population abundance and density estimates elsewhere in the world.

5.2 | MATERIALS AND METHODS

5.2.1 Study area and survey design

Golfo Dulce is an inlet estimated to be 725–750 km^2 in the Puntarenas province of southwestern Costa Rica (Wolff et al. 1996, Bessesen 2015). Formed by shifting tectonic blocks, the marine embayment's fiord-like morphology is considered rare to the tropics (Berrangé 1989, Hebbeln & Cortés 2001, Malzer & Fiebig 2008). Golfo Dulce is characterized by a >200 m-deep inner basin (Wolff et al. 1996, Svendsen et al. 2006) sheltered from the broader Pacific masses by a 60-m sill at latitude 8°30' N (Hebbeln et al. 1996). Our ~400 km^2 study area encapsulates the full range and only known habitat of *H. p. xanthos* (Bessesen 2012, 2015, Bessesen & Galbreath 2017). A systematic distance sampling survey with a random starting point was designed in the software program Distance (version 7.3; Thomas et al. 2010) and resulted in 46 parallel transect lines spaced 0.75 km apart. Most transects were shore-to-shore (n=38), while the eight most south-easterly transects provided survey coverage only across the inner basin (Fig. 5.1).

5.2.2 Distance sampling

Both observers, the first author (BB) and research assistant Jorge Largaespada (JL), had previous experience detecting xanthic sea snakes, and conducted distance-estimation training prior to and during the survey. We completed 12 training sessions totaling 5 hours and 23 minutes with 165 trials (estimation attempts) following recommendations in Williams et al. (2017). Accuracy of visual estimates during training sessions was tested using an Aofar HX-700N/800H laser rangefinder (accurate to +/- 1m) and/or a small yellow buoy attached to a marked fishing line. Accuracy to +/- 1m was comparable between both observers with a combined precision rate of 98% achieved in the last 64 trials.

Transects were surveyed from 5–13 February 2020 following protocols in Buckland et al. (1993, 2001, 2015). As *H. p. xanthos* is nocturnal (Bessesen & González-Suárez 2022; Chapter 4), surveys were completed at night with observation hours typically beginning just after sunset and ending between 2200–0200 h. An expert local boat captain navigated our 7-m research vessel at 8–13 km per hour (generally 12 km/h) using a handheld Garmin GPSMAP 64 to maintain course following the transects. Three LED lamps were attached to the bow of the boat to illuminate forward waters from 90 degrees port (left) to 90 degrees starboard (right) and extending out to approximately 20 m distance. During the surveys, the observers remained at the bow (BB sitting and JL standing immediately behind) and continuously searched the area for snakes using additional handheld torches and headlamps as needed; visual coverage was not divided, but rather, both observers scanned the same span of water across the front and forward sides of the boat. Perception bias (the inability to detect snakes despite their presence) naturally occurs with increasing distance, a tenet of distance sampling, but neither darkness nor wave height caused additional perception bias because our lights shined through the water, eliminating most wave effect on visibility, and the reflectiveness of the yellow skin allowed ready detection of snakes within the defined observation area (Fig. 5.2). When a detection occurred, the boat was immediately slowed, and the perpendicular distance of the snake to the centerline was visually estimated to the agreement of both observers. Full-time observational coverage was maintained by JL during data recording, and all details were logged before the boat resumed speed.

Efforts were made to ensure detection of all snakes at the sea surface. To accurately utilize distance sampling methods, it is essential to obtain accurate perpendicular distances between the line and the detected snake before the snake changes its position in response to human presence. We first anticipated this would require us to obtain radial distance from the boat and the angle between the line and the snake at the time of first detection, which would then be converted into perpendicular distances; however, the snakes showed no reaction to our presence, allowing us to directly obtain perpendicular distances as we passed. In addition, the side of the boat (port or starboard) was recorded along with the date, time, GPS coordinates for boat location at detection, visibility, prevailing weather, and Beaufort wind force (BWF). Environmental variables were also recorded at the start and end of each track line and at 30-minute intervals during the search if no sightings were logged within the period.

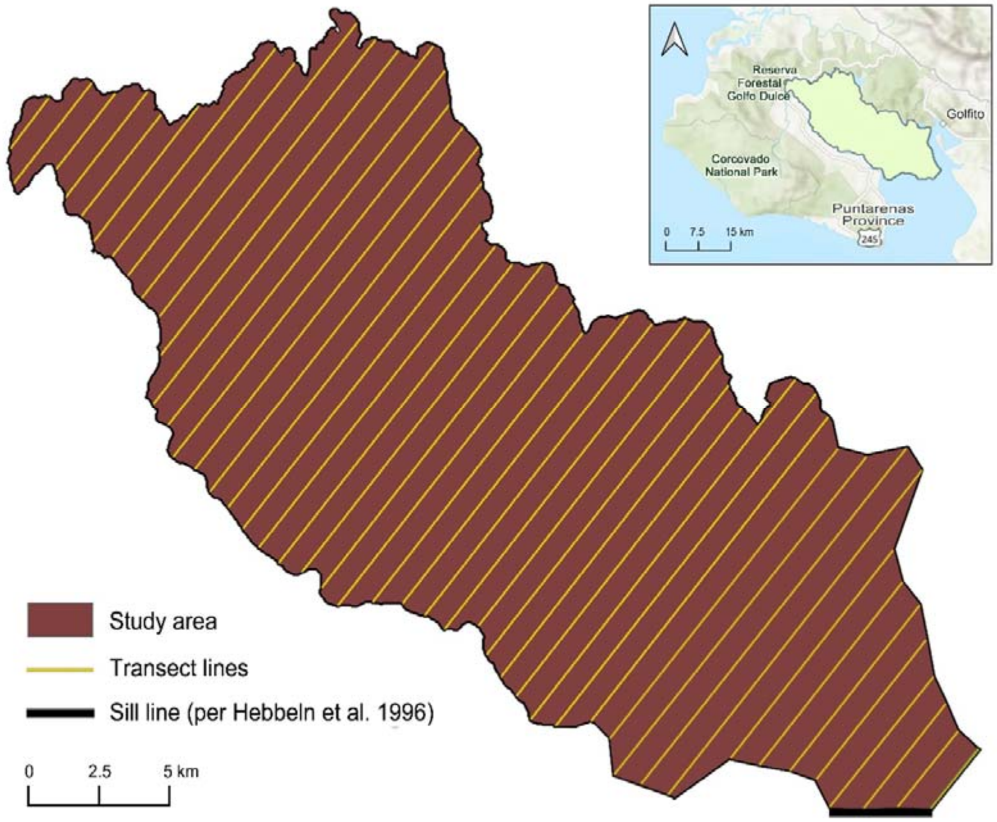

Figure 5.1. Study area with 46 transect lines spanning the inner basin of Golfo Dulce, Costa Rica; transects were generated in Distance 7.3 using a systematic design with a random starting point (Thomas et al., 2010), inset map created in ArcGIS (ESRI, 2011).

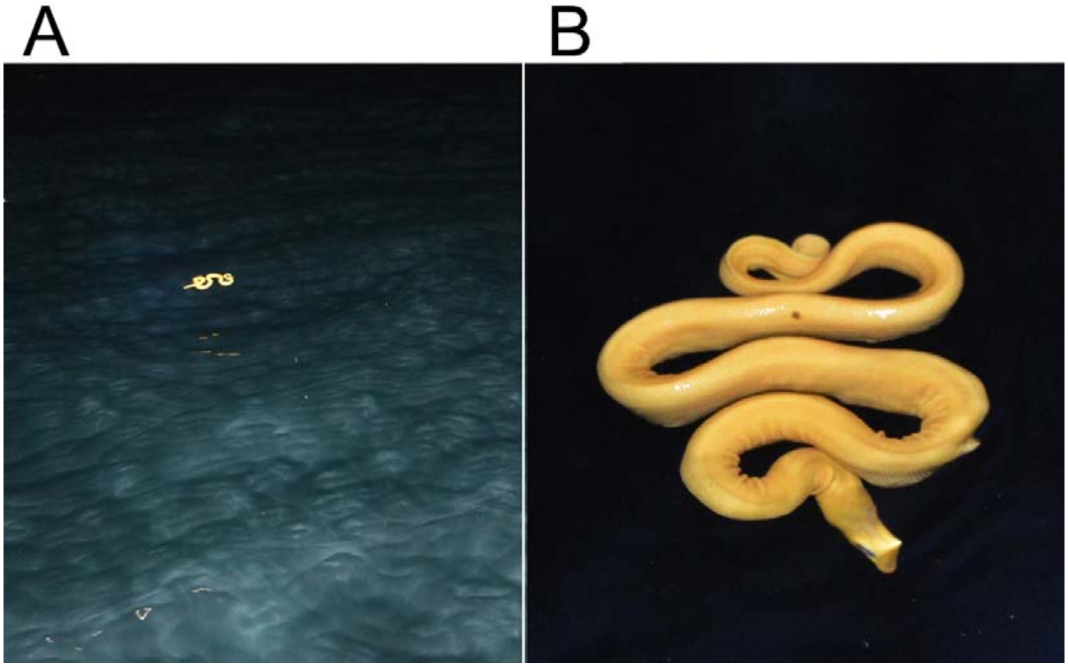

Figure 5.2. *H. p. xanthos* floating at the sea surface at night: **(A)** seen at ~9 m distance; photography rendered a background darker than it appeared in situ; and **(B)** photographed at closer range; the light-induced distortions are artifacts; photo credit: B. Bessesen.

5.2.3 Statistical modeling

We used the program Distance (Thomas et al. 2010) and the package 'Distance' (Miller et al. 2019) in R (version 4.0.3; R Core Team 2020) to model our line transect data. Three transect lines were repeated during the survey, and from each of these we analyzed the track with the highest recorded detections. Several conventional distance sampling and multiple covariate distance sampling models were explored. These included three key functions (half-normal, hazard rate, and uniform), with various adjustment terms (cosine or simple polynomial) and hour and BWF as covariates (Table 5.1). Hour and BWF were also tested for collinearity using a Kendall's Tau coefficient test (cor function in R). Models were compared using the Akaike information criterion (AIC; Akaike 1979) and the model with the lowest AIC score was deemed as the best fitting model. The input data for the models included the study area (A=394 km^2), number of transect lines (k=46), survey effort by line length (L=469 km), visibility-based truncation width (w=20 m), coverage area (2wL=18.76 km^2), and perpendicular distance of snake-centerline for each detection.

Because *H. p. xanthos* spends most of its time below the water surface, snakes at depth in the water column passed undetected violating the key assumption of distance sampling that detectability at the centerline is complete, often referred to as $g(0)=1$. As this is a common violation among diving marine animals, an availability bias correction has been proposed using dive data (Laake et al. 1997, Laake & Borchers, 2004). We used the R package 'hmltm' (Borchers et al. 2013) to compute a correction factor based on the probability of an animal being at depth (unavailable for detection) or near the surface (available for detection). Specifically, we chose the 'laake' model (Laake et al. 1997) as it considers boat speed and farthest visible distance during the distance sampling survey. Because dive data are not available for *H. p. xanthos* we relied on data from Rubinoff et al. (1986) who used ultrasonic pressure transmitters with boat-based hydrophones and receivers to track 15 *H. p. platurus* off the coast of Panama for 3.8 to 31.2 hours. The published data included track time, dive count and average dive duration for each specimen. To focus only on full dive cycles, we first adjusted the published track time by removing any initial surface time prior to the first dive (incomplete dives at the end of the tracking period were already truncated). We then calculated the average dive cycle for each individual by dividing the adjusted track time by dive count. Average dive duration served as 'unavailable' time per cycle and was subtracted from the dive cycle to obtain average time 'available' (Table 5.2). Finally, we averaged the unavailable and available times across individuals, weighted by the adjusted track time (as we expected individuals tracked for longer to provide more reliable data). We acknowledge that using Rubinoff et al. (1986) dive data assumes time-at-the-surface and time-below-the-surface of *H. p. platurus* is similar to that of *H. p. xanthos* and that the reported diving-surfacing behavior was 'normal' and not affected by capture and anesthesia or device attachment (all specimens reportedly swam normally in the lab prior to their release).

Diurnal sightings of *H. p. xanthos* are rare, so we conducted night surveys to maximize detection probability, but in doing so we violated the assumption that distance sampling data are collected at random times in relation to the organism's activity patterns. Also, the correction factor for availability, as described above, constitutes an average across a 24-hr period. To address potential biases resulting from this, we developed an activity bias correction method. We estimated surface activity rates using sighting data from a diel study with constant hourly survey effort across multiple 24 hours periods (Bessesen & González-Suárez 2022; Chapter 4). This was done by fitting a kernel density in the R package ‘activity’ (Rowcliffe 2021), with a 1.5 kernel bandwidth multiplier as recommended by Rowcliffe et al. (2014), to calculate surface activity rates for each clock hour. We then compared the overall average for the complete 24-hour period with the narrower night-time period weighted by time spent in each hour during the distance sampling survey (to account for variable effort within the survey interval). The activity bias correction factor was defined as the ratio between these two rates (24-hrs rate/night-time rate).

The best estimate and 95% confidence intervals of abundance from the best-fitting conventional distance sampling model were multiplied by both correction factors to obtain a final estimate of abundance with uncertainty. We note that we could not account for uncertainty in the correction factors, so the confidence intervals may be too narrow. Lastly, population density was calculated by dividing the final corrected abundance estimate by the range of the study area (in km^2). For comparison with pelagic sea snake studies that have reported an encounter-rate ‘density’ as snakes-per-hour (Kropach 1971a, 1973, Rubinoff et al. 1986, Lillywhite et al. 2015), we also report the average rate of snakes/ hr during the distance-sampling survey period.

Table 5.1. AIC values for conventional distance sampling (CDS) and multiple covariate distance sampling (MCDS; with covariates hour and BWF) models, using the key functions of uniform (UNI), half-normal (HN) or hazard rate (HR), and adjustment terms of 1–2 cosines (cos) or simple polynomial (simpol); covariates cannot be used with the uniform key.

CDS

Key	Adjust.	AIC
UNI	--	1192.3
UNI	1 cos	1114.0
UNI	2 cos	1115.9
HN	--	1114.3
HN	1 cos	1116.2
HR	--	1119.7
HR	simpol	1120.0

MCDS

Key	Covar.	AIC
HN	hour	1116.1
HN	BWF	1116.3
HN	hour + BWF	1118.1
HR	hour	1126.1
HR	BWF	1125.9
HR	hour + BWF	1127.8

Table 5.2. Summary of availability data used for 'laake' correction, including specimen identification, adjusted time tracked, dive count, means for dive cycle, dive duration per cycle (AveUn), and surface duration per cycle (AveAv), with percentage of time unavailable and available, respectively; these data were calculated from dive data for *Hydrophis [Pelamis] platurus* (see Rubinoff et al. 1986).

ID	Track	Dives	Cycle	AveUn	AveAv	% UA	% A
1	38220	12	3184.8	3168	16.8	99.47	0.53
2	18972	10	1897.2	1704	193.2	89.82	10.18
3	20268	6	3378	2880	498	85.26	14.74
4	13446	8	1680.6	1494	186.6	88.9	11.11
5	19188	11	1744.2	1734	10.2	99.42	0.59
6	11358	8	1419.6	1110	309.6	78.19	21.82
7	14052	7	2007.6	672	1335.6	33.47	66.52
8	23610	9	2623.2	2622	1.2	99.95	0.05
9	28146	11	2559	2544	15	99.41	0.58
10	37224	21	1772.4	1260	512.4	71.09	28.92
11	15918	13	1224.6	1164	60.6	95.05	4.94
12	90126	20	4506.6	3270	1236.6	72.56	27.43
13	26982	6	4497	4476	21	99.53	0.47
14	59118	25	2364.6	2262	102.6	95.66	4.34
15	112254	35	3207	3018	189	94.11	5.9

Time durations given in seconds

5.3 | RESULTS

During 45.9 observation hours over 9 nights of sampling, 203 *H. p. xanthos* sightings were recorded in sea states of BWF 2–5; no detections were made on the eight most south-easterly transect lines. After removal of data from repeated transects we analyzed 199 detections, all were estimated to be within 20 m from the centerline, a natural truncation of distance created by the limitations of our lights. The best conventional distance sampling model (lowest AIC; Table 5.1) fitted a uniform + cosine detection function, with the data grouped in 0.95-m intervals for an χ^2 goodness-of-fit statistic of p=0.997 (Figure 5.3), although estimates from all models were comparable. Multiple covariate distance sampling models showed no effect of hour and/or BWF on detection by distance with the best model (lowest Delta AIC; Table 5.2) having no covariates. Likewise, we found no collinearity between hour and BWF (corr [Kendall]=-0.29, p<0.0001).

Using the uniform + cosine model, we estimated a baseline of 7705 individuals (95% CI =5202–11414). This value was then corrected applying the availability bias correction (=0.1287575) and the activity bias correction (=0.4976385) to return a total abundance of *H. p. xanthos* at 29781 individuals (95% CI=20104–44115). Spatial density (abundance/area) was calculated at 76 snakes/ km^2. Over the course of the distance-sampling survey, our encounter rate averaged 4.8 ± 5.5 snakes/ h (range: 0–23).

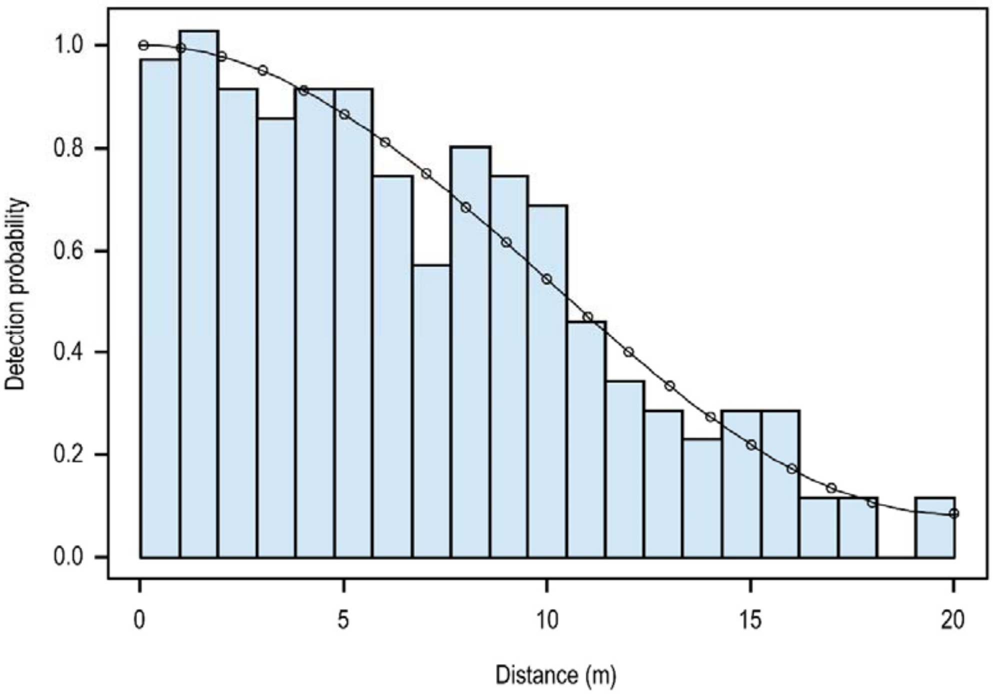

Figure 5.3. Detection function (uniform + cosine) fitted to 199 detections of xanthic sea snakes by distance with histogram of observed distances between the transect line and detected snakes; line indicates the estimated detection probabilities.

5.4 | DISCUSSION

Hydrophis platurus xanthos is one of only two sea snake taxa in the Americas. Unlike transitory pelagic sea snakes, *H. p. platurus,* in the Pacific Ocean, the yellow sea snake is an obligate resident of the inner basin of Golfo Dulce, Costa Rica. We estimate its total population size as fewer than 30,000 individuals. For comparison, Kropach (1973) estimated the local population of pelagic sea snakes in the Gulf of Panama to be up to a million individuals. Unlike the sizeable aggregations of *H. p. platurus* (100s or 1000s at a time) reported off Central America (Kropach 1971a, Dunson & Ehlert 1971, Tu 1976, Vallarino & Weldon 1996), no aggregations of *H. p. xanthos* have been observed in Golfo Dulce (Chapter 2), and the lead author (BB) has recorded only 765 individual sightings working in the embayment since 2010 (>880 observation hours). To our knowledge this study is the first quantitative abundance estimate for the global population of any sea snake taxon. Of the 47 species in the genus *Hydrophis* listed on The IUCN Red List (2022), abundance trends are unknown for 40 of them, and no global population estimates are provided. Obtaining abundance estimates on the species level is challenging because most sea snakes have wide and/or fragmented ranges and studies are typically site-specific with animals potentially leaving or arriving to the study area (Kropach 1973, Bonnet et al. 2014). Studying a geographically bound population provided a substantial and uncommon advantage; still, we hope our methods may prove of some value to future studies of sea snake abundance in other areas.

Although distance sampling has been described as a viable method for snakes (Dorcas & Willson 2009), studies of terrestrial species reported underestimations of population size due to small samples and low or inconsistent detections (Rodda & Campbell 2002, Stellati et al. 2019). We obtained a sample size greater than three times the 60–80 detections recommended by Buckland et al. (2001, 2015). Also, given the snakes were at the surface, they were readily observable and did not react to our presence, hence, potential biases including perception bias and bias due to distance-errors were effectively eliminated. We still had to address some limitations in the data, as our observed detections could not account for the number of snakes below the sea surface. Additional steps included the novel application of a known availability bias correction (Laake et al. 1997) and the proposal of a new correction for activity bias. These corrections required making some assumptions, especially using dive data from a related species when diving behaviors may differ. For example, pelagic sea snakes dive to avoid turbulent waters (Rubinoff et al. 1986) while xanthic sea snakes regularly surface in higher sea states (BWF 3–5; Bessesen & González-Suárez 2022; Chapter 4). If having more flexibility in surfacing conditions and/or a steady diel pattern results in *H. p. xanthos* spending more time at the surface, our corrections could have overestimated the population size. Greater accuracy may be derived with taxon-specific dive data, but our estimates provide a first approximation to the total abundance of this unique yellow sea snake and serve as markers for future trend studies.

Density provides another gauge by which change can be assessed. We estimated a considerably lower spatial density than reported for other marine snake taxa. Judging density by square meter (0.000076 snakes/ m^2 for *H. p. xanthos* in our study area) allows comparison with marine snake studies more commonly conducted in small, designated areas. Saint Giron (1964), for example, estimated *Laticauda colubrina* in just one small inlet of New Caledonia at a density of 0.20/ m^2. Lading et al. (1991) recorded 721 *L. colubrina* on Kalampunian Damit Island (a study area of <0.5 km^2), indicating a density estimate of 0.0014/ m^2. In a stretch of 3000 m along the edge of the Great Barrier Reef, Burns and Heatwole (Heatwole 1999) estimated *Aipysurus laevis* density to be 0.70–0.94/ m^2. Shine et al. (2021) studied *Emydocephalus annulatus* at three 20 x 350 m sites in New Caledonia and found annual densities of 0.005–0.036/ m^2 (estimates based on published data).

For herpetofauna, an encounter rate is sometimes used as a relative ‘density’ measurement, though rates are influenced by boat speed and searching protocols. In the Pacific Ocean, Rubinoff et al (1986) reported up to 165 pelagic sea snakes per hour, and Kropach (1971) recorded 4–180 pelagic sea snakes per hour in Panama. In northern Costa Rica, Lillywhite et al. (2015) once counted 1029 pelagic sea snakes in a single hour, though their average was only ~19 snakes/ hr. Inside Golfo Dulce, that team published an encounter rate of ~21 xanthic sea snakes per hour during two nights of collection (17/ h the first night and 25.7/ h the second night). This is comparable to the highest encounter rate for xanthic sea snakes ever recorded by the lead author (29/ hr during an around-the-clock diel study; Bessesen & González-Suárez, 2022; Chapter 4); however, across all studies, variance between nightly counts was apparent, likely associated to environmental conditions that are more or less suitable for surfacing. Hence, Lillywhite’s team may have benefitted from a small sample collected under ideal conditions. Multiple environmental variables are likely to influence surfacing behavior, including the photoperiod, wind force, red tide (which does occur in Golfo Dulce; pers.

obs.), weather, lunar phase, productively, and other factors that have not yet been identified (Lillywhite et al. 2015, Bessesen & González-Suárez 2022; Chapter 4). Precipitation, for example, could draw more individuals to the surface and/or extend the surfacing duration at a particular moment since sea snakes are known to drink from fresh-water lenses formed by rain (Lillywhite et al. 2014, 2019). Relatedly, seasonality could also contribute. Counts of xanthic sea snakes were generally the same during dry- and rain-season sighting surveys (Bessesen 2015), though the data were too limited for robust comparisons. When searching for pelagic sea snakes in the northern Pacific waters off Costa Rica, Lillywhite et al., (2015) reported similar numbers year-round but with a tendency for more sightings in the dry season. If the same is true for *H. p. xanthos* in Golfo Dulce, then our February distance-sampling detections could have overrepresented the number of surfacing snakes, leading to an overestimation of the population.

Our findings suggest the *H. p. xanthos* population is quite small and because sea snakes are known to exhibit k-selected traits, including low fecundity (clutch size of *H. p. platurus* is 1-6: Visser 1967), which can reduce resistance to negative impacts (Heatwole 1999, Rao et al. 2021), Golfo Dulce's endemic sea snake may be particularly vulnerable to threats. Current anthropogenic hazards include boat strikes and water contamination. There has been a substantial increase in boat traffic over the last decade (Bessesen & González-Suárez 2021; Appendix), and snakes can be injured in collisions (pers. obs.), plus water quality in the gulf is declining (Spongberg 2004, Fournier et al. 2019). The destabilizing effects of climate change may be creating additional challenges. Sea snakes exhibit thermal sensitivity (Heatwole et al. 2012) and surface waters in Golfo Dulce appear to be rising (Murayama et al. 2018). To presumably help *H. p. xanthos* avoid overheating in the relatively warm waters of their habitat, these snakes have already lost the melanistic dorsum of their ancestors (Solórzano 2011) and switched to a nocturnal diel cycle (Bessesen 2012, Lillywhite et al. 2015). During the day, light skin and eyes risk damage from solar radiation and it is possible that conspicuous yellow coloring exposes the snakes to predation, especially by avian hunters (Bessesen & González-Suárez 2022; Chapter 4), as well as harassment by dolphins (Bessesen et al. 2021; Appendix); because they must regularly surface to ventilate, nocturnal feeding mitigates but does not eliminate those risks. For sea snakes, access to fresh drinking water is limited in the marine environment (Rash & Lillywhite, 2019), making rainwater lenses critical for hydration (Lillywhite et al. 2019). Regional precipitation is naturally reduced during the dry season, and climate-induced environmental changes, including stochastic periods of drought, could reduce long-term sustainability of the xanthic population (Lillywhite et al. 2018, Udyawer et al. 2018). If *H. p. xanthos* has existed as a small population since its origin, selection may have naturally purged deleterious alleles and thereby mitigated potential genetic decline, providing some resistance to bottlenecking (Morin et al. 2021). Nevertheless, because this unique and geographically rare population occurs in a single location with small area of occupancy, it is inherently vulnerable.

Importantly, *H. p. xanthos* is not just a residential colony of *H. p. platurus.* Although a few all-yellow specimens have been found outside Golfo Dulce (Kropach 1971b, Bolaños et al. 1974), suggesting individuals may occasionally escape (Bessesen 2015) and rarely a pelagic snake may be carried into the embayment (Bessesen & Galbreath 2017), interbreeding is unlikely (unpub. data). The population appears allopatric (Sheehy et al. 2012) and has been isolated from its yellow-bellied conspecifics sufficiently long to show morphological and behavioral divergence (Bessesen & Galbreath 2017, Bessesen & González-Suárez 2022; Chapter 4). Indeed, lacking genetic exchange with sea snakes from the broader Indo-Pacific, *H. p. xanthos* has become a highly discrete organism, an 'evolutionarily significant unit' (ESU; per Ryder 1986, Casacci et al. 2014), which may ultimately be considered for full species status (Bessesen & Galbreath 2017). Our first population and density estimates of *H. p. xanthos* fill an important knowledge gap, but future work will be necessary to evaluate change in abundance, range size, and extinction risk. Count comparisons from three sighting surveys conducted over a ten-year period encouragingly suggest a stable or possibly growing population (Chapter 2), but caution is needed as we lack historical estimates or true time series of abundance. In the meantime, a conservative approach is recommended.

Since *H. p. xanthos* is part of a larger biotic community, and Rasmussen et al. (2021) demonstrated sea snakes to be bioindicators, monitoring this population could provide insights into the status of other marine fauna in its habitat. Costa Rica's Ministry of Environment (MINAE) and National System of Conservation Areas (SINAC) have made considerable efforts to preserve their country's rich biodiversity with increasing focus on marine resources (Alvarado et al. 2012, Palacios Martinez 2016). Our study highlights the importance of additional protections and regulatory enforcement in Golfo Dulce, which could serve to ensure the future of their unique endemic sea snake, *H. p. xanthos*.

4.5 ACKNOWLEDGMENTS

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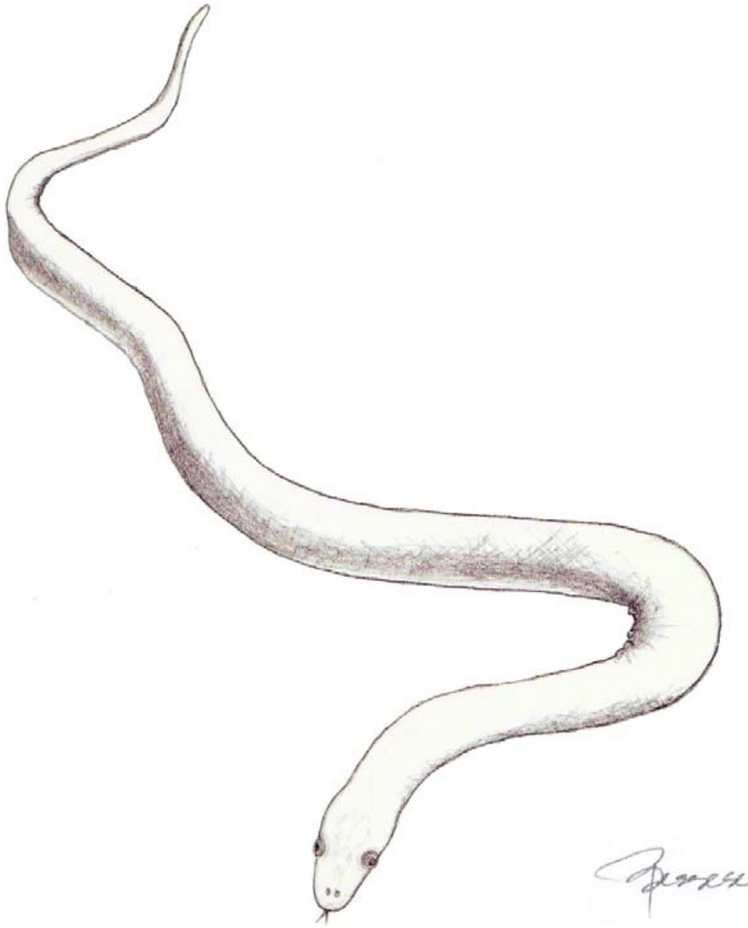
Chapter 6



CHAPTER 6: Coalescing new knowledge

6.1 | INTRODUCTION

Our understanding of the ophidian family tree continues to evolve (Zaher et al. 2019). There are now nearly 4000 recognized extant snake species, of which less than 2% are sea snakes (Uetz et al. 2022). Inhabiting the marine environment, these fascinating reptiles are inherently difficult to study (Udyawer et al. 2018), rendering more than a third Data Deficient per the International Union for Conservation of Nature (IUCN; IUCN 2022). *Hydrophis platurus xanthos* was a recently described taxon relatively new to science when this work began, so this research reduces a sizeable knowledge gap while confirming the taxon to be an intriguingly divergent endemic (Table 6.1; Fig. 6.1). My third boat-based sighting survey with boat captain and research assistant Jorge Largaespada garnered updated estimates of relative abundance. Repeating 30 days of on-water observations along with longitudinal and retrospective interviews with fishermen and tour boat guides suggested the population is not currently in decline (Bessesen & González-Suárez, in review; Chapter 2). As in our 2010 pilot study, interviewees attested that only xanthos is ever seen in the upper gulf, and their comme-nts denoted growing awareness and appreciation for the snake as a special marine vertebrate found nowhere else on Earth (Bessesen & González-Suárez 2021).

A rigorous examination of sea snake distribution in relation to marine conditions revealed interesting aspects of natural history. For example, sighting records from all three field seasons allowed us to quantitatively assess drift line use, which was for xanthos virtually nonexistent. Given the subspecies' conspicuous site fidelity to the inner basin of Golfo Dulce we also compared survey data with published bathymetry data and verified depth as a defining factor in its separation from the pelagic population (Bessesen & González-Suárez, In review; Chapter 2). After collecting two seasons of hydrographic readings, we then modelled several environmental variables for habitat suitability (Bessesen et al., In review; Chapter 3). While depth was still a major contributor, several other factors also had effect, especially salinity, environmental pH, and dissolved oxygen. Using our species distribution maps we measured xanthos' area of occupancy to be just 260 km^2, which is considerably smaller than the earliest proposed extent (320 km^2; Bessesen 2012).

In view of the hypothesis that temperature influenced the colonizers of Golfo Dulce to undergo evolutionary adaptations and recognising the influence of solar radiation on the thermal environmental, we then undertook an around-the-clock survey to systematically investigate correlations between sea snake surfacing behavior and the photocycle. That study demonstrated a divergent diel activity pattern: xanthos is generally nocturnal with peaks of crepuscularity (Bessesen & González-Suárez 2022; Chapter 4). Finally, by modelling data from a distance-sampling survey, I was able to answer a key question at the root of my research: how many yellow sea snakes are there? The total population is estimated at less than 30,000 individuals, with relatively low density across their range (Bessesen et al. 2022; Chapter 5).

TABLE 6.1. Marked differences between xanthos (*H. p. xanthos*) and its pelagic sister (*H. p. platurus*); REFERENCES: Chapters 2–5; Cogger 1975; Graham et al. 1971; Kropach 1971a; Leeders 2019; Lillywhite et al. 2015; NatureServe 2022; Rasmussen et al. 2011; Rubinoff et al. 1986; VIMS 2022; Wellington & Dunbar 1995; *Eastern Tropical Pacific.

	Xanthos	Pelagic sea snake
HABITAT		
location	Golfo Dulce, inner basin	Indo-Pacific Ocean
area (km^2)	260	>2,500,000
suitable water depth (m)	>100	≥10
ave. surface temp (°C)	30	28.5*
ave. surface salinity (ppt)	<31	35
ave. dissolved O_2 (mg/ L)	6.5	7.0–8.0
POPULATION		
global abundance	<30,000	>1,000,000
body color	yellow	black, yellow
eye color	light	dark
ave. length (cm)	49.1	70
ave. weight (g)	46.6	91–140
BEHAVIOR		
feeding posture	sinusoidal	elongate
diel pattern	crepuscular-nocturnal	diurnal
drift line use	no	yes
ave. surfacing wave height (m)	0.1–0.5 m	smooth water
relatively timid	yes	no

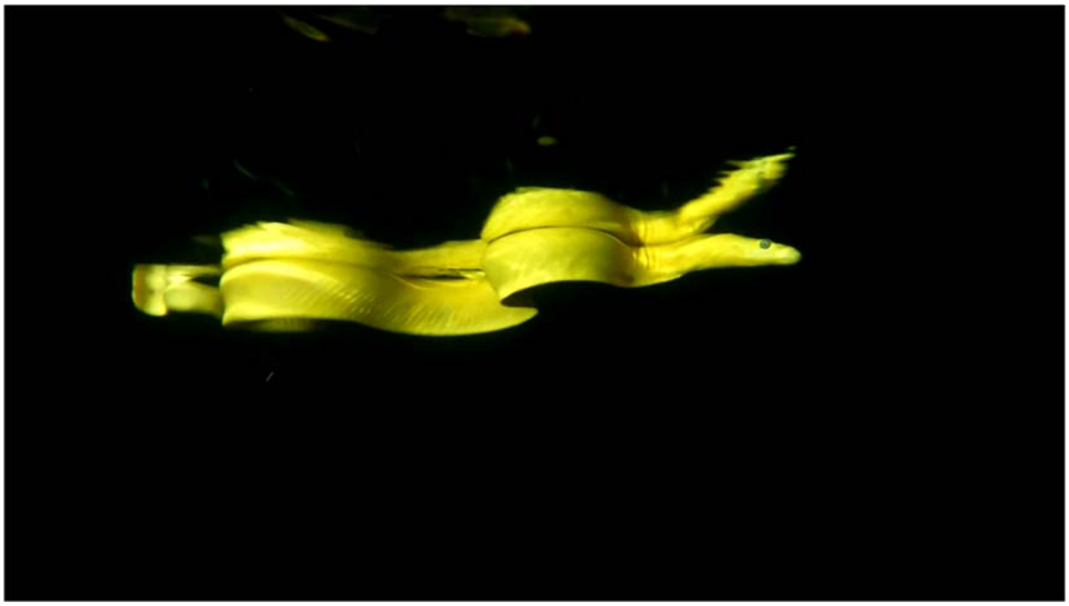


Figure 6.1. The yellow sea snake, *Hydrophis platurus xanthos,* floating at the sea surface at night as viewed from underwater (note the striking appearance of its light eye); the reflection is photo-induced; photo credit: B. Bessesen.

6.2 | FRAMING OUR FINDINGS

6.2.1 Unique among sea snakes

Despite the pelagic sea snake being the most widely distributed squamate in the world (Lillywhite et al. 2018), xanthos is the only sequestered and morphologically deviating subpopulation ever reported. The findings of our studies when considered comprehensively draw together elements of behavior, range, and habitat, and sharpen the image of *H. p. xanthos* as an evolutionarily significant unit (per Casacci et al. 2014), distinctly different from its sister group (Table 6.1) or any other species. The true sea snakes (Hydrophiini) of the Elapidae subfamily Hydrophiinae (distinct from kraits, Laticaudini, which took to the ocean on a separate timeline) are currently divided into two clades: ‘Aipysurus’ and ‘Hydrophis’ (Sanders et al. 2013). As its generic name suggests, xanthos belongs to the latter. The earliest record of pelagic sea snakes off Costa Rica dates to 1519 (Taylor 1953), but by that time an endemic was likely already emerging in Golfo Dulce, where partitive bathymetry placed a singular population in reproductive isolation sufficiently long for the entire clade to transition to a monochromatic state and considerably smaller stature (Bessesen & Galbreath 2017). Crepuscular-nocturnality was another dramatic shift for the population as pelagic sea snakes are considered diurnal across their extensive range. In this aspect, xanthos also contrasts with more distant relatives (Bessesen & González-Suárez 2022). Despite two semi-aquatic mangrove sea snakes, *Hydrelaps darwiniensis* and *Parahydrophis mertoni,* exhibiting crepuscularity, this pattern has not been identified in any congeners of the *Hydrophis* clade (Simões et al. 2020).

In the Western Hemisphere, *H. p. platurus* and *H. p. xanthos* are the only sea snakes found. However, in other geographic areas multiple sympatric species often share space in the neritic zone. This is especially the case from northern Australia upward into Indonesia and Papua New Guinea, a range that supports dozens of species (Heatwole 1999, Rasmussen et al. 2014). Few are bound to such a narrow extent as xanthos. Several Australian hydrophiines have notably restricted distributions, but most have historical records in more than one location (Cogger 1975, Heatwole 1999). The Taal Lake snake, *H. semperi,* may be most like xanthos given its 250-km^2 extent of occurrence (Gatus 2010); endemic to a lake in the Philippines, it is the only true sea snake known to reside full time in fresh water (Elfes et al. 2013). *Hydrophis sibauensis* was found living more than 1000 km up Borneo's Sibau River, but little is known about the species' range or whether it ever migrates to the ocean via the Kapuas River mainstem (Rasmussen et al. 2001). Several species occupy rivermouths (Voris 2015), such as *H. donaldi*, recently described from the estuarine habitat of the Gulf of Carpentaria in northern Australia (Ukuwela et al. 2012), and many others tolerate low salinity, including *H. p. platurus*. Two vagrant pelagic sea snakes were recorded in riverine tracts of Kerala, India, ≤5 km from the sea (Palot & Radhakrishnan 2010) and specimens have been successfully maintained in freshwater tanks for up to nine months (Kropach 1973).

Xanthos resides full time in a reduced-saline environment. When compared with the Pacific waters of its pelagic ancestors, the habitat in Golfo Dulce is undeniably different. We confirmed surface salinity to be ~5 ppt lower than in the adjacent ocean with temperatures up to three degrees warmer and oxygen concentrations possibly reduced 1–2 mg/ L. Considering the physical and behavioral adaptations already identified in the yellow sea snakes, one cannot help wondering if additional morphological and/or ecological modifications might boost individual fitness. Having switched to a nocturnal feeding strategy, for example, are xanthos' eyes adapted for better night acuity, exploiting whatever light is available from celestial bodies? If not, and darkness impairs vision, might it rely more heavily on sensory sensilla for detecting prey? When the deeper waters of the inner basin become anoxic, does xanthos keep to shallow isobaths or surface more frequently to ventilate its lungs, or is it physiologically adapted to endure or exploit oxygen-deficient waters in some special way? Looking at this account of phenotypic plasticity from a global perspective, could xanthos be a bellwether? Meaning, if higher water temperatures drove the Golfo Dulce population to abandon dark pigmentation, might the long-term environmental pressure of climatic warming elsewhere in the world drive other resident populations of *H. p. platurus*—perhaps, given enough time, the whole species—to a xanthic state?

6.2.2 Threats and protection

At a time when the current rate of species extinctions reaches upwards of a thousand times the normal background rate, endemic populations are at the greatest risk of disappearing (Pimm et al. 1995). Approximately 20% of reptile species are currently at risk of extinction (Bohm et al. 2013, Cox et al. 2022). While only three true sea snakes are currently listed on the IUCN Red List: *Hydrophis pacificus* as Near Threatened, *H. semperi* as Vulnerable, and *Aipysurus fucus* as Endangered (IUCN 2022), two more, *A. apraefrontalis* and *A. foliosquama,* are considered critically endangered under the Australian Environment Protection and Biodiversity Conservation Act (SPRAT 2022) despite Data Deficient listings under IUCN (Sanders et al. 2021a, 2021b). Other species also appear in decline with several potential drivers being considered, including increased predation, boat traffic, disease, and climate change (Udyawer et al. 2018, Somaweera et al. 2021). The first of those drivers is not a major concern for xanthos because any reduction in aposematism due to adaptive coloration has been in effect since its origins and there are no current reports of rising predator counts in its habitat. The other three drivers, however, are well worth consideration. Indeed, having conducted research in Golfo Dulce for more than decade, they are my chief concerns for xanthos.

As ecotourism gains ground in Golfo Dulce, boat traffic continues to increase (Bessesen & González-Suárez 2021), and with every vessel there is opportunity for a boat strike. We accidentally ran over a snake ourselves while speedily crossing the inner basin. It had been resting at the surface and went unseen until it passed under our bow. When we circled back, we found the animal floating in an uncoordinated posture with its mouth open, suggesting an agonal state, although no obvious external injuries could be discerned. Its survival status is unknown. Our 2010 sighting survey took place in quiet, pristine waters, but now myriad sport-fishing, tour boats, cruise liners and cargo ships mark the seascape. To meet growing demand for development and tourism, Golfito became a commercial port in 2020, and now receives tri-weekly freight ships, each carrying 80 containers (Phoebe Edge, pers. comm.). The Hilton property in Puerto Jiménez, Botanika Osa Peninsula (previously Crocodile Bay), is designing a controversial marina to attract private yachts. The project, which had been delayed for several years because the proposed area serves as critical habitat for sea turtles, dolphins, and birthing humpback whales (SETENA 2012, Bessesen 2015, Herra-Miranda et al. 2016), is now in development (Botanika by Hilton 2022). Fuel and oil leakage is an associated concern. Oil spills are devastating to sea snakes (Yaghmour et al. 2022) and a single large-scale event could cause mass mortality, potentially wiping out the xanthic population. Community chemical waste is already detectible the marine environment, from dish detergents to discarded paints and pharmaceuticals (Spongberg et al. 2011), as well as agricultural runoff (Sarmento et al. 2016, Fournier et al. 2019). In fact, the resident bottlenose dolphins evince dermal lesions resembling paracoccidiodomycosis ceti (Vilela & Mendoza 2018; also known as lacaziosis-like disease, or LLD), which is associated with compromised immunity, possibly due to contact with chemical contaminants (Bessesen et al. 2014). With xanthos trapped between shores, cumulative pollutants and resulting water degradation could negatively affect the snakes' health and/or resistance to pathogens.

In the effort to preserve diversity, we must recognize that biological losses do not normally occur over night (McGill et al. 2015). The effects of climate change are increasingly visible and xanthos may suffer potentially severe habitat compression due to ocean deoxygenation (Global Ocean Oxygen Network 2018), acidification (Raven et al. 2005), and warming. As the tropical belt widens (Seidel at al. 2008), regional temperatures in the Eastern Tropical Pacific are slowly rising (Morales-Ramírez et al. 2015). Murayama et al. (2018) reported elevating sea surface temperatures in Golfo Dulce, a trend that could affect sea snake behavior and metabolism (Udyawer et al.

2016). If xanthos has already strategically adapted to a warmer environment through skin color, body size, and diel cycle, intensifying thermal pressure could prove catastrophic. Unable to migrate away, the snakes are destined to face whatever comes.

Because rarity often spurs human interest (Angulo et al. 2009), there is another potential threat worthy of mention: harassment and exploitation. A 2016 YouTube Channel documentary based on its host's 'dare-devil' handling of wild animals aired a segment about Golfo Dulce's yellow sea snake (Peterson 2016). The animal was aggressively wrangled as a 'highly venomous species' (a true statement: Tu 2011) and presented in the traditional trophy-pose of being clutched at the neck with its body dangling. The experience almost assuredly resulted in death for the snake. Lacking the robust musculature of its terrestrial cousins, xanthos is a soft-bodied and structurally delicate animal, unaccustomed to intense gravitational pressure. Tilted into a vertical attitude, the animal's circulatory system is prone to collapse (Lillywhite 1987, 1988). Sea snakes are also susceptible to spinal fractures, and the act of pinning or grasping the head can cause damage to fragile bones (Gillett 2015). Furthermore, xanthos is acutely susceptible to human disturbance while floating. Unlike terrestrial serpents, it spends most of its time underwater, which means a snake observed at the surface is engaged in vital and time-sensitive behavior(s): breathing, feeding, rest/recovery, or reproduction. Any disruption of those activities could profoundly affect critical life processes. Herpetologists seeking hands-on experience have been known to capture and place serpents in containers of cold water to slow their metabolism, employing hyperthermia to render them immobile. Lillywhite et al. (2017) consider cooling methods 'inappropriate for restraint and anesthesia' and such techniques have been deemed inhumane by nearly all global ethics committees, including the American Veterinary Medical Association and the Institute for Laboratory Animal Research. Nevertheless, unsafe handling techniques may persist in practice with reptile enthusiasts unintentionally diminishing health and survivability in the subjects of their interest.

At present, xanthos is jointly assessed with *Hydrophis platurus,* a species listed of Least Concern under IUCN (Guinea et al. 2017). The actual size of the pelagic population is unknown due to severe fragmentation (Guinea et al. 2017), but it is reported as abundant (Lillywhite et al. 2015) and may number into the millions (Kropach

1973, NatureServe 2022). With waif dispersal across the Indian and Pacific Oceans (Lillywhite et al. 2018), the species is considered the most widely ranging snake in the world (Pickwell 1972). Although many questions remain, we now have a much clearer understanding of *H. p. xanthos* as a small, allopatric population warranting a separate assessment.

6.2.3 An allopatric population

As the Hydrophis clade is a rapidly speciating group (Sanders et al. 2020), xanthos may in fact be a separate species, although studies using nuclear microsatellite loci for more fine-scale resolution will be needed (Sheehy et al. 2012, Nankivell et al. 2020). In the meantime, the allopatric nature of the population is worth considering. If separate species are defined as groups of animals that cannot or do not effectively interbreed in nature, then we must examine the potential for genetic exchange between xanthos and the pelagic sea snake. It is currently unclear whether mating selection, size disparity and/or other factors preclude copulation or the creation of viable progeny, but we can cogitate on the likelihood of one taxon arriving to the other's habitat and surviving long enough to make contact and successfully hybridize.

We know that waif *H. p. platurus* are occasionally transported into the upper gulf (Bessesen & Galbreath 2017), possibly by storms (Heatwole 1999) and/or carried in ship ballast (Hernández-Camacho et al. 2006), yet no healthy adults have been recorded in the distribution area of xanthos. Approximately seven weeks after the powerful effects of Hurricane Otto caused record-breaking precipitation around the Osa Peninsula, I found three pelagic sea snakes in the inner basin of Golfo Dulce: an emaciated adult covered in epibiota, sagging limp in the water and seemingly near death, with two youngsters in proximity. The sex of the adult was undetermined, but it was presumably a female who had given birth after being washed into the embayment in a gravid state. A reduced feeding rate prior to parturition could help explain the anorexia (Lillywhite 2017), but feeding should have resumed, and prey-sized fish were incidentally caught in my net when I captured the snake for examination. It is also possible the animal arrived sick or injured or was simply at the end of its natural life span. Because it has been demonstrated that pelagic sea snakes are not suited to acclimation (Heatwole et al. 2012), the snake's poor body condition could alternatively be explained by prolonged diurnal surfacing in the warm gulf waters leading to overheating and physiological decline. Whatever its ailment, the adult probably died within hours of our observations, and it remains questionable whether either of the neonates survived since no other pelagic specimens were observed in the inner basin during future fieldwork.

Phoebe Edge (pers. com), a beach-front resident in Golfo Dulce and the owner of a tour-boat company working inside the gulf, has only ever seen two pelagic sea snakes above the sill line. They were identified by their solid black dorsal coloring and spotted tail paddles. Both exhibited peculiar behavior. In February 2021, Edge videotaped a large pelagic sea snake less than 50 m from the beach in Golfito Bay. It was mid-morning and the animal showed signs of extreme stress: undulating non-stop in a swimming-like style but progressing nowhere. As Golfito is the main port of call in Golfo Dulce, hosting both cargo and passenger ships, it is quite possible the snake was carried into that small inlet in a ship's ballast water and discharged at the marina. The second sighting occurred in February 2022 in the far northeast corner of the gulf, where a 'juvenile' (<40 cm) was discovered swimming in place at the water surface near the outlet of large river. During thirty minutes of observation, it occasionally made short dives but immediately resurfaced to continue its stereotypic undulations, often holding its head up. How the animal arrived in the north is unknown, but February is high season for tourism and cruise ships do visit that area, again pointing to the potential for ballast water to act in the transport of pelagic sea snakes into the gulf.

While such evidence suggests pelagic sea snakes do not fare well in the inner basin, there is still a conceivable chance for crossbreeding, so I have looked for phenotypic hybrids. Some proportion of an F1 generation would presumably inherit 50% black pigmentation on the dorsum and tail. Given almost 900 observation hours and 765 sighting records of xanthos, only two individuals met that criterium, having large disconnected black blotches along the dorsal ridge (no spots on the tail; Fig. 6.2). Another specimen with a slim black dorsal stripe and faintly blotched tail was photographed by Solórzano (2011). Natural selection in Golfo Dulce appears to favor xanthophores over melanophores, so if hybridization does not occur there, perhaps inherited latent melanistic features occasionally manifest.

Figure 6.2. The only two unusually melanistic *H. p. xanthos* recorded by the author; photo credit: B. Bessesen.

Given that the story of xanthos began with reports of all-yellow sea snakes off Central America (Voris et al. 1970, Kropach 1971b, Bolaños et at. 1974, Tu 1976), perhaps it is even more interesting to consider the potential for reproduction outside Golfo Dulce. It has been hypothesized that the all-yellow sea snakes found off Pacific shores in the 1970s were 'escapees' from the inner basin (Bessesen 2012, Bessesen & Galbreath 2017). This is supported by observations indicating xanthos may occasionally leave Golfo Dulce. During my fieldwork, only one xanthic specimen was ever found below the sill line: in August 2011 we came upon an individual apparently swept from its normal range by the higher wind and waves that mark the rainy season (Bessesen 2015). More recently, during the rainy season of August 2020, Phoebe Edge (pers. comm.) recorded another xanthic specimen in the southern sector of the gulf. It is unknown how frequently sea snakes are emancipated from the embayment or whether they breed with *H. p. platurus* outside the gulf. One individual with a thin black dorsal stripe (no tail spots) was photographed by Tu (1976) off northern Costa Rica, so it is possible that hybridization does occur there. If so, the phenotypic coloring of xanthos does not appear to persist, evidently disadvantageous in that habitat.

Circulation models suggest ocean currents are conducive for dispersal of sea snakes born in the Eastern Tropical Pacific to travel westward, theoretically all the way to the Australasian region (Brischoux et al. 2016). Hence, a dearth of a yellow specimens found anywhere beyond Central America seems noteworthy. Perhaps F2 generations are less viable. Habitat suitability modelling described considerable differences between the inner basin and the Pacific, suggesting that—much like pelagic sea snakes struggle to survive inside Golfo Dulce—xanthic sea snakes may struggle in the open ocean. Lower temperatures could reduce metabolism (Greene 1997), and increased salinity could promote dehydration, potentially disrupting physiological processes (Lillywhite 2014, Lillywhite et al. 2014). A nocturnal diel cycle, lack of drift-line exploitation, and/or other divergent ecological patterns could further hinder success. In any case, based on currently available data, the two populations do not appear to regularly interact or procreate, and viability of progeny is uncertain at best. If *H. p. xanthos* and *H. p. platurus* do not interbreed, then the evolutionary importance of the former is even more pronounced.

6.3 | FUTURE WORK

As this thesis reaches completion, I am focused on the work ahead. Golfo Dulce was recently declared a Hope Spot by oceanographer Sylvia Earle (Mission Blue 2019), underpinning the relevance of marine conservation in that embayment. Using the ecological data presented in this thesis, I have commenced an IUCN conservation status assessment for *H. p. xanthos,* which may provide additional scientific footing for the protective management of the population and its habitat. Having spent time underwater with xanthos during my PhD studies, I have also garnered new data (and perspective) on its feeding behavior, which is more dynamic than previously understood, a topic that will undoubtedly prompt further writing. Most substantially, I have coordinated a multi-institutional postdoctoral research project to unify experts in a close examination of xanthos' taxonomic distinctiveness using both molecular and morphological analyses. We hope to determine how long ago and by what means the xanthic population was separated and potentially solve whether the 1970s specimens are genetically aligned with *H. p. platurus* (suggesting all-yellow morphs exist in some, seemingly low, proportion of the pelagic population) or xanthos (confirming they were escapees from the inner basin and supporting the theory that xanthism is driven by atypical environmental pressures). I am thrilled to be collaborating with these esteemed colleagues as we work toward describing a new species: *Hydrophis xanthos.*

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APPENDICES

Offprints of two additional peer-reviewed articles by the author during the academic period of 2019–2022 to follow in this order:

A.1 Bessesen BL, González-Suárez M. 2021. The value and limitations of local ecological knowledge: Longitudinal and retrospective assessment of flagship species in Golfo Dulce, Costa Rica. People and Nature 3(3): 627–638.

A.2 Bessesen BL, González-Suárez M, Herra-Miranda D, Oviedo L. 2021. *Hydrophis platurus xanthos* (Golfo Dulce Yellow Seasnake): Harassment by dolphins. Natural History Note. Herpetological Review 52(2): 425–426.

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RESEARCH ARTICLE

The value and limitations of local ecological knowledge: Longitudinal and retrospective assessment of flagship species in Golfo Dulce, Costa Rica

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Abstract

1. Anthropogenic activities and climate change are affecting marine ecosystems world-wide, but systematic biodiversity assessments through periodic biomonitoring can be challenging and costly. Local ecological knowledge (LEK), obtained from experienced residents, can complement other approaches and provide improved understanding of the conservation status of marine areas. Here we explore the value and limitations of LEK to assess the status of several flagship species of tourism interest: cetaceans, sea turtles, whale sharks and sea snakes in a unique tropical fiord and biodiversity hotspot, Golfo Dulce, Costa Rica.
2. We analysed the interviews conducted with fishermen and tour boat guides in 2010 and 2020 and compared their responses to biomonitoring data obtained through boat-based sighting surveys during the same two time periods. Our questionnaire asked for the estimates of sighting frequencies in both years, and in 2020 it also inquired about perceived changes over the time gap.
3. A key limitation was that many interviewees from 2010 could not be relocated in 2020, though 13 repeat participants served as a panel. Their responses suggest shifts in abundance that vary across taxa. For example, changes in reported sighting frequencies from 2010 to 2020 indicate a possible decline in whales but an increase in sea snakes. Those changes were also reflected in our biomonitoring data, suggesting respondents were fairly accurate in their reports of current abundance. However, when asked about perceived changes over the decade we found their answers were not consistent with changes detected through their reported frequencies nor though biomonitoring.
4. Our results suggest LEK can be a good source of information for current assessment but highlight the potential biases of perceptions of change. Evaluating changes through LEK may best be done by obtaining interview data at multiple points in time and systematically assessing trends, though, notably, there can be challenges with acquiring consistent sample sizes. Interviews should not replace but can complement biomonitoring while also providing further value via

community engagement and as an avenue to gain insights into local opinions regarding conservation measures.

KEYWORDS

abundance trends, biodiversity monitoring, comparative frequencies, Costa Rica, Golfo Dulce, interview surveys, LEK, marine vertebrates

1 | INTRODUCTION

Given the current rates of species extinctions, upwards of 1,000 times the normal background rate (Carlton et al., 1999; Pimm et al., 1995), active conservation efforts are needed to preserve the diversity of life. We know that marine ecosystems world-wide are being affected by anthropogenic activity and climate change (Costello et al., 2017; Dulvy et al., 2003), and that habitat alterations can lead to reductions in ecosystem stability, resilience, productivity and irreversible species loss, impacting human communities that financially, culturally or aesthetically benefit from the environment (Chapin III et al., 2000). While periodic biomonitoring is effective for assessing trends in marine biodiversity, the costs associated with on-water sighting surveys can preclude frequent replication, making additional methods of data collection worthy of pursuit.

For many years, traditional ecological knowledge (TEK) passed down through generations and local ecological knowledge (LEK) gained by individuals over their lifetimes have been recognized as important sources of biological information (Anadón et al., 2009; Berkes et al., 2000; Leedy, 1949; Zimmerer, 1991). Despite a lack of integration into mainstream science (Hind, 2015), their use is generally advocated, especially when other data sources are limited (Folke, 2004). While TEK has benefitted conservation research and resource management in numerous indigenous territories (Ferguson et al., 1998; Huntington, 2000; Moller et al., 2004), LEK may be better suited for studies in mixed history communities, as it can include all resource users (Gerhardinger et al., 2009). Differing definitions of LEK may cause confusion (Usher, 2000; Yli-pelkonen & Kohl, 2005), but we follow Rehage et al. (2019) in defining it as the cumulative knowledge of long-term residents regarding ecological relationships within their environment, shaped through personal observations and experiences as well as communications and beliefs shared within their community. Obtained through interviews, LEK can complement biomonitoring in assessing the presence and status of various species (Beaudreau & Levin, 2014; Gilchrist et al., 2005; Turvey et al., 2013; Vaughan et al., 2003).

Whether survey methods are cross-sectional (sampling a group at a single point in time), longitudinal (interviewing the same panel over time) or retrospective (calling on respondent memory), certain biases and errors must be considered (Rafferty et al., 2015; Rindfleisch et al., 2008). Retrospective bias, for example, manifests as inadequate recall and/or inaccurate perception of historic declines and can hinder the accuracy of resulting assessments (O'Donnell et al., 2010). Stakeholders are also biased to their needs (Gerhardinger et al., 2009), and human characteristics including familiarity with the study area, age, gender, personality and even interactions with the interviewer can further influence respondents' answers (Brook & McLachlan, 2005; Moser, 1951). When potential bias is properly mitigated and reported, social surveys can have substantial collaborative power (Thornton & Maciejewski Scheer, 2012), and LEK can provide insight into species abundance in regions of ecological interest where periodic biomonitoring is limited (Anadón et al., 2009; Turvey et al., 2013).

Within the ecologically rich country of Costa Rica, Golfo Dulce (Figure 1) has been classified as a biodiversity hotspot (Nielsen Muñoz & Quesada Alpízar, 2006). This semi-closed embayment, measuring 50 km long and 10–15 km wide with an unusual fiord-like structure (Svendsen et al., 2006), supports at least 1,028 species (Morales-Ramírez, 2011). Among an array of iconic fauna, visitors may see humpback whales *Megaptera novaeangliae*, two resident species of dolphins (*Tursiops truncatus* and *Stenella attenuata*), at least three species of sea turtles (*Chelonia mydas*, *Eretmochelys imbricata* and *Lepidochelys olivacea*; Bessesen & Saborío-R, 2012, Bessesen, 2015), as well as the world's largest fish, the whale shark (*Rhincodon typus*; Pacheco-Polanco et al., 2015). The habitat is also home to a unique endemic sea snake, *Hydrophis platurus xanthos* (Bessesen & Galbreath, 2017).

The Golfo Dulce region is not heavily populated and there remains a strong human-to-sea bond. Of the fewer than 30,000 people who reside in the area (INEC, 2016), most depend on Golfo Dulce for food, entertainment and employment. At least 60% of citizens engage in small-scale fishing (Fargier et al., 2014) and 60%–80% of the local economy is in ecotourism (Hunt et al., 2015; Zambrano et al., 2010). Income-earning activities such as whale-watching, dolphins tours, kayaking, snorkelling trips and sport-fishing make Golfo Dulce a socio-economically essential habitat. Most tour boats and fishing vessels depart from one of two main marinas: Golfito, the regional municipality located on the mainland, or Puerto Jiménez, positioned on the Osa Peninsula (the base of our research). Golfo Dulce officially became a Marine Area of Responsible Fishing in 2010. The designation was initiated by local fishermen organizations to manage small-scale (artisanal) fisheries, and among other strategies, banned shrimp trawling and gillnets inside the gulf with mixed results (Fargier et al., 2014; García Lozano & Heinen, 2016). As a habitat, Golfo Dulce is still relatively healthy, but the threats of water contamination (Fournier et al., 2019; Spongberg, 2004), boat traffic (Bessesen, 2015) and illegal fishing (Fargier, 2012) are increasing. Hence, biodiversity monitoring efforts are critical to

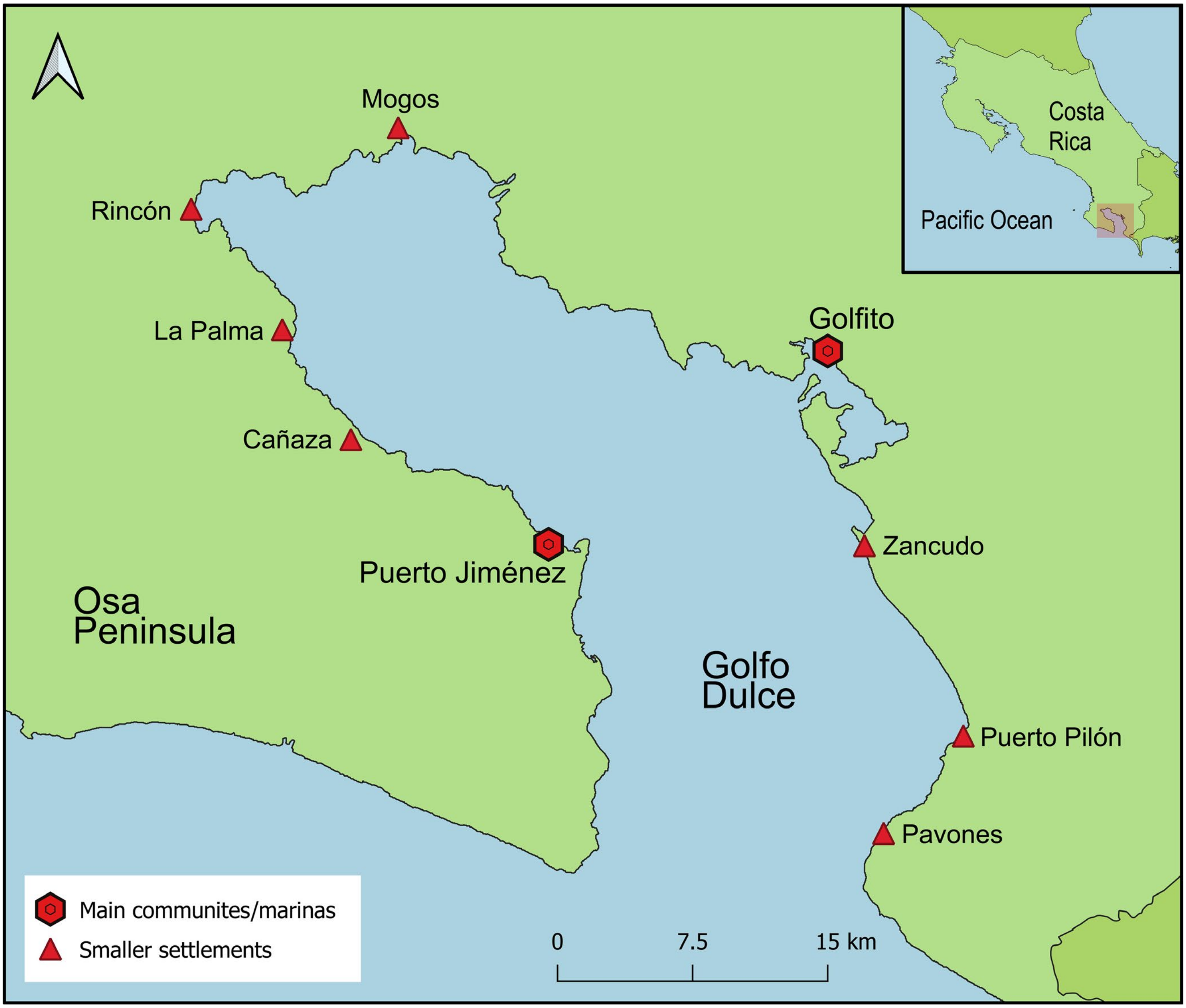

FIGURE 1 Map of Golfo Dulce showing the ports of Puerto Jiménez and Golfito along with several outlying communities. Inset: location of Golfo Dulce within Costa Rica

ensure negative trends cannot take hold without the opportunity for corrective action.

We conducted on-water multi-species marine sighting surveys in Golfo Dulce in 2010 and 2020, and to supplement this biomonitoring, we garnered LEK through interviews with fishermen and tour boat guides. Our interview surveys aimed to provide additional insights into the abundance of key marine vertebrates, and we compared reported responses between study periods to assess change. Respondents who participated both years also shared their perceptions of change over the time gap. We hypothesize that changes could have occurred in the presence, abundance and distribution of various species of marine fauna and that some of those changes detected through systematic analysis might not be directly recognized by the participants. Testing reported change (change in frequencies reported between 2010 versus 2020) against perceived change (recorded in 2020) and comparing results with our on-water sighting data, we illustrate some advantages and challenges of using LEK for biomonitoring. Because few studies have managed to compare LEK against empirical scientific data collected for the same species during the same time periods (Gilchrist et al., 2005), there exists a knowledge gap, which we strive to help fill.

2 | MATERIALS AND METHODS

2.1 | Interviews

From 6 January to 21 February 2010, interviews were conducted with local fishermen and tour boat guides using a standardized questionnaire. A decade later, from 9 January to 13 March 2020, we attempted to locate and interview respondents from that 2010 survey along with new participants to conduct a longitudinal LEK survey. Informed consent was obtained from all participants, interviews were mostly conducted face to face and responses were recorded onto a standardized form (see Supporting Information). The initial questions in 2020 were the same as those from the original 2010 questionnaire. Respondents were asked to provide details related to their work experience in Golfo Dulce, including occupation, classified as fishing (*private*, *artisanal* or *sport*), tourism (*wildlife-sighting*, *kayaking* or *diving*) or both; number of years working in the area; and average days per workweek. Respondents were then asked to categorize the frequency with which they sighted whales, dolphins, sea turtles, whale sharks and sea snakes (reported as *always*, *frequently*, *occasionally*, *rarely* or *never*). Sea snake coloration (*all-yellow* or *bicolour*) and location were also recorded. In 2020, for respondents who had participated in 2010 (termed panelists), we added a categorical estimate of perceived change in sighting frequency over the decade for each taxon (recorded as *increase*, *same* or *decrease*); we focused on repeat participants because several newcomers had fewer than 10 years' experience, so their perceptions did not span the studied time gap. Switching to a semi-structured format near the end of the interview, we asked all the respondents whether they were aware that the all-yellow sea snake, *H. p. xanthos*, is endemic to Golfo Dulce (*yes* or *no*) and whether they believed local communities benefit from marine conservation (*yes* or *no*). Respondents were then encouraged to elaborate any related opinions in their own words while the conductor (BLB) took notes. Interview protocols and questionnaire were approved by the University of Reading School of Biological Sciences' Ethics Committee (reference number SBS19-20 11). The interview data (with personal information removed for data protection) are available in a Figshare repository (Bessesen & González Suárez, 2021: https://doi.org/10.6084/m9.figshare.14442029.v1).

2.2 | Boat-based biomonitoring

Multi-species marine sighting surveys were conducted across all waters of Golfo Dulce in 2010 and 2020 during the same periods as our interviews (B. L. Bessesen & M. González Suárez, unpublished data). Replicating the methods described by Bessesen (2015), 30 days of boat-based observations were recorded each year. The gulf was divided into four geographical areas, labelled GA1–4. One quadrant was searched per day, generally rotating GA1, GA3, GA2, GA4, and traversing in a variable pattern to cover as much area as possible along the coast and in the midwaters. Target taxa were prescribed as cetaceans, sea turtles, whale sharks and sea snakes, and all sightings of those fauna made during the observation periods were documented. Sightings were logged using Global Positioning System (GPS), data fields included time, species and group size, and photographs were collected whenever possible. Environmental conditions were logged at the start and end of each observation period, including time, Beaufort Wind Force, air and sea surface temperatures, visibility and prevailing weather.

2.3 | Data analyses

We examined the data to address several goals: to assess LEK for current species abundance, we analysed data from all 2020 interviews; to assess changes in abundance, we compared panelist responses from 2010 and 2020; to test the accuracy of human perception, we compared reported and perceived change; and finally to determine the reliability of LEK for assessing current abundance and trends, we compared all interview data against boat-based data. For the interview data, reported frequencies and perceived changes were converted into numerical values for analyses (frequencies as *never* = 1 through *always* = 5, and changes as *decrease* = 1, *same* = 2 and *increase* = 3). We analysed the interview data using linear mixed models (LMM) to test how reported frequencies differ across taxa and respondent characteristics. For panelists, we also calculated reported change by comparing frequencies from both survey periods as the difference between the numerical frequencies (e.g. if 2010 frequency was *always* and 2020 frequency was *never*, the reported change was −4). We then used LMM to test the calculated reported changes as a function of the perceived changes recorded in 2020, while also testing if reported changes varied across taxa and respondent characteristics. All models included respondent ID as a random factor modifying the intercept. Models were fitted using the lmer function from the LME4 package (Bates et al., 2015) with the LMERTEST package (Kuznetsova et al., 2017) used to generate *p*-value in R (R Core Team, 2020). We visually inspected model residuals to check the assumptions of homogeneity of variance and normality.

We evaluated reported and perceived change against empirical evidence of change by directly comparing the results of our interviews with the results of our on-water sighting surveys. Boat-based biomonitoring data were converted into sighting frequencies by dividing the number of sightings for each taxon by the total observation hours (2010 = 233 hr, 2020 = 232.5 hr). Frequency proportions were labelled as 0 = *never*, 0.01–0.10 = *rarely*, 0.11–0.20 = *occasionally*, 0.21–0.30 = *frequently* and >0.30 = *always* (no frequencies were >0.35, which represented sightings nearly every day and generally more than once per day).

3 | RESULTS

3.1 | Current abundance of taxa

In 2010, we conducted a cross-sectional interview survey with 82 participants. Among those questioned, 72% were professional fishermen (artisanal and/or sport; *n* = 59), 13% were non-fishing guides (boat tours and excursions; *n* = 11) and 15% did both (*n* = 12). On average, respondents worked 5 days per week and had 12 years of experience (range 1–40 years). In 2020, we interviewed a total of 23 individuals, 13 of whom had participated in the 2010 survey. Among all respondents, 22% were professional fishermen (*n* = 5), 43% were non-fishing guides (*n* = 10) and 35% did both (*n* = 8). Respondents averaged 4 workdays per week and had 20 years of experience (range 3–50 years). Overall, respondent characteristics related to their years of experience did not influence their reported sighting frequencies, but those who worked as tour guides reported lower sighting frequencies. While length of workweek had effect in 2010, in 2020 it did not and neither did previous participation in our survey (Table 1). While we did not specifically inquire about the respondents' history of residency, participants were known to be a blend of locally born individuals, Costa Ricans who had relocated to the Golfo Dulce region and expats from other countries.

Different taxonomic groups were reported with significantly different sighting frequencies, and as such, interviewees mostly reported seeing dolphins *always* but whale sharks *rarely*. When comparing LEK with biomonitoring data for each study period, respondent frequencies generally matched boat-based estimates, although in 2010 our on-water frequency fell a category lower than reported by most interviewees for whales and a category higher for sea snakes. The most prominent difference was a complete lack of whale shark sightings during biomonitoring (Table 2, Figure 2). Here we note a limitation due to the nature of the ordinal sighting frequencies: the category *never* is finite and was reported only when a respondent had not ever seen that fauna, meaning the category of *rarely* was reported even if a respondent had merely one or two sightings within their career. This created a particular challenge when comparing the whale shark results. Whale sharks only occasionally visit Golfo Dulce (Pacheco-Polanco et al., 2015), so while experienced respondents were bound to report whale shark frequency at a minimal category of *rarely* (with ≥1 sighting, they could not report *never*), our periodic boat-based surveys, which failed to record the species given narrow time frames, were constrained to the category *never*.

3.2 | Abundance trends between study periods

By the time we conducted our 2020 interviews, most of the respondents from 2010 had moved away, switched occupations, retired, died or were untraceable, but the 13 who were interviewed during both study periods comprised a small longitudinal panel, which we used to evaluate the use of LEK in assessing biodiversity changes between study periods. Reported change, calculated by comparing panelist responses from 2010 and 2020, showed potential trends in relative abundance of target taxa. As with current abundance assessments (see Section 3.1), longitudinal LEK seemed fairly reliable, since reported change between years was generally consistent with change found through boat-based biomonitoring (Figure 3.) The trends varied by taxa but suggested decreases in whales, sea turtles and whale sharks and an increase in sea snakes. Dolphin abundance appeared stable; however, we acknowledge the ordinal system we employed imposed limitations on certain calculations of change: sighting frequencies of *always* in 2010 meant reported change could not be *increase*, as there was no higher frequency category. Because dolphins were predominantly reported as *always* sighted in 2010 and reported change for that taxon was largely *same*, we were unable to determine whether an upturn might have occurred.

3.3 | Longitudinal versus retrospective

To determine whether LEK was equally good at measuring change over the time gap using hindsight (compared to present-day judgement), we asked panelists what changes in taxa abundance they thought they had witnessed over the decade. When perceived change was compared to reported change, no relationship was detected. Indeed, reported changes were not predictable from perceived changes or influenced by occupation or changes in workweek (Table 3). Although we focus here on the panelists because their work history covered the full span of our study, it is worth noting that we found no statistical variance between the direction of change reported by the 13 repeat versus 10 new respondents (whales χ^2 = 4.4, p = 0.111; dolphins χ^2 = 4.3, p = 0.115; sea turtles χ^2 = 0.8, p = 0.676; whale sharks χ^2 = 1.4, p = 0.488; sea snakes χ^2 = 2.3, p = 0.314), suggesting the panel was a representative sample of all 2020 participants. Overall, panelist data showed high variability in perceived change, and we

TABLE 1 Model coefficients for linear mixed random intercept regressions predicting sighting frequencies (converted to a numerical scale: 1 = *never* to 5 = *always*) for five target taxa as reported during 82 interviews completed in 2010 and 23 interviews in 2020. For each tested predictor, we report the best estimate, its standard error (*SE*) and *p*-value (in bold when $p < 0.05$). The 2010 model had a marginal $R^2 = 0.538$ (variance explained by fixed factors only) and conditional $R^2 = 0.598$ (total variance explained including fixed and random factors). The 2020 model had a marginal $R^2 = 0.607$ and conditional $R^2 = 0.714$

	2010			2020		
Predictors	Estimates	*SE*	*p*	Estimates	*SE*	*p*
(Intercept)	2.59	0.23	**<0.001**	3.18	0.42	**<0.001**
Taxa: **Dolphin**	1.74	0.12	**<0.001**	2.04	0.20	**<0.001**
Taxa: **Sea Turtle**	1.34	0.12	**<0.001**	1.35	0.20	**<0.001**
Taxa: **Whale Shark**	−0.40	0.12	**<0.001**	−0.52	0.20	**0.010**
Taxa: **Sea Snake**	−0.04	0.12	0.760	0.87	0.20	**<0.001**
Fisherman	−0.18	0.15	0.238	−0.48	0.29	0.114
Tour guides	−0.53	0.20	**0.007**	−0.72	0.29	**0.024**
Worked days	0.09	0.03	**0.013**	−0.01	0.07	0.914
Years of experience	−0.01	0.01	0.144	−0.01	0.01	0.277
Interviewed in 2010				0.38	0.27	0.185

TABLE 2 Frequency statistics for 2010 and 2020 by taxa: means and standard deviations of interviewee reported sighting frequencies converted to numerical values (*never* = 1, *rarely* = 2, *occasionally* = 3, *frequently* = 4, *always* = 5) and biomonitoring data converted into sighting frequencies (*never* = 0, *rarely* = 0.01–0.10, *occasionally* = 0.11–0.20, *frequently* = 0.21–0.30, *always* >0.30), dividing sightings by observation hours

	2010 (233 observation hours)				2020 (232.5 observation hours)			
	Interviews		Biomonitoring		Interviews		Biomonitoring	
	Mean	*SD*	Sightings	Proportion	Mean	*SD*	Sightings	Proportion
Whales	2.9	0.9	2	0.01	2.7	0.8	3	0.01
Dolphins	4.6	0.6	81	0.35	4.7	0.4	74	0.32
Sea Turtles	4.2	0.8	80	0.34	4.0	0.9	69	0.30
Whale Sharks	2.5	0.8	0	0.00	2.2	0.7	0	0.00
Sea Snakes	2.9	1.2	37	0.16	3.6	1.0	57	0.25

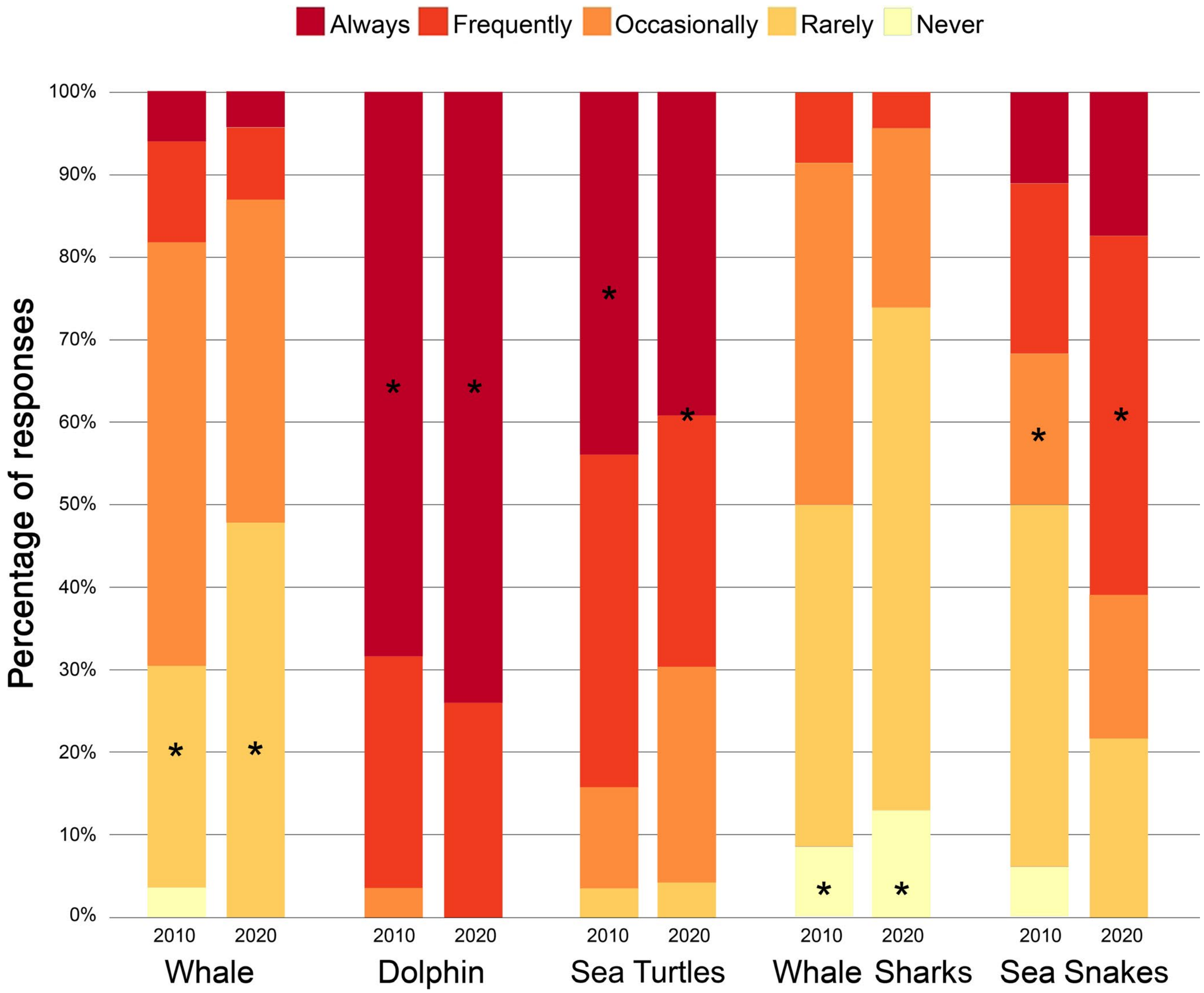

FIGURE 2 Sighting frequencies for five target taxa in 2010 and 2020, as reported by all respondents. Asterisks are positioned in the colours that represent our on-water sighting frequencies during the same time periods (also see Table 2)

found some dramatically conflicting patterns when mapping against reported change. For instance, most panelists perceived whales as having increased but reported equal or lower sighting frequencies in 2020 compared to 2010 (Figure 3). Individual responses for reported and perceived changes for sea snakes were also inconsistent, but in both cases the majority of panelists indicated an increase in sea

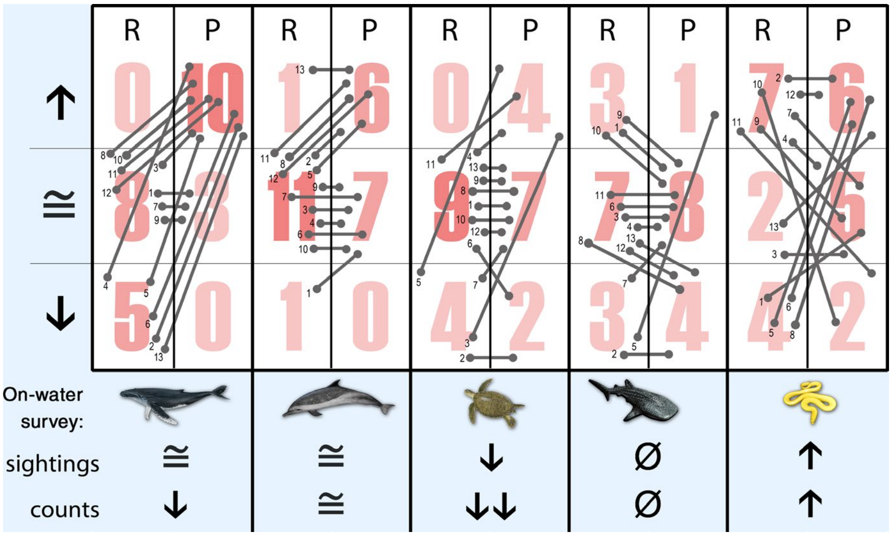

FIGURE 3 Changes in sighting frequency for each taxon between 2010 and 2020 shown as increase (↑), same (≅) and decrease (↓). Angled lines (labelled 1–13) represent 13 interview panelists and connect reported change (R columns) versus perceived change (P columns), with total counts for each block in red (shaded: light 0–4, medium 5–8 and dark 9–11). Changes seen during biomonitoring are presented below the grid as sightings (number of encounters) and counts (number of individuals seen)

TABLE 3 Model coefficients for a linear mixed random intercept regression predicting the changes in reported frequencies, comparing 2010 and 2020 responses, as a function of perceived change in 2020 and changes in occupation and number of workdays. Responses from 13 panelists interviewed in both 2010 and 2020. For each tested predictor, we report the best estimate, its standard error (*SE*) and *p*-value (in bold when $p < 0.05$). The model had a marginal $R^2 = 0.170$ (variance explained by fixed factors only) and conditional $R^2 = 0.210$ (total variance explained including fixed and random factors)

Predictors	Estimates	*SE*	*p*
Intercept	−0.38	0.48	0.430
Perceived change: Same	0.13	0.37	0.725
Perceived change: Increase	−0.32	0.40	0.424
Taxa: Dolphin	0.40	0.35	0.256
Taxa: Sea Turtle	0.04	0.36	0.905
Taxa: Whale Shark	0.11	0.39	0.773
Taxa: **Sea Snake**	0.88	0.35	**0.015**
Occupation change	−0.09	0.27	0.760
Working more days	0.34	0.36	0.359
Working fewer days	0.10	0.26	0.710

snakes, as was detected during biomonitoring (Table 3, Figure 3). On the other hand, there was higher individual consistency in responses for sea turtles, with most panelists reporting and perceiving no change. Biomonitoring actually indicated a decrease in sea turtles; although this decline was minimally reflected through reported change, it is notable that no reported change suggested an increase while several panelists perceived an increase (Figure 3).

3.4 | Additional interview insights

When given the opportunity to elaborate on their perceptions, respondents who suggested an increase in whales most often cited better protections or the elimination of commercial fishing vessels inside Golfo Dulce. Some respondents commented that more whales are seen during the rainy season, something also documented through biseasonal biomonitoring (Bessesen, 2015). Certain respondents who perceived dolphins to be increasing stated that less commercial fishing inside the gulf results in more food for them, and those who perceived an increase in sea turtles said conservation efforts are helping, although they acknowledged there is still minimal enforcement against egg poaching on the beaches. The respondents who perceived fewer sea turtles named several reasons for the decline: escalating boat traffic causing more propeller-strike fatalities (from 2008 to 2020 the number of working tour boats reportedly went from seven to 25 and 'everyone accidentally hits them', meaning sea turtles); longlines are regularly deployed outside the gulf and may be further increasing turtle bycatch by using live bait, while illegal gillnets are increasing incidental capture inside the gulf; and some conservation organizations are said to be causing additional disturbances by catching and handling sea turtles 'over and over' for research. Among interviewees who perceived a decline in whale sharks, one suggested offshore tuna seines as an issue, while others pointed to the impact of increasing boat traffic and over-eager tourists. Respondents again conveyed that only all-yellow sea snakes are seen inside the gulf and some noted that their awareness of the snakes had increased since our first survey in 2010 (which could also be a factor in their reports of *increase* for the species). Most realized that *H. p. xanthos* is endemic to Golfo Dulce and a thematic analysis of their comments consistently underscored three main qualities about the serpent: it is beautiful, it is venomous (although respondents were often quick to add that they did not fear the snake) and it is valued as a unique animal in Golfo Dulce. When asked about marine conservation in Golfo Dulce, 19 of the 23 (83%) respondents in 2020 agreed that environmental protection efforts benefit the local community, three suggested that downsides and benefits coexist and one participant saw no benefit to the community. Those in support of conservation reported the benefits as stabilizing or increasing their fishery resources as well as the financial infusion created by ecotourism. Eight respondents (37%) spoke specifically to the need for stricter enforcement of laws that protect marine life. Those who saw less advantage to conservation cited a dearth of profitable work due to fishing regulations and pointed out that large international companies reap most of the revenue from ecotourism while local citizens are hired as low-wage labourers.

4 | DISCUSSION

Throughout the years, LEK has been derived from many types of experienced informers, including farmers (Leedy, 1949; Vaughan et al., 2003), fishermen (Carter & Nielsen, 2011; Lozano-Montes et al., 2008; Rehage et al., 2019; Turvey et al., 2013), even urban-nature enthusiasts (Yli-pelkonen & Kohl, 2005), and it has been used to assess a wide range of land and marine species. By collecting and cross-comparing interview data and empirical scientific data from the same time periods to evaluate sighting frequencies for several charismatic marine species, however, our work fills a specific research gap and helps us understand the potential limitations and strengths of LEK. Our findings suggest that LEK could be a valid, complementary approach to assessing current abundance of charismatic marine taxa in Golfo Dulce. Sighting frequencies for cetaceans, sea turtles, whale sharks and sea snakes provided via interviews with local fishermen and tour boat guides generally matched sighting frequencies observed during on-water surveys. This work complements other LEK studies for species abundance with similar results: Anadón et al. (2009) and Turvey et al. (2013) both reported good agreement between data from cross-sectional interviews and field studies (land-based distance sampling for tortoises and boat-based surveys for porpoises respectively). Silvano and Begossi (2010) also compared LEK against biological surveys, but for various ecological aspects of bluefish, and they reported mixed results, such as agreement for the animals' diet but disagreement for their reproduction period. Although comparative studies are most easily realized with readily encountered fauna, such convenience is not always possible. As such, were unable to provide comparable biomonitoring data for whale sharks. In Golfo Dulce, resident species (dolphins, sea snakes and certain sea turtles) are more commonly seen than migratory visitors (whales and whale sharks), which are seasonally and/or sporadically present and harder to assess. LEK suggests whale sharks are not only rare in Golfo Dulce but also in decline. As a species becomes less available for documentation, estimates of its abundance simultaneously become more important for conservation. Hence, when a species is sighted infrequently by even the most experienced interviewees and is unlikely to ever be recorded through periodic biomonitoring, LEK should be considered more reliable for assessing abundance so long as respondents have substantial and ongoing experience in the study area. Of course, relying on LEK alone without any evidentiary standards is not recommended (Gilchrist et al., 2005). Furthermore, when 'testing' the assumptions and limitations of LEK against a biomonitoring scheme, it is essential to consider the assumptions and limitations of the biomonitoring scheme itself (Brook & McLachlan, 2005); our full boat-based methods are reported in Bessesen (2015).

An additional and important contribution of our study is the comparison of results of two fields' seasons a decade apart. Much of the literature focuses on single interview surveys to obtain LEK for species abundance trends rather than systematically comparing panel responses from 2 or more years (Thornton & Maciejewski Scheer, 2012). When we took the opportunity to examine our LEK data from a longitudinal perspective, evaluating sighting frequencies provided by a decade apart, overall trend patterns showed general consistency with abundance trends established through comparative biomonitoring. This suggests the strength of LEK. Unfortunately, we found retrospective perceptions of change much less reliable. Our panelists' perceived changes over the same period failed to agree with changes seen during boat-based surveys. Incongruence was apparent on an individual level as well: a person's perceived change for a particular taxon often conflicted with their own reported change (Figure 3). No individual leaned entirely in one direction, but overall perceived trends tended to be optimistic; for example, respondents reported an equal or lower frequency of whale sightings yet strongly perceived an increase. Comparing two points in time, our results suggest that respondents may not recollect changes accurately over a decade gap, even if their estimates of current abundance appear accurate and could be used to measure change over time using a longitudinal interview survey scheme. Retrospective bias appears to be a commonly reported phenomenon (Finney, 1981; Rafferty et al., 2015). Our respondents tended to over-estimate perceived abundance, though human perceptions could also sway in the opposite direction. LEK data reported by O'Donnell et al. (2010), for example, suggested a historical decline in seahorses that fisher logbooks did not corroborate. Granted, their LEK might have been accurate if seahorses had decreased due to factors other than fishing. Depending on the study, methodologies and framed objectives, retrospective bias may not be an issue. Rehage et al. (2019) and Santos et al. (2019) combined fishery-dependent data (i.e. reported landings) with LEK, applying a life-history calendar approach (as described by Freedman et al., 1988) to examine the spatial changes in bonefish in Florida over several decades. They found a good agreement between the datasets, both indicating an overall trend of decline.

The variance within social surveys is complex and interview bias has long been recognized (Moser, 1951). Our assessment of LEK was based on relatively few respondents possessing varying levels of expertise and differing characteristics, which could have limited our ability to identify all the factors that shaped respondent perceptions (Davis & Wagner, 2003). It is possible that a respondent's place of origin, being born locally versus elsewhere, could bias their perceptions but our data do not allow us to test this potential effect. We generally did not find responses to be influenced by the considered respondent attributes, although tour guides reported lower sighting frequencies overall. Tour guides likely pay closer attention to charismatic fauna as these are important for their livelihood (Mazzoldi et al., 2019), and greater interest could lead to greater expectations but also perhaps more accurate estimates. We divided fishing and tourism for our analyses, but there is some cross-over since sport-fishing is primarily a tourism activity, although it does not focus on the taxa explored in our interviews. Reported sighting frequencies may also be influenced by changes in awareness (i.e. learning about the uniqueness of the yellow sea snake might prompt more attention), or by the metrics applied. As our on-water survey showed, counting whale encounters versus counting individual whales can offer different pictures (Figure 3). Using quantitative descriptors that separate those items on a questionnaire, such as 'individuals or groups sighted at least once every 1–2 working days', would have been helpful to disentangle those effects. Belief systems can also influence LEK and change-focused assessments (Begossi, 2015). Believing conservation efforts are working (i.e. restriction of shrimp trawlers inside the gulf and fewer turtle eggs sold) could lead to the general perception that marine life is (must be) rebounding. Conversely, believing environmental problems have worsened (i.e. more boat traffic, illegal fishing and increased agricultural runoff) could lead to a sense that marine life is suffering and therefore must be in decline. Personal experience may also influence response. Unlike Ainsworth (2011) and Lozano-Montes et al. (2008), we did not find shifting baselines where older respondents report higher historic abundance than younger respondents, though that might be due to sample size and/or length of study, because many older fishers in 2010 did report an overall decline in Golfo Dulce fauna since their youth (Bessesen, 2010).

All previous participants who were located agreed to be interviewed again and our panel included many of the most experienced fishermen and guides in Puerto Jimenez. Notably, our smaller sample size in 2020 ($n = 23$) was not a factor of unexpectedly fewer participants but rather a windfall of participants in 2010 ($n = 82$). The original goal for the 2010 survey based on the size of the accessible community was 25 participants. Had we collected that number, our sample sizes between years would be comparable. Instead, over a hundred fishermen from all around the Golfo Dulce region were called to a political meeting in Golfito in 2010, and an author (BLB) received a last-minute invitation, subsequently garnering a substantially larger pool of data. Inadequate mobility and traceability made it impossible to locate or identify most of those men a decade later. Concerns regarding a repeat survey were not anticipated, and so some people might also have been untraceable because they provided their given names for the 2010 interviews but are known within their community only by their nicknames. Having both names might have aided our efforts. Given the importance of re-interviewing for accurate assessment of change, measures should be taken to ensure traceability, all within the limits of careful personal data protection. Over a 10-year time gap, it is also likely that some of the unlocated persons had moved away, switched occupations, retired or died, which emphasizes the problem of attrition over time. Identifying new participants in 2020 brought a different challenge: young fishermen were less willing to engage than in 2010. Illegal fishing with gillnets and spear guns is said to be on the rise, as is over-water drug trafficking, and it is possible that illicit activities created some perceived risk in discussing topics related to marine work. Although our sample was smaller in 2020 than in 2010, it was nevertheless in alignment with our expectations, as we knew we would be unable to contact all the regional fishermen who had previously participated. Indeed, our smaller sample more accurately reflects the limited access to interviewees common in remote geographical areas. Furthermore, statistical analyses indicated the perceptions of the 13 panelists were reflective of all of 23 respondents from the second study period, increasing confidence in our results.

Local ecological knowledge is not confined, of course, to assessments of faunal abundance (Castellanos-Galindo et al., 2011; Thornton & Maciejewski Scheer, 2012). The value of marine workers to expose or define the factors involved in a particular species' decline and/or shifts in human behaviour that pose threat to biodiversity should not be underestimated (Carter & Nielsen, 2011). The use of live bait by long-liners, clandestine poaching activities and admissions of propeller strikes are but some of the insights gained from our interviews. Despite the official ban on gillnets, we observed several fishermen setting and hauling those gears during our sighting survey and we were told that poaching reef fish with spearguns is also becoming a serious, although less visible, problem. That interviewees openly discussed these challenges demonstrated their overarching support of marine conservation. Most showed clear appreciation for the ecological beauty of the region and they largely saw conservation as a means to protect their natural resources and provide a robust tourism-based economy. Importantly, such honesty and support could change over time and/or may not be the norm in other regions of study, thus potential community-specific biases or agendas merit careful consideration.

Periodic biomonitoring is essential for measuring changes in marine biodiversity but is also costly. Combining systematic biodiversity assessments with LEK surveys may provide an economical solution. Longitudinal interview surveys may have the greatest value when conducted periodically *between* on-water sightings surveys, as changes found through systematic analysis of responses could serve as an early warning for negative trends. Although we found limited reliability of human perception for tracking faunal abundance trends, it would be worth exploring whether perceptions of change are better at shorter intervals (e.g. every 2–3 years rather than every decade). Interviews can also engage local communities and stakeholders, and represent their voices, something key to the successful management of ecological resources. Our study provides valuable assessment data for policymakers and practitioners about a bio-rich area of Costa Rica that is currently under pressure. We therefore hope the results inform marine conservation, appreciating that successful long-term protection of Golfo Dulce as a biodiversity hotspot and international ecotourism destination will depend wholly on Costa Rica's legislative and enforcement bodies, along with the collaboration of dedicated NGOs and the motivated involvement of local citizens in the welfare of their waters.

On a global level, the data presented here offer valuable insights concerning LEK as a complementary scheme to biomonitoring, which could benefit future studies no matter the locale. Our study, while small in scale, suggests that LEK can be a good source of information for current abundance estimates and for assessing trends by systematically comparing abundance estimates between periods but that it fails as a retrospective measure of change. Large-scale research projects combining longitudinal LEK interviews with on-water sighting surveys are needed to flush out the dynamics of this interdisciplinary approach. Our methods proved successful, although certain adjustments, such as clarifying the term 'sighting frequency' (how often versus how many) and taking greater care to ensure respondent traceability over sizeable time gaps, are highly recommended. Testing new research methods requires time, resources and unique problem-solving skills, but with anthropogenic activities causing ecosystem collapse and species declines throughout land and sea (Briggs, 2011; Costello et al., 2017; Pimm et al., 1995), we encourage every effort to explore interdisciplinary techniques that might aid the understanding of human–nature relationships and contribute to the protection of biodiverse life on Earth.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

B.L.B. conceived and designed the study; collected and analysed the data; and led the writing of the manuscript. M.G.-S. contributed to data analyses and manuscript writing.

DATA AVAILABILITY STATEMENT

Data are archived in Figshare at https://doi.org/10.6084/m9.figshare.14442029.v1 (Bessesen & González Suárez, 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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FIG. 3. Eggshells from failed nest of *Heterodon simus*, Scotland County, North Carolina, USA.

and no longer appeared gravid. On 10 August 2020, she was found dead and partially consumed by a predator. The condition of the remains suggested a raptor.

We suspected eggs had been deposited in the burrow the snake used for the longest period (6 June–14 July). From 25 August–5 October, a hardware cloth nest protector was placed over that burrow, as well as over each of the four additional burrows known to have been used between 6 June and 1 August. Each burrow was monitored daily. No indications of hatching or emergence were noted. On 31 October 2020, we carefully excavated the most-utilized burrow. A nest chamber was located off a side tunnel ca. 61 cm lateral distance from the burrow entrance. The chamber measured ca. 7 × 7 cm and was situated at the interface of the topsoil and roots of a tussock of *A. stricta* and the underlying layer of sandy soil (Fig. 2). The bottom of the chamber was ca. 25 cm below the surface. The chamber contained six non-adherent eggshells in an advanced state of degradation; none appeared to have hatched (Fig. 3). Although it was difficult to determine the precise number of ova visible in the radiograph, it was clearly more than six and may have been greater than 13. It is possible that some eggs were either reabsorbed or never developed fully, were infertile or otherwise deteriorated completely before we discovered the nest chamber, were deposited in another location, or were consumed by an underground predator. JCB and SJH found the shed skin of an adult *Cemophora coccinea copei* (Northern Scarlet Snake), a known reptile egg predator, within ca. 1 m of the nest burrow on 3 July. The remains of the female and eggshells are deposited in the herpetology collection of the North Carolina State Museum of Natural Sciences (NCSM 104650).

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***HYDROPHIS PLATURUS XANTHOS* (Golfo Dulce Yellow Seasnake). HARASSMENT BY DOLPHINS.** Within the true sea snakes (Elapidae: Hydrophiinae), *Hydrophis platurus xanthos* is a recently described subspecies endemic to the inner basin of Golfo Dulce, Costa Rica (Bessesen and Galbreath 2017. ZooKeys 686:109–123). Golfo Dulce is a semi-enclosed embayment with a profound inner basin (>200 m) and effective sill and shallow outer basin that prevent free exchange with the Pacific Ocean masses (Svendsen et al. 2006. Rev. Biol. Trop. 54:147–170). In contrast to black-and-yellow conspecifics residing outside the gulf, the geographically bound *H. p. xanthos* is bright canary yellow with significantly smaller body size (49 cm average total length; Bessesen and Galbreath 2017, *op. cit.*).

At 1239 h on 21 January 2012, two *Tursiops truncatus* (Bottlenose Dolphins) travelling in Golfo Dulce with a larger group broke off and began harassing an adult *H. p. xanthos.* Loose skin covering the snake's body indicated it may have been in the process of ecdysis when it was attacked (Fig. 1). This species employs a knotting behavior to aid shedding (Pickwell 1971. Copeia 1971:348–350; BLB, pers. obs.) which might have attracted the cetaceans. The dolphins tossed the serpent back and forth for 5–7 min in what appeared to be play, and then moved away to follow their group. The snake remained at the surface, knotting itself into a ball. It was netted for brief examination and deemed limp but alive, with teeth marks on the skin, especially around the head and neck (Fig. 1). After being returned to the water, its fate was unknown.

Hydrophis platurus outside Golfo Dulce possess black dorsums with yellow ventral surfaces and black spots or bands on the tail paddle (Bessesen 2012. Herpetol. Rev. 43:22–26). This coloration is considered aposematic as the species possesses neurotoxic venom and appears noxious, having few natural predators (Kropach 1975. *In* Dunson [ed.], The Biology of Sea Snakes, pp. 185–213. University Park Press, Baltimore, Maryland). Nevertheless, there are reports of *H. platurus* being attacked by octopus (van Bruggen 1961. Basteria 25:73–74), pufferfish (Pickwell et al. 1983. Calif. Fish Game 699:172–177), Lava Gulls (Reynolds and Pickwell 1984. Copeia 1984:786–789), pelicans (Álvarez-León and Hernández-Camacho 1998. Caldasia 20:93–102), Magnificent Frigatebirds (Sheehy et al. 2011. Herpetol. Rev. 42:443), Wood Storks (Solórzano and

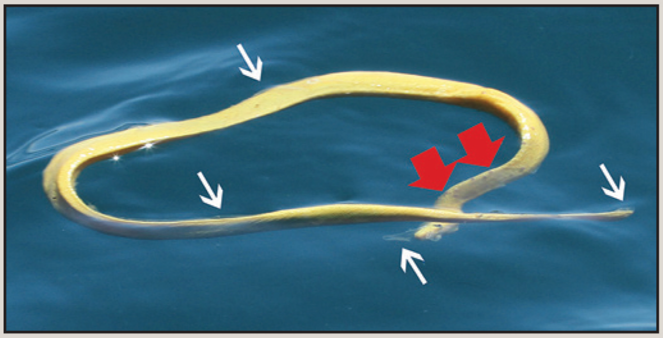

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FIG. 1. *Hydrophis platurus xanthos* floating limp in Golfo Dulce, Costa Rica after being tossed around by two *Tursiops truncatus* (Bottlenose Dolphins) and left with multiple tooth marks (red arrows; white arrows point to loosened skin).

Kastiel 2015. Mesoam. Herpetol. 2:121–123), and Common Black Hawks (Solórzano and Sasa 2017. Mesoam. Herpetol. 4:431–433), suggesting it is vulnerable to harm by a variety of organisms. Although dolphins apparently do not predate *H. platurus* (Kropach 1975, *op. cit.*), Ineich and Loyer (1998. Bull. Soc. Étud. Océan. 276:86) and Durso et al. (2015. Herpetol. Rev. 46:104) described *T. truncatus* in French Polynesia and Mexico, respectively, playing with one in a similar fashion to our observations. This is the first documented attack on *H. p. xanthos*, but local fishermen have reported seeing dolphins harassing yellow sea snakes on other occasions as well, and it remains unclear whether xanthic coloration has greater or less aposematic effect with respect to marine mammals or other potential assailants.

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***LEPTODEIRA NIGROFASCIATA* (Black-banded Cat-eyed Snake). DIET.** *Leptodeira nigrofasciata* is found along the Pacific versant from Mexico to Costa Rica (Leenders 2019. Reptiles of Costa Rica: A Field Guide. Comstock Publishing Associates, Ithaca, New York. 470 pp.). Rarely encountered, this semi-arboreal snake species is mostly nocturnal, feeding on skinks, anoles, leptodactylid and hylid frogs (Duellman 1958. Bull. Am. Mus. Nat. Hist. 114:1–152; Solórzano 2004. Serpientes de Costa Rica. Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica. 321 pp.). Here, we report the predation of the lizard *Marisora brachypoda* by *L. nigrofasciata*.

On the afternoon of 17 June 2019, in the Heloderma Natural Reserve in the Zacapa Department, Guatemala, we captured an *L. nigrofasciata* by hand and placed it in a cotton bag to hold for photos. While in the bag the snake regurgitated what was later identified as a juvenile *M. brachypoda*. The skink's tail was found separated from the body, most likely occurring after it had been injested. *Marisora brachypoda* is a species of short-limbed skink native to much of Central America, ranging throughout Mexico, Costa Rica, El Salvador, Guatemala, and Nicaragua (Hedges and Conn 2012. Zootaxa 3288:1–244). This species is diurnal and is typically found living in xeric habitats with low vegetation and numerous open basking spots (Leenders 2019, *op. cit.*). Records of predation on *M. brachypoda* by snakes are not well-reported but it may be inferred that most appropriately sized lizard eating snakes would prey upon this species (Hedges and Conn 2012, *op. cit.*). To the best of our knowledge, this is a first report of *L. nigrofasciata* preying upon this species of skink. The snake was released soon after.

Fig. 1. *Leptodeira nigrofasciata* (A) and regurgitated *Mesoscincus managuae* (B) from Zacapa Department, Guatemala.

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***LYCODON CAPUCINUS* (Common Wolf Snake). ECTOPARASITISM.** *Lycodon capucinus* is a common colubrine snake with a wide distribution throughout the Philippines and southeast Asia; it is frequently found in agricultural and residential areas at low elevations (Brown et al. 2013. ZooKeys 266:1–120). Ticks have been recorded parasitizing snakes particularly in captive python, cobras, and rat snakes in India (Catherine et al. 2017. J Parasit Dis. 41:952–958). To our knowledge, there are no records of tick parasitism from Philippine Colubridae.

On 13 February 2017, by a corn field near Mt. Cagua in Barangay Santa Clara, Gonzaga, Cagayan Province, Luzon, Philippines (18.228°N, 122.060°E; WGS 84; 278 m elev.), we found a dead *L. capucinus* with a damaged head (Fig. 1A), likely killed by local residents. Upon preservation, it was found that the snake was being parasitized by a partly engorged tick attached at its anal plate (Fig. 1B), identified as a female *Amblyomma helvolum*. To the best of our knowledge, *L. capucinus* appears to

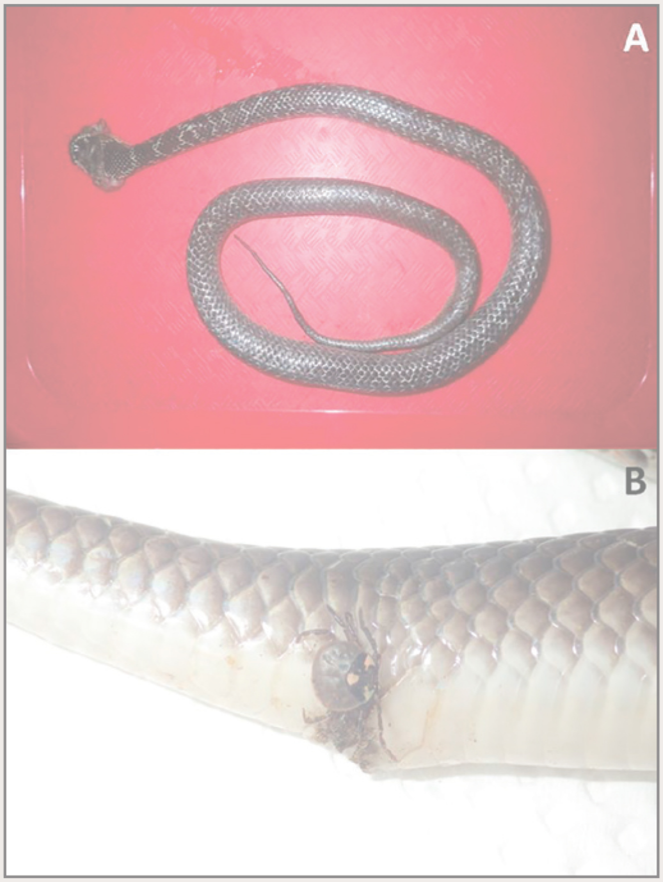

Fig. 1. *Lycodon capucinus* (A) parasitized by female *Amblyomma helvolum* (B) from Luzon Island, Philippines.

The unique ecology of an endemic sea snake *Hydrophis platurus xanthos* is the PhD thesis of Brooke L. Bessesen. It presents findings derived from fieldwork and analyses undertaken between 2019 and 2022 and builds on Bessesen's earlier research in Golfo Dulce, Costa Rica. This work was supervised by Dr Manuela González Suárez at University of Reading. Dr Gary J. Galbreath at Northwestern University in the United States provided additional support to the author.

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