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CONTRIBUTED PAPER

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

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Abstract

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 *H. p. 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 averages of temperature, salinity, dissolved oxygen, turbidity, and pH at 0.5 and 10 m based on probe readings 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 for *H. p. xanthos* and we estimate its extent of occurrence (282 km²) and current area of occupancy (260 km²) to inform conservation assessments and guide protection measures.

KEYWORDS

area of occupancy, Costa Rica, extent of occurrence, Golfo Dulce, habitat suitability, *Hydrophis platurus xanthos*, species distribution modeling

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

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deemed “suitable”) and can aid assessments of conservation status for potentially vulnerable taxa. *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-closed 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 *H. p. xanthos*' closest relative, the pelagic sea snake, *H. p. platurus*, which has a wide distribution ranging across the Indo-Pacific. The pelagic sea snake inhabits cooler waters and has a thermal tolerance of 18–33°C (Dunson & Ehlert, 1971). It is also exposed to oceanic salinity averaging 35 ppt and has sublingual salt-excretion glands (Dunson, 1968) and a sodium-blocking dermal layer to aid osmoregulation (Dunson, 1975). The pelagic sea snake spends most of its time in long slow dive cycles to an average max depth of 15 m (Rubinoff et al., 1986). It ventilates at the surface but also depends on dissolved oxygen in the marine environment as it respire up to 33% of its oxygen requirements through its skin (Graham, 1974). 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). Although the population appears to be restricted to the deepest, presumably coolest, waters of Golfo Dulce (Bessesen, 2015), habitat suitability has remained largely undefined.

Among available tools for SDM, Maxent (machine learning maximum entropy modeling) 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 *H. p. xanthos* considering more than 400 sea snake sightings accrued through

multiple surveys in Golfo Dulce over longer than a decade and 13 fundamental hydrographic variables known to influence the ecological patterns of marine species. Depth appears to be an important factor in sea snake habitat (Udyawer et al., 2020); temperature can define sea snake range (Graham et al., 1971; Hecht et al., 1974;) and is proposed to have modified behavioral patterns in *H. p. xanthos* (Bessesen, 2012; Bessesen & González-Suárez, 2022); salinity can impose adaptive pressure in the evolution of marine reptiles (Rash & Lillywhite, 2019); dissolved oxygen can affect both the biology and ecology of marine vertebrates (Global Ocean Oxygen Network, 2018), which could be particularly interesting to consider in a species utilizing cutaneous respiration (Graham, 1974); pH can provide insight into a population's response to potential ocean acidification (Raven et al., 2005); and Beaufort wind force (BWF) and turbidity are also of direct relevance because *H. p. xanthos* reportedly surfaces in relatively rougher waters than the pelagic snakes (Bessesen & Galbreath, 2017). Our work fills a sizeable knowledge gap about the potential effect of near-surface water conditions on a geographically isolated sea snake.

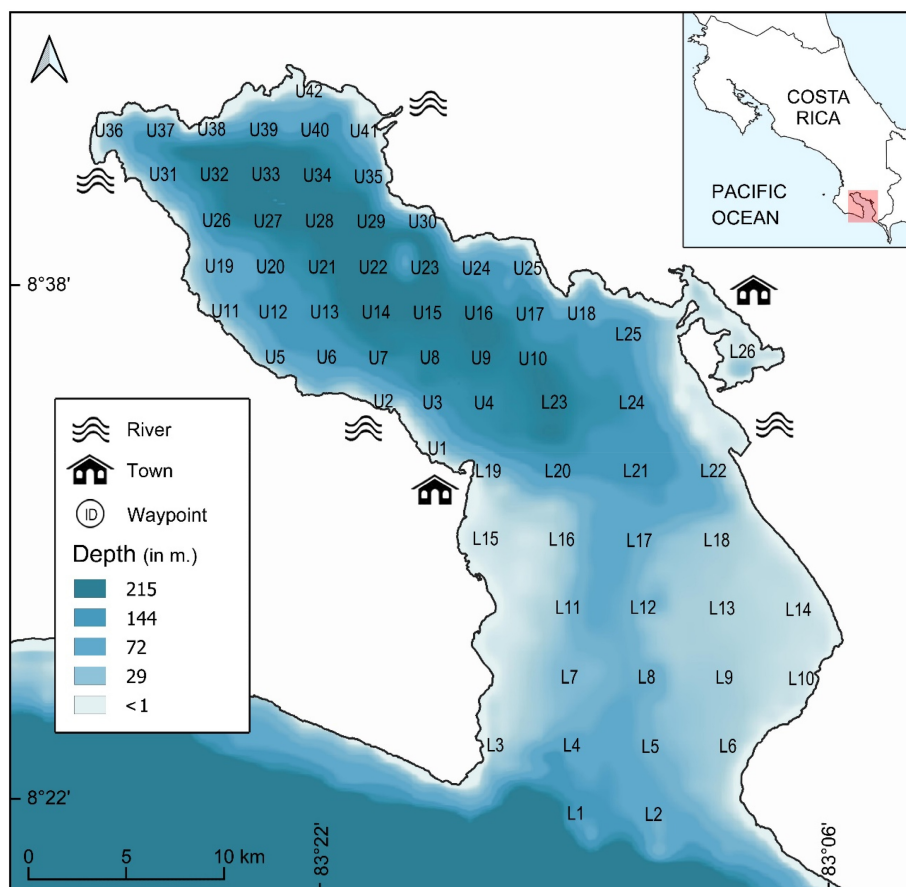
2 | METHODS

2.1 | Study area

Golfo Dulce is a semi-enclosed embayment located along the southwestern shoreline of Costa Rica just above Panama (Figure 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 (Figure 1). 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/month rainfall)

FIGURE 1 Bathymetric map of study area (Golfo Dulce, Costa Rica) with 68 water-testing waypoints divided by zone: 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)



and rainy season May through November (>500 mm/month 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 & Ballester-Sakson, 2015). Sea surface temperatures (SST) in Golfo Dulce vary but remain relatively warm, averaging approximately 30°C and occasionally reaching 32.5°C (Rincón-Alejos & Ballester-Sakson, 2015) as compared with SST of 28.3 – 28.6°C in the adjacent Pacific (Wellington & Dunbar, 1995; Rasmussen et al., 2011a, 2011b; 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 ≈ 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 (Rincón-Alejos & Ballester-Sakson, 2015).

2.2 | Hydrographic 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 (Figure 1). Sampling was conducted in shallower depths (0–10 m) where sea snakes breathe, rest, and feed. During 7 days in 2020 (between 12 and 29 January) and 3 days in 2021 (from 15 and 17 March), we used a lab-calibrated YSI ProDSS multi-parameter probe to collect hydrographic data. Readings of temperature ($^{\circ}\text{C}$), salinity (ppt), dissolved oxygen (optic; mg/L), turbidity (NTUs), and pH (scaled 0–14) were taken at depths of 0.5 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 BWF 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 (06:00 p.m. to 08:30 p.m.; these sites were also sampled multiple times during the day). For comparison, we also report 88 SST readings and 709 BWF records at actual *H. p. xanthos* sightings collected over approximately 11 years (not always during daylight hours). At 10:21 a.m. on March 14, 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.

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, they are 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 modeling 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 artifacts 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 *H. p. xanthos* (Bessesen, 2012, 2015), 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 artifacts 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 m²), which was the finest scale available for our corresponding depth data.

Additionally, we inspected long-term average sea surface temperature and salinity variables from the MARSPEC dataset (Sbrocco & Barber, 2013) but did not include them in our models as the raster resolutions were considerably coarser than our data and on the local level values were found to be inconsistent with the literature for Golfo Dulce: waters near a northern rivermouth represented the highest salinity with lower salinity nearer the open ocean, and SSTs were ≤4°C cooler than those reported in situ (23.0–30.0°C vs. 26.9–32.5°C per Acuña-González et al., 2006; Morales-Ramírez et al., 2015; Rincón-Alejos & Ballester-Sakson, 2015). 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.

2.3 | Presence-absence data

Between 2010 and 2021, a total of 765 occurrence records of *H. p. xanthos* were collected during multiple studies: three large multispecies surveys covering all waters of Golfo Dulce ($n = 125$; Bessesen, 2012, 2015), a sampling survey with 46 shore-to-shore transect lines above the sill ($n = 203$; Bessesen et al., 2022), a diel study ($n = 358$; Bessesen & González-Suárez, 2022), 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 h, 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 *H. p. xanthos* were recorded in the field but from data collected during the multispecies 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).

2.4 | Maxent modeling

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 m

(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's $R > 0.70$) correlated variables, so we used the `aster.cor.matrix` function in the R package "ENMTools" (Warren and Seifert, 2011) to test for correlations among predictors. A correlation of 0.72 was detected between SST and temp05 (Appendix S1). 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 modeling. 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 $\Delta AIC_c = 0$), and outlines the best Maxent settings for feature classes (linear, quadratic, hinge, product, threshold, referred to as L, Q, H, P, T) and 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 Dudik (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 *H. p. 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 nonsuitable (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-km² grid cells identified with sighting records or with suitable habitat encircled by grid cells with sighting records within the EOO; IUCN, 2022).

3 | RESULTS

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 1, Appendices S2 and S3). Both BWF 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 mid-waters, 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), with waters consistently cooler and more stable at 10 m depth. Measurements of pH were also lower at depth. Conversely, dissolved oxygen, and salinity were higher at 10 m than at 0.5 m. 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.

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
pH 05	8.20 ± 0.02	8.21 ± 0.02	8.21 ± 0.06	8.19 ± 0.06
pH 10	8.18 ± 0.02	8.19 ± 0.02	8.19 ± 0.08	8.18 ± 0.06

TABLE 1 Environmental conditions in Golfo Dulce (Costa Rica), including depth and 12 hydrographic variables describing the entire area (EA) and suitable habitat for *Hydrophis platurus 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, temp10, sal05, sal10, do05, do10, turb05, turb10, ph05, ph10); values are reported as means and standard deviations; depth obtained from GEBCO (2014)

TABLE 2 Environmental variables related to the presence of *Hydrophis platurus 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, temp10, 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

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 2; Appendix S4). 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 $PI \geq 3.5$, 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 2). The individual response curves for the most important variables suggest a higher probability of presence in areas where the water is >100 m, salinity is <32 ppt, pH is close to 8.2, dissolved oxygen is higher, temperatures are cooler, and turbidity is lower (Figure 2).

Suitable habitat for *H. p. xanthos* was primarily restricted to the Upper Gulf in the full model (Figure 3a) but also when depth was excluded as a predictor (Figure 3b). 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 (Figure 3a,c); this appears solely as an effect of depth because when considering only hydrographic variables the area is deemed unsuitable with high certainty (Figure 3b,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

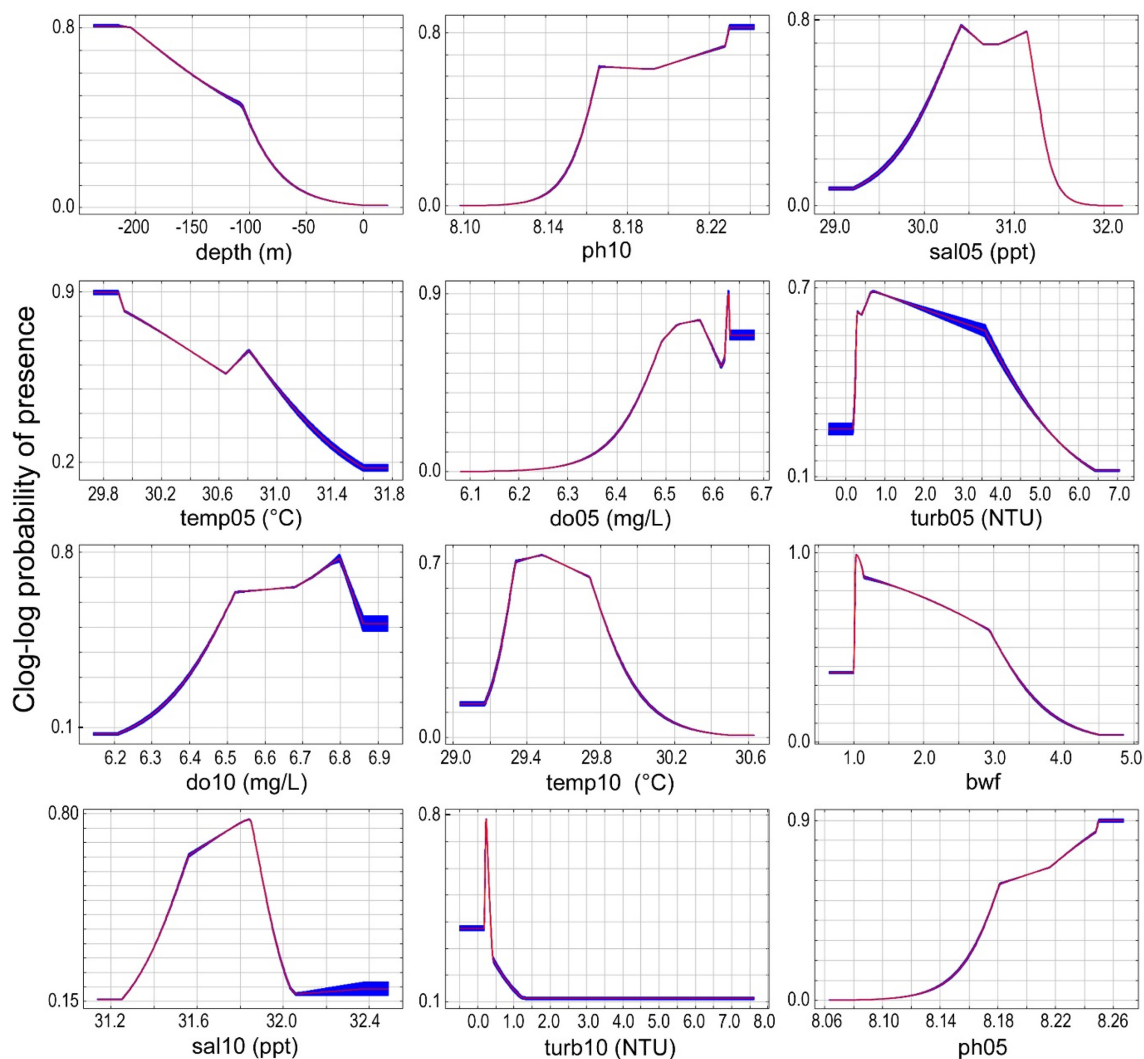


FIGURE 2 Response curves in order of permutation importance showing probability of presence for *Hydrophis platurus xanthos* in Golfo Dulce (Costa Rica) across values of 12 environmental variables: Depth, Beaufort wind force (bwf; 1–5 scale), and temperature, salinity, dissolved oxygen, turbidity, and 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) \pm one standard deviation (blue)

recorded sea snakes in the most southerly sector of the inner basin where suitability is low. Near the sill area, where the slow-moving inner basin circulation transitions to the rapid three-layer current structure of the outer basin, “disorderly” surface circulation patterns occur (Svendsen et al., 2006) that may be disadvantageous for sea snakes as they could become caught in eddies or swept away. All sightings of *H. p. xanthos* (765 observations, excluding one clear vagrant) delineate a contiguous extent of occurrence (EOO = 282 km²; Figure 3a) 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 *H. p. 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 1), readings at 88 sea snake 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 1), but records from 709 sea snake sightings in the same zone averaged 2.87, indicating a preference for rougher conditions within its territory.

4 | DISCUSSION

Our results identified environmental conditions suitable for *H. p. xanthos*, and we also delineated its extent of

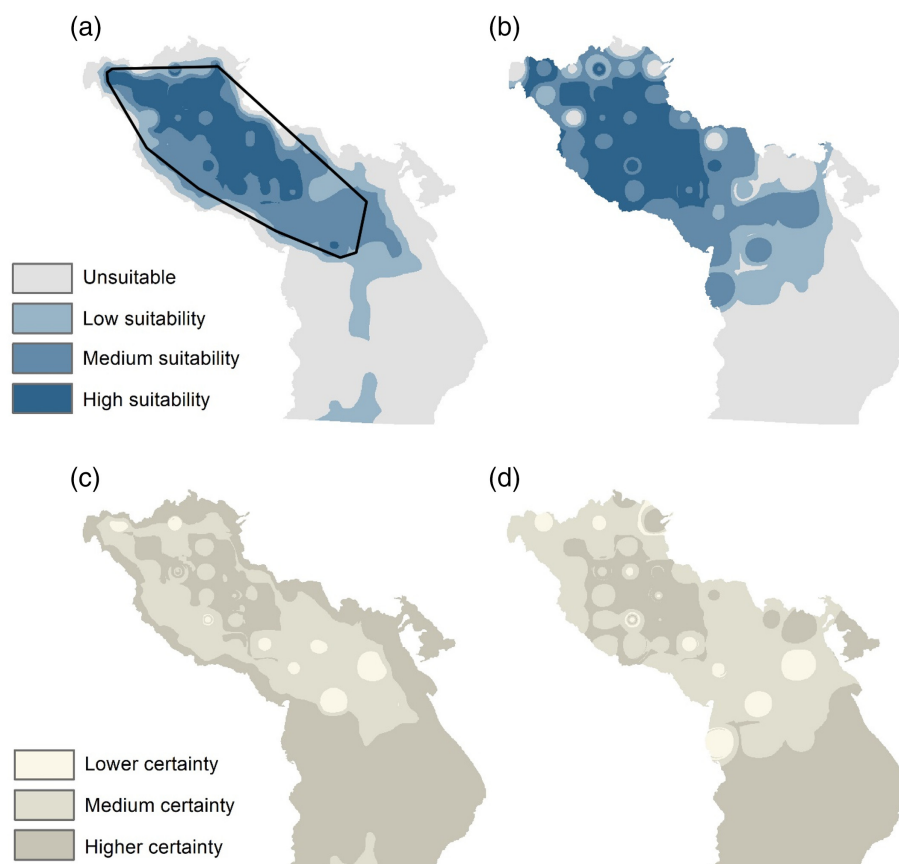


FIGURE 3 Habitat suitability maps (blue; A–B) with associated model uncertainty (tan; C–D) for *Hydrophis platurus xanthos* in Golfo Dulce, Costa Rica, based on Maxent cloglog thresholds of minimal training presence (mtp) and maximum probability (maxP) from 100 replicates; (a) mean suitability from 100 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); extent of occurrence (EOO) outlined in black; (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)

occurrence (EOO = 282 km²) and area of occupancy (AOO = 260 km²), which can be used in assessing risk of extinction. Suitable conditions were based on depth, along with 11 other hydrographic variables, among which salinity, pH, dissolved oxygen, temperature, and turbidity showed importance. Our analyses provided quantitative evidence to confirm the influence of depth on the distribution of *H. p. xanthos*, as has been found for several sea snake species (Udyawer et al., 2020). Depth alone, however, does not explain sea snake presence and even excluding this variable suitability was still limited to the Upper Gulf. We therefore expect the deepest waters of that zone to provide the most beneficial conditions for the snakes' physiological needs. Importantly, residing in deep water does not necessarily mean the snakes dive deeply (average max dive depth for pelagic sea snakes is

15 m, per Rubinoff et al., 1986). Our study suggests only that conditions between 0 and 10 m depth over areas of >100 m are more suitable for survival and presence of prey. *H. p. xanthos* opportunistically feed on larval–juvenile marine fish that gather near them at the surface; although, unlike pelagic sea snakes, they do not utilize drift lines for feeding (Bessesen, 2012; Lillywhite et al., 2015). The golden trevally, *Gnathanodon speciosus*, is the fish most sighted near *H. p. xanthos*, observed year-round, and confirmed as prey (pers. obs.); a member of the Carangidae family, it is known to inhabit deep lagoons, swimming closely around larger animals (Froese & Pauly, 2022).

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 *H. p. xanthos* was 30.5–31.25 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 and 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 *H. p. xanthos* has physiologically adapted to low-saline conditions, which presumably require less salt excretion and 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 *H. p. xanthos*. Infrequently, all-yellow individuals have been found in the broader Pacific Ocean (Kropach, 1971; 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 *H. p. 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), and *H. p. 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 CO₂ 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 *H. p. 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-Alpizar & 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 *H. p. xanthos* in the water column. Dissolved oxygen levels are declining in seas worldwide, and fauna that utilize both shallow and deep strata, like *H. p. xanthos*, may suffer habitat compression (Global Ocean Oxygen Network, 2018). Furthermore, unless these serpents have adapted to endure or exploit oxygen-deficient water conditions in some special way, when levels are reduced, cutaneous respiration could 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, 2014; Udyawer et al., 2016). Sea snakes are sensitive to thermal shifts (Heatwole et al., 2012) and water temperature can define their range (Hecht et al., 1974; Lillywhite et al., 2018). Matching the biseasonal data of Rincón-Alejos & Ballester-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 *H. p. 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 SST readings at nearly a hundred sea snake sightings in the Upper Gulf to average a full degree lower than SST readings at waypoints in that zone, suggesting *H. p. xanthos* spends more time on the surface when the upmost ocean layer is cooler than average. High temperature has been proposed as a driver of the endemic's all-yellow coloring (Solórzano 2011), and a nocturnal feeding cycle may also be related to thermal pressure and/or could help protect pale skin and eyes from solar sensitivity (Bessesen & González-Suárez, 2022). We found cooler and more stable thermal conditions below the surface, where the snakes spend most of their daytime hours. 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 & Ballester-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), *H. p. 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 *H. p. 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 (Rincón-Alejos & Ballester-Sakson, 2015). While pelagic sea snakes favor calmer, clearer waters (Kropach, 1973; Brischoux & Lillywhite, 2011), *H. p. 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 *H. p. 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 *H. p. 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, especially currents, but also tides, wind, and weather, and hydrographic conditions at greater depths likely affect *H. p. xanthos* both directly and indirectly and could also influence habitat suitability. 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 *H. p. 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., 2011a, 2011b; 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 stenotopic 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, *H. p. 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.

AUTHOR CONTRIBUTIONS

BLB conceived and designed the study, collected the data, undertook most of the analyses, including inverse 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.

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CONFLICT OF INTEREST

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

DATA AVAILABILITY STATEMENT

The datasets generated during this study are available on reasonable request from the corresponding author.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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