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Geospatial and Behavioral Observations of a Unique Xanthic Colony of Pelagic Sea Snakes, *Pelamis platurus*, Residing in Golfo Dulce, Costa Rica

Golfo Dulce is a curved tropical fiord positioned between 8.3666°N and 8.7500°N on the South Pacific coastline of Costa Rica. The embayment is approximately 50 km in length and 10–15 km wide, supplied with fresh water from four main rivers (Svendsen et al. 2006). The inner basin in the upper region of the inlet, north from 8.5000°N, is of tectonic origin and periodically anoxic (Hebbeln and Cortés 2001). Bathymetric studies show the waters there reach 215 m in depth and are protected by an effective 60 m sill and a submerged valley, ≤ 80 m deep, which extends southward to the mouth of the Gulf. This topography prevents free exchange between the deeper waters of the inner basin and adjacent coastal water masses (Svendsen et al. 2006).

The venomous pelagic sea snake, *Pelamis platurus* (Elapidae: Hydrophiinae), is the most widely distributed snake in the world. This monotypic genus (Pickwell and Culotta 1980) has been reported along the Pacific shores of Latin America since the early 1500s (Taylor 1953) and is the only sea snake on the west coast of Costa Rica (Solórzano 2004). Generally reliant on ocean currents for long distance movement, pelagic sea snakes are often associated with drift lines, and groups of a few to several thousand may aggregate in narrow bands of smooth water on the ocean surface, possibly for the purpose of passive transportation, feeding, and/or reproduction (Kropach 1971a; 1975). However, despite being a true pelagic species that ranges far out to sea, *P. platurus* is most commonly found 1–20 km off shore (Savage 2002). It opportunistically feeds on a wide array of small and young fish species at the water surface (Hecht et al. 1974) and can thrive in lower saline conditions (Dunson 1971).

Pelamis platurus displays diverse color variations (Kropach 1971b). In the Eastern Pacific, the majority of Yellow-bellied Seasnakes are tricolored with black dorsal coloring and brownish ventral coloring separated by yellow lateral stripes. The second most common are bicolored snakes, black and yellow with no brown (Bolaños et at. 1974; Tu 1976). Both variations display black spots or bands on the flat paddle-shaped tail. Such coloration is suggested to be aposematic (Kropach 1975); indeed, predation on *P. platurus* appears practically nonexistent (Rubinoff and Kropach 1970), and the species rarely dives due to disturbances at or above the surface (Dunson and Ehlert 1971; Tu 1976), suggesting there is limited, if any, predation pressure from that direction (Kropach 1975). Unicolor snakes have been considered very rare, merely noted in the Western Hemisphere (Leenders 2001; Mattison 2007; Solórzano 2004; 2011). Smith's (1926) seven color forms did not include an all-yellow variety and Kropach offered the first definitive description (Pickwell and Culotta 1980) after seeing individuals of the variety in both Golfo Dulce and the Gulf of Panama. During a 1970 expedition, Kropach (1971b; 1975) observed 278 *P. platurus* inside Golfo Dulce. Nine of the specimens, about 3%, were of the all-yellow variety. In 1973, Bolaños et al. (1974) captured 102 specimens of *P. platurus* in five localities along the northern Pacific coastline of Costa Rica, including one snake that was "yellow with a few black dorsal dots." Tu (1976) later reported collecting 3077 pelagic sea snakes on the Pacific Coast of Costa Rica. Of that sample, four specimens, approximately 0.1%, were all-yellow. Tu (pers. comm.) confirmed he did not find any of his snakes in or near Golfo Dulce. Those findings show that all-yellow individuals along coastal Costa Rica are not limited to the waters of Golfo Dulce and may naturally represent a small percentage of the population-at-large.

During previous work on the Osa Peninsula (Bessesen and Saborío-R. 2009), local residents described to me a population of all-yellow specimens of *P. platurus* living in Golfo Dulce. Based on that information, a marine sighting survey was designed to collect baseline distribution data for the yellow sea snakes during the dry season of 2010. These findings, which suggest a separate and behaviorally distinct xanthic (defined here as all-yellow or primarily yellow) colony, are reported here.

METHODS

With the aid of a Costa Rican research assistant/boat captain, 82 preliminary interviews were conducted with local fishermen and tour boat guides. Interviewees were asked to estimate the frequency with which they saw pelagic sea snakes inside Golfo Dulce (never, rarely, occasionally, frequently or always) and the color of those snakes. Photographs were made available but all interviewees seemed familiar with the snakes.

After interviews, 30 daily on-water surveys were undertaken, systematically investigating surface waters around the entire Gulf to document first-hand sightings of *P. platurus*. January–February study dates were selected in part because local sources reported pelagic sea snakes as being seen more frequently at the surface during the dry season, an observation also noted by researchers in other areas of Costa Rica (Bolaños et al. 1974).

The embayment was divided into four geographical areas, labeled GA1–4. GA1 and GA4 were designed smaller to account for distance from the operations base of Puerto Jiménez and additional time spent in GA2 and GA3 as corridors. The boat captain selected delineating landmarks he found clear and familiar, resulting in GA3 being slightly larger than intended. Each day we concentrated on a single area, traversing its full breadth in a large loose pattern, e.g., perimeter, figure-eight, zigzag, to ensure time near each coast and in the midwaters. A rotation of GA1, GA3, GA2, GA4 was generally employed. Waters outside the embayment, designated as GA5 (Fig. 1), were not actively surveyed; however, some sea snake sightings occurred in that area after inadvertently crossing the boundary of GA4. Typically we departed Puerto Jiménez just after sunrise and traveled 65–80 km per day, with daily observation periods lasting an average of 7 h and 46 min. We carried out three night surveys in GA1 and GA2 to observe yellow sea snakes in low-light conditions.

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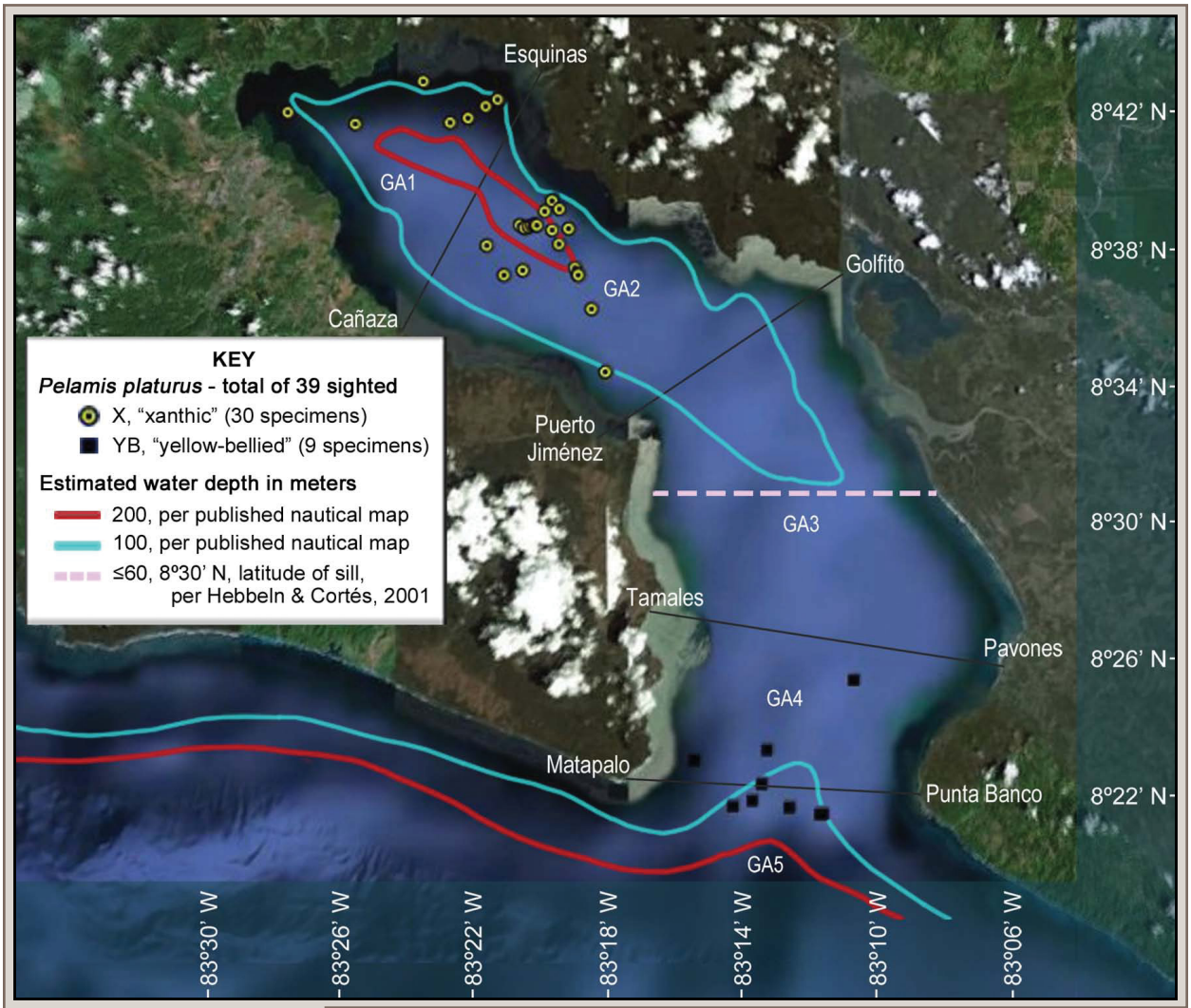

FIG. 1. GPS points for 39 first-hand sightings of *Pelamis platurus*, represented by 30 Xanthic sea snakes (yellow dots) and 9 Yellow-bellied sea snakes (black squares). Note the significant spatial gap that coincides with the graphic demarcation of the inner basin sill. Also shown, delineation of survey areas (grey lines).

GA1 = ↑ Cañaza 8.5948°N, 83.4006°W / Esquinas 8.7208°N, 83.3316°W;

GA2 = ↑ PJ 8.5425°N, 83.3038°W / Golfito 8.6217°N, 83.1821°W;

GA3 = ↑ Tamales 8.4521°N, 83.2820°W / Pavones 8.4203°N, 83.1086° W;

GA4 = ↑ Matapalo 8.3742°N, 83.2906°W / Pt Banco 8.3663°N, 83.1456°W;

GA5 = ↓ GA4 (outside gulf).

FIG. 2. Two typical Xanthic sea snakes found in upper Golfo Dulce. (A) This specimen was identified by two small black marks caudal and slightly medial to the supraocular scales (arrows). (B) Although predominantly yellow, some individuals retain larger black spots along the dorsal ridge. This sinusoidal posture was commonly seen when approaching at night. The slight halo effect was caused by the camera flash on the water.

COLOR REPRODUCTION SUPPORTED BY THE THOMAS BEAUVAIS FUND

TABLE 1. Geographical areas in Golfo Dulce with surface size, survey effort, and quantitative sighting distribution for Yellow-bellied and Xanthic specimens of *Pelamis platurus*.

Geographical areas		Survey effort		Snakes by color variation	
Location	Estimated surface size	Days of rotation	Approximate survey hours	Xanthic	Yellow-bellied
GA1, highest sector of gulf	130 km²	7.25	55.50	6	0
GA2, mid-upper gulf	192 km²	8.25	65.75	24	0
GA3, mid-lower gulf	256 km²	7.25	63.25	0	0
GA4, lowest sector of gulf	147 km²	7.25	47.50	0	4
GA5, outside gulf	—	—	01.00	0	5

Sightings were recorded using Global Positioning System (GPS; Garmin handheld GPS III) with 72% of sea snakes right next to the boat and none further than 5 m away. Typical bi- or tricolored *P. platurus* with black and yellow striae were logged as Yellow-bellied while all-yellow or primarily yellow individuals were logged as Xanthic. Two cameras, a Nikon D50 SLR digital camera and a Canon GL-1 mini DV video camera, were used to obtain photographic records. Daily solar and tidal charts were logged and time was recorded at the start and end of each observation period, along with environmental conditions, including air and sea surface temperatures, Beauford Wind Force, visibility and prevailing weather.

RESULTS

Interviews.—Of the 82 interviewees polled during this study, 72% (59) were professional fisherman (commercial and/or sport-tourist), 13% (11) worked in nonfishing tourism (boat tours/excursions), and 15% (12) of the subjects did both. The number of years experience in Golfo Dulce ranged from 1–40 with the average at 12 years. Average number of work days per week was 5. When asked how often pelagic sea snakes were seen inside Golfo Dulce, 44% reported that they were "rarely" seen, 18% answered "occasionally," 21% said "frequently," and 11% said "always." Only 6% of the interviewees had "never" seen *P. platurus* inside the Gulf.

Interviewees consistently reported that Xanthic sea snakes were found in the upper, deep water regions of Golfo Dulce, while Yellow-bellied sea snakes were down near Matapalo at the inlet's entrance, and that this was not a seasonal phenomenon. Some interviewees from the pueblo of Pavones on the southeastern shores of Golfo Dulce, who worked solely in the lower half of the Gulf, had never seen a Xanthic sea snake. The project's research assistant (Largaespada, pers. comm.) had observed Xanthic snakes in the upper Gulf for more than 35 years and never a Yellow-bellied snake in that region. Two resident biologists (Boston, pers. comm.; Bernal, pers. comm.) confirmed witnessing only Xanthic snakes around the inner basin, including possible reproductive aggregations in the month of July. Boston also reported never seeing a Xanthic sea snake in a drift line.

Field counts.—Between the dates of 13 January and 24 February 2010, a total of 233 observation hours was logged across all areas of Golfo Dulce (Table 1); most (89%) were conducted during daylight hours. In general, weather conditions presented minimal precipitation, relatively calm water and average visibility greater than 15 km. Daily temperatures, recorded near the marina of Puerto Jiménez, averaged 28.6°C for air and 30.5°C for sea surface. (The upper lethal temperature for *P. platurus* is from 33°C [Dunson and Ehlert 1971] to 36°C [Graham et al. 1971].)

A total of 39 pelagic sea snakes were documented, divided as 30 Xanthic and 9 Yellow-bellied. For the Xanthic variety, 80% (24) were seen in GA2 with the remaining 20% (6) found higher up in GA1. All Yellow-bellied snakes were seen within 7 km of the Gulf entrance, most near the border of GA4/GA5, although one individual was recorded a little further into the embayment. The distance between the southernmost Xanthic and northernmost Yellow-bellied specimens was 21.6 km. No pelagic sea snakes were found in GA3 (Table 1, Fig. 1).

Overall, sea snakes were infrequently seen; however, if one was sighted, others usually were seen, sometimes several in a short stretch of time, suggesting certain days and/or conditions were more conducive for surfacing. One example occurred under a full moon on 30 January, when 8 Xanthic snakes were sighted within an hour (2017–2110 h), no more than 300 m apart. In another instance, 5 Xanthic specimens were sighted over a span of about 4 km in only 23 min (1618–1641 h; 20 February). Although snakes were sometimes seen swimming across the water, most were found simply floating at the surface.

We were able to collect photographs and/or video footage in 77% of our total sea snake sightings, allowing for identification of individuals. Individual Yellow-bellied snakes were easy to recognize by the unique configuration of their markings and it was confirmed that nine different Yellow-bellied snakes were encountered. Although Xanthic specimens appeared unicolored and were consistently yellow with neither lateral demarcations nor prominent tail patterns, photos revealed that most had at least one black speck on the head or body. A few individuals (1–2% of the total Xanthic sampling) had one or more larger black spots (estimated <5 mm in diameter) along the dorsal ridge. One specimen had decidedly heavier dorsal markings, yet none of its spots were estimated at >20 mm. Using markings, it was determined that every Xanthic snake photographed during the investigation was also a distinct individual (Fig. 2A, B).

Behavioral observations.—Photographs were taken for 100% of the nine Yellow-bellied sightings, all of which took place during daylight hours. All of the Yellow-bellied snakes reliably remained on the surface while approached for documentation; two surfaced next to the boat when the motor was off; and 6 snakes were still on the surface after departure. On the two separate occasions that we touched the tails of Yellow-bellied snakes facing away from us, they both turned back and struck at the boat hull. Neither dove. All Yellow-bellied sea snakes were seen in relatively still water or smooth rolling waves and two snakes (22%), were floating in or near a defined drift line.

Photographing Xanthic snakes proved a greater challenge. They never surfaced near the boat and, in daylight conditions,

tended to dive if we slowed down anywhere near them. Despite clear views at every sighting, photographs of Xanthic snakes were captured only 50% of the time (5 of 10) in full daylight. Low-light conditions increased the success rate. For evening sightings from 1400–1600 h, photos were collected for 71% (5 of 7) of Xanthic sightings. During night surveys conducted after 1800 h, 85% (11 of 13) were photographed. Because the Xanthic snakes did not dive as readily at night, it was possible to directly approach and obtain close-range photographs and videotape using flashlights. However, the snakes often assumed a tight sinusoidal shape (Fig 4B; this posture was not observed in Yellow-bellied snakes). On the one occasion we touched a Xanthic snake, it did not respond by striking but immediately dove. Most Xanthic snakes were recorded in choppy water; a few were seen in slightly calmer morning and evening waters; none was found in smooth water. We occasionally saw drift lines in the upper half of the embayment; however, only one Xanthic snake was observed several feet outside a slick of floating scum and debris. The occurrence rate of drift lines in the upper and lower regions of the Gulf is unknown. One Xanthic snake was also videotaped while shedding its skin, using the knotting behavior described by Pickwell (1971, 1972).

DISCUSSION

After many interviews with local biologists, fishermen, and tour boat guides, and an expansive on-water survey of Golfo Dulce during the dry season, we have determined that all the sea snakes above about mid-Gulf appear bright canary yellow. The consistently yellow skin coloring of sea snakes found in the northern region of the Gulf and absence of yellow snakes below the sill suggest this population may be genetically disjunct from those in the Pacific. The data show clear geospatial, morphological, and behavioral distinctions between the Xanthic and Yellow-bellied populations, and phylogenetic studies would be of significant interest to determine if morphology has given rise to a distinct form of *Pelamis platurus* in Golfo Dulce.

Golfo Dulce's topography may help explain the almost 22 km gap between the Xanthic and Yellow-bellied populations and complete lack of sea snake sightings in GA3. Although the Xanthic colony appears to reside high up in the inner basin and no sea snakes were sighted near the sill, shallower waters south of the sill may play a role in habitat boundaries.

Hecht et al. (1974) listed several limiting factors for the establishment of resident populations of pelagic sea snakes, including annual range of surface temperatures, depth of water, prevailing currents, and storm pathways. They suggested that, demarcated by the 26°C isotherm correlated with the 100 m isobath, permanent breeding colonies should occur in many areas worldwide, including the western coast of Central America. Given the favorable yet insulated bathymetrics of Golfo Dulce, the idea of one such breeding population becoming sequestered, possibly by shifts in currents, is conceivable. Furthermore, the pelagic sea snake's nonspecialized food habits and ability to thrive in lower saline conditions would have allowed the original colonizing snakes to inhabit the fiord-like waters. Because *Pelamis platurus* spends about 87% of its time submerged (Rubinoff et al. 1986), and respires partially through its skin, meeting 12–33% of its oxygen requirements and excreting carbon dioxide by that mechanism (Graham 1974b), it would be interesting to investigate whether and/or how the Gulf's periodic anoxia affects the resident snakes.

Kropach (1971a, b) first reported the all-yellow variety of pelagic sea snake after conducting a one-year study of *P. platurus* in the Gulf of Panama, where "regular trips were made in the northern part of the [gulf]." Although the yellow variety was seen during that study, Kropach made no indication that the number of yellow specimens made up a greater concentration than the 3% he reported in Golfo Dulce. This decreases the likelihood that yellow snakes are predominant in the Gulf of Panama or are in any way isolated from the prevailing color varieties in that embayment, and suggests the Golfo Dulce population may be unique.

What are the adaptive advantages of xanthic coloring in Golfo Dulce when that variety exists in only a small percentage of the general population? Solorzano (2011) suggests temperature might play a role. Because *P. platurus* naturally collects solar energy while basking (Graham et al. 1971; Graham 1974a) and sea surface temperatures in Golfo Dulce are higher than other areas within the species' range (Hecht et al. 1974), perhaps lighter dorsal coloring reduces chances of overheating at the surface where it feeds.

Xanthic sea snakes were commonly found in rougher water than expected for *P. platurus*. Such conditions might play a role in surfacing and/or detectability. Xanthic snakes were also more likely to dive when approached, especially during daylight hours, and often took a seemingly defensive sinusoidal posture. Boat traffic and other human activity may influence sea snake behavior within the embayment and/or all-yellow coloring may not be entirely aposematic in Golfo Dulce. It also appears that Xanthic snakes make limited, if any, use of drift lines.

The findings of this study raise several interesting questions about the Xanthic sea snakes residing in Golfo Dulce and there remains much to learn about this unique colony.

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