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Amphibian & Reptile Conservation
19(1): 1–10 (e338).

Coloration and Crypsis in a Pelagic Sea Snake

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***Abstract.*—The Yellow-bellied Sea Snake ranges across the tropical Indo-Pacific and is the most widely distributed squamate reptile. The bicolored form, *Hydrophis platurus platurus*, has a black dorsum and is cryptic while floating among wavelets that produce dark streaks resembling the snake. When flotsam is present on slicks that are its favored foraging sites, the snakes also resemble sticks or debris, while the mottled coloration of the tail resembles the froth that is a common component of flotsam. A second color morph is the all-yellow xanthic subspecies, *H. p. xanthos*, which has a discrete population restricted to an inner basin of Golfo Dulce. These yellow snakes are conspicuous, and floating specimens are highly visible. Predation pressures from birds, fishes, and marine mammals are potentially great on this species. Whereas the bicolored snakes are diurnal, the highly conspicuous xanthic snakes tend to be nocturnal. In both forms, brilliant yellow coloration is a presumptive aposematic signal that is reinforced by chemical detection of noxious skin. Scarring of snakes is indicative of predatory strikes, but overall predation appears to be less than expected and conceivably mitigated by crypsis and aposematic signals. Understanding features of coloration is important to the conservation of this species, which may serve as an important bioindicator of changes in climate and habitat.**

Keywords. Aposematism, bioindicator, camouflage, climate change, diurnal, *Hydrophis platurus*, Indo-Pacific, marine, nocturnal, predation

Citation: Lillywhite HB. 2025. Coloration and Crypsis in a Pelagic Sea Snake. *Amphibian & Reptile Conservation* 19(1): 1–10 (e338).

Accepted: 26 January 2025; **Published:** 09 March 2025

Introduction

The antipredator, protective, and adaptive values of background color matching (camouflage, crypsis, or "substrate mimicry") have been convincingly demonstrated and are of widespread occurrence (e.g., Sumner 1935; Dice 1947; Kettlewell 1961; Endler 1978; Gibbons and Lillywhite 1981; Rosenblum 2006; Marshall et al. 2016; Micheletti et al. 2016; Ruxton et al. 2018; Stevens and Merilaita 2011). Most studies of cryptic coloration have involved the distributional patterns or survival rates of different color morphs within a species, most often in terrestrial environments. Although crypsis is important for species in aquatic environments, there are no well-studied examples of marine organisms in pelagic environments.

Here I discuss coloration and crypsis in the sea snake *Hydrophis platurus* (Elapidae: Hydrophiini), the only pelagic and surface-feeding marine snake species (Heatwole 1999). This snake has the widest distribution of any squamate reptile and occurs across the entire tropical Indo-Pacific (Dunson and Ehlert 1971; Hecht et al. 1974; Heatwole 1999; Sheehy et al. 2012; Brischoux et al. 2016). Much of its time is spent floating in the water column at depths of 20 to 50 m or floating on slicks where it forages for small pelagic fishes (Kropach 1971a; Rubinoff et al. 1986; Brischoux and Lillywhite 2011; Cook and Brischoux 2014). Bouts of diving are interrupted by surfacing to breathe in air or to ambush small fishes that are concentrated beneath debris while 'float-and-wait' foraging at the ocean's surface (Dunson and Ehlert 1971; Rubinoff et al. 1986; Brischoux and Lillywhite 2011; Cook and Brischoux 2014). The Yellow-bellied Sea Snake is considered to be the only marine air-breathing predator that forages specifically at the oceanic surface on labile features such as slicks or drift lines. Cryptic coloration has not previously been demonstrated or discussed for this species.

Colors of *Hydrophis platurus*

There are two principal color morphs of *Hydrophis*

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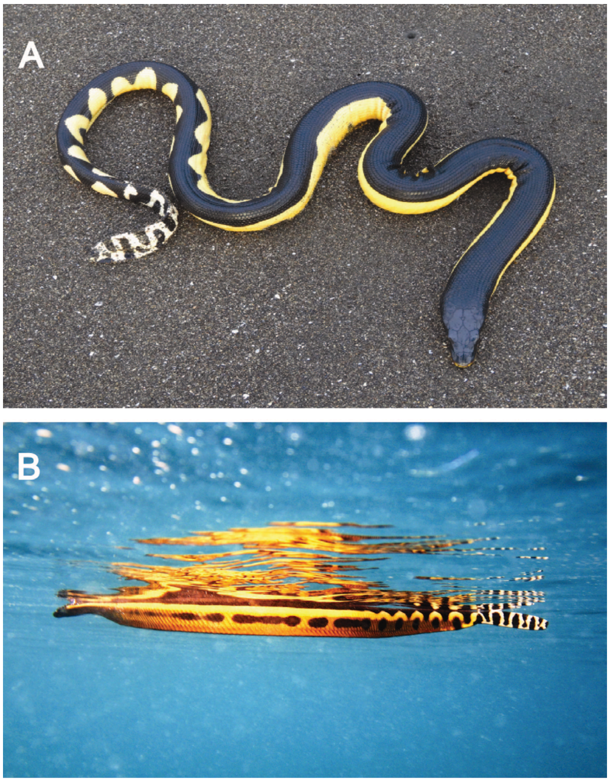

Fig. 1. Views of the bicolored *Hydrophis platurus platurus* featuring the black dorsum of a beached specimen **(A)** and the yellow underside with posterior mottling as seen from underwater **(B)**. *Photos by the author* **(A)** *and Joe Pfaller* **(B)**.

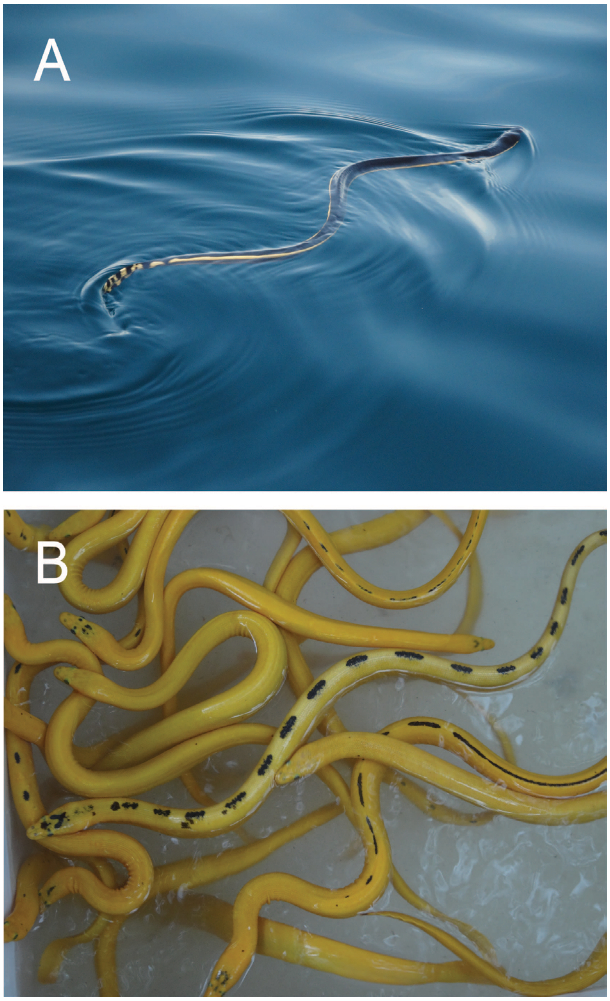

Fig. 2. Dorsal view of *H. p. platurus* swimming in coastal water offshore of northwestern Costa Rica **(A)** and a group of xanthic *H. p. xanthos* from Golfo Dulce being held temporarily for research purposes **(B)**. Most specimens of the latter subspecies are all-yellow, but some individuals are marked with small spots or stripes of black pigment. *Photos by Shauna Lillywhite* **(A)** *and the author* **(B)**.

platurus, each representing a distinct subspecies. The more common is the well-known bicolored black and yellow subspecies making up the larger number of snakes that range across the Indo-Pacific oceans (*H. p. platurus*). These snakes have a black dorsum, including the head, with yellow to orange-yellow coloration on the ventral and lateral aspects of the body (Fig. 1). The lateral yellow coloration can be variably interrupted with streaks or spots of black, but the ventral body is typically completely yellow. Beginning at or near the tail, or in many cases somewhere about two-thirds or three-fourths of the distance from the head, the black color is interrupted with yellow or white blotches, which almost always represent a mottling of the two colors on the full height of the tail (Fig. 1). In various views, this bicolored subspecies appears largely black when seen from above (Fig. 2A), and variably yellow when viewed from below (Fig. 1B).

The second color morph is a xanthic subspecies that is restricted to the inner basin of Golfo Dulce, southwestern Costa Rica (*H. p. xanthos*; Bessesen and Galbreath 2017; Solórzano and Sasa 2024). These snakes are entirely yellow, but many individuals have various amounts of black skin limited to diffuse narrow blotches or a mid-dorsal stripe (Fig. 2B). Compared with *H. p. platurus*, specimens of *H. p. xanthos* are notably smaller and generally exhibit a uniformly yellow color (Fig. 2B). The xanthic subspecies is significantly isolated from the broader-ranging bicolored subspecies due to the nature of the currents and bathymetry of its habitat (Bessesen and Galbreath 2017; Bessesen et al. 2023). The xanthic snakes appear allopatric (Sheehy et al. 2012) and likely seldom interbreed with the bicolored conspecifics, even though there is occasional exchange between Golfo Dulce and the western Pacific (see also Solórzano and Sasa 2024).

The bright yellow of the xanthic subspecies is obviously not cryptic when these snakes are at the ocean's surface. Therefore, the discussion that follows focuses on the bicolored subspecies, while the xanthic snakes are considered only in contexts where it is appropriate.

Behavior of *Hydrophis platurus* at oceanic slicks

Yellow-bellied sea snakes spend most of their routine time (up to 99%) floating in the water column at depths of 20–50 m (Rubinoff et al. 1986). Bouts of diving

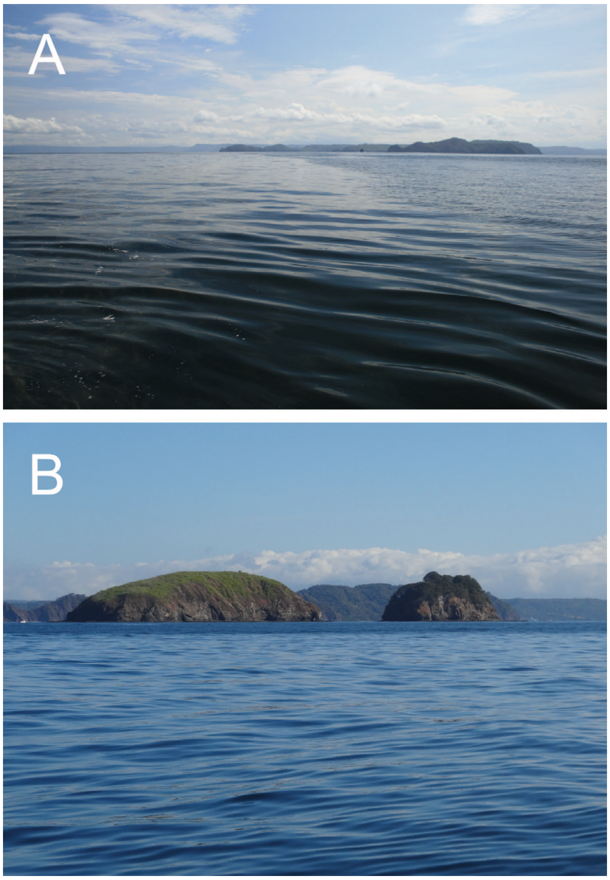

Fig. 3. Scenes of ocean water in Golfo Papagayo, northwestern Costa Rica, featuring contrast between calm surface water of a slick and rougher water adjacent to the slick. The slick shown in **(A)** (left half of photo) shows the length of a broad slick extending to the horizon. The breadth of a large slick can be seen in **(B)** (much of foreground). *Photos by the author.*

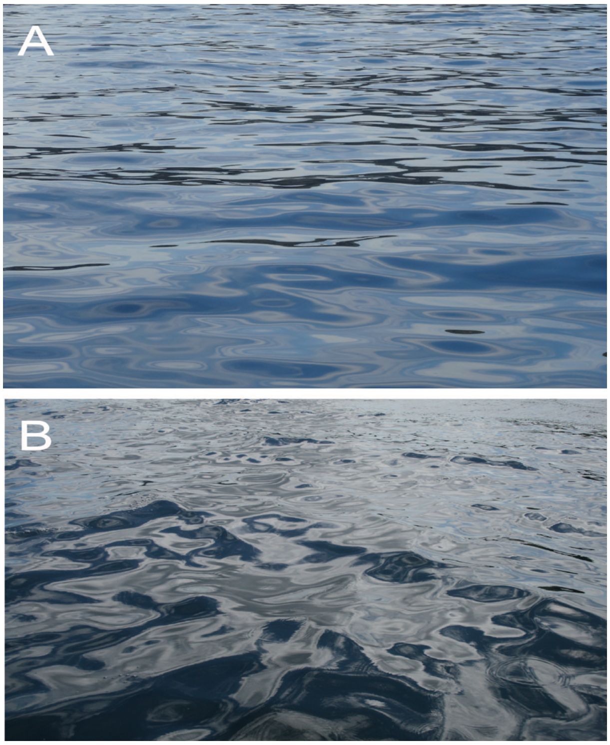

Fig. 4. Two conditions of the surface waters of a slick featuring surface patterns of wavelets in different sea and lighting conditions. Note the wavelets shown in **(A)** create dark streaks that resemble outlines of the black surfaces of sea snakes that float on the ocean surface. The water conditions shown in (B) produce variable surface features that obscure the outline of floating snakes. *Photos by the author.*

alternate with surfacing events, which are either very brief to breathe in air or longer to forage (Rubinoff et al. 1986). This species ambushes small fishes that are concentrated under debris while 'float-and-wait' foraging at the oceanic surface on slicks (Dunson and Ehlert 1971; Rubinoff et al. 1986; Brischoux and Lillywhite 2011). Evidently, the Yellow-bellied Sea Snake is the only marine air-breathing predator that forages at the oceanic surface on labile features such as slicks or drift lines.

Slicks (or drift lines) are typically short-lived, mobile oceanic structures formed as the result of Langmuir circulations or convergent currents created by a variety of physical processes involving internal waves and eddies (Ewing 1950; Barstow 1983). Slicks can be variable in width, relatively small, and short-lived, or they can form drift lines that extend for hundreds of meters or kilometers (Fig. 3). They typically form stretches of calm glassy water surrounded by rougher areas (Figs. 3 and 4), and they frequently have high quantities of positively buoyant flotsam containing both seaborne and terrigenous items (Figs. 5 and 6). Due to their dynamic features, planktonic organisms including larval and juvenile fish concentrate on the slicks (Barstow 1983; Dempster and Kingsford 2004; Kingsford and Choat 1986; Pineda 1994; Shanks 1995). How sea snakes aggregate on slicks is not clear, but they could arrive at slicks by passive drift on currents, similar to the inert flotsam (Dunson and Ehlert 1971; Hecht et al. 1974), or they might actively seek out slicks possibly using currents, vision, or vomerolfaction underwater (Rubinoff et al. 1988). Indeed, Yellow-bellied Sea Snakes might visually detect flotsam or the refractive properties of glassy water, or even fish, from an underwater viewpoint, as has been shown for the detection of potential prey by 'float-and-wait' foraging fish (Cronin 2005). The presence of flotsam appears to be important in attracting snakes to slicks, whether actively or passively, and conceivably enhances their visual detection of such structures from beneath the water (Brischoux and Lillywhite 2011). Hence, a reasonable hypothesis is that the presence of calm, glassy water and the presence of flotsam might influence a snake's 'decision' to surface at a slick (Brischoux and Lillywhite 2011) (Figs. 3, 5, and 6). Floating snakes are generally more abundant on slicks when atmospheric conditions include clear sky and bright light (Brischoux and Lillywhite 2011).

Slicks with any amount of flotsam attract smaller pelagic species of fishes which habitually hide beneath floating objects, including the snakes themselves (Hunter and Mitchell 1967). Floating snakes characteristically

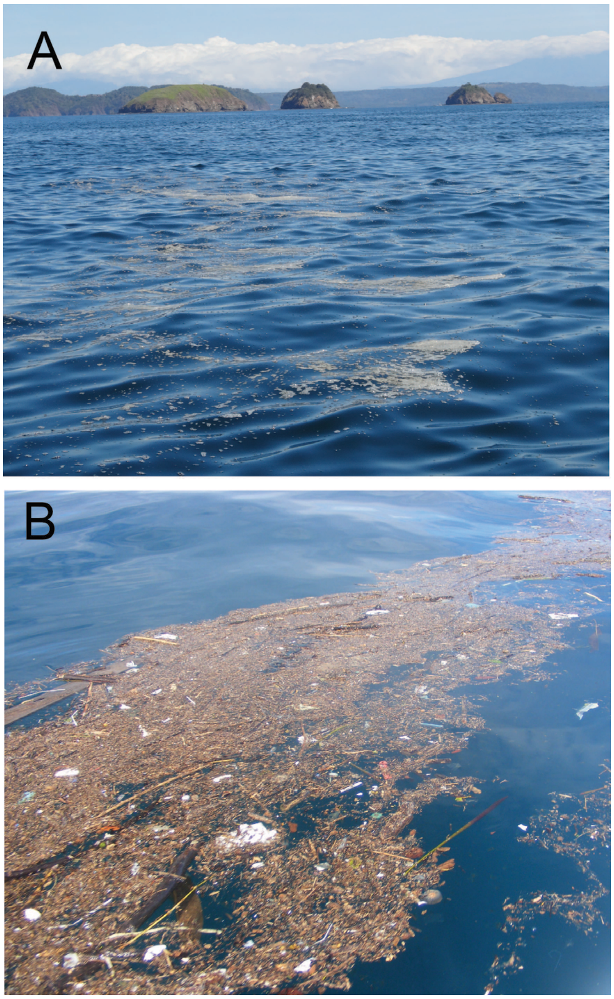

Fig. 5. Views of flotsam on a slick. **(A)** Froth extends toward the horizon on a small slick in Golfo Papagayo, Costa Rica. **(B)** Debris that accumulates on slicks as result of washout from coastal river mouths during the wet season. As a result there are numerous sticks and other objects of variable colors that resemble floating snakes, although there is no snake in this scene. *Photos by the author*.

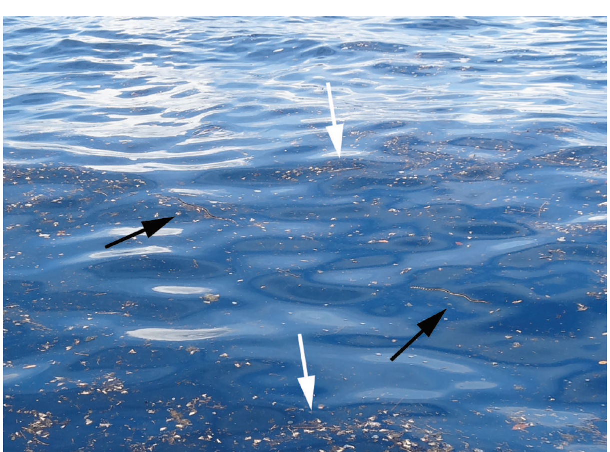

Fig. 6. Crypsis in snakes floating on a slick with small amounts of flotsam. The black arrows point to two snakes, and the white arrows point to floating sticks that resemble the yellow edge of a snake's outline. The posterior mottling on the snake at the left is shown to resemble a small patchwork of leaves that are part of the flotsam. *Photo by the author*.

adopt a floating posture with the dorsal surfaces variably exposed to air and the head angled downward beneath the water's surface (Figs. 1B and 6). Such 'float-and-wait' behavior employed by floating aggregations of *H. platurus* on slicks enhances the foraging success of this species (Dunson and Ehlert 1971; Kropach 1971a; Brischoux and Lillywhite 2011).

Are the black and yellow sea snakes cryptic at the ocean's surface?

Animals that are effectively camouflaged exhibit colors, patterns, and movements that render them indistinguishable from their background or as irrelevant objects in it. Two related but distinct aspects of camouflage are matching the background pattern (crypsis; Endler 1978, 1984) and disruptive coloration (Cott 1940; Cuthill et al. 2005; Merilaita and Lind 2005). Crypsis embodies all traits that reduce an animal's risk of being detected when it is potentially perceivable to an observer (Stevens and Merilaita 2009). Typically, the term crypsis includes features of physical appearance such as coloration and behavioral traits that prevent detection.

With respect to the latter, the time spent by sea snakes floating on slicks involves little swimming or movement. The swimming that I have observed involved snakes that were disturbed by humans during attempts to capture them. In the absence of provocation, the snakes floated motionless at the surface of calm waters that were part of a slick. In other situations when snakes were surfacing for short periods to breathe air, swimming entailed vertical movement up or down in the water column, and their time at the surface was brief. These statements are based on observations of two to four persons during 14 trips to Costa Rica, when boat time on slicks was additive for several hours per day over the course of about seven days per trip. The total observation time was conservatively about 900 person-hours. Dismissing active movements by floating snakes, I will now consider aspects of crypsis related to background color and pattern-matching.

Black dorsal coloration

In most circumstances, floating *H. platurus* appear dark when viewed from a distance, and especially from overhead (Figs. 2A, 6, and 7). The surface of the ocean also appears dark, with some variation depending on the lighting of the sky and roughness of the sea (Figs. 3 and 5). Regardless of atmospheric conditions, ripples or wavelets characteristically appear dark, and moving ridges often resemble the length and outline of a sea snake (Fig. 4). Figures 7 and 8 illustrate the cryptic nature of *H. platurus* floating on a slick, with an appearance resembling the dark outlines of various riffles present in the surrounding water.

When snakes are floating on slicks with flotsam, including sticks and plant debris that are washed out

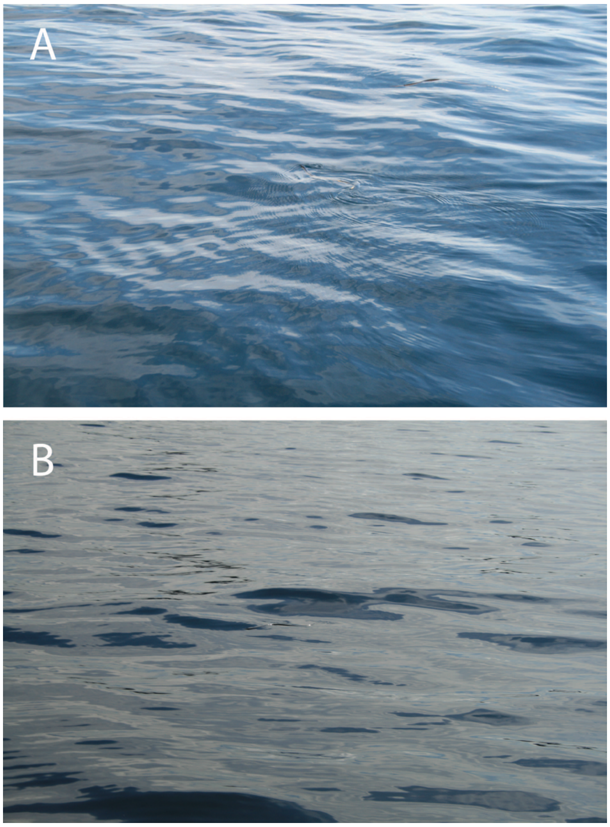

Fig. 7. Views of snakes that appear cryptic while upon surface waters of a slick in Golfo Papagayo, Costa Rica. **(A)** A swimming snake, barely visible in the center of the photo, produces wakes that blend well with wavelets in the surrounding water. **(B)** A snake is floating near the center of the photo and resembles the many dark streaks from wavelets in the surrounding water. *Photos by the author.*

to sea from mainland streams and rivers during the wet season, the yellow edges on the lateral aspects of a snake's body can resemble floating sticks (Figs. 5 and 6). The white and black mottling of the tail also takes on the appearance of froth that is formed as part of the flotsam in various circumstances (Figs. 5 and 6).

The black dorsal coloration of *H. platurus* has been suggested to function as countershading which disrupts the silhouette in a gradient of downstreaming light and obscures the appearance of the body, rendering it less distinguishable from the background (Graham et al. 1971). This aspect of coloration adds to the camouflage function of the black pigments but also involves the yellow pigments. With respect to other possible functions, the dorsally dark coloration might provide some filtering of ultraviolet light that can be damaging to internal organs (Porter and Norris 1969; Graham et al. 1971). Some authors have suggested that the black coloration being exposed at the water-air interface might function in thermoregulation, involving alternate basking and diving (Brattstrom 1965; Dunson and Ehlert 1971; Graham et al. 1971; Graham 1974). For example, Graham et al. (1971) found that snakes exposed to sunlight in still water over a range of normal water temperatures from 20 to 30 °C maintained a body temperature "slightly warmer than ambient,' whereas the snakes were not warmer at

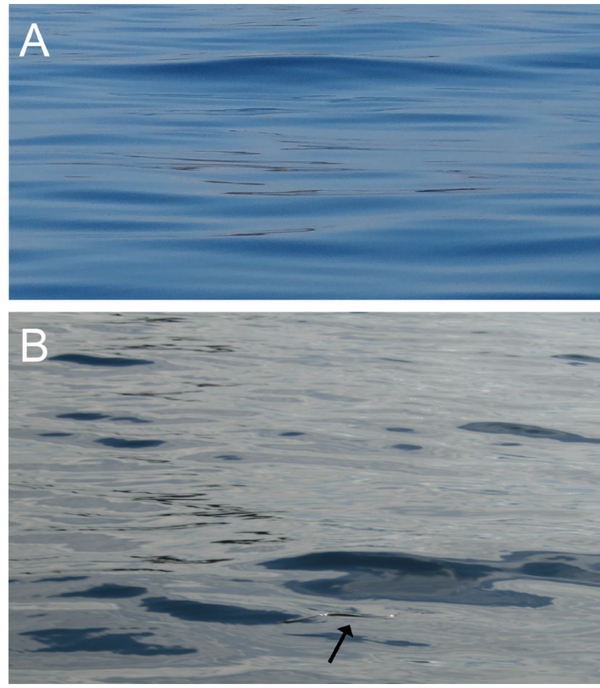

Fig. 8. **(A)** Dark streaks are shown in the water of a slick and are easily confused with the dark outline of floating snakes seen in the other figures. **(B)** Close-up view of a floating snake (arrow) resembling dark streaks in surrounding water. Compare also with the streaks seen in **(A)**. *Photos at a slick in Golfo Dulce, Costa Rica, by the author.*

night. In the field, Dunson and Ehlert (1971) found that *H. platurus* had body temperatures ranging from 2.48 °C above to 1.98 °C below that of the surrounding seawater. The case for the role of black integument in the thermoregulation of *H. platurus* is controversial and not well-established (Graham 1974; Heatwole 1981; Shine et al. 2003). Although black coloration can enhance rates of heating in snakes exposed to sunlight, even shallow water was shown to completely remove this effect (Shine et al. 2003). When *H. platurus* are maintained artificially in water that is cooler than 22 °C, the snakes tend to float at the surface continuously, which in nature would expose them to the warmest conditions available (Heatwole et al. 2012). Clearly, multiple functions are conceivably associated with the color pattern of *H. platurus,* as well as multiple selection forces that might interact in complex ways and on variable time scales.

Yellow coloration

The brilliant yellow colors of *H. p. platurus* may contribute to countershading and disruptive coloration (especially near the tail), as well as reverse countershading. The yellow color imparts countershading when snakes are viewed from above (e.g., aerial predators), but this color is a strong visual signal that could also be aposematic with respect to potential predators viewing the snake from below (e.g., various fishes).

Predation pressures in the tropical Pacific are markedly intense (Vermeij 1978), and sea snakes are potentially impacted both by aerial and marine predatory birds,

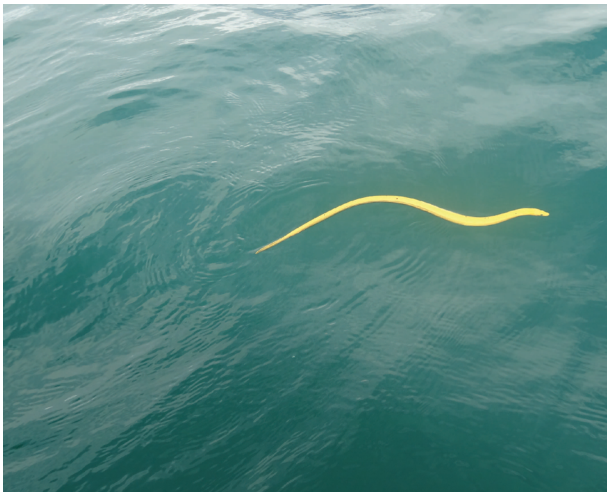

Fig. 9. A xanthic snake, *Hydrophis p. xanthos*, floating on ocean water in Golfo Dulce. Note how conspicuous is this snake in comparison with the black dorsum of the bicolored subspecies seen in the other figures. *Photo by the author.*

fishes, and mammals (Heatwole 1975; Masunaga et al. 2008; Sheehy et al. 2011; Ridgway et al. 2022; Solórzano and Sasa 2024). Wounds and scarring on *H. platurus* have been interpreted as indications of attempted predation (Heatwole 1975; Rubinoff and Kropach 1970; Kropach 1973; Pickwell et al. 1983; Weldon and Vallarino 1988; Sheehy et al. 2011; Solórzano and Sasa 2024), and there are reports of these snakes being attacked by birds and fish, as well as harassment by mammals (see discussion in Weldon and Vallarino 1988; Sheehy et al. 2011; Solórzano and Sasa 2024). However, observations of birds and fishes reacting to *H. platurus* suggest this snake is avoided, and predatory vertebrates have been observed to drop, spit out, or regurgitate snakes that were attacked (Weldon 1988; Sheehy et al. 2011; Escalante and Benavides 2021). Therefore, this species of sea snake appears to be unpalatable to many fishes as well as egrets and herons (Caldwell and Rubinoff 1983), and evidence suggests that chemicals in the skin of *H. platurus* are avoided and very likely noxious (Weldon 1988). Evidence suggests that the bright yellow coloration of bicolored *H. p. platurus* possibly evolved as an aposematic signal (Kropach 1973; Heatwole 1975; Rubinoff and Kropach 1970; Kropach 1975; Caldwell and Rubinoff 1983). Hence, both crypsis and warning signals might combine to mitigate predation on this species.

All-yellow snakes, *Hydrophis platurus xanthos*

Smith (1926) recognized different color morphs of *H. platurus*, which conceivably might be related to variations in physical conditions or predation pressures. Kropach (1971b), Solórzano (2011), and Bessesen (2012) reported a population in the northern basin of Golfo Dulce that is exclusively composed of xanthic (all-yellow or primarily yellow) sea snakes that are rarely seen outside the Gulf along the southwestern coast of Costa Rica. Later studies revealed a geographically restricted marine habitat in which 100% of the sampled sea snakes exhibited a diagnostic character (Bessesen and Galbreath 2017). The xanthic population is spatially separated from the oceanic bicolored snakes by a gap of about 22 km and has been given subspecies status (Bessesen 2012; Bessesen and Galbreath 2017), although the taxonomy remains controversial (Solórzano and Sasa 2024). The topography of Golfo Dulce and associated currents generally prevent free exchange between the deeper waters of the inner basin and the adjacent coastal water (Svendsen et al. 2006; Bessesen and Galbreath 2017), but various observations suggest that some snakes likely wash out from the Gulf to the Pacific from time to time (Bessesen and Galbreath 2017; Solórzano and Sasa 2024). Moreover, the presence of some bicolored specimens inside Golfo Dulce (even mating with yellow specimens) suggests that the movement of snakes occurs in both directions (Solórzano and Sasa 2024).

Clearly, the xanthic *H. p. xanthos* snakes are not cryptic, as they are highly visible when floating on the surface of the ocean (Fig. 9). Noteworthy differences in behavior between the xanthic and bicolor populations of *H. platurus* have been reported. Unlike the bicolor snakes that spend time resting or foraging while floating on the surface during daylight hours, the xanthic snakes tend to be markedly nocturnal with respect to this behavior (Bessesen 2012; Lillywhite et al. 2015; Solórzano and Sasa 2024). They tend not to be attracted to slicks like the bicolor snakes, and they surface in rougher water. Why the xanthic subspecies lost its dark coloration is not known, but the lighter yellow skin likely risks damage from solar radiation and presumably exposes the snakes to avian predators (Bessesen and González-Suárez 2022) and harassment by dolphins (Bessessen et al. 2021). Although multiple factors (including surface temperatures) might have influenced the evolution of nocturnal surfacing behavior of the xanthic snakes, the reversal of activity that is seen in the less conspicuous bicolor snakes is clearly compatible with the hypothesis for crypsis in the latter population.

Conservation of *Hydrophis platurus*

Sea snakes are important components of the vertebrate marine fauna, and the very broad range of *H. p. platurus* is especially significant. The bicolored subspecies can therefore serve as a possible harbinger for climate change, both in contexts of temperature and drought as well as changes in trophic ecology and community structure. Sea snakes have been generally acknowledged as important bioindicators that are relevant to monitoring marine habitats and assessing the effects of climate change, changes or loss of habitat, declines in biodiversity, and other anthropogenic impacts (Lillywhite et al. 2018; Udyawer et al. 2018; Rasmussen et al. 2020). Increasing our knowledge and insights related to the biological properties, behavior, and survival of sea snakes is especially important, particularly in the pelagic species.

Crypsis is seemingly important for this species because of its periodic association with the ocean's surface. Intermittent air-breathing is essential and foraging while floating on slicks is an evolved behavior that is necessary for successful foraging. The pelagic *H. platurus* consumes at least 34 species of fishes from 27 different families, and thus its foraging ecology is a centrally important aspect of its pelagic life history (Brischoux and Lillywhite 2013). Crypsis might well be important to the successful foraging of *H. p. platurus* on slicks.

In addition, access to fresh water for osmoregulation is important for sea snakes, although it is limited in marine environments, and drinking from lenses of rainwater is critical for hydration in *H. platurus* (reviewed by Rash and Lillywhite 2019). Sea snakes were once thought to drink seawater and eliminate excess salts by means of sublingual salt glands. However, recent investigations have demonstrated that sea snakes do not drink seawater. Dehydrated sea snakes avoid drinking seawater but rather drink fresh water to maintain their water balance (Lillywhite et al. 2012). *Hydrophis platurus* dehydrate at sea during periods of drought, and in offshore waters near Guanacaste, Costa Rica, they potentially withstand as long as six months of drought. When the dry season ends, these snakes drink from the freshwater lenses that form on the surface of the ocean during periods of heavy rainfall (Lillywhite et al. 2014, 2019). Following drought, these snakes are in a low state of body condition and have significantly lower total body water than conspecifics captured during the wet season (Lillywhite et al. 2014). Logically, free-ranging snakes would not be in a dehydrated condition if they drank and processed seawater. Regional precipitation over the ocean is reduced during the dry season, and climatically induced stochastic periods of drought could pose serious threats to the well-being of sea snake populations. Cryptic features of *H. platurus* could be important in protecting snakes from aerial predation during critical behaviors such as drinking fresh water from oceanic surface lenses.

In summary, cryptic coloration is important to the wide-ranging *H. p. platurus* because of the diel behaviors that position these snakes on the ocean's surface where they are subject to possible predation from above as well as attacks from fishes or mammals in pelagic waters. In contrast, the conspicuously colored xanthic subspecies *H. p. xanthos* has evolved more nocturnal behavior that involves resting or floating at the surface, and they do not appear to aggregate specifically along slicks. Both subspecies and color forms are subject to predation, and the brilliant yellow coloration is likely to function in aposematic contexts, reflecting the significant pressures of predation upon this species. Actual observations or other evidence of predation on the xanthic snakes in Golfo Dulce are less numerous than expected, which offers some credence for the effectiveness of the aposematic signal (Solórzano and Sasa 2024). Conservation is important in the context of the broader ranging services of this subspecies as a bioindicator of marine health and climatic impacts, and for the xanthic subspecies in the context of its limited geographic isolation where it is inherently vulnerable to climatic and anthropogenic impacts (Bessesen et al. 2023). Indeed, with the lack of much genetic exchange with sea snakes from the broader Indo-Pacific, *H. p. xanthos* has become a highly discrete organism and 'evolutionarily significant unit' with unknown risks of extinction, and it may ultimately be considered for status as a full species (Bessesen and Galbreath 2017). Monitoring populations of both subspecies of *H. platurus* may provide insights into the status of other marine fauna and the health of marine habitats.

Acknowledgements.—I am grateful to numerous persons who assisted me in the field during numerous visits to Costa Rica, over which time I developed ideas concerning the camouflage of Yellow-bellied Sea Snakes. Adán Barrera provided excellent boat transportation and assistance in locating sea snakes. I am grateful to A. Solórzano and M. Sasa for managing the permits (018-2009-ACAT, DNOP-002-2010, DGT-013-04-2010, ACG-PI-012-2010, 129-2011-SINAC, 069-2012-ACAT, PI-ACAT-053-2012, DGVS-171-2013, ACT-OR-DR-055-17). I also thank C. Sheehy III, J. Pfaller, J. Wixson, H. Heatwole, M.-C. Tu, M. Edwards, M. Sandfoss, J. Lillywhite, S.R. Lillywhite, S.M. Lillywhite, and J. Crowe-Riddell for assistance with the observations of snakes. S. Boucher provided accommodation during our studies and was helpful in many ways. Harold Heatwole and Coleman Sheehy III provided comments for improving an earlier draft version of the manuscript. This research was conducted within guidelines and approval of the University of Florida IACUC (200902798; IC00000701; IC00001629; IC00003534) and was supported by the National Science Foundation (IOS-0926802 to HBL).

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