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On the Abundance of a Pelagic Sea Snake

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Abstract.— **We quantified the abundance of pelagic sea snakes, *Hydrophis* (= *Pelamis*) *platurus*, while following slicks that formed drift lines during 3 yr of research in the Golfo de Papagayo, Costa Rica. The number of snakes we observed floating on slicks varied greatly and ranged from 0 to 1,029 per hour. The largest number we observed was highly unusual in recent experience but comparable to earlier reports of sea snake aggregations in the historical literature. Snakes were more abundant on slicks with flotsam during early morning hours on clear, calm days. However, 'decisions' of sea snakes to spend time floating on slicks are also influenced by other factors that are not known or are poorly understood. Neither temperature nor salinity influenced the number of snakes we observed within the range of the parameters we encountered. We observed only a single snake during 13 days of searching during which there were red tide conditions with cold and turbid water disturbed almost daily by high winds. We also counted floating snakes at the inner basin of the Golfo Dulce in southern Costa Rica, where the population of *H. platurus* contains almost exclusively xanthic (all-yellow) individuals. These snakes are behaviorally different and are most-commonly observed while floating at night, without any strong association with slicks. Mean counts of these xanthic snakes suggest the abundance of pelagic sea snakes is essentially similar in Golfo Dulce (21.4 ± 4.4 snakes/h) and Golfo de Papagayo (19.3 ± 4.4 snakes/h, neglecting the single, unusually high count of 1,029 snakes/h).**

Despite sometimes elusive behavior and patchy occurrence, there is considerable information on the abundance and demography of snakes (Mullin and Seigel, 2009; Miller et al., 2011; Rose et al., 2013). Information on the population biology of sea snakes is more problematic, however, owing to three-dimensional living space, aquatic or amphibious habits, patchy usage of habitat through time (especially sea kraits), and difficulty of detection when living in, or moving through, open water. As with some species of terrestrial snakes, population estimates of high densities are obtained where sea snakes are concentrated at resting sites (Brischoux and Bonnet, 2008), but dispersal occurs to unknown areas during feeding or other activities (Heatwole, 1999). Sometimes regular migrations occur, but these have not been well chronicled or quantified (Heatwole, 1999).

Huge numbers of sea snakes have been counted in association with aggregations, either in sea caves, nesting sites, or rarely on drift lines in the open ocean. Large numbers of Yellow-Bellied Sea Snakes, *Hydrophis* (= *Pelamis*) *platurus* (Linnaeus, 1766), sometimes wash ashore and die on beaches during episodic circannual events that appear to involve upwelling of cold water on the Guanacaste coast of Costa Rica (Boucher, pers. obs.). Willoughby Lowe (1932) observed a spectacular aggregation of sea snakes in the Malacca Straits. From the deck of a ship he reportedly saw a nearly solid mass of snakes, many intertwined with each other, occurring in a line about 3 m wide and perhaps 100 km long. The total number of snakes, reported to be *Hydrophis* (= *Astrotia*) *stokesii*, must have been huge and possibly involved either passive or active attraction to a 'slick' (or drift line) where currents converged. Slicks are smooth, calm-water streaks forming drift lines in the ocean because foam, floating objects, and debris accumulate as flotsam. These zones of convergence are formed by a variety of physical processes and currents such as internal waves and eddies (Ewing, 1950). Such slicks can be variable in width and relatively small and short-lived, or they can form drift lines that extend for hundreds of meters or kilometers. Plankton becomes concentrated there, and smaller pelagic fishes are attracted to feed and to hide beneath objects.

Hydrophis platurus is the only truly pelagic sea snake. It also is the only species found well beyond the centers of origins, abundance, and diversity of sea snakes in the central Indo-Pacific (Brischoux et al., 2012). This species has the broadest distribution of any squamate reptile and is the only sea snake that occurs in the eastern Pacific. It ranges from the southern tip of Africa, across the Indo-Pacific to the shores of Central America, where the latitudinal distribution includes the Gulf of California to the north and Ecuador to the south. Molecular phylogenetic analyses place *H. platurus* within a core group of *Hydrophis* spp. having origins about 2 Ma, which postdates the closure of the Isthmus of Panama and is consistent with its exclusion from the Caribbean (Sanders et al., 2013). *Hydrophis platurus* associates closely with oceanic surface currents, and it seems likely that this species migrated to the eastern Pacific via the Equatorial Countercurrent (Kropach, 1975). Such dispersal also appears likely to be an ongoing, continuous process that maintains a 'fluid' and potentially evolving distribution of the species. Low levels of genetic divergence suggest that rates of gene flow are relatively high throughout the Pacific and that range expansion to the eastern Pacific is relatively recent (Sheehy et al., 2012). Both phenomena could be because of passive drifting of these snakes on oceanic surface currents that sometimes waft individuals to latitudes where they are not breeding residents (Dunson and Ehlert, 1971). On the other hand, diving and subsurface swimming behaviors of these snakes offer some independence from the horizontal direction and velocity of surface currents (Rubinoff et al., 1988).

Because of its uniquely pelagic ecology involving passive drifting with currents, estimating abundance and population structure of such a species is problematic. The majority of observations or counts of these snakes have been made on the surface of the ocean, but *H. platurus* is capable of diving to depths of 50 m (Rubinoff et al., 1986). At any given location where pelagic sea snakes are evident from surface sightings, the 'underwater' component of the population is totally unknown.

Hydrophis platurus are found in the greatest numbers in association with oceanic 'slicks' (Dunson and Ehlert, 1971; Kropach, 1971, 1975), and some of the earlier reports of the number of *H. platurus* floating on the ocean surface mention

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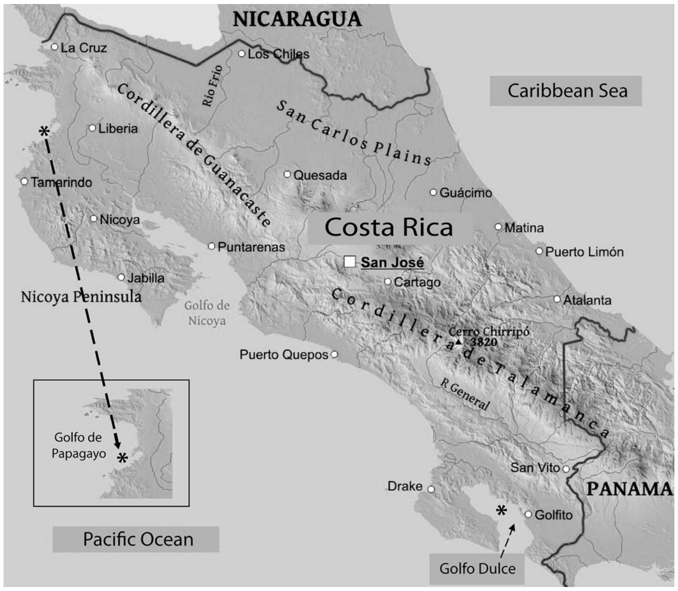

FIG. 1. Map of Costa Rica with inset to feature location of sites where *Hydrophis platurus* were collected in the Golfo Papagayo during this study. The general site of collections is indicated with an asterisk (*), and the dashed arrow connects the locations on the map as shown at two different scales. The asterisk in the Golfo Dulce indicates where the yellow *H. platurus* were collected in southern Costa Rica. The map was modified from an image from Freeworldmaps.net, with permission.

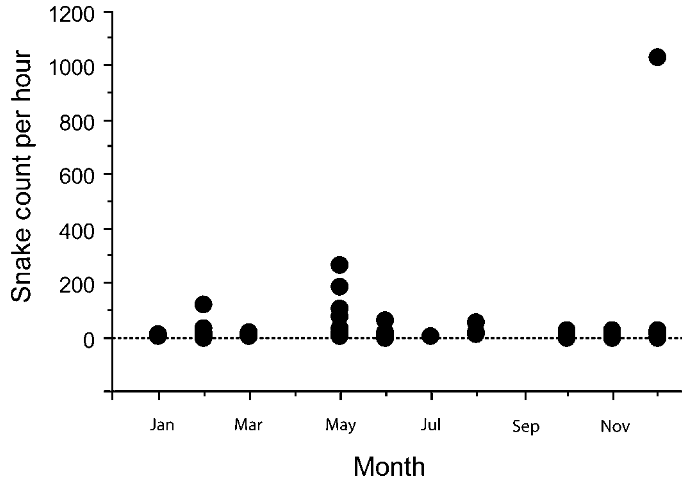

FIG. 2. Counts of pelagic sea snakes (*Hydrophis platurus*) floating on slicks at Golfo de Papagayo, Costa Rica, in relation to time of year. Note that numerous data points are superimposed in this figure and the high count for December (2012) is unusual.

'thousands' of snakes on slicks (Kropach, 1971). The extent to which such aggregations reflect the local population density is unknown. Clearly, however, there are circumstances in which sea snakes can be very abundant. We have been conducting research with *H. platurus* in the Golfo de Papagayo, Costa Rica (Fig. 1), where snakes are common but not typically seen in very large numbers. Therefore, we have wondered whether earlier sightings of very large numbers of snakes are rare events or whether the population might have declined, as is the case with numerous vertebrates, including terrestrial as well as marine species of snakes (Reading et al., 2010; Lukoschek et al., 2013). Here we report sightings of sea snakes during the course of 3 yr of field work. Our observations were sufficient to enable us to assess the 'average' expectation of numbers, variability of numbers, one observation of exceptional numbers, and some of the factors that influence the appearance and aggregation of these snakes.

MATERIALS AND METHODS

Snake Counts.—The data reported here are based on counts of live *H. platurus* during research expeditions when snakes were collected for laboratory investigations related to other research (Brischoux and Lillywhite, 2011, 2013; Lillywhite et al., 2012, 2014; Pfaller et al., 2012; Sheehy et al., 2012). The majority of snakes that we collected were returned alive to their approximate locations of capture. The majority of counts and collections (see below) were made in the Golfo de Papagayo, usually within 1–10 km from the Guanacaste coast of northwestern Costa Rica.

All counts involved sightings (and usually captures) of floating snakes by 2–4 persons aboard a small, 6-m long boat during slow movement along slicks at an average speed of 8 km/h. We scanned for, and sighted, snakes that were within a distance of approximately 15 m to either side of the boat. In most cases snakes were captured using a dip net. Each snake was placed in a bucket or large tub and subsequently transferred to an individual mesh bag (for storage in an insulated cooler) while other persons continued to watch for snakes on the water. Searches for sea snakes were conducted generally during early morning hours between 0700 h and 1100 h when snakes were most common at the ocean surface (see also Tu, 1976). We made such searches during each of 98 days distributed among every month except April and September during 2010 through 2013 (Fig. 2).

We recorded the time and subtracted the running time of the boat while it was traveling off-slick during movement from one slick to another. We noted whether each slick had a dense or sparse amount of flotsam and, during most trips, we recorded the temperature and salinity of water within the upper 3 cm of ocean surface. We also noted the cloud condition of the sky. Temperature was measured with a standard laboratory thermometer, and salinity of water samples was quantified using a Fisher hand-held salinity refractometer with automatic temperature compensation. To quantify the wave condition of the water, we estimated the maximum height of smaller waves that disturbed the ocean surface between larger wave ('swell') movements. We considered the smaller waves ('wavelets') to more-consistently represent the disturbance to floating snakes, as water conditions ranged from calm to choppy or rough.

On one occasion, 3 December 2012, there were unusually large numbers of snakes floating on a slick with calm water and flotsam. After we captured snakes for research, we cruised along this slick and simply counted the snakes for a considerable distance to record a representative number.

During two nights in May of 2013, we similarly captured floating sea snakes that were part of the xanthic population of *H. platurus* in the interior of Golfo Dulce in southern Costa Rica (Solórzano, 2011) (Fig. 1). These snakes differed from the bicolored sea snakes that we captured in northwestern Costa Rica, not only in color but also in behavior. The yellow snakes in Golfo Dulce evidently do not aggregate in large numbers along slicks but can be found floating in open water as well as on slicks. Also, these snakes are most abundant during early evening hours following sunset (Solórzano, pers. obs.). Counts of these snakes were analyzed separately from the others.

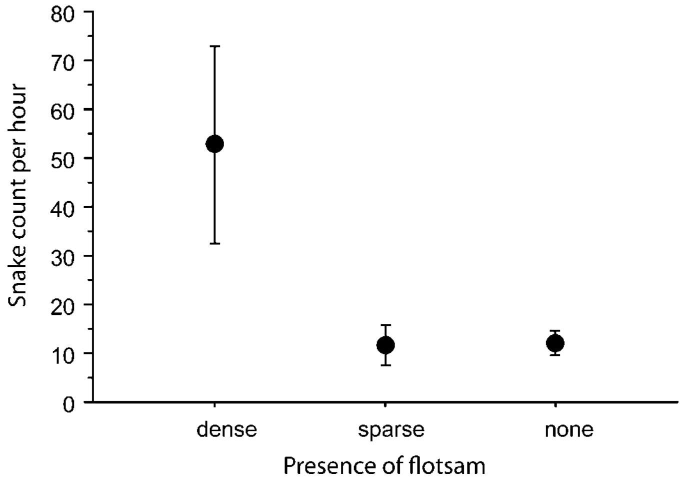

FIG. 3. Relationship of snake counts (*Hydrophis platurus*) to presence of flotsam on slicks at Golfo de Papagayo, Costa Rica. Flotsam was categorized according to 'dense' presence with froth, floating objects, and debris ('sparse' with some bubbles and very few floating debris, or 'none'). Symbols denote mean ± SE.

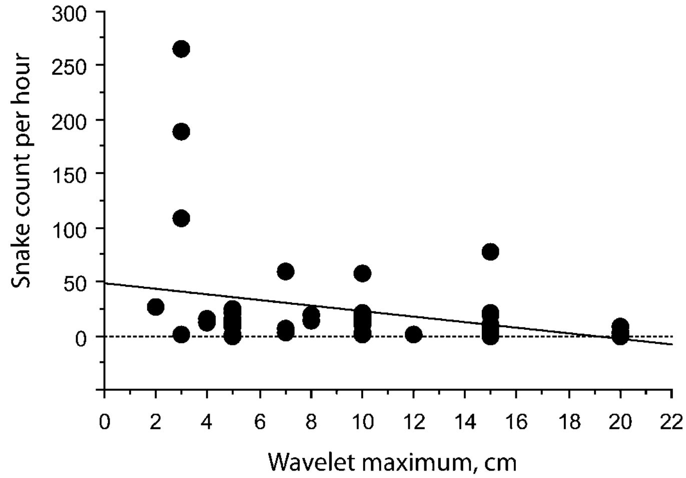

FIG. 4. Relationship of snake counts to estimated maximum height of wavelets on the ocean surface at Golfo de Papagayo, Costa Rica. Regression equation: count/h = 49.33 − 2.62 × wavelet maximum. $F_{1,53} = 6.231$, $R^2 = 0.107$, $P = 0.0158$.

Analysis and Statistics.—All data are presented as mean ± SE. Counts are expressed as the number of snakes seen or captured per hour. This seems to be the most practical expression for comparative purposes given that 1) snakes tend to aggregate along slicks, 2) snakes in fact distribute vertically throughout a volume of water and are not restricted solely to an area of ocean surface, and 3) numbers/time are best compared with data previously published. To evaluate the influence of factors on the number of snakes we used analysis of variance (ANOVA) or analysis of covariance (ANCOVA) with number of snakes as the dependent variable; flotsam, maximum height of wavelets, temperature, or salinity as the factor; and time as the covariate. Fisher's protected least significant difference (PLSD) was used for post hoc tests of differences. Simple (least squares) regression analysis also was used to evaluate the influence of month and maximum height of wavelets on the counts of snakes. All statistical analyses were performed using Statview 5.0.1.0., without the highest count value included, insofar as it was clearly an outlier (Fig. 2).

RESULTS

Golfo de Papagayo.—In the Golfo de Papagayo, counts of snakes ranged from zero to 1,029/h with a mean count of 31.5 ± 12.9 snakes/h. The counts with the highest (unusual) value removed ranged from 0–265 snakes/h and the mean count was 19.3 ± 4.4 snakes/h. These data also exclude counts that were made during a research trip during 3–16 March 2012 when there was a red tide, exceptionally high wind conditions, and unusually cold and turbid water; we sighted only a single snake during 11 boat runs in an attempt to locate snakes in the usual manner.

We have been able to collect generally similar numbers of snakes throughout the year, but data suggest a tendency for snakes to be more common during drier months (December to May) (Fig. 2). Counts were significantly higher on slicks that contained denser amounts of flotsam (ANCOVA with flotsam as the factor and run time of boat the covariate, $F_{2,80} = 4.468$, $P = 0.0146$) (Fig. 3). Counts were generally higher during sunny conditions and were greater when water conditions were calm (regression with $F_{1,53} = 6.231$, $R^2 = 0.107$, $P = 0.0158$; Fig. 4).

Water temperatures varied from 23–30.5°C (mean = 28.4°C), and the salinity of water ranged from 30–34 parts per thousand (ppt) (mean = 32.4 ppt). Neither temperature nor salinity of water influenced the count of snakes within the range of values we encountered ($F_{1,55} = 0.391$, $R^2 = 0.007$, $P = 0.5342$ and $F_{1,64} = 3.199$, $R^2 = 0.048$, $P = 0.0785$, respectively). Regression analysis indicated that water temperature did not vary significantly in relation to month of the year ($F_{1,55} = 3.670$, $R^2 = 0.064$, $P = 0.0607$), whereas salinity decreased from dry to wet season ($F_{1,64} = 17.143$, $R^2 = 0.214$, $P = 0.0001$).

Golfo Dulce.— We counted snakes in Golfo Dulce during 13–15 May 2013. One morning count yielded five snakes in 30 min, for a count of 10 snakes/h. Evening counts after dark yielded 17 and 25.7 snakes/h on two different nights. Snakes were commonly seen at night and were not aggregated solely on slicks, as in the Golfo de Papagayo.

DISCUSSION

Association of Pelagic Sea Snakes with Slicks.—Our central question with respect to the data for counts of *H. platurus* we acquired during the course of 3 yr was whether this species is abundant in numbers comparable to both anecdotal and scientific accounts previously published. The answer came during 3 December 2012 when we counted 1,029 snakes/h while observing a slick having an aggregation of snakes that, in our experience, was exceptionally dense. This number is greater than any similar measurement published for this species (Table 1), and it appears to be comparable to observations of 'thousands' of snakes on slicks reported previously for both *Hydrophis* (= *Pelamis*) *platurus* (Dunson and Ehlert, 1971; Kropach, 1971) and *Hydrophis* (= *Astrotia*) *stokesii* (Lowe, 1932). What remains unknown is from how far and over what area or volume of ocean these snakes were drawn to the slick and how many individuals might have been submerged within the volume of water beneath the slick.

The mechanism by which *H. platurus* aggregate along slicks is unknown but almost certainly involves passive drifting in response to movements of currents that converge to form a slick (Kropach, 1971, 1975; Lillywhite et al., 2010). During all of our numerous trips to the Golfo de Papagayo over the course of 3 yr,

TABLE 1. Exceptionally high counts of *Hydrophis* (= *Pelamis*) *platurus*.

Location	Date	Measure of abundance	Habitat features	Source
Gulf of Panama	Sep–Oct 1969	Several thousand on slicks; 4–180 snakes sighted/h	Aggregations on slicks	Kropach, 1971
Near Bahía de Culebras, Costa Rica	19 Jan 1973	185 snakes/h	Calm water, probably with drift line(s)	Tu, 1976
Gulf of Chiriquí, Panama	7 Sep 1986	12 snakes/m^2	4 km × 30 m drift line with deep layer of flotsam	Vallarino and Weldon, 1996
Mouth of Golfo Dulce, Costa Rica	Not given	19.7/h; and 278 snakes/'few hours'	Slick or drift line with flotsam and calm water	Dunson and Ehlert, 1971
Golfo de Papagayo, Costa Rica	3 Dec 2012	1,029 snakes/h	Slick or drift line with flotsam and calm water	This study

we have seen very few snakes floating in water away from a slick (<0.5% of all sightings). Also, during extensive searching and travel by boat, we have never seen what appeared to be multiple snakes floating or swimming toward a slick to form an aggregation. Therefore, it seems likely that snakes passively drift to slicks while at various depths in the water column and subsequently surface to 'float-and-wait' forage (Brischoux and Lillywhite, 2011) on a slick when conditions are favorable during early morning hours. In the months of January and February, 1973, Tu (1976) collected more than 3,000 *H. platurus* in the same area as our study during early morning hours, but during the afternoon he was not able to find a single specimen despite extensive searching.

Our results reaffirm the importance of flotsam in attracting *H. platurus* to slicks, whether actively or passively, as reported by Brischoux and Lillywhite (2011) and further illustrated in Figure 3. It seems reasonable to hypothesize either that presence of flotsam influences the 'decision' of a snake to surface at a slick, possibly by enhancing visual detection from beneath the ocean surface (Brischoux and Lillywhite, 2011), or the flotsam is passively related to a stronger influence of currents which also passively brings a larger number of snakes to a given slick. Floating snakes also are generally more abundant on slicks when there are bright light and clear-sky conditions. This was evident in our observations, but we did not attempt to evaluate this further because the influence of light levels has been determined previously based on quantitative data we obtained during part of the research period reported here (Brischoux and Lillywhite, 2011). Slicks, and especially those with flotsam, attract smaller pelagic species of fishes that tend to hide beneath floating objects, including the sea snakes we are discussing. Considering all the available information, we conclude that floating aggregations of *H. platurus* on slicks is a behavior related to foraging success (Hunter and Mitchell, 1967; Dunson and Ehlert, 1971; Kropach, 1971; Brischoux and Lillywhite, 2011).

Ocean surface temperature varied by 7.5°C and salinity varied by 4 ppt during the course of our study. The latter correlated significantly with the seasonal influence of rainfall. However, neither of these variables influenced the numbers of snakes we observed. One possible exception was the nearly complete absence of snakes floating on the ocean surface during a period of red tide we investigated in March of 2012. At this time, water temperatures were measured as low as 22.5°C and salinity measurements were 34.5 ppt. However, the water was turbid and high wind conditions prevailed as well, so we cannot assess which factor or combination of factors were responsible for discouraging snakes from floating. We observed one snake during the 6 days we spent searching, so we assume snakes were present but did not spend time floating. On most days the wind either obscured or prevented slicks from forming, and this might have been the single-most important factor affecting our failure to observe snakes during the red tide.

We emphasize that there is great variation in the numbers of snakes that float together on slicks, and the factors we investigated are not absolute predictors for the presence of snakes. Two days in sequence might involve very similar or identical parameters of environment, yet one day there are numerous snakes floating and the next day there are none. We conclude there are other factors influencing behavior that we have neither investigated nor understand.

What seems exceptionally interesting is the entirely different behavior of the xanthic specimens of *H. platurus* that inhabit the inner reaches of the Golfo Dulce in southern Costa Rica. Our observations, in addition to those of A. Solórzano (pers. obs.), indicate that these snakes are more commonly seen floating during early evening hours after dark without forming aggregations on slicks. These observations are unrelated to visibility during different times of day. Our counts suggest that these snakes are perhaps equally abundant as the bicolored snakes in the Golfo de Papagayo, although they appear to form a separate population (Solórzano, 2011; Bessesen, 2012; Sheehy et al., 2012). Because this population might be somewhat 'entrapped' within the inner basin of Golfo Dulce (Solórzano, 2011; Bessesen, 2012), perhaps fewer slicks or their manner of formation account for the behavioral differences between this population and the snakes outside the Golfo Dulce, including those in Golfo de Papagayo.

Global Abundance of Hydrophis platurus.—During 2010 and 2011, we collected tissues from *H. platurus* for genetic analysis, and this involved clipping the terminus of the tail (Sheehy et al., 2012; unpubl. data). All of these snakes were returned to locations where they were captured. During the sampling of hundreds of snakes, we are confident that fewer than three were recaptures, representing less than 1% of the snakes that were sampled. The low recapture rates we observed are consistent with those described in a previous mark and release study in the Gulf of Panama (Kropach, 1975). Because of the drifting ecology of these snakes, we consider the population at Golfo de Papagayo to be highly transient, with individuals moving in and out by passively drifting with currents.

Hydrophis platurus is the most widely distributed species of squamate reptile, ranging from the Cape of Good Hope westward across the Indo-Pacific to the western coastline of Central America (Minton, 1975). This species is widely distributed in tropical seas except for the Atlantic Ocean, Caribbean Sea, Red Sea, and possibly the central Pacific (Smith, 1926). Because of its passive drifting ecology, *H. platurus* is frequently wafted to locations where it does not maintain a resident breeding population (e.g., California, Hawaii, New Zealand, Tasmania, the Sea of Japan, and the Galápagos). Because of the breadth of its range, and the indication that aggregations on slicks may include thousands of snakes at various locations, the pan-oceanic population of this species must be exceptionally large and probably represents the most-abundant species of snake. With respect to the much-quoted account by Lowe (1932), reporting dense aggregations of a sea snake in one of the more-heavily used waterways in the world, no other such sightings have been reported since the first publication in 1932. The identification of the species as *Astrotia* (= *Hydrophis*) seems doubtful, as other aggregations of this species are not known, and the identification came some time after the sighting and was based on a preserved museum specimen of *Astrotia* (which can be highly variable in coloration). The true identification of Lowe's species may never be known, but the behavior of the snakes in the slick matched that of *H. platurus*.

Conclusions

With respect to the Guanacaste coast of northwest Costa Rica, very large numbers of sea snakes aggregate on slicks and are likely to be especially abundant on calm, clear mornings where slicks are associated with flotsam. Day-to-day occurrence of such aggregations is highly variable, and there appear to be factors that are not understood driving the surfacing and floating behavior of snakes. The global abundance of this species must be exceptionally large, with transoceanic movements and reproductive replacement of individuals that waft away from the main oceanic currents to poleward locations where they cannot sustain a reproductive population. Future research poses a challenge to better understand the drifting ecology of this species and to determine how drifting with currents relates to the absolute abundance and global circulation of these snakes. It will be important to know if the Pacific bays of Central America are the last locations where large aggregations can still be found on our planet.

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