SYMPOSIUM

Dehydration and Drinking Responses in a Pelagic Sea Snake

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Synopsis Recent investigations of water balance in sea snakes demonstrated that amphibious sea kraits (*Laticauda* spp.) dehydrate in seawater and require fresh water to restore deficits in body water. Here, we report similar findings for *Pelamis platurus*, a viviparous, pelagic, entirely marine species of hydrophiine (''true'') sea snake. We sampled snakes at Golfo de Papagayo, Guanacaste, Costa Rica and demonstrated they do not drink seawater but fresh water at variable deficits of body water incurred by dehydration. The threshold dehydration at which snakes first drink fresh water is -18.3 ± 1.1 % (mean $\pm$ SE) loss of body mass, which is roughly twice the magnitude of mass deficit at which sea kraits drink fresh water. Compared to sea kraits, *Pelamis* drink relatively larger volumes of water and make up a larger percentage of the dehydration deficit. Some dehydrated *Pelamis* also were shown to drink brackish water up to 50% seawater, but most drank at lower brackish values and 20% of the snakes tested did not drink at all. Like sea kraits, *Pelamis* dehydrate when kept in seawater in the laboratory. Moreover, some individuals drank fresh water immediately following capture, providing preliminary evidence that *Pelamis* dehydrate at sea. Thus, this widely distributed pelagic species remains subject to dehydration in marine environments where it retains a capacity to sense and to drink fresh water. In comparison with sea kraits, however, *Pelamis* represents a more advanced stage in the evolutionary transition to a fully marine life and appears to be less dependent on fresh water.

Introduction

Secondary evolutionary transitions between terrestrial and marine environments pose great difficulties for organisms and are not well understood. Such transitions involve numerous adaptations of morphology, physiology, and behavior of organisms (Mazin and de Buffrenil 2001). The maintenance of water balance in hyperosmotic environments is especially a problematic aspect of secondary marine transitions and is possibly the principal deterrent to successful marine life (Dunson 1979; Brischoux et al. 2012). Seawater (SW) is hyperosmotic to body fluids of most vertebrates, and therefore marine forms will tend to lose water and gain salts across permeable surfaces. Additional salts will be gained by drinking SW, whether incidentally or intentionally, and additional body water will be lost via pulmonary evaporation, defecation, and excretion of waste products. Thus, living in SW incurs severe risk of dehydration.

Secondarily, marine vertebrates have evolved means of conserving water including specialized excretory structures that eliminate excess salt. Although these aspects of hydromineral balance are generally well studied, less is known regarding the means of replacing lost body water and the sources from which this water comes. Observations of drinking and behavioral responses to freshwater (FW) sources are especially scant, and recent observations suggest that some generalizations regarding drinking of SW may not be correct (Lillywhite et al. 2008).

Several independent lineages of reptiles have successfully colonized coastal waters, but comparatively few are capable of permanent residence in SW, especially in vast open seas. Sea snakes are the exception,

being widely distributed throughout much of the world's tropical marine waters (Heatwole 1999). Recent studies of amphibious sea kraits (*Laticauda* spp.) indicate that these species dehydrate in SW and require FW for water balance, in spite of possessing functional salt glands (Lillywhite et al. 2008). We do not yet know, however, whether the principal lineage of "true" sea snakes—some 60 species of Hydrophiini that are viviparous and entirely marine—also require FW. Therefore, to further understand the FW drinking requirements of sea snakes requires examination of this important marine clade.

Here, we report that yellow-bellied sea snakes *Pelamis platurus* drink FW and restore water balance when experimentally dehydrated, but, like sea kraits, do not drink SW. This finding is significant because it emphasizes some dependence on FW in what is arguably one of the more fully marine-adapted species of sea snake.

Methods

Animals and study site

We investigated dehydration and drinking behaviors in yellow-bellied sea snakes (*P. platurus*) at coastal sites in Golfo de Papagayo, Guanacaste, Costa Rica during three research trips conducted in 2010 and 2011. Snakes were collected 2–10 km offshore, during morning hours beginning after sunrise. Each snake was captured individually, either by hand or by using a handheld dip net, while the snake floated in a "float-and-wait" posture on the ocean surface (Brischoux and Lillywhite 2011). The snake was immediately transferred to a plastic container, inspected for epibionts and size, then transferred into a mesh bag for transport to shore.

Dehydration and drinking

In principle, we followed methods that were used in previous studies of sea kraits and reported by Lillywhite et al. (2008). Snakes ($n = 29$) were weighed following their return to the laboratory after brief exposure to room air while lying on a dry towel until their skins were dry to the touch. Snakes were weighed to the nearest 0.1 g using a Sartorius ELT2001 electronic balance. Each snake was dehydrated by exposure to room air while being held individually inside a marked mesh bag. Mean air temperature was $25.8 \pm 0.6°C$ and the mean relative humidity was $53.6 \pm 4.5\%$ during the times snakes were dehydrating.

Each animal was weighed daily (without bag) during the period of dehydration and testing, which varied from 3 to 13 days (mean 6.4 ± 1.3 days). The bags containing dehydrating snakes were kept separated on shelves and exposed to laboratory air during periods between weighings. Snakes in bags appeared remarkably calm, assumed relaxed loose coils, and moved little. After snakes had lost variable amounts of the original body mass, each was placed individually inside a plastic container half-filled with SW (approximately 2–4 l, depending on the size of snake) and observed for drinking (Fig. 1). Each snake was held overnight and re-weighed the following morning, 18–20 h later. Prior to each weighing, a snake was placed on an absorbent cloth towel, patted lightly to remove surface water, and then exposed to room air until the skin reached a dry condition as determined by touch (5–15 min). Each snake was treated similarly, and we attempted to be consistent with respect to the final condition of the skin prior to weighing.

After being weighed, each snake was then placed individually into a plastic aquarium half-filled with FW ($\sim$2–4 l, depending on the size of the snake) and observed for drinking (Fig. 1). Each snake was held in FW overnight and re-weighed the following morning, 18–20 h later. If a snake did not drink FW, it was placed inside a mesh bag and the dehydration process was continued (in air) until the snake's mass was further reduced by variable amounts; the above protocol was then repeated. These steps were continued until drinking occurred, or until the loss of mass reached 27% of initial body mass (see below).

Drinking resulted in a gain in mass by snakes, but, to account for possible measurement error, we judged that drinking had occurred if a snake gained ≥ 1 g following 18–20 h in water. The majority of snakes that were kept in FW or SW and did not drink lost mass during similar periods.

The snakes used in these tests were collected on two different occasions. The second group of snakes ($n = 11$) was returned to the laboratory and tested immediately for drinking FW using the protocol described above. These snakes were then dehydrated as above and subsequently used for further drinking tests. Also, when we tested this second group of snakes, we already knew (based on data from the first group) that the dehydration threshold for drinking FW usually exceeded a loss of 12% body mass. Therefore, we dehydrated snakes to greater deficits
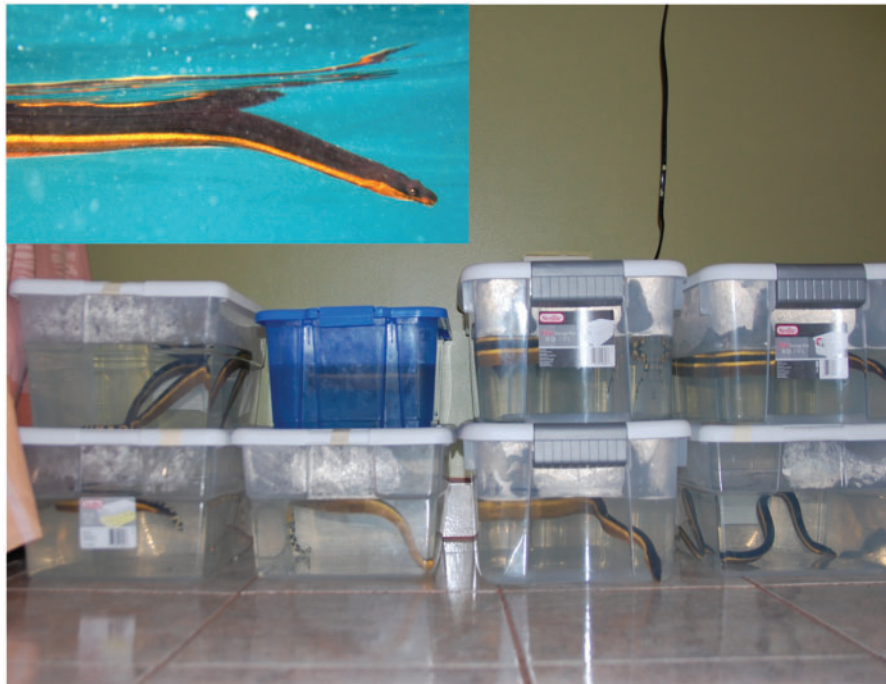
Fig. 1 Yellow-bellied sea snakes (*P. platurus*) resting in FW inside containers that were used in experiments on dehydration and drinking. The head down position of some of these snakes is typical of postures that are assumed by snakes floating at the ocean's surface (inset).

than that before we tested them for FW drinking at further intervals of dehydration (e.g., Fig. 2).

Tests of drinking in brackish water

In addition to the above experiments, 19 snakes (48.6 ± 9.1 g body mass) were tested for drinking FW immediately following capture, then dehydrated to $-19.2 \pm 1.1\%$ of their original body mass and subsequently tested for drinking in a regressive series of brackish water beginning at full SW (32 ppt), then 70% SW, 50% SW, 25% SW, 10% SW, and ending with FW (0 ppt). For each discrete step in the series, snakes were subjected to the drinking protocol described above, except that time in each salinity was 8 h. Each snake was placed in the next sequential water immediately following weighing, without any additional time in air between the salinities tested. Each snake went through the entire series of drinking tests regardless of the concentration at which drinking was first observed.

Dehydration in seawater

Five snakes were held in SW and their mass measured each day over a period of 11 days. Each snake was dried externally before weighing, as described

above. Snakes rested in SW in various positions, but usually with the head angled slightly downward, which is typical of the "float-and-wait" posture seen when snakes are floating on the ocean's surface (Fig. 1).

Data analysis

All data are expressed as mean $\pm$ SE and were analyzed using Statview 5.0.1.0. Differences among variables were tested for significance using ANOVA and Fisher's PLSD *post hoc* tests. Percentages were log-transformed prior to analysis. Rates of loss of mass were determined using standard regression analysis.

Results

Dehydration and drinking

During two separate visits to the field site, we collected a total of 29 snakes (mass $= 68.2 \pm 6.3$ g; range 14.6–155.8 g). Three snakes died during the initial dehydration process, with one individual refusing to drink even when dehydrated to -16.7% of original body mass. Three of the 11 snakes collected in the second sample drank FW amounting to 9.2%,
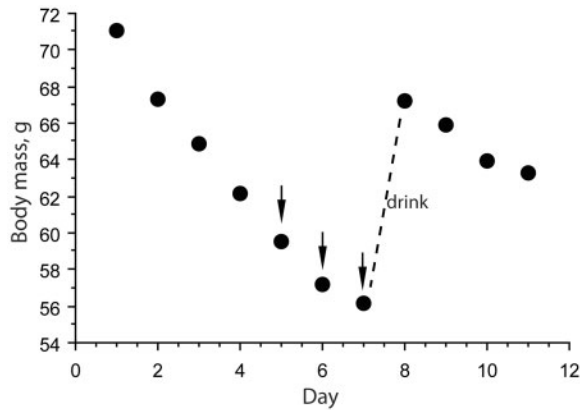
Fig. 2 Changes of body mass in an individual snake that was dehydrated by exposure to air in the laboratory. The arrows indicate points during the dehydration schedule when snakes were offered FW according to the protocol described in the text. This individual drank at the third opportunity when FW was offered at −21.4% loss of body mass. Drinking made up approximately 3/4 of the mass deficit.
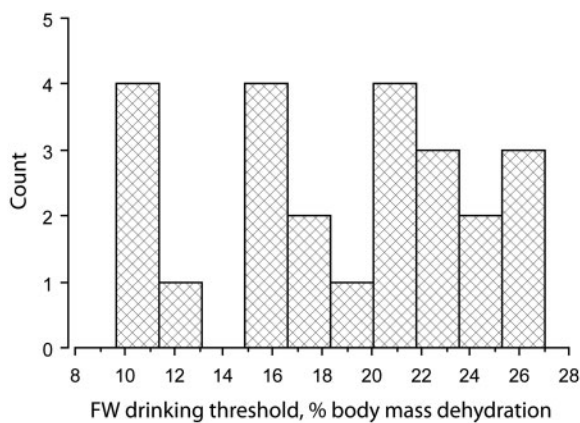

Fig. 3 Histogram illustrating variability in the threshold for drinking FW by *P. platurus*. The counts are number of snakes that drank at the indicated % loss of body mass.

10.4%, and 11.5% of the snake's body mass, respectively, immediately following capture.

Not a single snake drank SW in the laboratory. When held in FW, snakes drank measurable volumes at varying levels of dehydration (Fig. 2). The majority of snakes (85%) drank FW at dehydration deficits varying from 9.7% to 26% loss of body mass (Fig. 3). Four snakes (15% of total) refused to drink during dehydration up to 14.5%, 23%, 26%, and 27% of body mass, respectively. In comparison with sea kraits studied previously (Lillywhite et al. 2008), *Pelamis* dehydrated to greater deficits of body mass

and drank relatively greater volumes of water to replenish a greater percentage of the dehydration deficit (Table 1; Fig. 4).

Few snakes were observed drinking, but ingestion of water was evident from increases in body mass. In some cases, ingested water was also evident from a distended stomach and from water dripping from the lips. Care was taken to keep snakes level or with the head elevated during drying and weighing. In the few cases when snakes were observed to drink FW, movements of the mouth usually involved short to medium gapes with relatively rapid closure. Such drinking movements usually occurred at or near the surface of the water and were reflected in increases of mass by the snakes that we observed expressing this behavior.

Tests of drinking in brackish water

Of the 19 dehydrated snakes presented with the opportunity to drink from a regressive series of brackish water, none drank SW or 70% SW, and 5 snakes did not drink at any of the concentrations tested (Table 2). Snakes tended to drink relatively a greater volume of water at values up to 25% SW, then somewhat less at 50% SW (Fig. 5). Each of the snakes that first drank at 50% SW also drank further upon subsequent exposure to more dilute values. One of the snakes that first drank at 25% SW also drank at 10% SW, but none of the snakes that first drank at 10% SW drank again at FW. One of the 19 snakes drank 30.6% of its body mass in FW immediately following capture and prior to dehydration and subsequent testing in brackish water.

Dehydration in seawater

Regression analysis indicated that snakes kept in full SW lost mass at a rate of $0.54 \pm 0.03\%$ body mass per day. This rate was roughly an order of magnitude less than the rates of loss in air ($4.32 \pm 0.82\%$ body mass per day) at equivalent temperatures.

Discussion

We have explored the drinking behaviors of a pelagic sea snake and report that *P. platurus* does not drink SW but will drink FW when dehydrated sufficiently to induce a drinking response. This has important implications for the little-explored question of how marine vertebrates might respond to the distribution of FW sources (Lillywhite and Ellis 1994; Lillywhite et al. 2008, 2010; Lillywhite and Tu 2011;

Table 1 Dehydration parameters (mean ± SE) for four species of sea snakes dehydrated for 2 weeks in air, then offered SW followed by FW

Species (n)	Body mass (g)	Cumulative dehydration deficit		SW ingested	FW ingested		
		g	% Mass		g	% Mass	% Deficit
Laticauda colubrina (14)	258.1 ± 65.5[a]	21.9 ± 3.7[a]	9.6 ± 0.5[a]	0	11.1 ± 2.5[a]	4.9 ± 0.7	51.8 ± 7.1[a]
L. laticaudata (9)	205.1 ± 16.2[a]	31.5 ± 2.3[a]	15.5 ± 0.5[b]	0	15.8 ± 2.6[a]	8.0 ± 2.6	51.2 ± 7.2[a,b]
L. semifasciata (12)	554.6 ± 38.4[b]	75.5 ± 4.8[b]	13.7 ± 0.4[b]	0	29.9 ± 4.4[b]	5.4 ± 0.6	39.5 ± 4.5[b]
P. platurus (27)	68.2 ± 6.3[c]	12.29 ± 1.6[c]	18.3 ± 1.1[c]	0	8.24 ± 0.9[c]	13.06 ± 1.0[c]	77.3 ± 7.8[c]

Species are listed in order of decreasing terrestrial tendencies. *L. colubrina* spends considerable time on land, hiding among rocks near shoreline; *L. laticaudata* emerges onto rocks but spends most time in water; and *L semifasciata* is nearly fully aquatic except for egg laying. *P. platurus* is pelagic and entirely marine. Data for *Laticauda* spp. are from Lillywhite et al. (2008).
Parameters with different symbols are statistically different for comparisons of species within a column (ANOVA, $P < 0.05$).
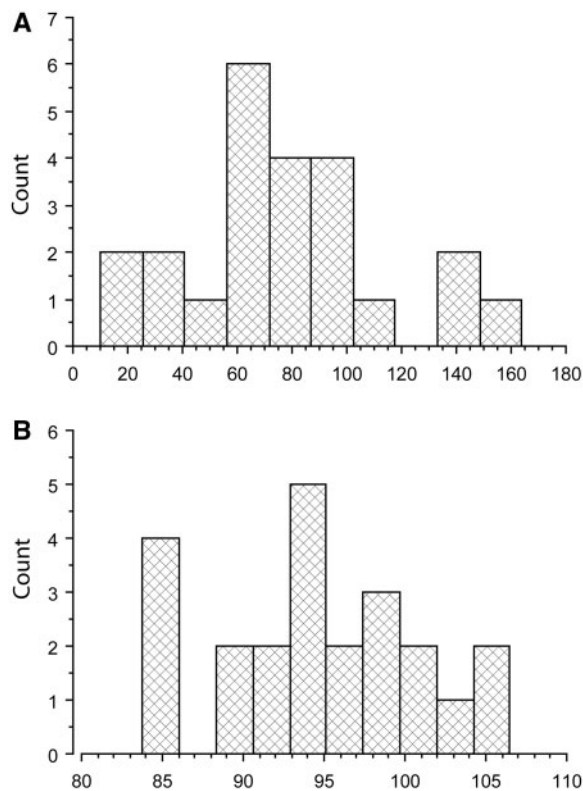

Fig. 4 Histograms illustrating variability in the amount of (**A**) body mass deficit that was made up by drinking FW (expressed as percentage of the mass deficit rehydrated), and the resulting (**B**) hydration status of the snakes (*P. platurus*) following drinking, expressed as percentage of original body mass.

Brischoux et al. 2012). In the context of water balance and responses to FW resources, *P. platurus* is especially important for two reasons: (1) It represents the only clade of marine snakes (Hydrophiini) that was previously not investigated with respect to drinking FW. (2) It is pelagic, being the most widely distributed species of snake (southern Africa through Indo-Pacific to Central America) and the only sea snake to range into the eastern Pacific Ocean (Heatwole 1999). This species is totally marine, whereas laticaudine sea kraits we investigated previously (Lillywhite et al. 2008) are amphibious and represent separate and less advanced (transitional) stages in the adaptation to marine life by sea snakes. *Pelamis platurus* is part of the Hydrophiini clade of elapid snakes, which contains about 60+ species of viviparous, completely marine sea snakes (Slowinski and Keogh 2000; Sanders et al. 2008). Because of its pelagic habits and extensive range, *Pelamis* is arguably one of the more highly adapted species of marine snakes. Indeed, it offers a useful model for exploring distributional constraints in relation to water salinity and the evolutionary transitions from land to sea (Brischoux et al. 2012).

We found *Pelamis* to be different from sea kraits (1) in being far less inclined to drink FW (roughly two-fold higher threshold) (2) and in drinking a higher percentage of body water deficits during replenishment (Table 1; Figs. 3 and 4). Drinking a relatively larger volume of water is likely the result of the greater dehydration threshold at which these snakes first drink. Clearly, there is an evolutionary suppression of drinking response in *Pelamis* relative to sea kraits, the latter representing an earlier lineage of elapid sea snakes that evolved marine adaptations independent of the Hydrophiini (Slowinski and Keogh 2000). Because *Pelamis* exhibit a high dehydration threshold before drinking, we could not know the dehydration deficit of snakes before they were dehydrated in the laboratory. Therefore, the

Table 2 Summary of salinity thresholds at which 19 snakes (*P. platurus*) that had been dehydrated to −19.17 ± 4.69% of their original body mass drank brackish or FW when exposed to a regressive series of salinities at the end of the dehydration period

SW	70% SW	50% SW	25% SW	10% SW	0% SW (FW)	No drinking
0	0	4 (9.3 ± 2.6)	5 (15.4 ± 3.0)	2 (13.9 ± 0.8)	3 (6.9 ± 2.0)	5

Table entries for each species indicate the number of snakes drinking from indicated water source when offered in series: 100% SW, 70% SW, 50% SW, 25% SW, 10% SW, 0% SW (FW).
Numbers in parentheses indicate the percentage of the original body mass of water ingested. Numbers are mean ± SE.
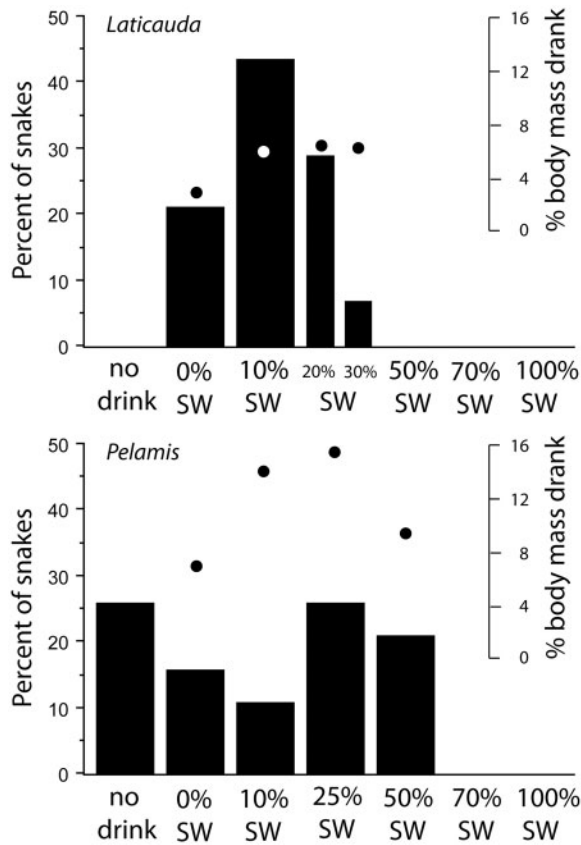
Fig. 5 Percentages of tested snakes that first drank at various salinities when tested in regressive order (100% SW to FW). The dots indicate the mean amounts of water drunk, scaled to the vertical axis on the right-hand side of the graph. The upper graph is based on data reported previously for *Laticauda* species (Lillywhite et al. 2008), and the lower graph illustrates data for *P. platurus* from the present study. All snakes were initially dehydrated to the species' mean threshold for drinking before exposing them to indicated salinities.

true body water deficit might be even greater than those we measured when snakes first drank FW. This fact renders our estimates of drinking threshold to be conservative and possibly contributes to the variation in the drinking responses measured.

Importantly, four of the snakes that were tested for drinking immediately following capture drank FW, thus indicating they were thirsty and, therefore, in a dehydrated state (Bonnet and Brischoux 2008; Lillywhite et al. 2008). We are presently conducting further research to assess the extent to which *Pelamis* are naturally dehydrated at sea.

Our data also indicate that *Pelamis* drink brackish water up to 50% SW, whereas *Laticauda* spp. voluntarily drink brackish water only up to 30% SW (Fig. 5) (Lillywhite et al. 2008). Moreover, 20% of the *Pelamis* we tested did not drink water at all, and one snake refused to drink even after dehydration to a loss of 27% of its body mass. This observation reinforces the conclusion that the drinking response in this species is suppressed (or less sensitive) relative to that of *Laticauda*. Note that at lower salinities, both sea kraits and *Pelamis* drink progressively greater volumes as the salinity of the water increases (Fig. 5). However, there is a tendency in both species for the amount of water ingested to stabilize at higher salinities, and in the case of *Pelamis* to decrease at 50% SW (Fig. 5). This pattern likely reflects a trade-off between the relative amounts of water and salt that are ingested as the salinity of the water increases. None of the numerous snakes we tested ever ingested SW (Lillywhite et al. 2008; this study; unpublished observations).

The evolutionary origin of *P. platurus* is nested within the *Hydrophis* clade of sea snakes, which speciated rapidly within the past 5 Myr (Sanders et al. 2008). This and other species of sea snake conceivably represent middle to late evolutionary transition along a continuum leading to full physiological independence from FW sources. The evolution of viviparity (Sanders et al. 2008) and comparatively high rates of secretion from salt glands (Dunson 1968) bestow hydrophiine sea snakes with a high degree of adaptation to marine life compared with many other marine reptiles, including *Laticauda* spp. These conditions are reflected in a higher degree of

diversification than is characteristic of any of the other groups. Yet, *P. platurus* remains subject to dehydration in marine environments where it retains a capacity to sense and to drink FW.

The only potential sources of FW available to a pelagic species living in the open ocean are (1) fresh or brackish water lenses formed during heavy rains (Tomczak 1995) and (2) water in prey. Digestion of prey, however, incurs losses of water attributable to digestion, defecation, and excretion of salts and nitrogenous wastes via the salt glands and kidney. Increasing theoretical and empirical evidence suggests that consumption of prey might actually incur a net loss, rather than gain, of water (Peterson 1996; Henen et al. 1998; Longshore et al. 2003; Lillywhite et al. 2008; Davis and DeNardo 2010). The extent to which sea snakes of any species drink water from FW lenses in nature remains to be investigated (see also Lillywhite and Ellis 1994).

Dunson and Robinson (1976) also found that fasting *Pelamis* dehydrate in SW, and they documented drinking of FW when it was offered to dehydrated snakes. Snakes kept in SW survive for long periods if fed on FW fish (Dunson and Robinson 1976), but it remains unclear whether these snakes can survive for long periods if kept in full SW and fed marine species of fishes.

As with sea kraits, rates of net water efflux in SW are roughly an order of magnitude less than are those when snakes are in air at the same temperature. We estimated rates of net water loss using data for changes of mass in fasting snakes in SW, using the methods described by Lillywhite et al. (2008, 2009). Such rates of water loss in sea kraits vary with the aquatic tendencies of species, with more fully marine species having the lower rates (Fig. 6). We expected rates of water loss in *Pelamis* to be even lower due to its pelagic habits. Instead, net water efflux in *Pelamis* was intermediate in comparison with the three species of *Laticauda* (Fig. 6). Nonetheless, using the mean rate and assuming that 25% of the loss of mass is attributable to metabolic carbon (Lillywhite et al. 2008), we estimate that *Pelamis* can remain at sea without a source of FW for about 3 months if the lethal dehydration is about 36% of its body mass. The actual rates of net water efflux in nature are likely to be different from those measured in the laboratory, however, due to the influence of temperature, hydrostatic pressure acting on the skin when snakes are below the ocean's surface (87% of the time according to
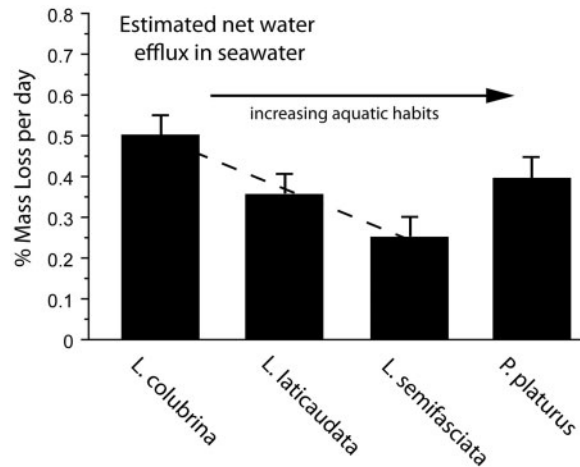

Fig. 6 Estimated rates of net water efflux for snakes kept in SW in the laboratory. Data are based on changes in mass and assume that 25% of the loss of mass is attributable to metabolic carbon (Lillywhite et al. 2008). The data for sea kraits (*Laticauda*) are from Lillywhite et al. (2009).

Rubinoff et al. 1986), and, importantly, behavior. In all likelihood, rates of water loss in freely ranging *Pelamis* are lower than those measured in the laboratory. Similarly, tolerance for dehydration might be greater than we suppose. All these factors require further investigation, which will be difficult due to the pelagic habits of this species. In spite of these limitations, knowledge of water balance in *P. platurus* and its behavioral response to water resources is important because of its position on the scale of evolutionary transition from the terrestrial to the marine habitat.

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