

# Trophic consequences of pelagic life-style in yellow-bellied sea snakes

François Brischoux<sup>1,2,\*</sup>, Harvey B. Lillywhite<sup>1</sup>

<sup>1</sup>Department of Biology, University of Florida, Gainesville, Florida 32611, USA

<sup>2</sup>Centre d'Etudes Biologiques de Chizé, CEBC-CNRS UPR 1934, 79360 Villiers en Bois, France

**ABSTRACT:** Snakes show a close relationship between their own size and that of their prey. This is especially true for marine species that forage on the sea floor. In these sea snakes, body size influences both the depth to which a snake dives and its ability to extract prey from crevices in which they shelter. These factors could be expected to have less influence in the case of strictly pelagic foragers. We examined the trophic ecology of the yellow-bellied sea snake *Pelamis platurus*, which is the only surface-feeding sea snake species. We based our study on 2 independent but complementary datasets: dietary data and stable isotopes. Our results confirm the pelagic trophic ecology of this species. However, in contrast to other marine species, *P. platurus* does not exhibit any ontogenetic shift in prey size despite having a relatively large range of body size. Although prey number increases with a snake's size, our results suggest a limitation on *P. platurus*' ability to accommodate very large prey. Functional attributes that are linked to a pelagic life-style such as swimming performance, buoyancy regulation, and osmoregulation—in addition to possible limitations of prey availability—are likely to constrain the trophic ecology of this species. Future investigations should explore the relative contributions of these different, but not mutually exclusive functional attributes, to unravel the foraging constraints in the context of evolutionary transition to marine life in secondarily marine vertebrates.

**KEY WORDS:** Diet · Marine life · Ontogenetic shift · *Pelamis platurus* · Sea snake · Stable isotopes

Resale or republication not permitted without written consent of the publisher

## INTRODUCTION

Many predatory species exhibit a correlation between their size and the size of the prey which they consume (Vézina 1985). This prey size to predator size relationship is especially tight in gape-limited predators in which morphology impedes processing of the food before ingestion (e.g. fish, Zaret 1980 and snakes, Shine 1991). In these predators, the size of the gape correlates with one or more dimensional measurements of their prey (Werner 1974, Webb 1986, Shine 1991, Arnold 1993, Belk et al. 2001, Hill et al. 2005), and the prey size increases with increasing predator size when prey items are available across a wide range of sizes (Werner & Hall 1974,

Wahl & Stein 1988, Shine 1991, Arnold 1993, DeVries et al. 1998).

In typically gape-limited predators such as snakes, some of the better examples of tight relationships between the size of a predator and its prey occur in both aquatic (Mushinsky et al. 1982, Shine 1986, Houston & Shine 1993, Willson et al. 2010) and marine species (Pernetta 1977, Voris & Moffett 1981, Shetty & Shine 2002, Brischoux et al. 2009, 2011b). In all these cases, the snake's size influences the size (and thus the species) of the prey that is consumed. In addition to gape-limitation, 2 complementary hypotheses have been suggested to explain such coherent trends in marine species (Shine 1991). (1) A snake's body size might determine its ability to dive deeper

\*Email: francois.brischoux@gmail.com

or longer; hence larger snakes can more easily take larger prey because the latter are generally found in relatively deep water (Pernetta 1977, Shine 1986, Shine & Shetty 2001, Shetty & Shine 2002). (2) A snake's body size might determine its ability to probe and successfully extract prey from the crevices in which it shelters (Shine 1991, Brischoux et al. 2009).

Although these hypotheses are compelling for snakes foraging on the seafloor, one would expect the constraints affecting the relationship between the size of a snake and that of its prey to be less severe in pelagic environments. For instance, surface feeding should cancel both the constraints linked to the allometry of diving, and to foraging in crevices. Thus, in pelagic environments, we should expect gape-limitation to be the principal constraint for determining the range of prey that is available to a species. With respect to piscivorous species, small snakes should consume small fish, but large snakes should consume both small and larger fish within the available size range, i.e. species should exhibit an ontogenetic telescope (Arnold 1993, Ménard et al. 2006).

We tested this hypothesis in yellow-bellied sea snakes *Pelamis platurus* (Hydrophiini), the only pelagic, surface-feeding marine snake species (Heatwole 1999). *P. platurus* is widely distributed over the entire tropical Indo-Pacific (Dunson & Ehlert 1971, Hecht et al. 1974, Heatwole 1999). The snakes spend up to 99% of their day-to-day life submerged in the water column (20 to 50 m deep), and they surface either very briefly to breathe or longer to forage on fish that are associated with floating debris (Rubinoff et al. 1986, Brischoux & Lillywhite 2011). We combined conventional dietary data (Klawe 1964, present study) with data for stable isotopes to explore the trophic consequences of pelagic life-style in *P. platurus*.

## MATERIALS AND METHODS

### Field procedures

We sampled a population of *Pelamis platurus* in the Papagayo Gulf, off the Pacific coast of Guanacaste, Costa Rica, during 4 research trips conducted in 2010 and 2011. Snakes were captured when lying motionless at the oceanic surface on slicks (or drift lines) between 07:00 and 10:00 h (Brischoux & Lillywhite 2011). Captured snakes were transferred to the laboratory where they were weighed to the nearest 0.1 g, measured for snout–vent length (SVL,  $\pm 0.5$  cm) and total length (TL,  $\pm 0.5$  cm), and sexed by eversion

of the hemipenes. Each snake was released at its approximate location of capture the following day.

### Diet

Because of the particular pelagic, surface-feeding life-style of *Pelamis platurus*, a precise description and quantification of the diet is complicated. Once a snake feeds, it dives and digests its meal while submerged in the water column. As a consequence, most of the accessible snakes floating at the surface have empty stomachs (~93% in our study). Additionally, if the few individuals captured with prey items in the stomach were forced to regurgitate, the spines of ingested fish might incur severe internal injuries (Brischoux & Bonnet 2009). As a consequence, prey items were opportunistically gathered when they were voluntarily regurgitated by snakes. We gath-

Table 1. *Pelamis platurus*. Identification and size (standard length, SL) of the fish found in yellow-bellied sea snakes in the Papagayo Gulf off Costa Rica. Identical superscript letters associated with measurements of snake snout–vent length (SVL) indicate the same individual snake

Period	Taxon	Prey SL (mm)	Snake SVL (cm)
<b>October 2010</b>			
	<i>Fistularia corneta</i>	70.7	29.0
	Gerreidae	14.2	45.5 <sup>a</sup>
	Gerreidae	11.8	45.5 <sup>a</sup>
	Gerreidae	8.9	45.5 <sup>a</sup>
	Gerreidae	13.9	45.5 <sup>a</sup>
	Gerreidae	16.3	45.5 <sup>a</sup>
	Gerreidae	16	45.5 <sup>a</sup>
	Gerreidae	14.8	45.5 <sup>a</sup>
	<i>Oligoplithes</i> sp.	18.6	45.5 <sup>a</sup>
	<i>Oligoplithes</i> sp.	79.0	32.0
	<i>Opistognathus brochus</i>	39.4	33.5
<b>March 2011</b>			
	Gempylidae	51.5	53.0 <sup>c</sup>
	Gempylidae	41.3	53.0 <sup>c</sup>
	<i>Oligoplithes</i> sp.	120.5	55.5
	Sparidae	13.9	49.5 <sup>b</sup>
	Sparidae	11.9	49.5 <sup>b</sup>
<b>May 2011</b>			
	Gerreidae	15.7	47.0 <sup>d</sup>
	Gerreidae	16.8	47.0 <sup>d</sup>
	Gerreidae	16.7	47.0 <sup>d</sup>
	Gerreidae	14.9	47.0 <sup>d</sup>
	Gerreidae	16.6	41.0 <sup>e</sup>
	Gerreidae	17.7	41.0 <sup>e</sup>
	Gerreidae	16.9	41.0 <sup>e</sup>
	Gerreidae	17.1	41.0 <sup>e</sup>
<b>August 2011</b>			
	Unidentified	24.13	36.5

ered 11 fish from 4 snakes in October 2010, 5 fish from 3 snakes in March 2011, 8 fish from 2 snakes in May 2011, and 1 fish from 1 snake in August 2011 (Table 1). Fish specimens were stored in 90% ethanol and brought to the University of Florida. Fish were counted, measured for standard length (SL,  $\pm 0.1$  cm) and identified to the nearest taxonomic level by fish specialists (W. Smith-Vaniz and R. H. Robins from the Florida Museum of Natural History, D. Johnson and A. Nonaka from the Smithsonian Institution; see Table 1). The staining processes that were required for identification of fish impeded further isotopic analyses of the prey of *P. platurus*. We complemented our data set with published data on prey species (Klawe 1964, Voris & Voris 1983; see Table 2) and number of prey and prey size (given as SL, Klawe 1964). Because Klawe's (1964) data were collected in a different geographic area (Ecuador) and with a different method (dissection) both datasets were analyzed separately.

### Stable isotope analyses

For isotopic analyses, we clipped a small piece of tissue ( $3 \times 3$  mm) from the tip of the tail in a subsample of snakes that were sampled in October 2010. To provide a representative and balanced range of body size, we selected snakes according to 3 categories: young-of-the-year (SVL  $\leq 35$  cm), medium-sized snakes ( $35 < \text{SVL} < 55$  cm) and large snakes (SVL  $\geq 55$  cm). For each size category, we sampled 5 males and 5 females, except for the larger category for which we sampled 6 males and 6 females ( $n = 32$  snakes). Tissue samples were stored in 90% ethanol and brought to the University of Florida for analyses. Tissues were dried

Table 2. *Pelamis platurus*. Fishes recorded as eaten by yellow-bellied sea snakes in different study locations. Some species names have been modified from the original source in accordance with current taxonomy

Family	Taxon	Location	Source
Acanthuridae	<i>Acanthurus xanthopterus</i>	Panama	Kropach (1975)
Atherinopsidae	<i>Melanorhinus cyanellus</i>	Panama	Kropach (1975)
Blenniidae	<i>Hypsoblennius brevipinnis</i>	Panama	Kropach (1975)
	<i>Hypsoblennius</i> sp.	Panama	Kropach (1975)
Carangidae	<i>Caranx caballus</i>	Panama	Kropach (1975)
	<i>Caranx hippos</i> <sup>a</sup>	Ecuador	Klawe (1964)
	<i>Chloroscombrus orqueta</i>	Panama	Kropach (1975)
	<i>Decapterus lajang</i>	South Africa	Visser (1967)
	<i>Hemicaranx bicolor</i>	Panama	Kropach (1975)
	<i>Oligoplithes</i> sp.	Costa Rica	Present study
	<i>Vomer declivifrons</i>	Panama	Kropach (1975)
Chaetodontidae	<i>Chaetodon humeralis</i>	Panama	Kropach (1975)
Clupeidae <sup>b</sup>	–	–	Voris & Voris (1983)
Coryphaenidae	<i>Coryphaena hippurus</i>	Panama	Kropach (1975)
Diodontidae	<i>Diodon histrix</i>	Colombia	Klawe (1964)
Engraulidae	<i>Anchoviella</i> sp.	Panama	Kropach (1975)
	<i>Engraulis</i> sp.	Panama	Kropach (1975)
Fistulariidae	<i>Fistularia corneta</i>	Costa Rica	Present study
	<i>Fistularia corneta</i>	Ecuador	Klawe (1964)
	<i>Fistularia corneta</i>	Panama	Kropach (1975)
Gempylidae	Unidentified	Costa Rica	Present study
Gerreidae	Unidentified	Costa Rica	Present study
Kyphosidae	<i>Kyphosus</i> sp.	Panama	Kropach (1975)
Lobotidae	<i>Lobotes pacificus</i>	Panama	Kropach (1975)
Lutjanidae	<i>Lutjanus</i> sp.	Panama	Kropach (1975)
Mugilidae	<i>Mugil cephalus</i>	Panama	Kropach (1975)
	<i>Mugil curema</i>	Panama	Kropach (1975)
	Unidentified	Ecuador	Klawe (1964)
Mullidae	<i>Mulloidichthys rathbuni</i>	Panama	Kropach (1975)
	<i>Pseudupeneus grandisquamis</i>	Ecuador	Klawe (1964)
Nomeidae	<i>Psenes whiteleggi</i>	South Africa	Visser (1967)
Opistognathidae	<i>Opistognathus brochus</i>	Costa Rica	Present study
Polynemidae	<i>Polydactylus approximans</i>	Ecuador	Klawe (1964)
	<i>Polydactylus approximans</i>	Panama	Kropach (1975)
Pomacentridae	<i>Abudefduf troschelli</i>	Panama	Kropach (1975)
Salmonidae	<i>Selar crumenophthalmus</i>	Ecuador	Klawe (1964)
Scombridae	<i>Auxis</i> sp.	Ecuador	Klawe (1964)
	<i>Thunus albacares</i>	Costa Rica	Klawe (1963)
	Unidentified	Panama	Kropach (1975)
Sparidae	Unidentified	Costa Rica	Present study
Sphyracidae	<i>Sphyracna</i> sp.	Panama	Kropach (1975)
Stromateidae	<i>Peprillus medius</i>	Panama	Kropach (1975)
	Unidentified	South Africa	Visser (1967)
Tetraodontidae	<i>Sphoeroides</i> sp.	Panama	Kropach (1975)

<sup>a</sup>*Caranx hippos* is currently known to occur only in the Atlantic Ocean, and this listing likely represents a misidentification

<sup>b</sup>Further data were not provided in the corresponding publication

in an oven at  $+60^\circ\text{C}$ . Because lipids are depleted in  $^{13}\text{C}$  relative to proteins and carbohydrates (Post et al. 2007), lipids were extracted from samples using

petroleum ether in a Dionex accelerated solvent extractor. The skin of the tail-clips was then removed, finely diced with a scalpel, and analyses were performed on skin samples (i.e. mainly keratin). Of each sample, ~500 µg was weighed and sealed inside a tin capsule. Samples were analyzed for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  in the Stable Isotope Geochemistry Laboratory at the University of Florida, Gainesville.

## RESULTS

### Dietary data

Our study adds 5 new prey species and 4 new fish families to the known diverse diet of *Pelamis platurus* (total of 34 species of fish, from 27 different families; Table 2).

We did not detect any correlation between prey SL and predator TL in either dataset (Papagayo Gulf: Spearman rank correlation,  $r_s = -0.21$ ,  $p > 0.05$ ; Ecuador:  $r_s = -0.13$ ,  $p > 0.05$ ; Fig. 1a). Snakes were shown to feed mostly on prey <60 mm long. Very few snakes had prey >60 mm long, and those belonged to all sizes including young-of-the-year (Fig. 1a, Table 1).

The number of prey and the TL of the predator were not correlated in both datasets (Papagayo Gulf:  $r_s = 0.39$ ,  $p > 0.05$ ; Ecuador:  $r_s = 0.24$ ,  $p > 0.05$ ; Fig. 1b). However, larger snakes tended to feed on a relatively larger number of prey items per feeding bout (Fig. 1b).

Prey number was negatively linked to the mean prey size (Papagayo Gulf:  $r_s = -0.74$ ,  $p < 0.05$ ; Ecuador:  $r_s = -0.47$ ,  $p < 0.05$ ). However, there was no relationship between the number of prey and the mean size for prey <60 mm (Papagayo Gulf:  $r_s = -0.55$ ,  $p > 0.05$ ; Ecuador:  $r_s = -0.30$ ,  $p > 0.05$ ; Fig. 2). All snakes that had fed on prey >60 mm contained only 1 prey item in their stomach, irrespective of the body size (Fig. 2).

### Stable isotope analyses

Overall,  $\delta^{13}\text{C}$  ranged from  $-17.9$  to  $-15.6\text{‰}$  (mean  $-16.6 \pm 0.5\text{‰}$ ) and  $\delta^{15}\text{N}$  ranged from  $12.9$  to  $14.6\text{‰}$  (mean  $13.9 \pm 0.5\text{‰}$ ) (Fig. 3). The size of the snakes did not affect either  $\delta^{15}\text{N}$  or  $\delta^{13}\text{C}$  values ( $F_{1,30} = 0.085$ ,  $r^2 = -0.003$ ,  $p = 0.77$  and  $F_{1,30} = 1.93$ ,  $r^2 = 0.06$ ,  $p = 0.17$ , for  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  respectively; Fig. 3). We did not detect any effect of the sex on snakes' isotopic

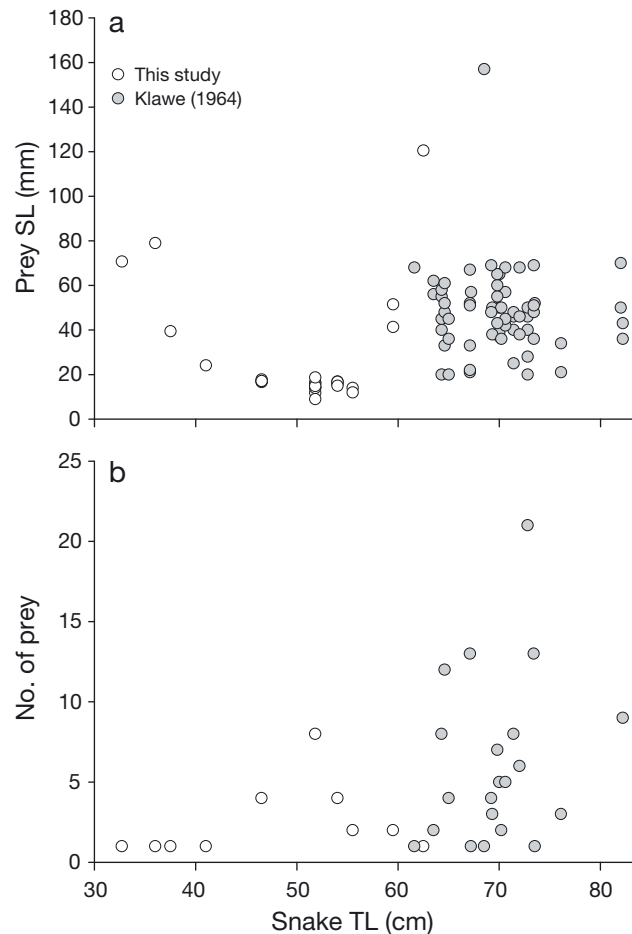


Fig. 1. *Pelamis platurus*. Relationship between snake size (total length, TL) and (a) prey size (standard length, SL) or (b) number of prey, based on our samples and data from Klawe (1964). Most prey items are within a 10 to 60 mm SL range, even those found in very large adult snakes. There is a tendency for larger snakes to feed on a larger number of prey items. Klawe's (1964) data are represented as individual prey measurements when available, and as minimum and maximum values when only the size range was given

signatures (ANOVAs:  $\delta^{15}\text{N} = 13.9 \pm 0.1$  versus  $13.9 \pm 0.1\text{‰}$  for females and males respectively,  $F_{1,30} = 0.004$ ,  $p = 0.95$ ;  $\delta^{13}\text{C} = -16.5 \pm 0.1$  versus  $-16.6 \pm 0.1\text{‰}$  for females and males respectively,  $F_{1,30} = 0.20$ ,  $p = 0.65$ ; Fig. 3).

Accordingly, within sexes the size of the snakes did not affect  $\delta^{15}\text{N}$  ( $\delta^{15}\text{N}$ :  $F_{1,14} = 0.31$ ,  $r^2 = 0.02$ ,  $p = 0.59$  and  $F_{1,14} = 0.77$ ,  $r^2 = 0.05$ ,  $p = 0.39$  for females and males respectively; Fig. 3). However, we detected a positive relationship between the size of the snake and  $\delta^{13}\text{C}$  in females, but not in males ( $F_{1,14} = 5.97$ ,  $r^2 = 0.30$ ,  $p = 0.03$  and  $F_{1,14} = 0.02$ ,  $r^2 = 0.001$ ,  $p = 0.89$  for females and males respectively; Fig. 3).

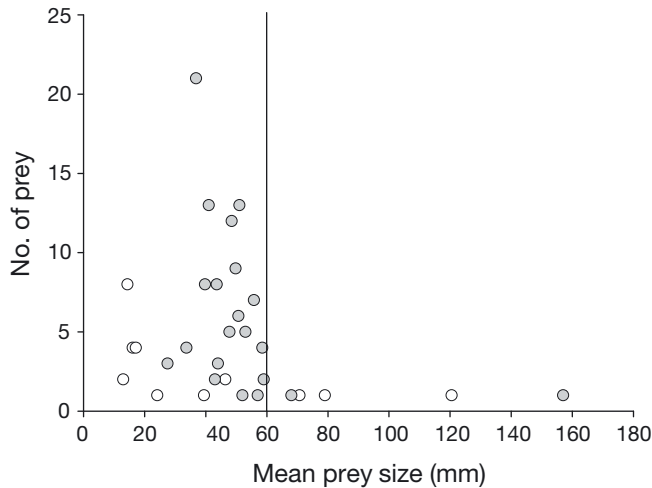


Fig. 2. *Pelamis platurus*. Relationship between mean prey size (standard length, SL) and number of prey, based on (○) our samples and (◐) data from Klawe (1964). Black line: prey size limit above which snakes had only 1 prey item in their stomach. There was no relationship between the number and mean size of prey for items <60 mm

## DISCUSSION

Our data expand the knowledge of the trophic ecology of the most widely distributed sea snake species which forages at the oceanic surface for larval and small fish associated with floating debris (Klawe 1964, Dunson & Ehlert 1971, Voris & Voris 1983, Brischoux & Lillywhite 2011). Both our datasets suggest a lack of ontogenetic shift in foraging ecology presumably linked to the pelagic life history of *Pelamis platurus*. Although we lack isotopic information for all of the potentially available prey, the combination of our conventional dietary data with isotopic signatures is informative and should not generate any spurious patterns (see Brischoux et al. 2011b for similar isotopic assessment of ontogenetic shifts in sea kraits). A complete dataset for isotopic signatures of all prey items, even within a limited geographic region, is not feasible due to the dramatic drifting ecology of *P. platurus* (Sheehy et al. 2012).

*Pelamis platurus* we investigated have mean  $\delta^{13}\text{C}$  signatures of  $-16.6\text{‰}$ , which suggests an oceanic, pelagic life-style in the tropical Pacific waters (Pajuelo et al. 2010). This is largely coherent with previous hypotheses about the ecology of *P. platurus*, which appear to wander broadly over the tropical Indo-Pacific while drifting in response to surface and sub-surface currents (Dunson & Ehlert 1971, Hecht et al. 1974, Rubinoff et al. 1986, 1988, Sheehy et al. 2012). The relationship between body size and

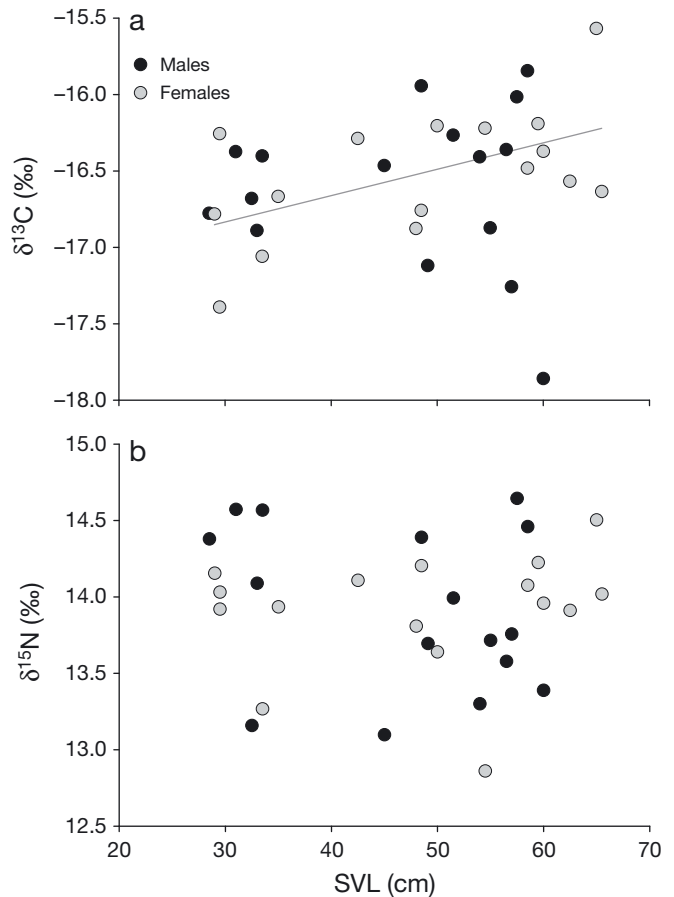


Fig. 3. *Pelamis platurus*. Relationship between female and male snake body length (snout-vent length, SVL) and (a)  $\delta^{13}\text{C}$  or (b)  $\delta^{15}\text{N}$ . The regression line in (a) indicates a statistically significant relationship between SVL and  $\delta^{13}\text{C}$  in females (see 'Results')

$\delta^{13}\text{C}$  suggests possible variations in the use of water masses during the life of female *P. platurus*. Although this result might be an artifact of our sampling, we suggest that it is equally likely to be a major phenomenon to explore owing to its general implications for the population dynamics of *P. platurus*, including putative sex-differences in dispersal strategies or abilities (see e.g. Lane & Shine 2011).

$\delta^{15}\text{N}$  values are similar among size and sex of *Pelamis platurus*, which suggests that whatever their body size, *P. platurus* occupy a similar trophic level and thus feed either on similar prey, or on prey that occupy similar trophic levels. Such a result implies that this species might not show any significant ontogenetic shift in foraging ecology. This hypothesis is supported by the very weak (if any) relationships between the size of predator and prey based on both our and previously published data (Fig. 1, Klawe 1964). Independently of body size, *P. platurus* seems

to be an opportunistic predator that is specialized to feed on relatively small fish that are attracted by floating debris (Klawe 1964, Kropach 1975, Voris & Voris 1983; Table 1). Indeed, a review of the available data shows that this species is known to feed on at least 34 different species of fish, from 27 different families (Table 2), a predictable trophic feature knowing the extensive distributional range of the species.

Although smaller fish are probably more abundant than larger fish underneath slicks where currents converge, relatively large fish species or individuals can also concentrate on slicks (Hunter & Mitchell 1967). Such fish can exceed 50 mm in length but are infrequently found in the stomach of *Pelamis platurus* (e.g. Pacific cornetfish, leatherjackets, bigscale goatfish; Table 1, Klawe 1964). These larger fish are well within the size range of prey theoretically edible by medium-sized or large *P. platurus* which have remarkably long jaws (~6% body length)—a crucial dimension for gape-limited predators such as snakes. Indeed, even young-of-the-year appear able to feed on prey >80 mm (Fig. 1a; see also Kropach 1975). Although large snakes can feed on a larger number of prey per feeding bout compared with smaller snakes (Fig. 1b), our results suggest there is a limitation on the ability of *P. platurus* to accommodate numerous larger prey. Indeed, whatever their body size, snakes feeding on prey >60 mm always had only 1 prey item in their stomach (Fig. 2).

Why longer *Pelamis platurus* do not seem to specifically target large prey items as do most other snakes, especially marine species, is not clear. Although this could simply reflect the relative abundance of small fish available on slicks, we propose 3 complementary hypotheses that are linked to the challenges of pelagic marine habits of snakes and might also bear on their pelagic trophic ecology. (1) Feeding on very small prey might allow a significant reduction in the bodily distension linked to the presence of a bulky prey in the stomach, which can greatly affect swimming ability (Shine 1988, Brischoux & Shine 2011, Brischoux et al. 2011a). Perhaps more importantly, bodily distension and the obligate stretching of skin might also affect skin permeability, and thus the susceptibility of *P. platurus* to dehydration in seawater (Lillywhite et al. 2012). Targeting specifically small fish (even in relatively large numbers, Fig. 1) should allow *P. platurus* to decrease the magnitude of bodily distension and thus reduce any subsequent locomotory or osmoregulatory detrimental effects. (2) As *P. platurus* spends most of the time in the water column (up to 99%, Rubinoff et al. 1986), drifting at a specific

depth range might require finely-tuned control of buoyancy. Having a large meal in its stomach might affect a snake's buoyancy by directly changing its density (Graham et al. 1975). In addition, the very elongated lung of *P. platurus* is thought to play a role similar to that of an air-bladder (Graham et al. 1975). Large prey in a snake's stomach, and the resulting localized lung compression, will likely affect movements of the air volume along the snake's body length and thereby impede the control of a snake's position. (3) As larger prey might take disproportionately longer to be ingested (Shine 1991), we can speculate that the time required to swallow a large fish would significantly increase either the quantity of saltwater ingested incidentally or the contact time between the thin oral mucosa and seawater. Both processes could inevitably affect a snake's osmotic balance, resulting in a significant energy expenditure linked to salt gland functioning (Schmidt-Nielsen 1983).

In summary, although the specialization of *Pelamis platurus* on a relatively large number of small or larval pelagic fish might be driven primarily by the prey that are available on slicks, there are other constraints linked to pelagic life-style in secondary marine vertebrates, such as efficient swimming, buoyancy regulation, and osmoregulation, that might play significant roles in the foraging ecology of *P. platurus*. Other species of hydrophiine sea snakes also show foraging specialization toward very small prey (e.g. fish eggs in the turtle-headed sea snakes *Emydocephalus annulatus* and *E. ijimae*, or the marbled sea snakes *Aipysurus eydouxii* and *A. mosaicus*; Voris 1966, Voris & Voris 1983, Sanders et al. 2012). Further studies could usefully explore the relative contributions of these different—but not mutually exclusive—hypotheses to unravel the foraging constraints in the context of the evolutionary transition to marine life in secondarily marine vertebrates.

*Acknowledgements.* We thank Joe Pfaller, Coleman Sheehy, Harold Heatwole and Joel Wixson for assistance in the field. Adán Barrera provided boat transportation and helped to locate slicks and snakes. Alejandro Solórzano and Mahmood Sasa helped with securing and managing the permits (018-2009-ACAT, DNOP-002-2010, DGT-013-04-2010). Serge Boucher provided kind assistance with lodging and other logistical support. We are grateful to William Smith-Vaniz and Robert H. Robins from the FLMNH and to David Johnson and Ai Nonaka from the Smithsonian Institution for fish identification. We thank Hannah Vander Zanden for her crucial help during removal of lipids from tissues, and Jason Curtis for isotope analyses. Thomas Fauvel, Yves Cherel, Luca Luiselli and 2 anonymous referees commented on earlier versions of the paper. Funding was provided by National Science Foundation grant IOS-0926802 to H.B.L., and by the CNRS (France).

## LITERATURE CITED

- Arnold SJ (1993) Foraging theory and prey-size-predator size relations in snakes. In: Seigel RA, Collins JT (eds), Snakes: ecology and behavior. McGraw-Hill, New York, NY, p 87–115.
- Belk MC, Whitney MJ, Schaalje GB (2001) Complex effects of predators: determining vulnerability of the endangered June sucker to an introduced predator. *Anim Conserv* 4:251–256
- Brischoux F, Bonnet X (2009) Life history of sea kraits in New Caledonia. *Memoir Mus Natl Hist* 198:133–147
- Brischoux F, Lillywhite HB (2011) Light- and flotsam-dependent 'float-and-wait' foraging by pelagic sea snakes (*Pelamis platurus*). *Mar Biol* 158:2343–2347
- Brischoux F, Shine R (2011) Morphological adaptations to marine life in snakes. *J Morphol* 272:566–572
- Brischoux F, Bonnet X, Shine R (2009) Determinants of dietary specialization: a comparison of two sympatric species of sea snakes. *Oikos* 118:145–151
- Brischoux F, Bonnet X, Shine R (2011a) Conflicts between reproduction and feeding in amphibious snakes (sea kraits, *Laticauda* spp.). *Austral Ecol* 36:46–52
- Brischoux F, Bonnet X, Cherel Y, Shine R (2011b) Isotopic signatures, foraging habitats and trophic relationships between fish and seasnakes on the coral reefs of New Caledonia. *Coral Reefs* 30:155–165
- DeVries DR, Bremigan MT, Stein RA (1998) Prey selection by larval fishes as influenced by available zooplankton and gape limitation. *Trans Am Fish Soc* 127:1040–1050
- Dunson WA, Ehlert GW (1971) Effects of temperature, salinity, and surface water flow on distribution of the sea snake *Pelamis*. *Limnol Oceanogr* 16:845–853
- Graham JB, Gee JH, Robison FS (1975) Hydrostatic and gas exchange functions of the lung of the sea snake *Pelamis platurus*. *Comp Biochem Physiol* 50:477–482
- Heatwole H (1999) Sea Snakes. Australian Natural History Series. University of New South Wales Press, Sydney
- Hecht MK, Kropach C, Hecht BM (1974) Distribution of the yellow-bellied sea snake, *Pelamis platurus*, and its significance in relation to the fossil record. *Herpetologica* 30:387–396
- Hill JE, Nico LG, Cichra CE, Gilbert CR (2005) Prey vulnerability to peacock cichlids and largemouth bass based on predator gape and prey body depth. *Proc Annu Conf Southeastern Assoc Fish Wildlife Agencies* 58:47–56.
- Houston DL, Shine R (1993) Sexual dimorphism and niche divergence: feeding habits of the Arafura filesnake. *J Anim Ecol* 62:737–749
- Hunter JR, Mitchell CT (1967) Association of fishes with flotsam in the offshore waters of Central America. *Fish Bull* 66:13–29
- Klawe WL (1963) Observations on the spawning of four species of tuna (*Neothunnus macropterus*, *Katsuwonus pelamis*, *Auxis thazard* and *Euthynnus lineatus*) in the Eastern Pacific Ocean, based on the distribution of their larvae and juveniles. *Inter-Am Trop Tuna Com Bull* 6: 447–540
- Klawe WL (1964) Food of the black-and-yellow sea snake, *Pelamis platurus*, from Ecuadorian coastal waters. *Copeia* 1964:712–713
- Kropach CM (1975) The yellow-bellied sea snake, *Pelamis*, in the Eastern Pacific. In: Dunson WA (ed) *Biology of the sea snakes*. University Park Press, Baltimore, MD, p 185–213
- Lane A, Shine R (2011) Intraspecific variation in the direction and degree of sex-biased dispersal among sea-snake populations. *Mol Ecol* 20:1870–1876
- Lillywhite HB, Brischoux F, Sheehy CM III, Pfaller JB (2012) Dehydration and drinking responses in a pelagic sea snake. *Integr Comp Biol* 52:227–234
- Ménard F, Labruno C, Shin YJ, Asine AS, Bard FX (2006) Opportunistic predation in tuna: a size-based approach. *Mar Ecol Prog Ser* 323:223–231
- Mushinsky HR, Hebrard JJ, Vodopich DS (1982) Ontogeny of water snake foraging ecology. *Ecology* 63:1624–1629
- Pajuelo M, Bjorndal KA, Alfaro-Shigueto J, Seminoff JA, Mangel JC, Bolten AB (2010) Stable isotope variation in loggerhead turtles reveals Pacific–Atlantic oceanographic differences. *Mar Ecol Prog Ser* 417:277–285
- Pernetta JC (1977) Observations on the habits and morphology of the sea snake *Laticauda colubrina* (Schneider) in Fiji. *Can J Zool* 55:1612–1619
- Post DM, Layman CA, Arrington DA, Takimoto G, Quattrochi J, Montaña CG (2007) Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. *Oecologia* 152:179–189
- Rubinoff I, Graham JB, Motta J (1986) Diving of the sea snake *Pelamis platurus* in the Gulf of Panama. I. Dive depth and duration. *Mar Biol* 91:181–191
- Rubinoff I, Graham JB, Motta J (1988) Diving of the sea snake *Pelamis platurus* in the Gulf of Panama. II. Horizontal movement patterns. *Mar Biol* 97:157–163
- Sanders KL, Rasmussen AR, Elmberg J, Mumpuni, Guinea M, Bias P, Lee MSY, Fry BG (2012) *Aipysurus mosaicus*, a new species of egg-eating sea snake (Elapidae: Hydrophiinae), with a redescription of *Aipysurus eydouxii* (Gray, 1849). *Zootaxa* 3431:1–18
- Schmidt-Nielsen K (1983) Animal physiology: adaptation and environment. Cambridge University Press, Cambridge
- Sheehy CM III, Solórzano A, Pfaller JB, Lillywhite HB (2012) Preliminary insights into the phylogeography of the yellow-bellied sea snake, *Pelamis platurus*. *Integr Comp Biol* 52:321–330
- Shetty S, Shine R (2002) Sexual divergence in diet and morphology in Fijian sea snakes, *Laticauda colubrina* (Laticaudidae). *Austral Ecol* 27:77–84
- Shine R (1986) Sexual differences in morphology and niche utilization in an aquatic snake, *Acrochordus arafurae*. *Oecologia* 69:260–267
- Shine R (1988) Constraints on reproductive investment: a comparison between aquatic and terrestrial snakes. *Evolution* 42:17–27
- Shine R (1991) Why do larger snakes eat larger prey items? *Funct Ecol* 5:493–502
- Shine R, Shetty S (2001) Moving in two worlds: aquatic and terrestrial locomotion in sea snakes (*Laticauda colubrina*, Laticaudidae). *J Evol Biol* 14:338–346
- Vézina AF (1985) Empirical relationships between predator and prey size among terrestrial vertebrate predators. *Oecologia* 67:555–565
- Visser J (1967) Color varieties, brood size, and food of South African *Pelamis platurus* (Ophidia: Hydrophiidae). *Copeia* 1967:219
- Voris HK (1966) Fish eggs as the apparent sole food item for a genus of sea snake, *Emydocephalus* (Kreffft). *Ecology* 47:152–154
- Voris HK, Moffett MW (1981) Size and proportion relationship between the beaked sea snake and its prey. *Biotropica* 13:15–19

- Voris HK, Voris HH (1983) Feeding strategies in marine snakes: an analysis of evolutionary, morphological, behavioral and ecological relationships. *Am Zool* 23: 411–425
- Wahl DH, Stein RA (1988) Selective predation by three esocids: the role of prey behavior and morphology. *Trans Am Fish Soc* 117:142–151
- Webb PW (1986) Effects of body form and response threshold on the vulnerability of four species of teleost prey attacked by largemouth bass (*Micropterus salmoides*). *Can J Fish Aquat Sci* 43:763–771
- Werner EE (1974) The fish size, prey size, handling time relation in several sunfishes and some implications. *J Fish Res Board Can* 31:1531–1536
- Werner EE, Hall DJ (1974) Optimal foraging and the size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). *Ecology* 55:1042–1052
- Willson JD, Winne CT, Pilgrim MA, Romanek CS, Gibbons JW (2010) Seasonal variation in terrestrial resource subsidies influences trophic niche width and overlap in two aquatic snake species: a stable isotope approach. *Oikos* 119:1161–1171

*Editorial responsibility: Matthias Seaman, Oldendorf/Luhe, Germany*

*Submitted: July 3, 2012; Accepted: November 14, 2012  
Proofs received from author(s): March 5, 2013*