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Marine Snake Epibiosis: A Review and First Report of Decapods Associated with *Pelamis platurus*

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Synopsis Under circumstances in which area for settlement is limited, the colonization of living substrata may become a highly valuable strategy for survival of marine invertebrates. This phenomenon, termed epibiosis, results in spatially close associations between two or more living organisms. *Pelamis platurus*, the yellow-bellied sea snake, is the only exclusively pelagic marine snake and its propensity for foraging along ocean slicks facilitates its colonization by pelagic epibionts. Herein, we report epibionts associated with *P. platurus* inhabiting the waters off the northwestern Pacific coast of Costa Rica. These associations include the first records of decapod epibionts from any marine snake. Decapod epibionts were found on 18.9% of *P. platurus*, and size of snake (total length) had a significant positive effect on the frequency and intensity of epibiosis. We discuss the spatial and ecological mechanisms that facilitate these interactions, as well as the suite of factors that either promote or deter epibiosis and ultimately dictate the frequency and intensity of these interactions. Finally, we provide a review of marine snake epibiosis. The intention of this review is to (1) provide contemporary researchers with a single, accessible reference to all known reports of epibionts associated with marine snakes and (2) discuss what is currently known with respect to diversity of epibionts from marine snakes.

Introduction

Competition for space is a major factor affecting the ability of marine invertebrates to successfully colonize a given substratum (Enderlein and Wahl 2004). Under circumstances in which area for settlement is limited—whether by high population densities (e.g., on benthic structures) or by low availability of substrata (e.g., on pelagic flotsam)—colonization of living substrata may become a highly valuable strategy for survival of marine invertebrates (Wahl 1989). This phenomenon, termed epibiosis, results in spatially close associations between two or more living organisms (Harder 2009), in which a single host (or basibiont) supports one or more typically facultative colonizers (or epibionts) (Wahl and Mark 1999). The relative costs and benefits of colonizing living hosts

are likely different among epibiont species and ultimately determine the composition of the epibiotic assemblages.

Marine snakes—Laticaudinae, Hydrophiini, and Acrochordidae—are common and conspicuous inhabitants of the warm tropical waters of the Indian and Pacific Oceans, and are known to host a variety of sessile epibionts (Zann et al. 1975). The study of epibiosis in marine snakes has a scattered history of anecdotal reports starting with Cantor (1841) and Darwin (1851, 1854), and very few accounts quantify the frequency of these interactions (Jeffries and Voris 1979; Key et al. 1995). Moreover, there has been limited discussion of the complex suite of factors that affect these interactions and the possible role that marine snakes play as epibiont hosts. In most

Table 1 Decapod epibionts associated with *Pelamis platurus* in Pacific Costa Rica

Decapod epibionts	Stage	2010			2011			Total (391)	I_0	F_0 (%)
		April (37)	June (100)	October (81)	March (49)	May (52)	July (72)			
Caridea (shrimps)										
<i>Macrobrachium</i> sp.	J	0 (0)	0 (0)	5 (3)	2 (2)	0 (0)	6 (4)	13 (9)	1.44	2.3
<i>Atya</i> sp.	J	0 (0)	0 (0)	13 (5)	0 (0)	0 (0)	7 (7)	20 (12)	1.67	3.1
Brachyura (crabs)										
Grapsidae	M	12 (10)	26 (12)	24 (12)	6 (5)	33 (6)	8 (7)	109 (52)	2.1	13.3
<i>Planes major</i> ^a	J	1 (1)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (1)	NA	0.3
<i>Plagusia squamosa</i>	M	4 (2)	1 (1)	2 (2)	0 (0)	2 (2)	0 (0)	9 (7)	1.29	1.8
<i>Portunus affinis</i>	J	2 (1)	0 (0)	1 (1)	1 (1)	0 (0)	1 (1)	5 (4)	1.25	1.0
Total		19 (13 ^b)	27 (13)	45 (17 ^b)	9 (6 ^b)	35 (8)	22 (17 ^b)	157 (74 ^b)	2.12	18.9
F_0 (%)		35.1 ^c	13.0	21.0	12.2	15.4	23.6	18.9	–	–

Notes. All parenthetical references indicate numbers of snakes. The duration of each field survey changed across the study period: April 2010 (4 days); June 2010 (10 days); October 2010 (13 days); March 2011 (7 days); May 2011 (7 days); July 2011 (8 days). I_0 , mean intensity of epibiosis (only snakes hosting at least one epibiont); F_0 , overall frequency of epibiosis (all snakes encountered); J, juvenile; M, megalopa.

^aThis taxon is also in the family Grapsidae.

^bSome *P. platurus* hosted more than one decapod taxon causing the “total” number of snakes (in parentheses) to be less than the sum within the column: three hosted grapsid megalopae and *Atya* sp.; two hosted grapsid megalopae and *Macrobrachium* sp.; one hosted grapsid megalopae and *P. affinis*; one hosted *P. squamosa* and *Atya* sp.; one hosted *P. squamosa*, *Atya* sp., and *P. affinis*; one hosted grapsid megalopae, *Macrobrachium* sp., and *P. affinis*.

^cSurvey for which we found a higher proportion of snakes hosting decapod epibionts compared to pooled data for the five other surveys (proportion test).

cases, these associations are assumed to be detrimental to the snakes (Pickwell 1971; Zann et al. 1975). Certain behaviors (“knotting” and frequent shedding) and physical attributes (e.g., color pattern) are thought to be antifouling mechanisms (Pickwell 1971; Shine et al. 2010).

Herein, we report epibionts associated with *Pelamis platurus* inhabiting the waters off the northwestern Pacific coast of Costa Rica. These associations include the first records of decapod epibionts from any marine snake. The primary goal of this study is to better understand these novel associations by (1) quantifying the frequency and intensity of their occurrence during six field surveys encompassing 15 months and (2) assessing the effect of size of snake on these interactions. The secondary goal of this study is to provide a review of marine snake epibiosis, including a summary of all known references to epibionts of marine snakes.

Methods

Study area

The Gulf of Papagayo is located off the northwestern Pacific coast of Guanacaste, Costa Rica, and spans

~1100 km² between the Santa Elena Peninsula to the north and the Nicoya Peninsula to the south. The average water depth is 10–60 m, and the average water temperature ranges from 21degC to 31degC (Jiménez et al. 2001). The climate of the Gulf of Papagayo and the adjacent Guanacaste Province is characterized by distinct dry (December–April) and rainy (May–November) seasons (Bednarski and Morales-Ramírez 2004), a factor that is associated with seasonal upwelling events in the area (Jiménez et al. 2001; Jiménez and Cortes 2003) and is known to affect the abundance of floating debris (Thiel and Gutow 2004).

Sampling

During the six field surveys between April 2010 and July 2011, individual *P. platurus* were captured by hand or net from a small boat while floating along ocean slicks—surface currents that tend to concentrate floating debris. Each day snakes were collected between 0700 and 1100 h for 1–4 h depending on the abundance of snakes. Immediately after capture, snakes were visually inspected for epibionts and placed in individually labeled mesh bags. Epibionts were placed in separate vials of 70% ethanol and

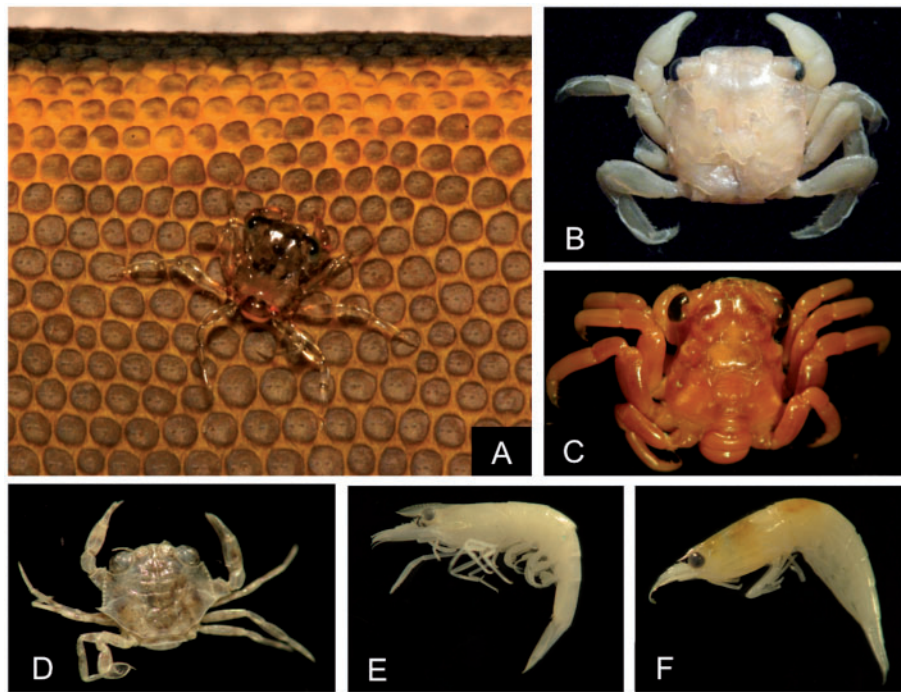


Fig. 1 Decapod epibionts from *P. platurus* in Pacific Costa Rica (A) Megalopal crab of the family Grapsidae on the side of *P. platurus*, (B) juvenile *P. major*, (C) megalopa of *P. squamosa*, (D) juvenile *P. affinis*, (E) juvenile *Macrobrachium* sp., and (F) juvenile *Atya* sp.

returned to the laboratory to be identified to the lowest taxonomic level possible, using a dissecting microscope equipped with an ocular micrometer. Standard body-size measurements were taken for each specimen and are reported as mean \pm SE. Snakes were returned to the laboratory, measured for total length (TL) (from the anterior tip of the head to the posterior tip of the tail) using a tape measure, and released the following day.

Statistical analyses

Overall frequency of epibiosis (F_0) was derived for each taxon separately and for all taxa combined by dividing the number of snakes hosting the epibionts by the total number of snakes surveyed. This value was derived for each field survey and for all surveys combined. The intensity of epibiosis was the number of epibionts per snake, and mean intensity (I_0) was derived for each epibiont taxon and all taxa combined for snakes hosting at least one epibiont. Nondecapod epibionts were not sampled consistently; thus, data on the frequency and intensity of occurrence were insufficient for statistical quantification.

To test for differences in occurrence of epibionts among the six field surveys, we used a series of

proportion tests in which the proportion of snakes hosting epibionts from each survey was compared against the pooled data from the other five surveys (Bonferroni correction for six tests: corrected alpha = 0.008). Data for the six field surveys were then pooled. To test if snake size affected the overall frequency of epibiosis (F_0), we performed a binomial logistic regression. Finally, to test if snake size had an effect on the intensity of epibiosis when epibionts were present (I_0), we used a Poisson regression (log-link function). All statistical analyses were performed in R for Windows v. 2.8.1 (R Development Core Team 2008).

Results

A total of 391 *P. platurus* was collected during the six field surveys. The number of snakes collected during each field survey varied depending on the duration of the survey (Table 1). Of the 391 snakes, 74 individuals (18.9%) hosted 157 decapod epibionts (range = 1–14 per snake) (Table 1). The survey conducted in April 2010 was the only survey in which the proportion of snakes hosting epibionts was significantly higher than the pooled data (proportion test: Pearson's $X^2 = 7.94$, $df = 1$, $P = 0.005$).

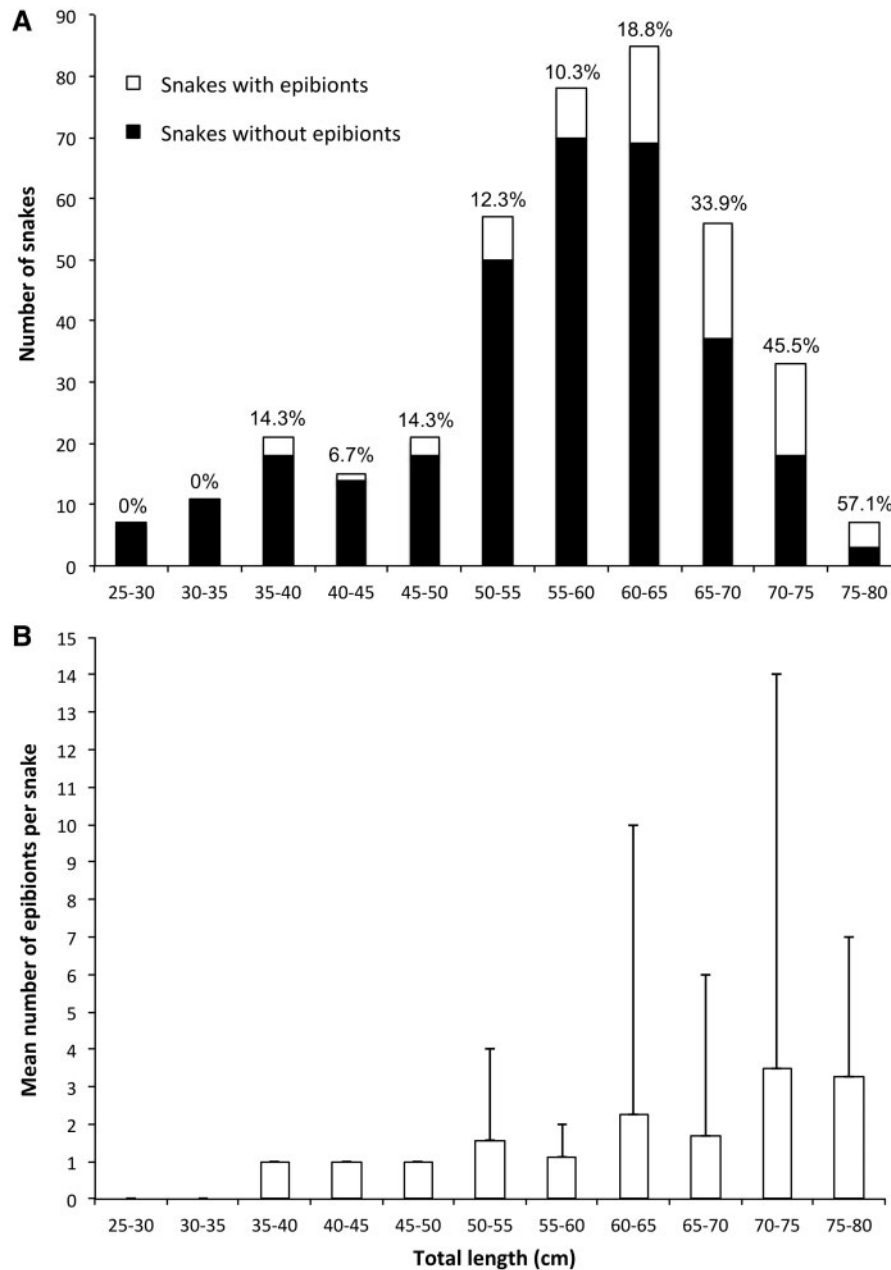


Fig. 2 Frequency and intensity of epibiosis against size of *P. platurus* in Pacific Costa Rica ($n = 391$). **(A)** Histogram showing the distribution of sizes of *P. platurus* (total length; TL). White bars and data labels indicate the number and frequency (F_0) of snakes hosting epibionts, respectively. **(B)** Mean number of epibionts per snake (l_0). Y-bars indicate the maximum number of epibionts observed in each snake size increment. Snakes on the border of two size increments were placed in the larger increment.

Of the 157 decapod epibionts, four brachyuran crabs and two caridean shrimps were identified (Table 1, Fig. 1). The crab taxa include megalopae of the family Grapsidae ($n = 109$, range = 1–14 per snake; mean carapace length/width = 2.57 ± 0.32 mm/ 1.86 ± 0.29 mm), megalopae of *Plagusia squamosa* ($n = 9$;

range = 1–2 per snake; mean CL/CW = 4.83 ± 0.98 mm/ 3.6 ± 0.83 mm), juvenile *Portunus affinis* ($n = 5$; range = 1–2 per snake; mean CL/CW = $2.8 \pm 0.7/3.87 \pm 0.75$ mm), and a juvenile *Planes major* ($n = 1$; CL/CW = $4.7/4.0$ mm), a taxon also in the family Grapsidae (Fig. 1A–D). The shrimp taxa

include juvenile *Atya* sp. ($n=20$; range=1–6 per snake; mean TL = 11.76 ± 1.56 mm) and juvenile *Macrobrachium* sp. ($n=13$; range=1–2 per snake; mean TL = 10.83 ± 1.13 mm) (Fig. 1E–F). Seventy-six individual *P. platurus* hosted just one decapod taxon, seven hosted two, and two hosted three (Table 1).

The percentage of snakes hosting decapod epibionts (F_0) increased with the size of the snake (Fig. 2A), and the snake size had a significant positive effect on the frequency of epibiosis (binomial logistic regression: $g(x) = -6.22 + 0.08$ (TL), z -value = 4.93, $df=390$, $P < 0.0001$). The mean number of decapod epibionts per snake (I_0) increased with the snake size (Fig. 2B), and the snake size had a significant positive effect on the intensity of epibiosis (Poisson regression: $\log(x) = -1.38 + 0.033$ (TL), z -value = 3.32, $df=73$, $P = 0.0009$).

Seven nondecapod epibionts were also identified (Table 2): *Atlanta inclinata* (snail, Atlantidae), *Obelia longissima* (hydroid, Campanulariidae), *Lepas anatifera* (barnacle, Lepadidae), *Conchoderma virgatum* (barnacle, Lepadidae), *Platylepas hexastylus* (barnacle, Platylepadidae), *Ascidia ceratodes* (tunicate, Ascidiidae), and *Tomiodon* sp. (fish, Gobiessocidae). See Table 2 for size measurements of representative nondecapod specimens. The frequency and intensity of epibiosis of these taxa were not quantified.

Discussion

Pelamis platurus is considered the only exclusively pelagic marine snake and is well known for its propensity for floating along ocean slicks—surface currents that tend to concentrate pelagic organisms and floating debris (Shanks 1983; Kingsford and Choat 1986). Most reports suggest that *P. platurus* aggregates on slicks when foraging for small pelagic fishes (Kropach 1971, 1975; Heatwole 1999), which tend to seek refuge beneath floating debris (Hunter and Mitchell 1967). In addition, aggregating on slicks might provide abundant mating opportunities (Kropach 1971). Whether *P. platurus* actively pursues slicks or passively drifts into them is still a matter of some debate (Lillywhite et al. 2010; Brischoux and Lillywhite 2011). Nevertheless, for a pelagic “float-and-wait” predator (Brischoux and Lillywhite 2011), the dense faunal concentrations found along ocean slicks increase the opportunity of encountering possible prey items and facilitate the colonization of organisms that are commonly found among pelagic

rafting communities (Kropach 1975; Thiel and Gutow 2005).

Decapod epibionts associated with *P. platurus*

Pelamis platurus in Costa Rica hosts a diverse array of decapod crustaceans, all of which represent previously undocumented epibionts of marine snakes. Collectively, these decapods were found on 18.9% of snakes, suggesting that these associations are not inconsequential. The most frequent ($F_0 = 13.3\%$) and most intense ($I_0 = 2.1$) of these epibiotic associations was from crab megalopae of the family Grapsidae *sensu stricto* (Ng et al. 2008). The specific identities of these megalopae could not be determined because megalopae of different grapsid species are morphologically very similar, and formal descriptions of some species are either insufficient or lacking. These specimens may represent up to six different grapsid species known to inhabit Pacific Costa Rica (*Grapsus grapsus*, *Goniopsis pulchra*, *Geograpsus lividus*, *Pachygrapsus socius*, *Planes marinus*, and *P. major*) (Vargas and Wehrmann 2009). The *Planes* crabs are plausible candidates as they are obligate rafters of flotsam and pelagic organisms (Donlan and Nelson 2003; Frick et al. 2011), and a juvenile *P. major* was found on *P. platurus* in this study. However, presence of other species cannot be ruled out. We are currently conducting molecular phylogenetic analyses to determine the specific identities of these megalopae. To a far lesser extent ($F_0 < 4\%$, $I_0 < 2$), *P. platurus* also hosts megalopal and juvenile stages of four other decapod taxa common to Pacific Costa Rica (*P. squamosa*, *P. affinis*, *Macrobrachium* sp., and *Atya* sp.).

The life stages represented by these decapod epibionts (either megalopal or juvenile) suggest that these individuals are making the transition from the plankton to their respective adult habitats (Dittel and Epifanio 1990; Anger 2001). Slicks are important features that might mediate these transitions (Shanks 1983, 1995). First, slicks tend to concentrate larval decapods and floating debris, providing rafting opportunities for settling larvae. Clinging to floating debris may provide protection from predators (Mitchell and Hunter 1970; Moreira et al. 2007) and allow larvae to remain at the surface by avoiding the downwelling currents inherent in the formation of slicks (Shanks 1985; Kingsford and Choat 1986). This phenomenon may be particularly important for obligate and facultative rafting taxa (*P. major* and *P. squamosa*, respectively), which must acquire a raft prior to metamorphosing and

Table 2 Nondecapod epibionts associated with *Pelamis platurus* in Pacific Costa Rica

Nondecapod epibiont	n	Body size (measurement) (mm)	New record for <i>P. platurus</i>	New record for marine snakes
Gastropoda				
<i>Atlanta inclinata</i>	3	1.0–1.5 (AL)	✓	✓
Hydrozoa				
<i>Obelia longissima</i>	15	0.5–2.3 (PH)	✓	✓
Cirripedia				
<i>Lepas anatifera</i>	15	3.4–18.5 (TH)	✓	–
<i>Conchoderma virgatum</i>	14	12.4–29.5 (TH)	–	–
<i>Platylepas hexastylus</i> ^a	1	2.5 (RCD)	–	–
Chordata				
<i>Ascidia ceratodes</i>	1	1.25 (TL)	✓	✓
<i>Tomocodon</i> sp.	1	15.0 (TL)	✓	✓

Notes. The frequency and intensity of nondecapod epibionts were not quantified. AL, axis length; PH, polyp height; TH, total height; RCD, rostro-carinal diameter; TL, total length.

^a*Platylepas indicus*, *P. krugeri*, *P. ophiophilus*, and *P. hexastylus* likely represent the same species, *P. hexastylus* variety (*sensu* Pilsbry, 1916); therefore, this taxon is not considered a new record.

beginning their pelagic existence. For these rafting taxa, upwelling events during the dry season may facilitate offshore transport (Jiménez et al. 2001; Jiménez and Cortes 2003). Second, under certain conditions, slicks will move shoreward (Shanks 1983, 1985, 1995), providing a mechanism for the recruitment of larvae to the habitats where adult populations are located. Clinging to floating debris also being transported shoreward may be energetically advantageous (Shanks 1985; Wehrmann and Dittel 1990) and would enable larvae to access favorable shoreward surface currents (Shanks 1983, 1995; Moreira et al. 2007). Megalopal-stage grapsid crabs mostly recruit either to rocky intertidal or mangrove habitats (Rathbun 1918; Shanks 1995), whereas the juvenile amphidromous shrimps (*Macrobrachium* sp. and *Atya* sp.) migrate from inland to freshwater streams and rivers (Wehrmann and Dittel 1990; Bauer and Delahoussaye 2008; Bauer 2011). Postmegalopal portunid crabs, like *P. affinis*, may recruit to neritic habitats or remain in the pelagic environment where free swimming juveniles and adults often seek shelter among floating debris (Stoner and Greening 1984). For these amphidromous and intertidal taxa, shoreward transport may

be disrupted during the dry season when upwelling events tend to drive surface water offshore (Jiménez et al. 2001; Jiménez and Cortes 2003).

The mutual attraction to slicks by larval decapods and *P. platurus*, and the tendency for larval decapods to cling to floating debris, provide the necessary ecological and spatial overlap required for epibiosis. Once in relatively close proximity, however, there is a suite of factors that may affect these interactions. These factors fall into three main groupings: (1) physical factors, (2) ecological factors that promote epibiosis, and (3) ecological factors that deter epibiosis. The relative importance of these factors will ultimately determine the frequency and intensity of these interactions.

Epibiosis of *P. platurus* by larval decapods might simply be a function of surface area availability, a purely physical factor. The relative abundance of *P. platurus* and flotsam on a given slick can vary considerably (Kropach 1975; Shanks 1983), and this may affect the frequency of epibiosis by changing the relative surface area provided by floating *P. platurus*. If larval decapods opportunistically cling to floating items (Shanks 1985), then the frequency of epibiosis may simply be proportional to the available surface area that *P. platurus* represents. When settlement area is limited (i.e., low abundance of flotsam), *P. platurus* may provide an important platform for larval decapods, at least temporarily. Conversely, when the relative abundance of flotsam increases, colonization of *P. platurus* become less important and therefore less frequent. This explanation is consistent with our observation that a significantly higher proportion of snakes was found hosting epibionts at the end of the dry season (April 2010), a period when flotsam is relatively sparse (J.B.P, personal observation). In addition, we found that snake size had a significant positive effect on the frequency and intensity of epibiosis, suggesting that the additional surface area provided by larger snakes is an important factor affecting these associations. Because surface area will increase with the square of snake length, longer *P. platurus* provide a proportionately greater area for settlement. Our data support the hypothesis that these associations are opportunistic and at least somewhat driven by available surface area.

Next, there are ecological factors that may act to promote epibiosis and increase the frequency and intensity of these associations. Most notably, *P. platurus* is highly venomous (Shipmen and Pickwell 1973) and unpalatable to many predatory fishes

(Rubinoff and Kropach 1970; Weldon 1988). For these reasons, epibiosis may be advantageous to larval decapods when predation pressure is high. As previously mentioned, predation may be an important factor causing larval decapods to cling to floating debris (Mitchell and Hunter 1970; Moreira et al. 2007); thus, active selection of *P. platurus* as a host may further reduce risk of predation. Another factor that may promote these associations would be a cleaning mutualism. *Pelamis platurus*, which generally does not tolerate debris attached to its skin (Zann et al. 1975), may tolerate the larval decapods if the decapods consume other potentially harmful epibionts (e.g., barnacle cyprids) or rid the snake of unshed skin. In turn, larval decapods would acquire the energy and nutrients needed for their development and eventual metamorphosis (Anger 2001). Both hypotheses regarding reduced predation and mutualistic cleaning would promote epibiosis, but neither has been tested empirically. Future studies may seek to quantify risk of predation and diet of larval decapods both on and off *P. platurus*.

Finally, there are ecological factors that may act to deter epibiosis and reduce the frequency and intensity of these associations. Host behaviors are thought to be the primary factors that deter epibiosis on marine snakes (Zann et al. 1975). *Pelamis platurus* will actively and vigorously remove unwanted skin and debris from the surface of its body by “knotting” (Pickwell 1971; Zann et al. 1975). Knotting is considered an antifouling mechanism that evolved in response to the heightened susceptibility to epibiosis in the pelagic environment (Zann et al. 1975). This behavior may certainly deter epibiosis of larval decapods. However, unlike sessile epibionts (e.g., barnacles), larval decapods do not become affixed to the skin of the snakes and do not appear to elicit the knotting response. In addition, knotting would also be far less effective against the removal of a motile epibiont, which can crawl to another part of the body to avoid being removed.

Although there may be functional reasons for *P. platurus* to avoid hosting larval decapods (see discussion below), there is likely a greater impetus for larval decapods to actively avoid or abandon *P. platurus* or remain on the snakes only temporarily. First, *P. platurus* frequently dives. Although *P. platurus* is considered to be a primarily surface-dwelling snake, dive profiles indicate that these snakes spend most of the time submerged and suspended in the water column (Rubinoff et al. 1986). Whether or not

larval decapods remain on *P. platurus* during dives is unknown. Diving may deter epibiosis if larval decapods actively abandon snakes to remain at the surface or if larval decapods become dislodged while the snake is swimming. A common factor thought to deter epibiosis in other marine vertebrates is that epibionts may not physiologically tolerate the often-extreme environments used by the host during diving (Key et al. 1995). However, diving depths for *P. platurus* are comparatively shallow (Rubinoff et al. 1986) and may not necessarily deter epibiosis. Second, *P. platurus* sheds its skin and is known to shed frequently regardless of body size (19.5–25.4 days between sheds) (Zann et al. 1975). Pshed individuals were found hosting the largest aggregations of decapod epibionts (up to 14 individuals). Therefore, shedding may be an important factor affecting the frequency and intensity of epibiosis. Third, *P. platurus* may actively avoid shoreward currents to keep from becoming stranded, an event that typically leads to the death of the snake (Kropach 1975). For those intertidal and riverine decapod taxa that may utilize floating debris for shoreward transport, this would deter any long-term association and reduce the frequency of their occurrence. This deterrent may be less important for those epibiont taxa that primarily inhabit floating debris (e.g., *P. major* and *P. squamosa*).

In this study, the frequency of these associations (total $F_0 = 18.9\%$) suggests that larval decapods probably colonize *P. platurus* opportunistically and temporarily, possibly in response to the availability of flotsam. Moreover, *P. platurus* appears to tolerate the presence of larval decapods, as the snakes presumably incur little to no physical or energetic cost by hosting these epibionts. Nevertheless, whether larval decapods actively select or avoid *P. platurus* or whether their occurrence is simply proportional to the available surface area provided by floating *P. platurus* remains unclear. Future studies will focus on assessing the frequency and intensity of larval decapods on floating debris so as to better evaluate which factors either promote or deter epibiosis of *P. platurus*.

Marine snake epibiosis

The study of epibiosis in marine snakes has a scattered history of anecdotal reports dating back to Cantor (1841) and Darwin (1851, 1854). For this reason, we have compiled a summary of all known references to epibionts from marine snakes (Table 3).

Table 3 Epibionts associated with marine snakes [Hydrophiini (Cantor 1841),¹ Acrochordidae (Darwin 1851),² and Laticaudinae (Darwin 1854)³]

Habitat	Marine pelagic	Marine benthic	Amphibious benthic	References	
SNAKE	<i>Pelamis platurus</i> ¹				
	<i>Distira kingii</i> ¹				
	<i>Distira major</i> ¹				
	<i>Distira nigroincta</i> ¹				
	<i>Acalyptophis peronii</i> ¹				
	<i>Astrota stokesii</i> ¹				
	<i>Aphysurus foliosquama</i> ¹	X			
	<i>Aphysurus fuscus</i> ¹	X			
	<i>Aphysurus laevis</i> ¹	X			
	<i>Aphysurus duboisii</i> ¹	X			
	<i>Aphysurus apraefrontalis</i> ¹	X			
	<i>Aphysurus eydouxi</i> ¹				
	<i>Lapemis curtus</i> ¹				
	<i>Hydrophis sp.</i> ¹				
	<i>Hydrophis fasciatus</i> ¹				
	<i>Hydrophis brooki</i> ¹				
<i>Hydrophis bituberculatus</i> ¹					
<i>Hydrophis cyanocinctus</i> ¹					
<i>Hydrophis elegans</i> ¹					
<i>Hydrophis spiralis</i> ¹					
<i>Hydrophis gracilis</i> ¹					
<i>Hydrophis caerulelescens</i> ¹					
<i>Hydrina schistosus</i> ¹					
<i>Emydocephalus annulatus</i> ¹					
<i>Thalassophis viperina</i> ¹					
<i>Acrochordus granulatus</i> ²					
<i>Laticauda laticaudata</i> ³					
<i>Laticauda semifasciata</i> ³					
<i>Laticauda saintgironsi</i> ³					
Diatoms and algae	Ceramiales (red algae)				
	<i>Cladophora</i> sp.				
	<i>Giffordia mitchellae</i>				
	<i>Navicula</i> sp.				
	<i>Spyridia filamentosa</i>				
	<i>Spyridia</i> sp. ^a				
	<i>Streblonema</i> sp.				
	<i>Ulva</i> sp.				
	Unidentified algae				
	Foraminifera	<i>Amphistegina lesson</i>			
		<i>Elphidium craticulatum</i>			
<i>Operculina</i> sp.					
Hydrozoa					
<i>Bimeria fluminalis</i>					
<i>Campanularia serrulata</i>					
<i>Clytia longicyathus</i> ^b					
<i>Dynamena quadridentata</i>					
<i>Obelia longissima</i>					
References					Shine et al. (2010)
					Zann et al. (1975)
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				Zann et al. (1975)	
				Zann et al. (1975)	
				Shine et al. (2010)	
				Wall (1921), Smith (1926), Zann et al. (1975), Ohba et al. (2005)	
				Smith (1926), Kropach and Soule (1973), F. Brischoux, personal observation	
				Zann et al. (1975)	
				Zann et al. (1975)	
				Zann et al. (1975)	
				Wall (1921)	
			Wall (1921)		
			Zann et al. (1975)		
			Zann et al. (1975)		
			present study		

(continued)

Table 3 Continued

Habitat	Amphibious benthic		References
	Marine pelagic	Marine benthic	
Epibionts			
<i>Octolasmis warwickii</i>	X		Annandale (1906), Yamato et al. (1996)
<i>Platylepas indicus</i> ^d			Daniel (1958)
<i>Platylepas krugeri</i> ^d	X		Kruger (1912), Pilsbry (1916), Wall (1921)
<i>Platylepas ophiophilus</i> ^d	X	X	Lanchester (1902), Gotto (1969), Kropach and Soule (1973), Zann et al. (1975), Zann and Harker (1978), Rasmussen (1992), Hayashi (2009)
<i>Platylepas hexastylus</i> ^d	X		present study
<i>Platylepas</i> sp. ^a	X		Darwin (1854), Wall (1921), Padate et al. (2009)
Decapoda			
<i>Macrobrachium</i> sp.	X		present study
<i>Atya</i> sp.	X		present study
Grapsidae ^e	X		present study
<i>Planes major</i> ^f	X		present study
<i>Plagusia squamosa</i>	X		present study
<i>Portunus affinis</i>	X		present study
Gastropoda			
<i>Atlanta inclinata</i>	X		present study
Bivalvia			
<i>Pinctada</i> sp.		X	Zann et al. (1975)

(continued)

In this summary, we found 35 different references that report 48 distinct epibiont taxa from 28 marine species of snakes. A similar review by Zann et al. (1975) provided numerous historical references, as well as many new reports at the time had not been described previously (Zann et al. 1975). However, we have included a number of older, more cryptic references that Zann et al. (1975) had overlooked, as well as all known references to epibionts from marine snakes published since 1975. The intention of this review is to provide contemporary researchers with a single, accessible reference to all known reports of epibionts associated with marine snakes.

Our review indicates that marine snakes are known to host a variety of epibionts that are typically associated with floating debris and other marine vertebrates (Thiel and Gutow 2005; Lazo-Wasem et al. 2011). Not surprisingly, the lepadomorph and balanomorph barnacles comprise a large percentage of the diversity with 13 distinct taxa. However, there are also references to various other phyla of marine organism, including bryozoans, hydrozoans, polychaetes, bivalves, foraminiferans, and alga. Moreover, the present study on *P. platurus* in Costa Rica has expanded the diversity of marine snake epibiota to include several decapod crustaceans, a gastropod, and two chordates. Almost all epibiont taxa in Table 3 are unspecialized and form facultative associations with marine snakes. However, there are three species of barnacle that are thought to be obligate on marine snakes: *Octolasmis grayi*, *Platylepas ophiophilus*, and *Platylepas krugeri* (Pilsbry 1916; Zann 1975; Jeffries and Voris 1979). More work is needed to confirm whether these species are truly specific to marine snakes or whether their distinct morphologies are actually plastic responses to living on snakes.

The diversity of epibionts on marine snakes also appears to depend on the habitat preferences of the various snake species. If we include the 11 new species of epibiont reported in this study, then *P. platurus* hosts almost half of all the epibiont diversity documented for marine snakes (Table 3, Fig. 3). As already described, *P. platurus* is the only exclusively pelagic marine snake and is often found floating motionless along ocean slicks (Kropach 1971, 1975; Heatwole 1999), making them particularly susceptible to colonization by pelagic epibionts. Other hydrophiines (e.g., *Aipysurus* spp. and *Hydrophis* spp.) and *Acrochordus granulatus* (Acrochordidae) utilize benthic habitats of varying depth and rarely,

if ever, come ashore (Heatwole 1999). These snakes also appear to host low diversity of epibionts relative to *P. platurus* (Table 3, Fig. 3), although some species (*Aipysurus duboisii*, *Enhydrina schistosa*, and *Lapemis curtus*) host comparatively more than others (Table 3). Contact with submerged structures (e.g., rocks and coral) in the benthic habitat likely deters the colonization and persistence of many epibionts on these benthic marine snakes. Moreover, specific color patterns in shallow, near-shore waters may act to deter epibiosis (Shine et al. 2010; Solórzano 2011). Although the amphibious sea kraits (*Laticauda* spp.) forage in benthic habitats (primarily shallow coral reefs), these snakes spend roughly half of the time on land (Heatwole 1999). For this reason, desiccation, as well as abrasion, would deter the settlement and growth of most epibionts on *Laticauda* spp. and likely explain why these snakes host few epibiont taxa (Table 3, Fig. 3). Concordantly, the most aquatic of the Laticaudinae, *Laticauda semifasciata*, also hosts more epibiont species than its more terrestrial congeners (Table 3).

Despite supporting the most diverse epibiont community of any marine snake, *P. platurus* does not appear to show a higher tolerance for epibiosis. Instead, its susceptibility to epibiosis in the pelagic environment is thought to have led to more specific mechanisms to deter epibiosis. First, *P. platurus* is known to shed more frequently than most marine snakes and frequency of shedding in *P. platurus* is

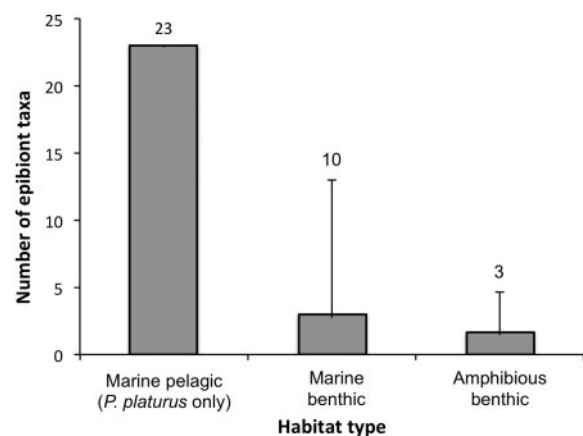


Fig. 3 Mean number of epibiont taxa recorded for marine snakes based on habitat type (marine pelagic, *P. platurus* only; marine benthic, $n = 24$; amphibious benthic, $n = 3$). Y-bars and data labels indicate the highest number of epibiont taxa recorded for a snake species in each category of habitat type. See Table 3 for designations of habitat type for species of marine snake.

not dependent on body size, as it is in other snakes (Zann et al. 1975). Second, *P. platurus* performs behavioral “knotting” (described above). As noted by previous authors, both presumed adaptations to deter epibiosis would be energetically costly and might have evolved in response to pressure from epibiosis in the pelagic habitat (Zann et al. 1975). Despite this very reasonable conclusion, little is known regarding the costs of epibiosis to marine snakes. Presumably, a sessile epibiont, such as a barnacle or bryozoan, attached to the skin of a snake may interfere with cutaneous gas exchange. Work on *P. platurus* suggests that while diving, these snakes absorb 33% of their oxygen and release 94% of their carbon dioxide through their skin (Graham 1974). Nevertheless, to our knowledge, there are no studies that investigate the costs of epibiont cover on cutaneous gas exchange (Shine et al. 2010). In addition, epibiosis is typically associated with increased weight and drag (Key et al. 1995), both are factors that might exact an energetic cost to a swimming snake. Shine et al. (2010) found that dense algal cover on *Emydocephalus annulatus* reduced the swimming speed by up to 20%. The authors attributed this decrease in speed to an increase in drag. Similar studies that are able to quantify the costs of epibiosis will lead to a better understanding of the patterns of epibiotic diversity we see in marine snakes, as well as in other marine vertebrates.

In summary, we discovered 11 previously unreported epibionts associated with *P. platurus*, 6 of which represent the first decapod epibionts to be reported from any marine snake. Moreover, we found 35 references to 48 distinct epibiont taxa associated with 28 marine species of snake from the past 150 years. The results of this study show how little attention has been given to the study of epibiosis in marine snakes. We do not believe that these results reflect the rarity of these associations. Instead, these results suggest that many observations of epibionts from marine snakes are not reported in the scientific literature. Scientists investigating the biology of marine snakes in the field provide the best opportunities to contribute valuable new information if attention is also paid to the presence of epibionts. Future studies should include (1) field and museum-based surveys to specifically quantify the diversity and frequency of epibiosis from many species of snake in many localities, (2) field surveys of inanimate substrata and snakes in the same area to quantify differences in surface area availability and

epifaunal diversity, (3) comparative studies between free-living and epibiotic individuals to assess the potential costs and benefits of epibiosis for the epibionts, and (4) empirical studies to quantify the energetic costs of epibiosis on marine snakes. Such studies would provide valuable insights into the complex suite of factors that affect these interactions and the possible role that marine snakes play as hosts to epibionts.

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References

- Alvarez F, Celis A. 2004. On the occurrence of *Conchoderma virgatum* and *Dosima fascicularis* (Cirripedia, Thoracica) on the sea snake, *Pelamis platurus* (Reptilia, Serpentes) on Jalisco, Mexico: Crustaceana. p. 761–64.
- Anger K. 2001. The biology of decapod crustacean larvae. Lisse: A.A. Balkema Publishers.
- Annandale N. 1906. Stalked barnacles (Cirripedia Pedunculata) in the Colombo Museum. Spolia Zeylanica 3:193–95.
- Annandale N. 1909. An account of the Indian Cirripedia Pedunculata. Part 1. Family Lepadidae. Mem Ind Mus Calcutta 2:59–137.

- Badrudeen M. 2000. On the occurrence of the cirriped barnacles, *Chelonibia patula* (Ranzani) on the sea snake, *Hydrophis cyanocinctus* (Daudin). Mar Fish Inf Serv Tech Ext Ser 164:25.
- Bauer RT. 2011. Amphidromy and migrations of freshwater shrimps. I. Costs, benefits, evolutionary origins, and an unusual case of amphidromy. In: Asakura A, editor. New frontiers in Crustacean biology, Proceedings of the TCS Summer Meeting, Tokyo, September 20–24, 2009. Leiden: Brill. p. 145–56.
- Bauer RT, Delahoussaye J. 2008. Life history of the amphidromous river shrimp *Macrobrachium ohione* from a continental large river system. J Crustacean Biol 28:622–32.
- Bednarski M, Morales-Ramírez A. 2004. Composition, abundance and distribution of macrozooplankton in Culebra Bay, Gulf of Papagayo, Pacific coast of Costa Rica and its value as bioindicator of pollution. Rev Biol Trop 52:105–18.
- Bennett I. 1971. The Great Barrier Reef. Melbourne: Lansdowne Press.
- Brischoux F, Lillywhite HB. 2011. Light- and flotsam-dependent ‘float-and-wait’ foraging by pelagic sea snakes (*Pelamis platurus*). Mar Biol 158:2343–47.
- Cantor T. 1841. Observations upon pelagic serpents. Trans Zool Soc Lond 2:303–13.
- Cuffey RJ. 1971. Pacific sea snakes: a highly mobile newly recognized substrate for bryozoans. International Bryozoology Association 2nd International Conference, September 6–16, 1971, Durham. London: Academic Press. p. 606. Abstract 37.
- Daniel A. 1958. On *Platylepas indicus* n. sp. a new barnacle from the Madras Coast of India. Ann Mag Nat Hist 1:755–57.
- Darwin C. 1851. A monograph on the sub-class Cirripedia. The Lepadidae. London: Ray Society.
- Darwin C. 1854. A monograph of the sub-class Cirripedia. The Balanidae and Verrucidae. London: Ray Society.
- Dean B. 1938. Note on the sea-snake *Pelamis platurus* (Linnaeus). Science 88:144–45.
- Dittel AI, Epifanio CE. 1990. Seasonal and tidal abundance of crab larvae in a tropical mangrove system, Gulf of Nicoya, Costa Rica. Mar Ecol Prog Ser 65:25–34.
- Donlan CJ, Nelson PA. 2003. Observations of invertebrate colonized flotsam in the eastern tropical Pacific, with a discussion of rafting. Bull Mar Sci 72:231–40.
- Enderlein P, Wahl M. 2004. Dominance of blue mussels versus consumer-mediated enhancement of benthic diversity. J Sea Res 51:145–55.
- Frick MG, Kopitsky K, Bolten AB, Bjorndal KA, Martins HR. 2011. Sympatry in grapsoid crabs (genera *Planes* and *Plagusia*) from olive ridley (*Lepidochelys olivacea*), with descriptions of crab diets and masticatory structures. Mar Biol 158:1699–708.
- Gotto RV. 1969. Marine animals. Partnerships and other associations. London: English Universities Press.
- Graham JB. 1974. Aquatic respiration in the sea snake *Pelamis platurus*. Resp Physiol 21:1–7.
- Harder T. 2009. Marine epibiosis: concepts, ecological consequences and host defence. Mar Ind Biofouling 4:219–31.
- Harmer SF. 1926. The Polyzoa of the Siboga Expedition, II, Cheilostomata Anasca, Siboga Expedition Report, Vol. 28b. Leiden: Brill.
- Hayashi R. 2009. The commensal barnacles (Cirripedia; Thoracica; Coronuloidea) attached on marine vertebrates in Japanese water. Unigame Newsletter of Japan 81:3–16.
- Heatwole H. 1999. Sea snakes. Sydney: University of New South Wales Press.
- Hoek PPC. 1887. On *Dichelaspis pellucida*, Darwin, from the scales of an Hydrophid obtained at Mergul. J Linn Soc Lond 21:154–55.
- Hunter JR, Mitchell CT. 1967. Associations of fishes with flotsam in the offshore waters Central America. Fish B-NOAA 66:13–29.
- Jeffries WB, Voris HK. 1979. Observations on the relationship between *Octolasmis grayi* (Darwin, 1851) (Cirrepedia, Thoracica) and certain marine snakes (Hydrophiidae). Crustaceana 37:123–32.
- Jiménez C, Cortes J. 2003. Growth of seven species of scleractinian corals in an upwelling environment of the eastern Pacific (Golfo de Papagayo, Costa Rica). Bull Mar Sci 72:187–198.
- Jiménez C, Cortés J, León A, Ruíz E. 2001. Coral bleaching and mortality associated with the 1997–98 El Niño in an upwelling environment in the eastern Pacific (Gulf of Papagayo, Costa Rica). Bull Mar Sci 69:151–69.
- Key MM Jr, Jeffries WB, Voris HK. 1995. Epizoic bryozoans, sea snakes, and other nektonic substrates. Bull Mar Sci 56:462–74.
- Kharin VE. 1981. A review of the sea-snakes of the genus *Aipysurus* (Serpentes, Hydrophiidae). Zool Zh 60:257–64.
- Kingsford MJ, Choat JH. 1986. Influence of surface slicks on the distribution and onshore movements of small fish. Mar Biol 91:161–71.
- Kropach C. 1971. Sea snake (*Pelamis platurus*) aggregations on slicks in Panama. Herpetologica 27:131–35.
- Kropach C, Soule JD. 1973. An unusual association between an ectoproc and a sea snake. Herpetologica 29:17–29.
- Kropach C. 1975. The yellow-bellied sea snake, *Pelamis*, in the Eastern Pacific. In: Dunson WA, editor. The biology of sea snakes. Baltimore: University Park Press. p. 185–213.
- Krüger P. 1912. Über ostasiatische Rhizocephalen. Anhang: Über einige interessante Vertreter der Cirripedia thoracica. Abhandlungen der Mathematisch-Physikalische Klasse der Königlich Bayerischen der Akademie Wissenschaften 8:1–16.
- Lanchester WF. 1902. On the Crustacea collected during the “Skeat Expedition” to the Malay Peninsula. Proc Zool Soc Lond 2:363–81.
- Lazo-Wasem EA, Pinou T, Peño de Niz A, Feuerstein A. 2011. Epibionts associated with the nesting marine turtles *Lepidochelys olivacea* and *Chelonia mydas* in Jalisco, Mexico: a review and field guide. Bull Peabody Mus 52:221–40.
- Lillywhite HB, Solórzano A, Sheehy CM III, Ingley S, Sasa M. 2010. New perspectives on the ecology and natural history

- of the yellow-bellied sea snake (*Pelamis platurus*) in Costa Rica: does precipitation influence distribution? IRCF Reptiles Amphib 17:69–72.
- Mitchell CT, Hunter JR. 1970. Fishes associated with drifting kelp, *Macrocystis pyrifera*, of the coast of southern California and Baja California. Bull Dep Fish Game St Calif 56:288–97.
- Moreira FT, Harari J, Flores AAV. 2007. Neustonic distribution of decapod planktonic stages and competence of brachyuran megalopae in coastal waters. Mar Freshw Res 58:519–30.
- Ng PKL, Guinot D, Davie P. 2008. Systema brachyurorum: part I. An annotated checklist of extant brachyuran crabs of the World. Raffles Bull Zool 17:1–286.
- Nilsson-Cantell CA. 1930. Cirripedes. Résultats Scientifiques du Voyage aux Indes Orientales Néerlandaises de LL. AA. RR. Le Prince et la Princesse Léopold de Belgique. Mémoires du Musée Royal d'Histoire Naturelle de Belgique 3:1–24.
- Nilsson-Cantell CA. 1934. Cirripeds from the Malay Archipelago in the Zoological Museum of Amsterdam. Zool Mededelingen 17:31–63.
- Ohba H, Fujioka Y, Tottori K, Shibuno T. 2005. Coral reefs 24:403.
- Padate VP, Baragi LV, Rivonker CU. 2009. Biological aspects of sea snakes caught incidentally by commercial trawlers off Goa, west coast of India. J Threat Taxa 1:609–16.
- Pickwell GV. 1971. Knotting and coiling behavior in the pelagic sea snake *Pelamis platurus*. Copeia 2:348–50.
- Pilsbry HA. 1916. The sessile barnacles (Cirripedia) contained in the collections of the U.S. National Museum; including a monograph of the American species. US Natl Mus Bull 93:1–357.
- Development Core Team R. 2008. R: a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing.
- Rasmussen A. 1992. Rediscovery of *Hydrophis bituberculatus* Peters, 1872 (Serpentes: Hydrophidae). Herpetologica 48:85–97.
- Rathbun MJ. 1918. The grapsoid crabs of America. US Natl Mus Bull 97:1–461.
- Reynolds RP, Pickwell GV. 1984. Records of the yellow-bellied sea snake, *Pelamis platurus*, from the Galapagos Islands. Copeia 1984:786–89.
- Rubinoff I, Kropach C. 1970. Differential reactions of Atlantic and Pacific predators to sea snakes. Nature 228:1288–90.
- Rubinoff I, Graham JB, Motta J. 1986. Diving of the sea snake *Pelamis platurus* in the Gulf of Panamá. Mar Biol 91:181–91.
- Shanks AL. 1983. Surface slicks associated with tidally forced internal waves may transport pelagic larvae of benthic invertebrates and fishes shoreward. Mar Ecol Prog Ser 13:311–15.
- Shanks AL. 1985. Behavioral basis of internal-wave-induced shoreward transport of megalopae of the crab *Pachygrapsus crassipes*. Mar Ecol Prog Ser 24:289–95.
- Shanks AL. 1995. Orientated swimming by megalopae of several eastern North Pacific crab species and its potential role in their onshore migration. J Exp Mar Biol Ecol 186:1–16.
- Shelford R. 1901. Report on the Sarawak Museum. Sarawak: Sarawak Museum.
- Shine R, Brischoux F, Pile AJ. 2010. A seasnake's colour affects its susceptibility to algal fouling. Proc R Soc Lond B 277:2459–64.
- Shipmen WH, Pickwell GV. 1973. Venom of the yellow-bellied sea snake (*Pelamis platurus*): some physical and chemical properties. Toxicon 11:375–77.
- Smith M. 1926. Monograph of the sea-snakes (Hydrophiidae). London: British Museum.
- Solórzano A. 2011. Variación de color de la serpiente marina *Pelamis platura* (Serpentes: Elapidae) en el Golfo Dulce, Puntarenas, Costa Rica. Cuadernos de Investigación UNED 3:89–96.
- Stoner AW, Greening HS. 1984. Geographic variation in the macrofaunal associates of pelagic *Sargassum* and some biogeographic implications. Mar Ecol Prog Ser 20:185–92.
- Thiel M, Gutow L. 2004. The ecology of rafting in the marine environment. I. The floating substrata. Oceanogr Mar Biol Annu Rev 42:181–264.
- Thiel M, Gutow L. 2005. The ecology of rafting in the marine environment: II. The rafting organisms and community. Oceanogr Mar Biol Annu Rev 43:279–418.
- Vargas R, Wehrtmann IS. 2009. Decapod crustaceans. In: Wehrtmann IS, Cortés J, editors. Marine biodiversity of Costa Rica, Central America. Berlin: Springer. p. 209–28.
- Wahl M. 1989. Marine epibiosis: I. Fouling and antifouling: some basic aspects. Mar Ecol Prog Ser 58:175–89.
- Wahl M, Mark O. 1999. The predominately facultative nature of epibiosis: experimental and observational evidence. Mar Ecol Prog Ser 187:59–66.
- Wall F. 1921. Ophidia taprobanica, or the snakes of Ceylon. Colombo: H.R. Cottle.
- Wehrtmann IS, Dittel AI. 1990. Utilization of floating mangrove leaves as a transport mechanism of estuarine organisms, with emphasis on decapod Crustacea. Mar Ecol Prog Ser 60:67–73.
- Weldon PJ. 1988. Feeding responses of Pacific snappers (genus *Lutjanus*) to the yellow-bellied sea snake (*Pelamis platurus*): behavioral biology. Zool Sci 5:443–48.
- Yamato S, Yusa Y, Tanase H. 1996. Distribution of two species of *Conchoderma* (Cirripedia: Thoracica) over the body of a sea snake, *Laticauda semifasciata* (Reinwardt), from the Kii Peninsula, southwestern Japan. Publs Seto Mar Biol Lab 37:337–43.
- Zann LP. 1975. Biology of a barnacle (*Platylepas ophiophilus* Lanchester) symbiotic with sea snakes. In: Dunson WA, editor. The biology of sea snakes. Baltimore: University Park Press. p. 267–86.
- Zann LP, Harker BM. 1978. Egg production of the barnacles *Platylepas ophiophilus* Lanchester, *Platylepas hexastylus* (O. Fabricius), *Octolasmis warwickii* Gray and *Lepas anatifera* Linnaeus. Crustaceana 35:206–14.
- Zann LP, Cuffey RJ, Kropach C. 1975. Fouling organisms and parasites associated with the skin of sea snakes. In: Dunson WA, editor. The biology of sea snakes. Baltimore: University Park Press. p. 251–65.