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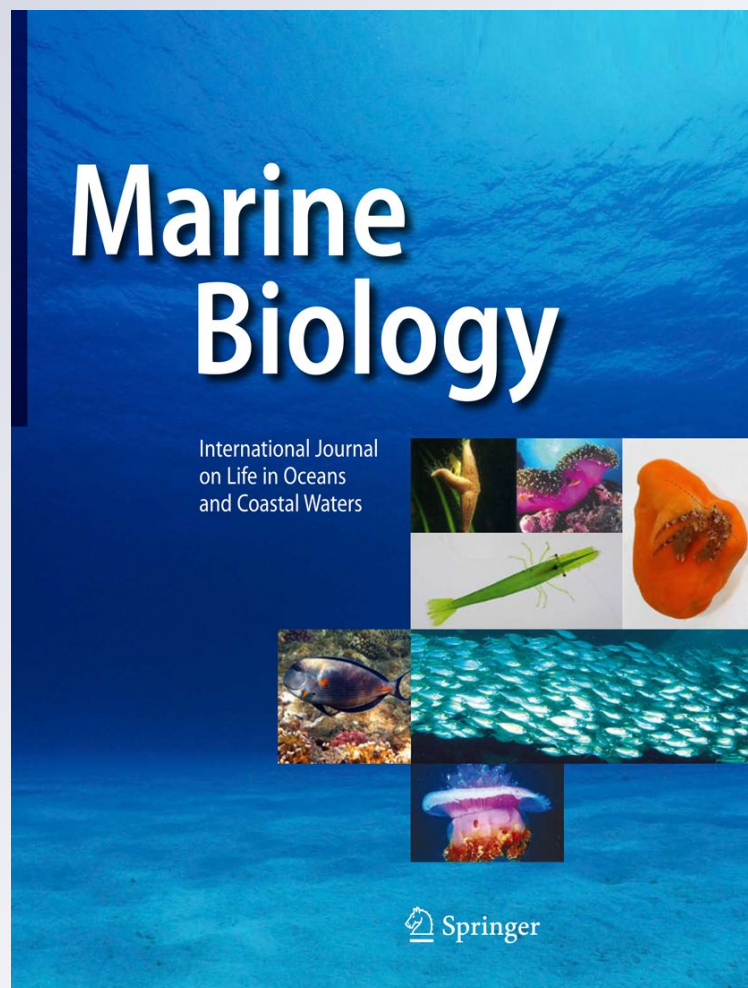
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Light- and flotsam-dependent ‘float-and-wait’ foraging by pelagic sea snakes (*Pelamis platurus*)

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Abstract Efficient detection of food patches in oceanic areas by pelagic predators is often linked to large-scale physical structures (e.g. fronts, upwellings) that are usually rich and predictable. At smaller scales, however, predictability of resource becomes less clear because of the lability of smaller physical structures such as slicks and drift lines. Here, we explore how light levels and quantity of flotsam affect the occurrence of foraging Yellow-bellied sea snakes (*Pelamis platurus*) on slicks. Although this pelagic species was formerly hypothesised to surface randomly and drift passively to reach slicks, our results show that foraging snakes are far more abundant on slicks if light levels are high and if slicks display flotsam. The combination of both light and flotsam should enhance the contrast between a potentially favourable slick and the adjacent waters as seen from an underwater viewpoint. Although our results do not unambiguously demonstrate the ability of *Pelamis platurus* to visually detect surface drift lines, they clearly suggest a role of both light levels and amount of flotsam on surfacing decision. Accordingly, this hypothesis is supported by several complementary traits that are specific to this species. ‘Float-and-wait’ foraging undoubtedly requires efficient detection of, and orientation to, oceanic slicks—processes that are likely less random and passive than formerly believed. Successful pelagic foraging is no doubt important to this species of sea snake that is the world’s most widely distributed snake species.

Introduction

Clear-cut examples of animals’ ability to locate food resources in complex, large-scale ecosystems come from the marine environment where resources are patchily distributed in space and time (Fauchald 1999). Accordingly, food patch localisation in marine apex predators has been a fruitful field of investigation over the last decades (see Bost et al. 2009 for a review). At large scales, some oceanic features (e.g. currents, fronts, upwellings, eddies) provide highly productive areas and harbour diverse ecological networks (Lutjeharms et al. 1985; Mann and Lazier 2006), which are often targeted by pelagic predators (Bost et al. 2009; Croll et al. 2005). These structures are usually stable in space and time and thus predictable, which allow experienced individuals to actively seek these foraging patches (Brown 2000; Krebs and Inman 1992). At finer scales, the predictability of resources in pelagic ecosystems is less clear (Fauchald et al. 2000; Levin 1992), because of stochastic processes inherent to oceanic features (Mann and Lazier 2006), but also due to prey–predator interactions (Fauchald et al. 2000; Hays et al. 2006).

Slicks or drift lines are typically small, short-lived, mobile oceanic structures formed as the result of Langmuir circulations, internal waves or convergent currents (Barstow 1983). They occur as stretches of calm glassy water surrounded by rougher areas, and accumulate high quantities of positively buoyant flotsam, constituted of both seaborne and terrigenous items. Due to their dynamic features, slicks concentrate planktonic organisms, including larval and juvenile fish (Barstow 1983; Dempster and Kingsford 2004; Kingsford and Choat 1986; Pineda 1994; Shanks 1995). In contrast with larger-scale structures, slicks do not seem to be generally attractive to foraging predators (Barstow 1983). Although some predatory species are often associated with floating

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objects, foraging on slick-associated fauna is not clearly supported by stomach content analyses (e.g. Tuna fish, Castro et al. 2002). The lability of slicks compared to larger structures probably impedes efficient and consistent localisation of these small oceanic food patches by most mobile pelagic predators.

The Yellow-bellied sea snake (*Pelamis platurus*, Hydrophiinae) is the only pelagic species of sea snake and has an extensive distribution covering the entire tropical Indo-Pacific (Heatwole 1999). Yellow-bellied sea snakes display a peculiar diving pattern (fast descent–very slow ascent; see Brischoux et al. 2007 for comparisons with other species) and spend most of their day-to-day life (up to 99% of the time) floating in the water column (20–50 m deep, Rubinoff et al. 1986). Diving bouts are interrupted by surfacing events, which are either very brief to air-breathe or longer to forage (Rubinoff et al. 1986). Indeed, this species uses a unique foraging strategy among marine air-breathing predators: it ambushes small fish that are concentrated under debris while ‘float-and-wait’ foraging at the oceanic surface on slicks (Dunson and Ehlert 1971; Rubinoff et al. 1986). To our knowledge, the Yellow-bellied sea snake is the only marine air-breathing predator foraging specifically at the oceanic surface on labile features such as slicks or drift lines.

The way these comparatively small (<1 m) sea snakes can efficiently reach oceanic slicks remains unclear, but two alternative hypotheses have been proposed. First, a foraging snake might randomly surface and rely on passive drifting, as inert flotsam, to reach a slick (Dunson and Ehlert 1971; Hecht et al. 1974). Second, a snake could actively detect a potentially favourable slick from underwater (Rubinoff et al. 1988). The use of vomerolfaction to detect a slick seems unlikely from deeper water. The different directions of surface versus deeper currents make long distance (20–50 m deep) olfactory detection of potential foraging slicks unlikely (see Rubinoff et al. 1986, 1988 for diving depth and surface vs. deep current directions). Moreover, *Pelamis platurus*, as other hydrophiine sea snakes, appear to have reduced olfactory abilities compared to amphibious sea kraits and terrestrial elapids (Kishida and Hikida 2010). However, Yellow-bellied sea snakes might visually detect flotsam or refractive properties of glassy water, or indeed fish, from their underwater viewpoint, as it has been shown for the detection of potential prey by ‘float-and-wait’ foraging fish (Cronin 2005). Indeed, a visual response would rapidly enable a snake to surface exclusively on potentially favourable foraging slicks. Herein, we examine how light levels and presence of flotsam affect the occurrence of foraging Yellow-bellied sea snake on slicks, as the combination of both parameters should accentuate the contrast between a

potentially favourable slick and the adjacent waters as seen from an underwater viewpoint.

Materials and methods

We investigated a population of Yellow-bellied sea snakes in the Papagayo Gulf off the Pacific coast of Costa Rica. Field-work sessions (7–15 days) occurred both during the rainy (June and October) and the dry season (February and April) of 2010. During searching bouts conducted between 700 and 1,000 h, we patrolled the sea in search of slicks whereon foraging snakes tend to be concentrated (Dunson and Ehlert 1971). For each bout, we counted the number of snakes observed lying at the surface (presumably foraging), and we recorded both ambient light levels and quantity of flotsam on slicks (see below).

Light levels above the surface should accentuate the contrast between a slick with flotsam and the adjacent waters when viewed from a submerged viewpoint. For each searching session, we scored the overall cloud cover, using two categories: no or light cloud cover versus medium or heavy cloud cover. In October 2010, we further measured the vertical solar irradiance every 15 min for each searching session using a pyranometer (DS-05A Digital Solar Meter, Daystar Inc.). Importantly, cloud cover scores were convergent with vertical solar irradiance (ANOVA with the mean vertical solar irradiance for a given survey as the dependent variable and cloud cover score as the predictor: $F_{1,11} = 6.72$, $p = 0.02$; $491.7 \pm 41.6 \text{ Wm}^{-2}$ for no or light cloud cover versus $344.8 \pm 38.5 \text{ Wm}^{-2}$ for medium to heavy cloud cover).

Because visible attributes of the slick—quantity of flotsam, pelagic organisms, foam and organic oils dampening wavelets—might affect its visual detection from underwater, we scored each surveyed slick for the amount of flotsam, using two categories: no or scarce debris versus high concentration of flotsam (see Lillywhite et al. 2010 for photographs). The sheen or flattened water surface was present on both categories of slicks, and foam usually accompanied the presence of flotsam.

Results

Both cloud cover and quantity of flotsam had an effect on the number of snakes sighted on slicks (ANCOVA with the number of snakes as the dependent variable, cloud cover and slick state as the predictors and the duration of the survey as the covariate: effect of the flotsam $F_{1,30} = 24.32$, $p < 0.0001$; effect of the cloud cover $F_{1,30} = 7.69$, $p < 0.009$, Figs. 1a, 2). Post hoc tests indicated that slicks

with much debris on cloudy days had a similar number of snakes as did slicks with little debris on sunny days.

Focusing on ambient light levels (October 2010), a logistic regression with the presence or absence of snakes as the dependent variable and the vertical solar irradiance as the continuous predictor (with the solar irradiance nested within the survey to take into account daily variations) showed that snakes were more likely to be floating on slicks if the solar irradiance was high ($df = 13$, $\chi^2 = 32.11$, $p = 0.002$, Figs. 1b, 2).

Discussion

Rubinoff et al. (1988) suggested that Yellow-bellied sea snakes might detect slicks from underwater before surfacing, but this hypothesis has been largely ignored (Dunson and Ehlert 1971; Heatwole 1999; Hecht et al. 1974; Ineich 1988). Our results clearly show that ambient light and the

quantity of flotsam influence the abundance of Yellow-bellied sea snakes on a slick. Although our results do not unambiguously demonstrate the ability of Yellow-bellied sea snakes to visually detect a surface drift line, the combined effects of both light levels and presence of objects on slicks support the ‘visual detection’ hypothesis.

The strong effect of light we detected clearly suggests a significant role of vision in the surfacing decisions of snakes, and the ‘visual detection’ hypothesis is further supported by various, but complementary, traits specific to this species. For instance, the retinal structure of Yellow-bellied sea snake suggests a specialisation for detection of form and motion (Hibbard and Lavergne 1972). Additionally, none of the free-ranging snakes tracked by Rubinoff et al. (1986) displayed any extended surfacing time overnight. Finally, Yellow-bellied sea snakes tend to avoid the nearshore turbid waters in favour of more transparent offshore waters (Dunson and Ehlert 1971).

Alternatively, the increased abundance of Yellow-bellied sea snakes under high light intensities could be related to surface basking by floating snakes (Dunson and Ehlert 1971). We discarded this thermoregulation hypothesis for several reasons. First, body temperatures of free-ranging Yellow-bellied sea snakes have been shown to be identical to those of the surrounding water (Graham 1974). Second, it has been shown experimentally that snake models will be thermoconformer once submerged, even in very shallow water (Shine et al. 2003). Finally, sea snakes, including *Pelamis*, are known to have very high surface area to volume ratios (Brischoux and Shine 2011); inevitably, any heat gain would be immediately lost to the water.

Our results also complement the peculiar diving pattern of Yellow-bellied sea snakes, characterised by a very fast descent followed by a very slow and progressive ascent phase (Rubinoff et al. 1986, see Brischoux et al. 2007 for comparison). Indeed, we can speculate that the slow ascent phase could be used to observe the sea surface and thereby orient to slicks that shelter flotsam and/or abundant prey, as it has been shown for the detection of potential prey by ‘float-and-wait’ foraging fish (Cronin 2005). Furthermore, the variable directions of surface versus deeper currents could enable snakes to drift passively relative to the surface water during the slow and progressive ascent phase, thereby visually sampling a significant surface area over the course of a day (Rubinoff et al. 1988). Additionally, but not exclusively, swimming underwater might require less energy expenditure than swimming at the surface against surface currents (Rubinoff et al. 1988). As a consequence, repositioning to potential food sources from underwater might also provide energetic advantages to *Pelamis*.

Detecting potentially favourable slicks prior to surfacing should convey advantages compared to ‘random surfacing passive drifting’. First, a snake might increase its foraging

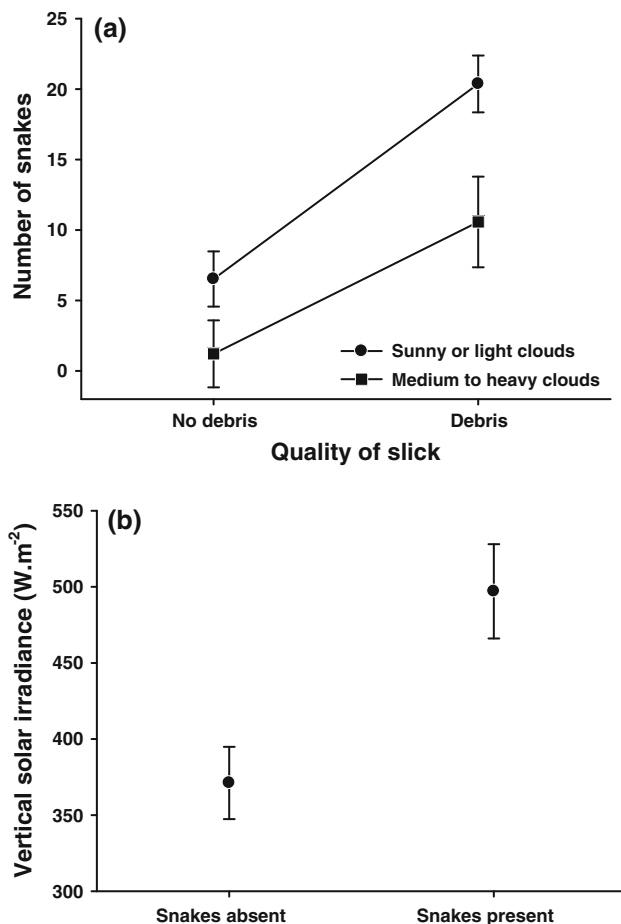


Fig. 1 **a** Number of snakes sighted on slicks with few versus heavy flotsam under contrasting weather conditions (no or light clouds vs. medium or heavy clouds). **b** Mean values of solar irradiance measured when snakes were present or absent (see text for details). Mean are given \pm SE

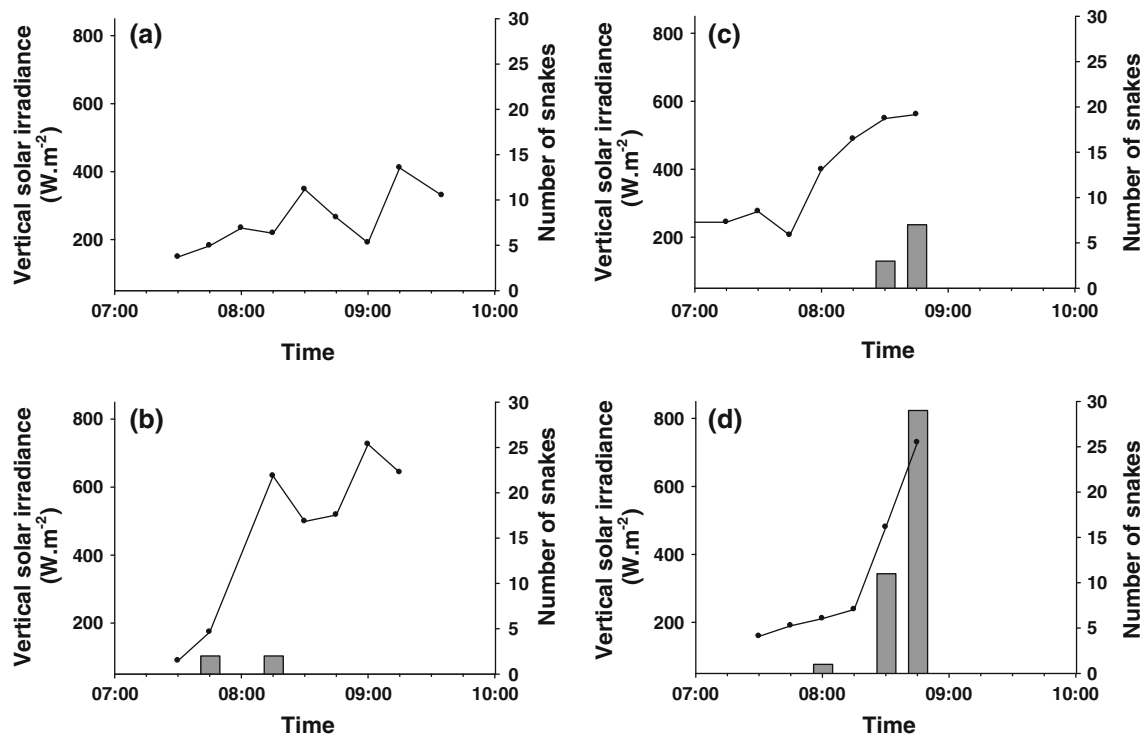


Fig. 2 Examples of snake counts (grey bars) and solar irradiance (connected points) for four contrasted surveys: **a** cloudy, few flotsam; **b** sunny, few flotsam; **c** cloudy, heavy flotsam; **d** sunny, heavy flotsam

opportunities by selectively surfacing on slicks with heavy flotsam, which shelter more abundant prey (Dempster and Kingsford 2004; Kingsford and Choat 1986; Pineda 1994; Shanks 1995). Second, clear conditions might increase the detection of prey as well as the striking precision of a snake that relies largely on vision to successfully forage (Hibbard and Lavergne 1972). Finally, the presence of flotsam might reduce the conspicuousness of a snake lying at the oceanic surface (Lillywhite et al. 2010), and thus both decrease the predation risks to *Pelamis* and increase its efficiency to capture wary prey.

The ecology of *Pelamis platurus* is poorly known, and numerous features of environment and behaviour might influence the foraging patterns we describe here. For instance, Yellow-bellied sea snakes might rely on cues other than the quantity of flotsam to surface on a slick. Because slicks with abundant flotsam also shelter abundant prey (Dempster and Kingsford 2004; Kingsford and Choat 1986; Pineda 1994; Shanks 1995), sea snakes might be able to directly assess prey availability (e.g. through shiny reflections, Cronin 2005), rather than indirectly rely on flotsam quantity. These factors could act together or independently, and the present data do not allow us to disentangle them. However, either outcome would not change our principal conclusion. Additionally, whether *Pelamis* possess visual capacities to detect floating debris from underwater is difficult to assess (but see Hibbard and

Lavergne 1972). However, similar detection has been suggested in ‘float-and-wait’ predatory fish (including deep fish species, Cronin 2005), for which vision seems to provide one of the main cues that might be used to detect prey situated above the predator in the water column. Such process might equally be true for progressively ascending *Pelamis*, as suggested by their diving pattern and the effects of light and flotsam that we detected.

The larger amount of information on the ecology of pelagic sea snakes is limited to observations of behaviours at the ocean surface, probably due to logistical constraints related to occurrence in vast areas of open ocean (e.g. foraging; Dunson and Ehlert 1971; Klauber 1935; Klawe 1964; Lillywhite et al. 2010; Rubinoff et al. 1988; Voris and Voris 1983; but see Rubinoff et al. 1986). We hope the data that we evaluate here will help to stimulate future investigations of this species, including its full range of movements and habitat use.

Pelamis platurus is the only species of snake occurring in open ocean habitat. We emphasise that its unique ‘float-and-wait’ surface foraging undoubtedly require discriminate detection of, and orientation to, oceanic slicks—processes that are likely to be less random and passive than formerly believed. Future investigations should usefully explore the orientation behaviours and dynamics of snake–slick associations in other contexts such as dispersal. Undoubtedly, the successful foraging in a pelagic environment contributes

importantly to the very broad distribution of this species and its survival in the open ocean.

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