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Oceanic circulation models help to predict global biogeography of pelagic yellow-bellied sea snake

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It is well recognized that most marine vertebrates, and especially tetrapods, precisely orient and actively move in apparently homogeneous oceanic environments. Here, we investigate the presumptive role of oceanic currents in biogeographic patterns observed in a secondarily marine tetrapod, the yellow-bellied sea snake (*Hydrophis* [*Pelamis*] *platurus*). State-of-the-art world ocean circulation models show how *H. platurus*, the only pelagic species of sea snake, can potentially exploit oceanic currents to disperse and maintain population mixing between localities that spread over two-thirds of the Earth's circumference. The very close association of these snakes with surface currents seems to provide a highly efficient dispersal mechanism that allowed this species to range extensively and relatively quickly well beyond the central Indo-Pacific area, the centre of origin, abundance and diversity of sea snakes. Our results further suggest that the pan-oceanic population of this species must be extraordinarily large.

1. Introduction

Animal movements and orientation in oceanic environments reflect a continuum between passive drifting and active swimming [1]. Yet intuition suggests that passive drifting can be a hazardous strategy, as the likelihood of being transported to detrimental environments can be considerable [2]. Accordingly, over recent years, it has been progressively suggested that strategies of active movement and orientation in relation to the moving medium are more widespread than previously suspected: even planktonic organisms such as larval fish or jellyfish can influence their oceanic trajectories [3,4]. Larger species such as secondarily marine vertebrates (e.g. seabirds, sea turtles, cetaceans) provide instructive examples of precise orientation and active movements that enable the animal to locate and travel to specific areas in apparently homogeneous oceanic environments [5]. Overall, a high degree of passive exploitation of oceanic currents (i.e. a strategy close to what is observed in planktonic organisms) does not appear viable in pelagic tetrapods.

Here, we investigate the role of oceanic currents in biogeographic patterns observed in a secondarily marine tetrapod, the yellow-bellied sea snake (*Hydrophis* [*Pelamis*] *platurus*). *Hydrophis platurus* is the only pelagic species of sea snake. This small-sized species (approx. 70 cm, 140 g) occurs over the entire tropical Indo-Pacific Ocean [6], a distribution range among the largest of any
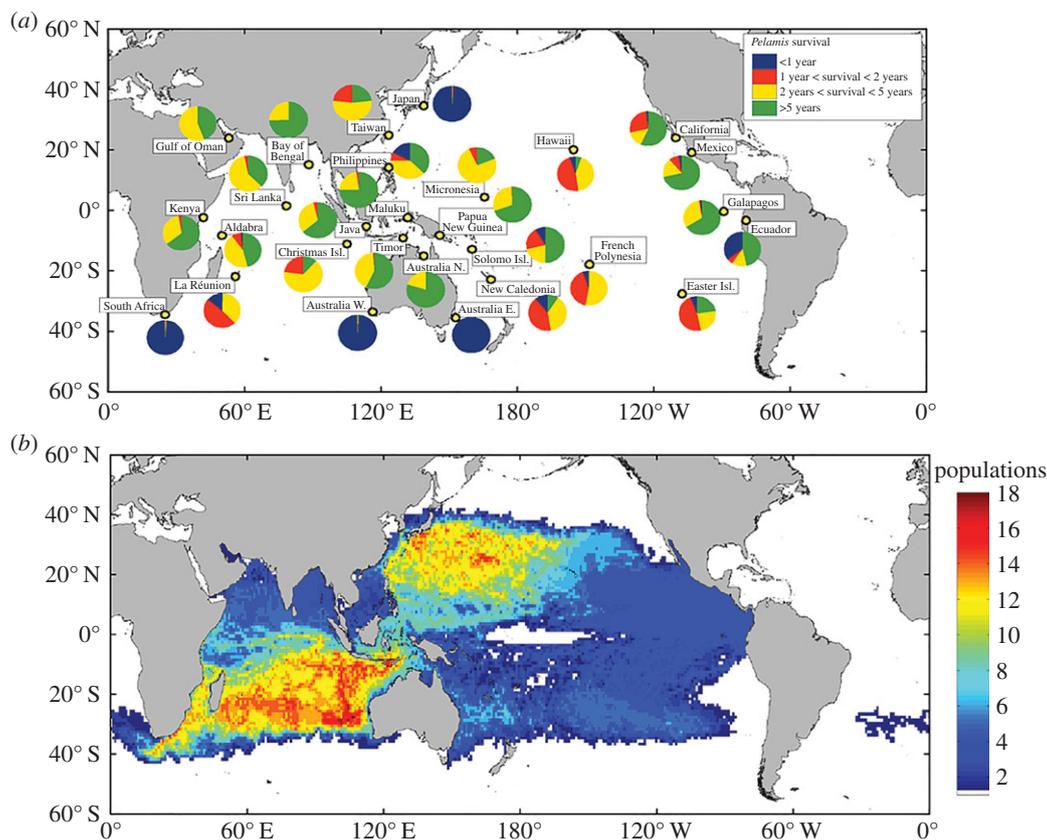
Figure 1. (a) *H. platurus* survival represented as circular diagrams representing each location of release (yellow dots). For clarity, survival was separated into four categories (<1 year (blue), 1–2 years (orange), 2–5 years (yellow) and >5 years (green)). (b) Population mixing patterns for drifting *H. platurus*. The colour chart indicates the number of snake populations (irrespective of snake number) that drifted through each pixel. (Online version in colour.)

living tetrapod, and the broadest of any species of squamate reptile despite a very recent evolutionary origin (less than 2 Ma [7]). Combined with traits such as shallow diving [8,9], surface foraging [10,11], association with slicks or drift lines [12,13], comparatively poor locomotor abilities to swim against waves and currents [10], and genetic homogeneity across the Pacific Ocean [14], the remarkably large distribution range of *H. platurus* strongly suggests a close association with surface currents. Despite previous speculations on the 'planktonic' character of *H. platurus* [10,14,15], no studies have yet attempted to evaluate the viability of such a strategy in this species. To test for this hypothesis, we use state-of-the-art world ocean circulation models to perform drift simulations and investigate survival and dispersal over a period of 10 years on snakes originating from 28 populations representative of occurrence area.

2. Methods

(a) Occurrence sites

The database for the presence of *H. platurus* was obtained from the published literature, from the GBIF website (http://www.gbif.org/species) and from the extent-of-occurrence range maps assembled by the IUCN (www.iucnredlist.org/technical-documents/spatial-data). Using this distribution, we designed a representative pattern of occurrence sites over the whole occurrence area. Care was taken not to *a priori* exclude anecdotal or extreme locations (e.g. South Africa, Easter Island) despite those being likely cases of vagrancy [6] (see also our results). We selected 28 sites representative of occurrence area for which we performed drift simulations (figure 1).

(b) Individual release and survival

We lacked detailed life-history traits for the species and this has two main consequences for our simulations:

First, because we lacked detailed data on reproductive season and frequency, we assumed a regular daily release of one individual from each population during the first year of drift simulations, representing a total of 10 220 individuals released. A 'point of origin' was chosen for each population, and snakes from each population were released in a $0.25° \times 0.25°$ area centred on this point of origin. The locations for release were randomly chosen, but uniformly distributed, inside this area.

Second, because we were unable to include life-history traits in our simulation (i.e. survival rate, age at maturity, reproductive frequency, lifespan, etc.), we assumed each individual to behave as an inert particle. We made the simplistic presumption that, in a stable population, natality counterbalances mortality and that the use of inert particles should not over-inflate either survival or mortality. For instance, 10 years may slightly overestimate the lifespan of *H. platurus*, but conservatively our simulations do not take into account offspring production by females.

The thermal habitat was used to estimate the survival of each simulated snake. *Hydrophis platurus* is known to cease feeding in water temperatures less than 19°C, a value below which locomotor abilities are strongly reduced and cold death can occur within 5–12 days [16,17]. We accordingly set a conservative lower lethal thermal limit at 18°C. A trajectory lasting more than one week in waters where temperature was below 18°C was considered lethal, and the simulation was ended for the particle.

(c) Simulation of drift

To compute the trajectories of snakes, we used the modelled surface current fields from the GLORYS-1 (G1) reanalysis of the
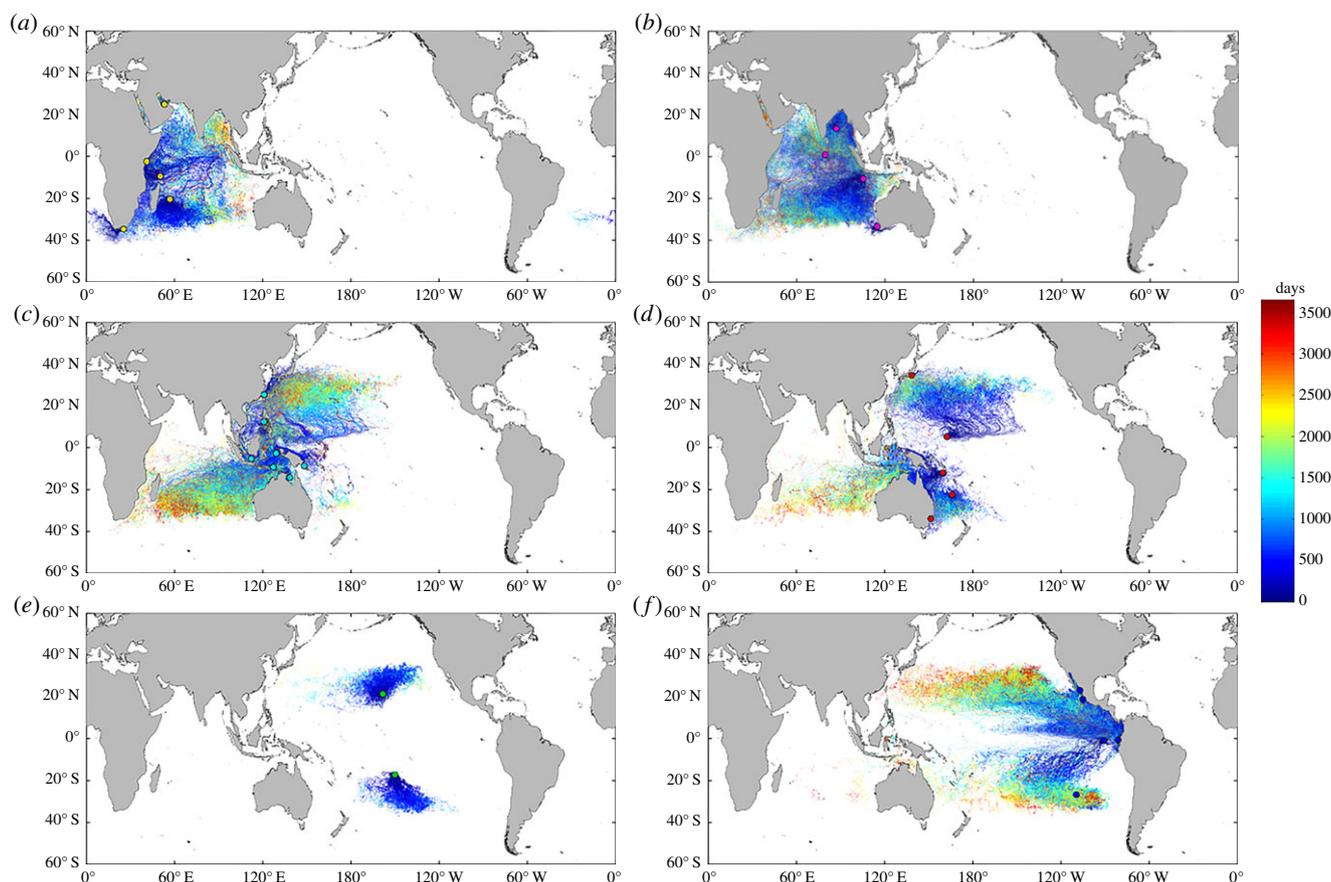
Figure 2. Summary of 10 year long passive drift trajectories of snakes for all the populations grouped by broad geographic area. (a) Western Indian Ocean, (b) eastern Indian Ocean, (c) Indonesian basin, Oceania and Japan, (d) western Pacific Ocean, (e) central Pacific Ocean and (f) eastern Pacific Ocean. Release locations are indicated by coloured dots, and the colour along each trajectory evolves as a function of the age of the simulated snake (blue, young; red, old). (Online version in colour.)

World Ocean circulation [18], performed by the Mercator Ocean centre (www.mercator-ocean.fr/) with the NEMO numerical ocean model (www.nemo-ocean.eu/). The G1 model has a horizontal resolution of $0.25°$ and 50 vertical layers. It covers the period 1 January 2002–31 December 2008. The G1 reanalysis provides a close-to-reality, 7 year long, three-dimensional simulation of the World Ocean dynamics as it assimilates satellite altimetry, temperature and salinity measurements.

Passive drift trajectories were computed using the Lagrangian trajectory simulation software ARIANE (freely available at www.univ-brest.fr/lpo/ariane/) and the G1-simulated currents in the first model layer (0–1 m). One location per day was recorded for analyses of trajectories. We used the water temperature in this first model layer to estimate temperatures along simulated trajectories. These temperatures closely match satellite-derived sea-surface temperatures that are assimilated into the model. To perform 10 year long drift simulations with this 7 year long current and temperature dataset, we simply looped the modelled data (i.e. the simulation continues after December 2008 using again data starting in January 2002).

3. Results and discussion

Overall, 1271 (12.4%) individuals remained in water masses more than $18°C$ and survived during the entire simulation. Survival rates were highly variable between populations (range 0–54.8%, figure 1a). The latitude of the population of origin negatively influenced survival of individuals ($F_{1,10218} = 4118.69$, $r^2 = 0.29$, $p < 0.0001$), with the highest survival rates found for individuals originating within latitudes $20°N–20°S$ (figure 1a). The three colonies with the largest

survival rates (more than 40%) originated from the Java, the Molucca and the Solomon Seas (figure 1a), locations that correspond remarkably well with the centre of origin of the species [7,19,20]. Conversely, the seven populations that became extinct in 1.5–8 years (figure 1a) point to occurrences that can be considered cases of vagrancy [6]. Similar to distribution of flotsam, *H. platurus* may be unevenly distributed (figure 1b) and drift into suboptimal accumulation zones [21]. These size-dependent processes [21] may have strong consequences for the demography of *H. platurus*. However, mortality can be reduced with minimal swimming behaviour [22], which seems plausible in *H. platurus* despite its comparatively poor locomotor abilities [10]. Similarly, diving includes long periods of hovering at selected depths [8,9] that possibly allow transitory disconnections between surface conditions and diving snakes.

The mixing of populations at the end of the simulation (figure 1b) strongly supports the remarkably low levels of genetic divergence found between the western and eastern Pacific [14]. These two independent sets of results along with the recent origin of the species (less than 2 Ma) indicate a relatively high rate of gene flow and a recent expansion of range [7,14], which are arguably strongly linked to the very close association of these snakes with oceanic surface currents.

For individuals surviving the entire simulation, the distance travelled averaged 30 495 km ($\pm 22\,879$, max = 108 718 km). Interestingly, the simulation shows that individual *H. platurus* can possibly travel remarkably large longitudinal distances across the Indo-Pacific Oceans (figure 2). Maximum longitudinal distances were $93.6°$ (approx. 10 000 km straight line

distance) eastward for a snake released near the Philippines that drifted east of Hawaii and 176.6° (approx. 20 000 km straight line distance) westward for a snake released along the coast of Mexico that reached Mauritius Island (figure 2). Overall, individuals from populations situated near the centre of origin of the species tended to drift afar both eastward towards the Pacific Ocean and westward toward the Indian Ocean (figure 2). These simulations are consistent with extremely low (if any) recapture rates of *H. platurus* [13,15].

4. Conclusion

Although exploitation of oceanic currents by *H. platurus* seems to be hazardous when individuals drift away from thermally compatible areas, it is clearly a highly efficient dispersal mechanism that allows this small species to exploit an extensive distribution that spread over two-thirds of the Earth's circumference. Drifting on oceanic gyres is the most likely explanation for *H. platurus* being the only species of sea snake to reach the Americas at the eastern end of the Pacific Ocean [6]. Drifting dispersal also maintains mixing of populations and thus gene flow between areas that are separated by more than 25 000 km. Together, these results further suggest that the pan-oceanic population of this species must be extraordinarily large [13] and likely represents one of the most abundant species of vertebrate tetrapod.

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