



# Demographics and reproductive biology of *Hydrophis schistosus* may make it more resilient to bycatch effects than other sea snakes

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## ABSTRACT

Mortality in fisheries bycatch is a threat to marine taxa globally. True sea snakes are viviparous marine reptiles found throughout tropical coastal waters, with varying reproductive strategies that differ from their terrestrial counterparts. *Hydrophis schistosus* and *H. curtus* are both caught frequently in large numbers as bycatch in gillnets, shore seines and trawlers on the west coast of India. In this study, we aimed to describe the population of *H. curtus* and *H. schistosus* in bycatch in terms of developmental stages; compare mortality rates across developmental stages and sexes; and discuss their breeding cycle and reproductive strategies in the context of fisheries threats. We sampled fishing nets for sea snakes from 2016 to 2019. The population structure of *H. schistosus* consisted primarily of breeding adults and did not change in the four years of sampling. However, the proportion of breeding adults of *H. curtus* in bycatch declined steadily. Gravid female *H. schistosus* appear to carry young from November to May, giving birth in April. We did not encounter any gravid *H. curtus* during our sampling. While the number of eggs increased with female snout to vent length in *H. schistosus*, the overall reproductive effort remained the same and investment per embryo reduced. Bycatch - induced mortality of *H. curtus* was significantly higher than *H. schistosus*. Adult *H. curtus* were most vulnerable to bycatch mortality of all demographic groups in both species. Reproductive strategies along with other ecological and life history differences may give *H. schistosus* an advantage compared to other taxa in the face of anthropogenic threats.

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## 1. Introduction

The study of animal populations is one of the foundations of ecology. Population characteristics such as growth rates and reproductive outputs are important to determine conservation actions and their efficacy. Vital rates such as juvenile survival (recruitment), age at first reproduction, reproductive rates, and adult survival in a given population may present as important indicators of population growth and stability (Eberhardt, 1977).

The stability of populations is further determined by several factors such as birth rates, death rates, immigration, and emigration. However, for sustained growth, abilities of young ones to reach breeding age and contribute to population growth is important. The reproductive effort (mass of eggs relative to female weight in each period) expended by a female over a lifetime remains constant across vertebrate taxa (around 1.4 times their body weight) (Williams, 1966; Charnov et al., 2007). Reproducing organisms can be placed on a spectrum of breeding strategies

based on the packaging of reproductive effort as *r* - strategists, i.e., those that produce large number of young with little reproductive effort and *k* - strategists, i.e., those that produce few young with higher effort per young, (Wilson and MacArthur, 1967).

The development of embryos also differs greatly across taxa. Females of viviparous species carry developing young in their bodies while oviparous species lay eggs. There are differences in how nutrition is provided to developing embryos. The mother may provide nutrition to embryos as they develop (matrotrophy), or the young may derive nutrition from the yolk (lecithotrophy) (Blackburn, 1999). While lecithotrophy is more common with oviparous animals and matrotrophy with viviparous animal, these are not mutually exclusive and may change through developmental stages. For instance, some squamate species display lecithotrophic viviparity and monotremes (Mammalia) display matrotrophic oviparity (Blackburn, 1992). Nine out of ten reptile families contain species that are viviparous (Fitch, 1970). Viviparity is particularly common in squamates (20% of species) (Blackburn, 1999).

Marine snakes belong to 3 families primarily: Acrochordidae, Elapidae and Colubridae. Two subfamilies of elapids; Laticaudinae

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(sea kraits) and Hydrophiinae (true sea snakes) have colonised marine habitats (Pyrón et al., 2013). There are around 70 extant hydrophiid species found throughout near shore waters in the tropics (except the Atlantic Ocean) (Sanders et al., 2013; Lillywhite et al., 2018). Reproductive modes and strategies differ among marine snakes. File snakes and true sea snakes are viviparous while sea kraits are oviparous, coming to land in order to lay eggs.

True sea snakes (Hydrophiinae) are a subfamily of Elapid snakes (Sanders et al., 2013). They are adapted to a completely aquatic life, spending their entire life cycles in near shore marine habitats (Rasmussen, 2000). Viviparity is plesiomorphic in hydrophiids (Keogh, 1998; Sanders et al., 2013). They also display variety in their breeding biology (Bergman, 1943; Lemen and Voris, 1981). *Hydrophis schistosus* is particularly unique as it produces the largest number of young (up to 31). Most sea snake species are r – selected with *H. curtus* producing the largest (at birth) young (Voris and Jayne, 1979; Lemen and Voris, 1981).

Despite being a speciose lineage, knowledge of sea snake ecology is scant, and little is known about their life histories (Udyawer et al., 2018). Sea snakes are threatened by anthropogenic activities throughout their range (Elfes et al., 2013; Goiran et al., 2017). Fisheries pose a threat to this taxon as they are often found in large numbers as bycatch in nets (Wassenberg et al., 1994; Ward, 1996; Fry et al., 2001; Milton, 2001; Rao et al., 2021).

Bycatch is the portion of the catch that was not targeted and is incidentally hauled up. It is a major issue in fisheries globally, threatening a whole range of charismatic taxa including marine turtles, sharks, and cetaceans. Milton (2001) estimated around 100,000 sea snakes are caught every year by the Northern Prawn Fishery in Australia. Coupled with these large harvests, mortality of some species is also high in fisheries bycatch. Most individuals end up drowning or crushed under the weight of the catch (Wassenberg et al., 2001). A comparison of trawler bycatch along the west coast of India from 2003 to 2019 revealed shifts in sea snake assemblages with potential declines in the populations of *Hydrophis curtus*. Simultaneously, the relative proportion of *H. schistosus* in bycatch increased over the same period (Rao et al., 2021).

In the current study, we aimed to (a) assess the populations of *H. schistosus* and *H. curtus* in bycatch of gillnets, shore seines and trawlers along the coast of Sindhudurg, Maharashtra, (b) compare mortalities rates in bycatch across species, developmental stages and sex and (c) analyse the breeding cycles and reproductive strategies of the sea snake species of the region. Finally, we discuss the life history and physiological differences between *H. curtus* and *H. schistosus* and the implications for their survival and management in the face of increasing anthropogenic pressures.

## 2. Methods

### 2.1. Study site

Sindhudurg is a coastal district in the state of Maharashtra on the west coast of India. The district has a large fisher population and many vessels employing multiple gears (Vidya et al., 2016). Malvan (16.0631° N, 73.4711° E) is a major fish landing centre in Sindhudurg, and around 100 trawlers and 500 gillnetters operate out of the natural harbour. Shore seining is also frequently practised on the shores of the region. Malvan Marine Sanctuary was established in 1978 to protect the region's marine biodiversity. The waters around Sindhudurg are characterised by patchy corals, rocky outcrops and sandy bottoms. The coastline is dotted by river mouths that bring in large amounts of silt and nutrients (United Nations Development Programme (UNDP), 2013).

### 2.2. Sampling for sea snakes

We conducted field work in 4 phases: January 2016–March 2016, December 2016–April 2017, December 2017–May 2018 and October 2018–May 2019. We sampled trawler and gillnet boats when they landed their catch. Trawlers were sampled in the evening around 17:00–19:00 and gillnets in the morning around 6:30–9:30. We sampled shore seines once they had pulled the nets in and were sorting the catch in the morning around 6:30–8:00. We collected the snakes (dead and alive) from the nets and recorded species identity and condition.

### 2.3. Morphometrics and dissection

All snakes were taken back to the field base in Malvan and kept in fresh sea water in 40 litre tubs, filled halfway. We measured the snout to vent length (SVL) and tail length (TL) (in cm) using a flexible measuring tape. We weighed the snakes using a bag and an electronic scale. We determined sex visually and confirmed by dissection (only dead snakes) or by everting the hemipenis (live snakes). We determined presence of eggs by palpation (Farr and Gregory, 1991). Live snakes were released back into the sea.

Dead gravid females were dissected by a longitudinal cut from the cloaca towards the head. The position and number of embryos were recorded. Eggs were then taken out of the mother and weighed in whole. Egg length was measured along the connective tissue fold that joins the eggs and width was measured perpendicular to the same. Depending on the developmental stage of the embryos, the eggs were opened, and each embryo was weighed, sexed, and tagged. Embryos and females were kept in a fixative (3% formalin) for 30–60 mins and transferred to a preservative (70% ethanol). Snout to vent length, tail length, weight and sex of embryos was recorded back at the lab in IISc, Bangalore. Females that were dissected have been preserved along with their embryos and deposited at the museum in the Centre for Ecological Science, IISc, Bangalore. Specimen numbers are included in the data file.

### 2.4. Analysis

We used SVL (cm) as proxy for developmental stage (Lemen and Voris, 1981). We determined length at maturity and length at birth from literature and classified individuals as neonates (*H. curtus* < 35 cm, *H. schistosus* < 35 cm), juveniles (35 cm < *H. curtus* < 54 cm, 35 cm < *H. schistosus* < 60 cm) and adults (*H. curtus* > 54 cm, *H. schistosus* > 60 cm) (Bergman, 1956; Voris and Jayne, 1979; Fry et al., 2001; Ward, 2001).

To understand shifts in the distribution of developmental stages over our sampling period, we used a multinomial Generalised Linear Model (GLM) with years as predictors and developmental stages as response. To understand distribution of sex ratios among sea snake species, we conducted z – tests for the difference in proportion of females from a null hypothesis of 0.5. To determine changes in sex ratios across years, we used a binomial GLM with sea snake sex as a response and years as predictors. To understand differences in mortality rates across species, we used separate binomial models with condition at encounter (dead or alive) as a response and species, sex, developmental stage, and reproductive status as predictor variables.

To understand the annual reproductive cycle of *H. schistosus*, we plotted the relative proportion ( $\pm$  SD) of gravid females encountered in each month using pooled data from 2018 and 2019. To determine differences in clutch sex ratios, we tested differences in proportion of females across all sampled clutches from null value of 0.5, i.e., equal sex ratios. To analyse foetal

nutritional regimes, we used linear regressions to test for change in yolk weight and total egg weight (g) with increasing embryo SVL (cm).

We evaluated the reproductive strategy of *H. schistosus* by first calculating the relative mass of the whole clutch to empty weight of the female (Williams, 1966; Lemen and Voris, 1981; Charnov et al., 2007). We then compared clutch sizes and relative clutch mass with increasing female SVL (cm) using Poisson and beta regression models respectively. Maternal investment per embryo was calculated as relative mass of the egg (g) to the empty female weight (g) (Voris and Jayne, 1979; Charnov et al., 2007). We tested change in relative egg mass with female SVL (cm) using a beta regression model. As embryos in our samples were at different development stages, we added embryo SVL (cm) as a term in our beta regression models to control for this effect. Similarly, we compared maternal investment with the sex of embryo using a beta regression model (Ferrari and Cribari-Neto, 2004; Douma and Weedon, 2019).

Data used in the current study and code for analysis in R is available at <https://github.com/cheesesnakes/sea-snake-demo-repro>.

### 3. Results

#### 3.1. Demographics of *H. schistosus* in bycatch

We sampled a total of 967 *H. schistosus* and 282 *H. curtus* from bycatch of trawlers (77 trips, 292.66 haul hours), gillnets (439 trips, 585.21 haul hours) and shore seines (46 sets, 190.45 h). Adults were the dominant developmental class in our sample of *H. schistosus* in all years ( $85.15 \pm 1.28\%$ ). However, juveniles were the dominant developmental stage in *H. curtus* ( $66.13 \pm 3.44\%$ ). The proportion of adult *H. curtus* decreased significantly across years in our sample but no such change was observed in *H. schistosus* (Supplementary materials Table A1, Figure 1).

The distribution of snout-vent length (cm) for *H. schistosus* changed seasonally and higher number of neonates were caught in March ( $2 \pm 1.4\%$ ), April ( $5 \pm 3.44\%$ ) and May ( $5.5 \pm 3.81\%$ , Fig. 3a). Sample sizes for *H. curtus* were too small for statistical comparisons but we did observe a high number of neonates in bycatch in March ( $50 \pm 35.35\%$ ) and in November ( $7.69 \pm 5.22\%$ ). Sex ratios of both *H. curtus* ( $P_{\text{female}} = 0.48 \pm 0.03$ ,  $Z_1 = 0.23$ ,  $p = 0.63$ ) and *H. schistosus* ( $P_{\text{female}} = 0.49 \pm 0.02$ ,  $Z_1 = 0.13$ ,  $p = 0.71$ ) were not significantly different from being equal. The proportion of female *H. schistosus* in bycatch was lowest in 2018 compared to other years sampled. The proportion of female *H. curtus* declined significantly across years from 2016 to 2019 (Supplementary materials Table A2).

#### 3.2. Mortality rates of sea snakes in bycatch

Overall mortality in bycatch of *H. schistosus* ( $17.99 \pm 1.23\%$ ) was significantly lower than *H. curtus* ( $42.55 \pm 2.94\%$ ,  $Z_{1241} = 8.37$ ,  $p = 5.62 \times 10^{-17}$ ). Neonates of *H. schistosus* exhibited high mortality ( $37.5 \pm 17.11\%$ ), however sample size is low ( $n = 8$ ) making comparisons unreliable. Juvenile *H. schistosus* ( $n = 105$ ,  $4.76 \pm 2.07\%$ ) had significantly lower mortality than adults ( $n = 648$ ,  $21.3 \pm 1.6\%$ ,  $\beta = -1.69 \pm 0.46$ ,  $Z_{755} = -3.61$ ,  $p = 0.0002$ ). Similarly, juvenile *H. curtus* ( $n = 125$ ,  $32.8 \pm 4.19\%$ ) also had significantly lower mortality in bycatch than adults ( $n = 62$ ,  $64.51 \pm 6.07\%$ ,  $\beta = -1.39 \pm 0.33$ ,  $Z_{183} = -4.18$ ,  $p = 0.00002$ , Fig. 2). *Hydrophis schistosus* males ( $n = 314$ ,  $22.92 \pm 2.37\%$ ) had similar mortality rates to females ( $n = 304$ ,  $20.39 \pm 2.31\%$ ,  $\beta = 0.14 \pm 0.19$ ,  $Z_{613} = 0.74$ ,  $p = 0.45$ ). *Hydrophis curtus* males ( $n = 110$ ,  $47.27 \pm 4.76\%$ ) had slightly higher mortality rates than females ( $n = 102$ ,  $35.29 \pm 4.73\%$ ,  $\beta = 0.55 \pm 0.28$ ,

**Table 1**

Summary of egg measurements, embryo morphometrics and clutch sex ratios of dissected *H. schistosus* females.

Measurement	Mean	Standard deviation
Egg length (mm)	39.71	11.72
Egg width (mm)	32.23	9.01
Egg weight (g)	14.30	5.45
Embryo snout to vent length (cm)	17.72	5.24
Embryo weight (g)	4.83	6.28
Sex ratio (female: total)	0.51	0.04

$Z_{207} = 1.94$ ,  $p = 0.052$ ). Gravid females of *H. schistosus* ( $n = 85$ ,  $18.82 \pm 4.23\%$ ) had slight lower mortality than non-gravid adult females ( $n = 151$ ,  $27.15 \pm 3.61\%$ ) but not significantly different ( $\beta = -0.49 \pm 0.33$ ,  $Z_{232} = -1.4$ ,  $p = 0.13$ ).

#### 3.3. Reproductive cycles and strategies of sea snakes

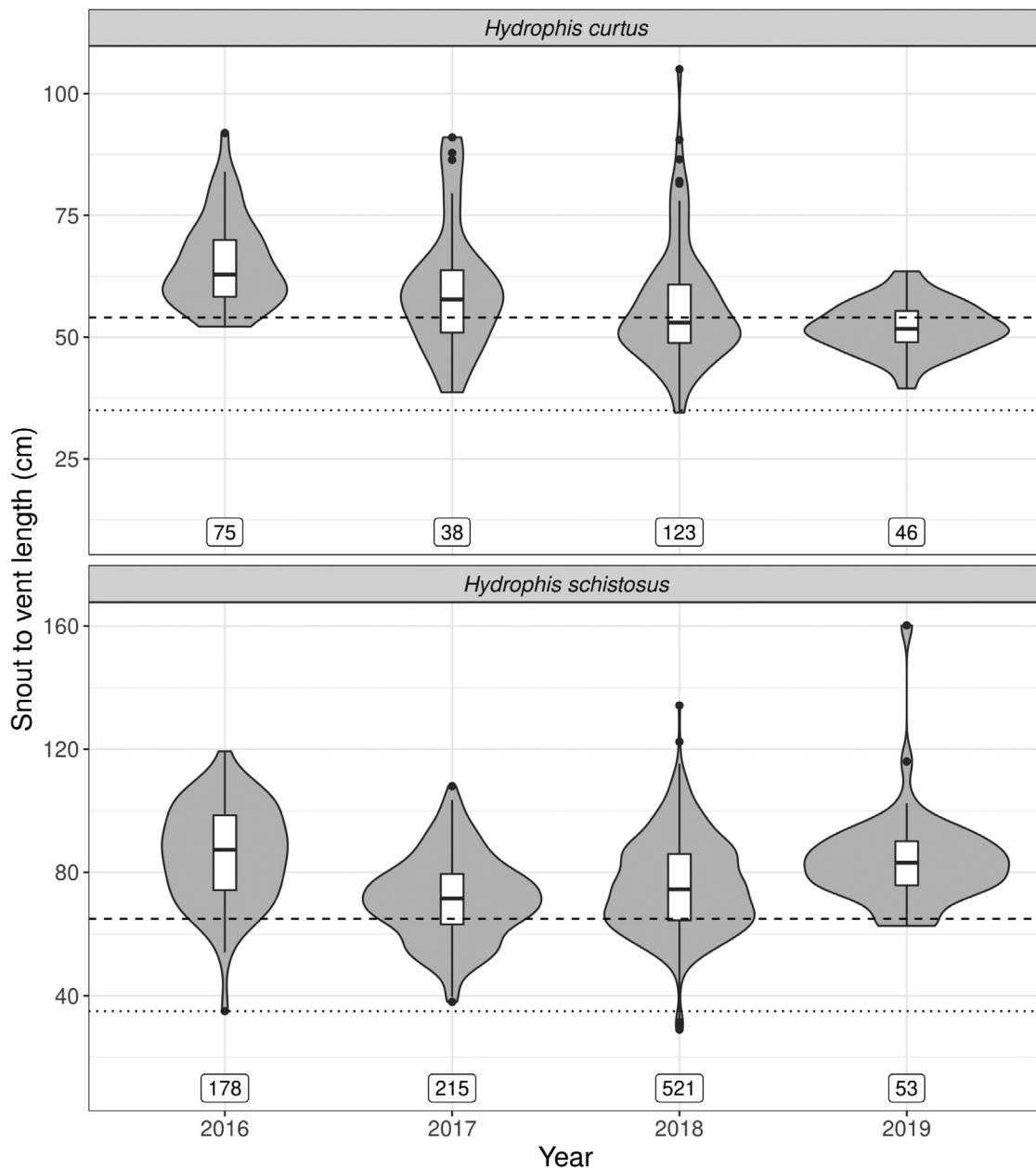
We encountered 75 gravid females of *H. schistosus* in 2018 and 12 gravid females of *H. schistosus* in 2019. We did not find any gravid females of *H. curtus* in bycatch. We encountered *H. schistosus* gravid females in January–May, November, and December. Thus, *H. schistosus* likely breeds between November and May. The number of gravid female *H. schistosus* peaked in February ( $25.37 \pm 3.75\%$ , Fig. 3b). We observed 2 females in April that gave birth in captivity (videos in supplementary materials C). The first gave birth to a single individual and was caught with a neonate in the net. The second female gave birth to 6 neonates, one of which was stillborn.

We dissected 29 female *H. schistosus* and found 235 eggs. *Hydrophis schistosus* had a high fertility rate with  $97.87 \pm 0.94\%$  of eggs containing embryos (see Table 1 for morphometrics of eggs and embryos). The proportion of females in *H. schistosus* clutches was not significantly different from 0.5 ( $0.51 \pm 0.03$ ,  $Z_1 = 0.15$ ,  $p = 0.69$ ). Yolk weight decreased significantly as embryo length increased ( $\beta = -0.45 \pm 0.04$ ,  $Z_{147} = -10.04$ ,  $r^2 = 0.40$ ,  $p = 2.09 \times 10^{-18}$ ). However, total egg weight increased with increasing embryo size ( $\beta = 0.36 \pm 0.05$ ,  $Z_{155} = 6.59$ ,  $r^2 = 0.21$ ,  $p = 6.48 \times 10^{-10}$ ).

The number of embryos carried by each gravid female of *H. schistosus* increased significantly with female SVL (cm) ( $\beta = 0.02 \pm 0.008$ ,  $Z_{15} = 3.10$ ,  $r^2 = 0.50$ ,  $p = 0.001$ ). However, relative clutch mass did not change with female SVL ( $\beta = -0.005 \pm 0.01$ ,  $Z_{13} = -0.52$ ,  $r^2 = 0.54$ ,  $p = 0.6$ , Fig. 4a). Maternal investment per embryo decreased with female length ( $\beta = -0.016 \pm 0.005$ ,  $Z_{54} = -3.21$ ,  $r^2 = 0.56$ ,  $p = 0.001$ , Fig. 4b). Maternal investment was slightly lower for male embryos than for female embryos ( $\beta = -0.13 \pm 0.8$ ,  $Z_{54} = -1.63$ ,  $r^2 = 0.47$ ,  $p = 0.1$ )

### 4. Discussion

Hydrophids are a diverse lineage of marine reptiles and are threatened by anthropogenic pressures throughout their geographical range from Australia to South Africa (Udyawer et al., 2018). In the current study, we described the demographics and reproductive strategies of two species caught as bycatch in trawlers, gillnets, and shore seines in the context of threats posed by fisheries. We observed that the population of *H. schistosus* along the Sindhudurg coast consists primarily of reproducing adults. In contrast, the proportion of adult *H. curtus* has declined over the sampling period (Fig. 1). Reproduction in *H. schistosus* is strongly seasonal with females giving birth to live young from March to May (Fig. 3a and b). *Hydrophis schistosus* females carry many embryos during each reproductive cycle. Bycatch mortality rates are significantly higher for *H. curtus* than *H. schistosus*. Finally, *H. curtus* adults are at higher risk of mortality than juveniles whereas risk across developmental stages and sexes are similarly low for *H. schistosus*.



**Fig. 1.** Population structure of *H. curtus* and *H. schistosus* in bycatch of gill nets, shore seines and trawlers at Malvan over 4 years of sampling. Sample sizes of each species in each year are indicated in the white boxes. Individuals below the dotted line in each panel were classified as neonates, individuals between the dotted line and the dashed line were classified as juveniles and individuals above the dashed line were classified as adults (Bergman, 1943; Lemen and Voris, 1981; Fry et al., 2001; Ward, 2001).

#### 4.1. Difference in age structure between *H. schistosus* and *H. curtus*

We observed a higher proportion of mature adults in *H. schistosus* compared to juveniles or neonates and a relatively smaller proportion of adults in *H. curtus* (Fig. 1). Fry et al. (2001) reported that large snakes of multiple species in prawn trawler catch had higher mortality rates than small snakes. In our case, mortality rates of adults in bycatch were relatively low for *H. schistosus* ( $21.3 \pm 1.6\%$ ) and much higher for *H. curtus* ( $64.51 \pm 6.07\%$ , Fig. 2). The relatively small number of neonates of *H. curtus* could be attributed to difference in habitat use across age classes (Udyawer et al., 2016b). The neonates that we found were caught in shore seines that operate in near-shore depths of around 2–6 m. Neonate and juvenile sea snakes, in particular, may use shallow tidal areas as refuges from fishing pressure (Udyawer

et al., 2016a). A larger proportion of breeding adults as well as high juvenile survival are necessary for the growth and stability of a population.

#### 4.2. Differences in mortality rates among species and demographic groups

Overall mortality of *H. schistosus* ( $17.99 \pm 1.23\%$ ) in bycatch in the region is low compared to *H. curtus* (Lobo, 2003; Rao et al., 2021). Lobo (2003) reported 65% mortality for *H. curtus* in trawler bycatch. Mortality across groups remains the same, indicating uniform risk across developmental stages and sex for *H. schistosus*. The high mortality of adult *H. curtus* may explain the change in population structure across years in our sample. Voris and Jayne (1979) estimated that 80%–90% of *H. schistosus* embryos

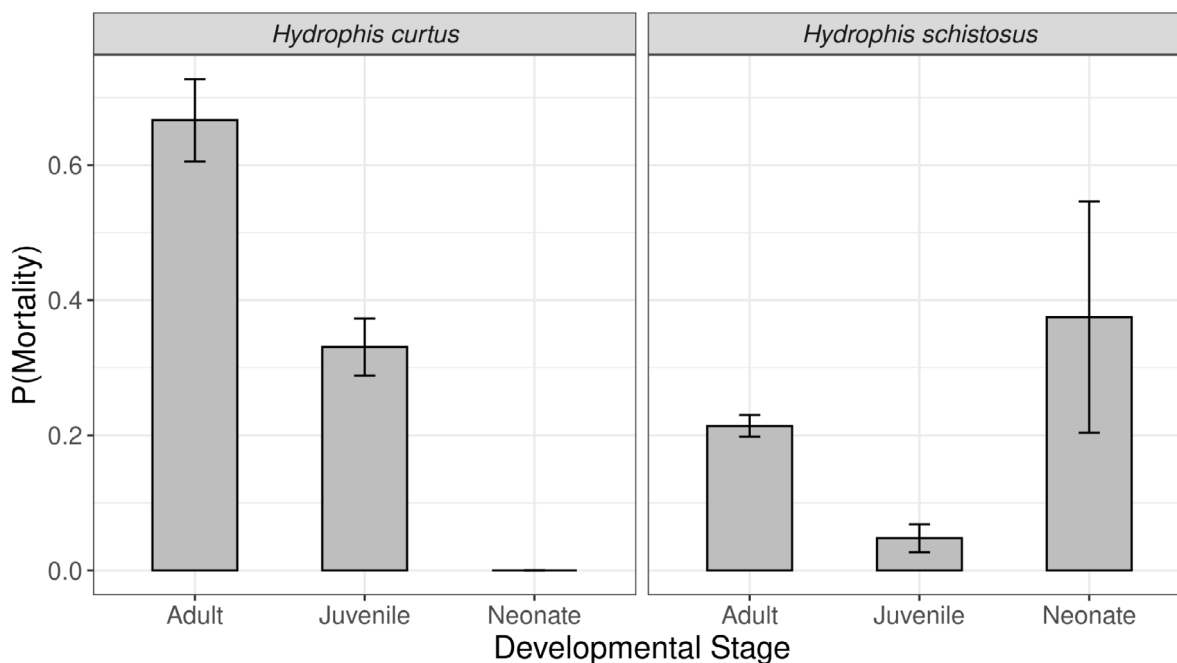


Fig. 2. Estimates of mortality rate ( $\pm$  SE) in bycatch by developmental stage across sea snake species.

do not survive to reproduce. Data on natural mortality rates and survival in sea snakes is scarce.

#### 4.3. Reproductive cycles of sea snakes and bycatch risk

We observed a relatively large number of gravid female *H. schistosus*, comprising around 25% of the sample at their peak in February (2018). There was a notable lack of gravid *H. curtus*. However, we did encounter a single gravid female of *H. viperinus* with fully developed embryos in November of 2017. This may suggest differing reproductive cycles among syntopic species.

The observed reproductive cycle of this population of *H. schistosus* is similar to other reports on their breeding biology (Bergman, 1956; Voris and Jayne, 1979; de Silva et al., 2011). However, the periods may vary by geographical region. Bergman (1956) observed that *H. schistosus* and other species gave birth around November at the end of the dry season in Surabaya, Java. We observed a similar trend, both with observed births in April and an increase in neonates from March to May, just before the onset of the monsoon on the Indian subcontinent (Fig. 1). This may put neonates at an advantage with respect to foraging and access to fresh water (Lillywhite et al., 2008).

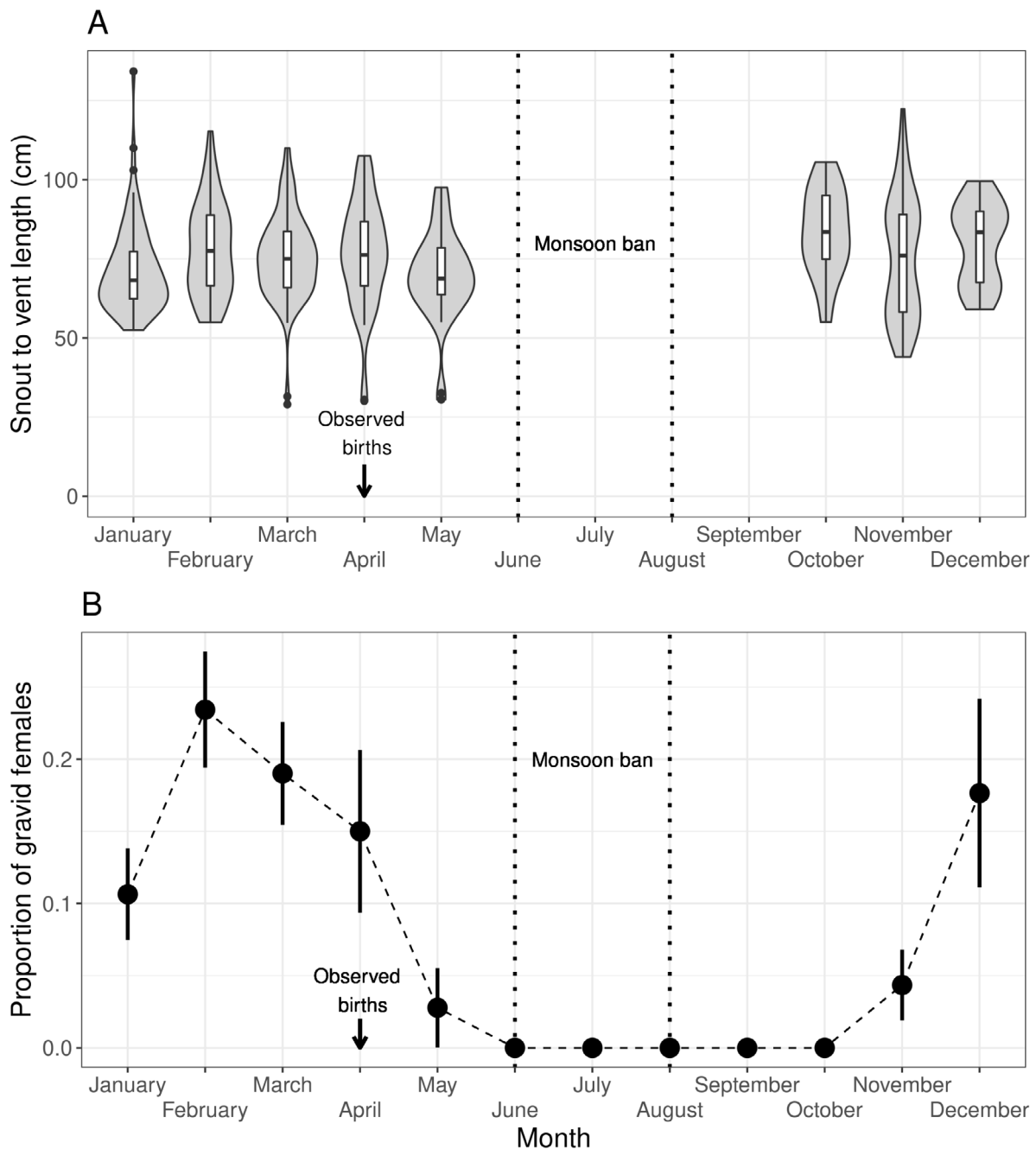
The period of reproduction for *H. schistosus* also overlap completely with intensive fishing for both trawlers and gillnets. In the Sindhurg region, trawlers peak in fishing effort around November and December, while gillnets use the most effort around February (pers. obs.). As this period coincides with the period of birth for *H. schistosus* (Fig. 3), the movement of females to shallower waters may increase their overlap and interactions with gill-netters and the associated risks as well. Conversely, change in female behaviour during pregnancy may explain the lack of *H. curtus* gravid females in bycatch during the current study. While mortalities of gravid females in bycatch remain low (~18%), it is difficult to determine the sublethal effects these interactions may pose such as increased stress and behavioural changes (Wilson et al., 2014).

#### 4.4. Reproductive strategies in relation to bycatch

Viviparity presents a unique set of trade-offs to marine snakes as compared to terrestrial snakes. Large clutches may hinder swimming performance and the female's ability to avoid predation and forage (Shine, 1988). Thus, marine sea snakes in general are  $k$ -strategists that have small clutches of larger embryos with the notable exception of *H. schistosus* (Lemen and Voris, 1981). During our study, the largest female (183 cm) also had the largest clutch (31 eggs) and this was observed in previous studies as well (Smith, 1926; Bergman, 1943; Voris and Jayne, 1979; de Silva et al., 2011). The large size of *H. schistosus* relative to its congeners in addition to their foraging habits may allow them to carry more embryos.

The ways in which females provide nutrients for embryonic development changes in the transition from oviparity to viviparity (Packard et al., 1977). We observed a stark increase in total egg weight, despite a reduction of yolk weight as the embryo develops. Assuming no transfer of matter and energy between females and embryos, total egg weight must remain more or less constant throughout development. Thus, our findings suggest that despite the presence of yolk *H. schistosus* females may provide some level of matrotrophic nutrition to embryos. Kasturirangan (1951) reported of a specialised placental tissue in *H. schistosus* (allanto-placenta) which may facilitate such nutrient transfer. We did not observe any gravid females with gut content. But we did observe large fat deposits in all gravid females we encountered, which may indicate the storage of energy for the gestation period (Figure 1 of supplementary materials B). It must be noted, however, that eggs of oviparous reptiles do exchange water and oxygen with their surroundings and thus also increase in weight during development (Cunningham and Hurwitz, 1936). In addition, physiological or energetic evidence for matrotrophic nutrition and capital breeding (using stored energy for reproduction) in sea snakes is not available yet.

Lemen and Voris (1981) reported an increase in reproductive potential (clutch size) with female age for all sea snake species. However, the reproductive effort over a lifetime remains constant



**Fig. 3.** (a) Seasonal changes in the population structure of *H. schistosus*. (b) Trend in the relative proportion of gravid females ( $\pm$  SD) caught in bycatch of gillnets, trawlers and shore seines in Malvan, Maharashtra. Two live births were observed during the month of April. Sampling was not conducted from June to September due to a uniform monsoon ban.

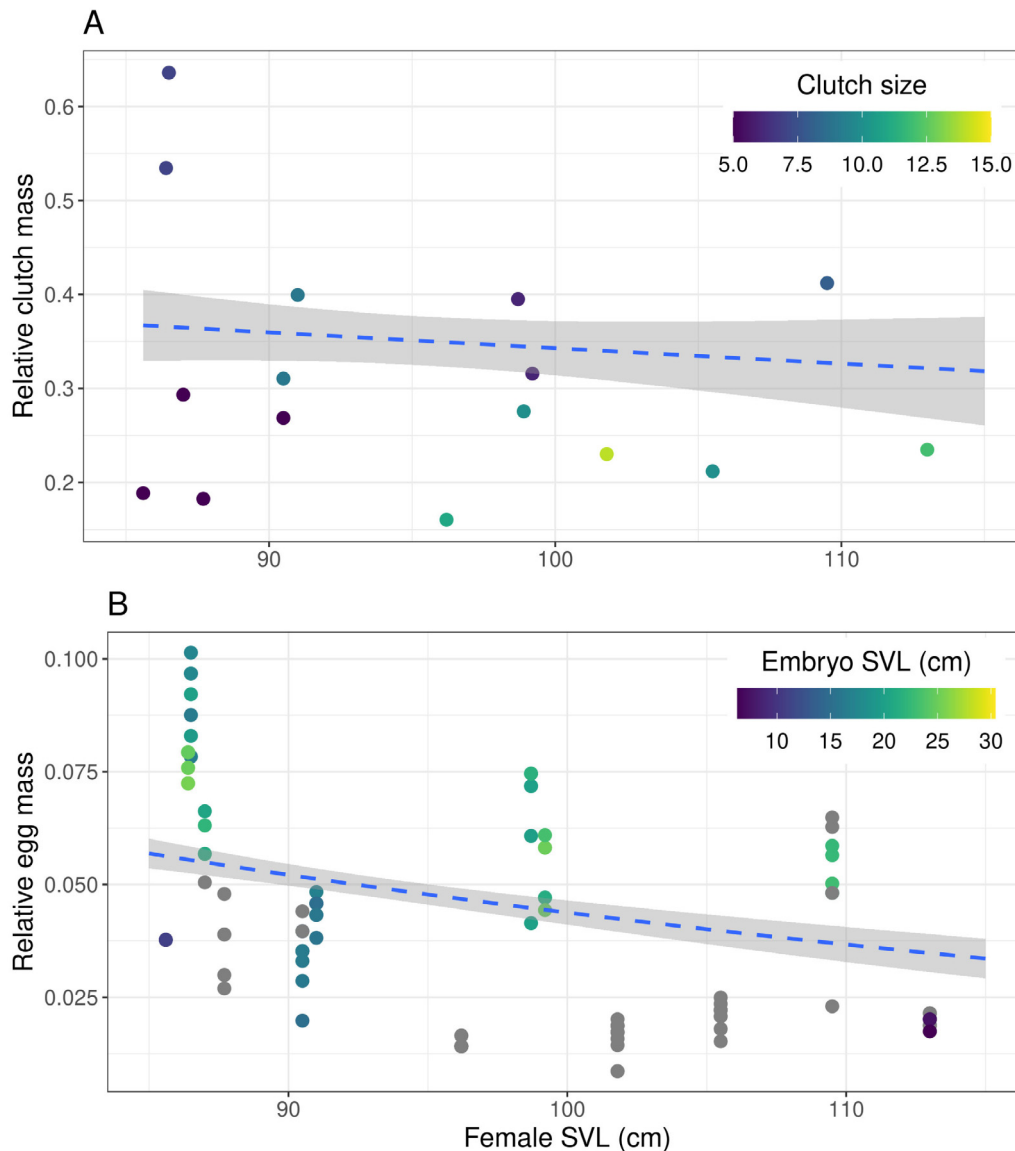
across taxa (around 1.4 times the female weight) (Charnov et al., 2007). We observed a similar trend of increasing clutch size with female length in *H. schistosus*. We also observed that maternal investment (relative clutch mass) did not change with increasing female SVL. Thus, investment per embryo likely reduces with female age in the case of *H. schistosus*, which is typical of  $r$ -strategists (Fig. 4). In addition, maternal investment in embryos was not very different across sexes, which may explain the equal sex ratios in clutches (Shine and Bull, 1977).

#### 4.5. Caveats and conclusions

*Hydrophis curtus*, like other Hydrophids, is a  $k$ -strategist producing few (5–6) large ( $\sim 29$  cm at birth) young (Lemen and Voris,

1981). The differences in reproductive strategies and apparent mortality rates between *H. schistosus* and *H. curtus* may put the former at a competitive advantage and contribute to assemblage shifts in the region. Rao et al. (2021) report a shift in sea snake assemblages in the Konkan region over the past two decades. The relative proportion of *H. schistosus* ( $P_{2002-2003} = 20\%$ ,  $P_{2016-2018} = 85\%$ ) in bycatch has increased with a corresponding decline in *H. curtus* ( $P_{2002-2003} = 85\%$ ,  $P_{2016-2018} = 20\%$ ).

The number of mechanised vessels in the region are increasing, indicating an increase in fishing pressure (Rao et al., 2021). While our findings suggest that *H. schistosus* populations in the Konkan region may continue to be stable despite increasing fishing pressures, we cannot be certain of the long-term effects that fisheries will have on them in the region. It is also important to



**Fig. 4.** (a) Change in relative clutch mass with increasing female snout to vent length (cm). Colour of the points indicate clutch size. (b) Reduction in relative egg mass (REM) with increasing female snout to vent length (cm). The colour of each data point indicates embryo SVL.

note that we cannot ascertain what makes *H. curtus* particularly vulnerable to bycatch mortalities due to lack of data throughout their range. It may be important to investigate what factors other than reproductive biology make sea snakes vulnerable or resilient to anthropogenic pressures. Further research is needed towards sea snake physiology and trophic ecology in anthropogenically dominated seascapes.

Sea snake populations around the globe are threatened by anthropogenic activity such as climate change, unregulated fishing, and pollution. Most sea snake species (~33%) are listed as data deficient in IUCN (Elfes et al., 2013; Udyawer et al., 2018). In India, sea snakes are protected under law, however, effective ground management is lacking. A better understanding of the risks faced by sea snake populations may lead to well informed and an effective conservation management strategy in the near future.

#### CRediT authorship contribution statement

**Shawn Dsouza:** Conceptualization, Formal analysis, Funding acquisition, Writing - original draft, Writing - review & editing. **Chetan Rao:** Supervision, Writing - original draft, Writing - review & editing, Project administration, Funding acquisition.

#### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary data

Supplementary material related to this article can be found online at <https://doi.org/10.1016/j.rsma.2021.101948>.

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