Resource use and the impacts of fisheries on two sympatric sea snake species on the west coast of India

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Abstract

We investigated differences in resource use between two sympatric sea snake species from the west coast of India, *Hydrophis curtus* and *H. schistosus*, and described the impacts of fishing on the interactions of these species. We compared habitat use, diet, and isotopic niche width between species to determine resource overlap. We then compared trophic overlap of each species with the fisheries in the region and tested the effect of fishing intensity on their isotopic niche width. *Hydrophis curtus* used deeper habitats than *H. schistosus*, resulting in increased spatial overlap with fisheries. The two species also had distinct trophic niches and *H. curtus* prey formed a larger proportion of fishery catch on average than *H. schistosus*. This greater overlap could make *H. curtus* more vulnerable to the effects of fisheries. Both species exhibited expansion in short-term and long-term isotopic niche width along a gradient of fishing intensity which may indicate behavioural changes associated with the presence of fisheries. *Hydrophis curtus* is a trophic generalist, competes with syntopic species and is dominant in most assemblages. However, *H. schistosus* exhibits higher plasticity in resource use and may have an advantage over *H. curtus*. Sea snakes play an important role as mesopredators and as intermediate links in coastal marine food webs. Thus, fishing could alter the relative abundance of these mesopredators with cascading effects through coastal food webs.

Introduction

Competition and predation are vital selective forces that determine assemblage composition in ecological communities (Paine 1966; Schoener 1974). The interaction of these top down and bottom-up forces along with processes such as dispersal, selection and speciation maintain diversity and ecosystem functioning (Vellend 2010; Terborgh 2015). Human interactions with these ecosystems such as fishing and agriculture can alter trophic interactions through the selective removal of predators, changing land use and exploitation of lower trophic levels. This can affect the state and stability of these systems resulting in widespread effects throughout food webs such as trophic cascades and mesopredator release (Jackson et al. 2001; Estes et al. 2011).

Overexploitation and bycatch are major issues faced by almost all fisheries globally (Bhathal and Pauly 2008; Soykan et al. 2008). The effects of fisheries on coastal ecosystems are wide ranging and historically well documented such as the collapse of top predator populations, mesopredator release, trophic cascades, and changes in behaviour of marine species (Jackson et al. 2001; Steneck 2012; Myers et al. 2007). Some recent examples of the fisheries effects on ecosystems and marine species are the decline of the Steller's sea lion in the Bering Sea, change in social behaviour of bottlenose dolphins in Sardinia, Italy, and the decline of the vaquita in Mexico due to gillnet bycatch (Hennen 2006; Rojas-Bracho and Reeves 2013; Díaz López 2018).

Fishing may involve the use of a diversity of gears with varying effects on the environment. Trawl fishing, for example, is a destructive practice which involves dragging a large net behind a powerful vessel. In addition to altering benthic habitats, gears such as trawls and long lines also result in large amounts of bycatch (Soykan et al. 2008). The composition of this bycatch ranges from polychaetes and juvenile fish to dolphins and marine turtles (Lobo 2007). Many vulnerable species suffer high mortalities in bycatch including

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sea turtles globally (see Gopi et al. 2007; Molina and Cooke 2012 for examples) and sharks in deep sea long lines (Cambiè et al. 2013).

True sea snakes (Hydrophiinae) are a recent lineage originating from terrestrial elapids around 6–8 million years ago (Sanders et al. 2013). They coexist with humans throughout their tropical range, often in areas of high fishing activity. They are threatened by anthropogenic activities and their consequences, such as rising ocean temperatures due to climate change, and habitat destruction due to fishing and pollution. Bycatch and interaction with fisheries cause large-scale mortality among sea snakes and pose a significant threat to them throughout their distribution (Fry et al. 2001; Lobo 2003; Milton 2001; Van Cao et al 2014).

Sea snake assemblages can consist of up to 20 sympatric species. This high degree of sympatry has led to a diversity of resource use strategies among the 70 extant species of hydrophids (Glodek and Voris 1982; Voris and Voris 1983). Species such as *Hydrophis curtus, Aipysurus laevis* and *H. platurus* are known to be generalists, feeding on between 12 and 31 families of fish depending on their geographical location (Voris and Voris 1983). Some species of sea snake specialise on a few prey items, such as *H. schistosus* which feeds primarily on plotosids and tetraodontids and *Emydocephalus annulatus* and *E. ijinae* which feed primarily on fish eggs (Voris 1966; Voris et al. 1978).

Diversity in resource use strategies manifest in a variety of foraging behaviours and habitat associations among syntopic and closely related species (Schoener 1974). For example, *E. annulatus* browses burrows of fish in rock crevices to forage fish eggs, *H. viperinus* and *H. schistosus* cruise benthic habitats to encounter prey, while *H. curtus* uses a sit and wait foraging strategy in the water column (Shine et al. 2004; Voris et al. 1978; Lobo et al. 2005). Resource specialisation may also lead to rapid morphological evolution, for example, in the case of microcephalic hydrophid species (Sherratt et al. 2018).

Sea snakes play a vital role as intermediate links in coastal ecosystems (Voris 1972). This also makes them useful bioindicators of ecosystem health (Brischoux et al. 2011). Rao et al. (2021) reported two hydrophid species, *Hydrophis curtus* and *H. schistosus*, as dominant in bycatch from trawl nets and gillnets in Sindhudurg, Maharashtra. They observed high mortality rates of both species in trawl nets. In addition, Rao et al.'s (2021) comparison of sea snake bycatch assemblages with Lobo et al.'s (2004) data suggests a shift in abundance of sea snakes in bycatch over the last 2 decades, indicating a decline in *H. curtus* populations. Similar declines in sea snakes have been reported from other parts of their range (Goiran and Shine 2013; Lukoschek et al. 2013; Lukoschek 2018).

Since such shifts in composition can have ecosystem level consequences, we aimed to understand the trophic ecology of these species and the effect of fishing on them. In the current study, our objectives were: (1) to determine habitat and resource use of the two dominant sea snake species in the Konkan region of India; *H. curtus* and *H. schistosus*; and (2) to examine the effects of fishing activity on their resource use and species interactions to understand assemblage shifts. We used a combination of approaches including (a) fisheries-dependent methods to characterise distribution and habitat use of the two species; (b) visual gut content analysis to characterise diet and trophic niche of the species and overlap between fisheries catch and sea snake diet; and (c) stable isotope analysis to characterise overall resource use in terms of isotopic niche, as well as the effect of fishing intensity on the niche width of both species.

Materials and methods

Study site

Sindhudurg is a coastal district in the south of Maharashtra on the west coast of India. There are 34 fish landing centres in the district out of which 1940 vessels operate. Most vessels are mechanised (929) with motorised (606) and non-motorised (405) boats also operating in the near shore waters of the district (Vidya et al. 2016). Malvan is one of the major landing ports in Sindhudurg with trawl nets, gillnets and shore seines being the most prominent of fishing practices (United Nations Development Programme (UNDP) 2013). Manual gillnets are operated off small (4–8 m) motorised or non-motorised crafts. Motorised gillnets are operated on crafts with an outboard motor (9–12 HP), targeting a variety of fish and crustaceans depending on the time of year. The trawl nets in the region are crafts of ~ 10 m with in-board motors (90–110 HP). Fishing in the region is operational from January to May and mid-August to December, with a uniform restriction during the monsoon months between June and August. Fishing effort remains constant for both trawl nets and gillnets throughout the fishing season (pers. obs.). Inshore areas around Sindhudurg are characterised by largely homogenous substrate of sand and silt with a few rocky outcrops. The coast has many river mouths that bring a large amount of silt along with fresh water to near shore areas (Hanamgond and Mitra 2008).

Field and laboratory methods

Fisheries-dependent sampling for sea snakes and fishing effort

We sampled sea snakes caught as bycatch in fisheries and landed at Malvan from January 2018 to May 2019. We sampled both gillnets and trawl nets for bycatch to ensure a

wider spatial coverage of the near shore areas. Boats were sampled when they landed their catch; mornings (7 am to 10 am) for gillnets and evenings (5 pm to 8 pm) for trawl nets. We conducted structured interviews with the crew to determine fishing location (nearest landmark), depth of fishing, and effort. The individuals caught were brought back to the field station, identified and examined for injuries. Snout to vent length (SVL), tail length (TL), weight and sex were recorded. Live snakes were released in near shore waters and dead snakes were dissected to check for gut content and confirm reproductive status.

Visual gut content analysis

We determined the presence of gut content in each snake visually or by mild palpation (Lobo et al. 2005). Live sea snakes were allowed to regurgitate their gut content in captivity on their own (i.e. without any palpation of their guts to force regurgitation) and gut content was extracted from dead snakes by dissection. Prey were identified to the nearest taxonomic unit (Family, Genus, or species), failing which they were recorded as unidentified (Fischer and Bianchi 1984). We gave each prey specimen a score for stage of digestion (1–5, 1 being intact and 5 being almost completely digested) based on a visual assessment. We measured the standard length, maximum width, and weight of all prey specimens; however, we used only specimens with a digestion score of less than 3 for morphometric analysis (Briand et al. 2015, 2016).

Tissue sampling for stable isotope analysis

We sampled blood from live individuals that weighed more than 150 g using caudal vein punctures. We sampled scale tissue from the mid body sections of dead snakes of all size classes. As whole blood and blood plasma have different metabolic turnovers (Reich et al. 2008), blood samples (approximately 1–1.5 ml) were taken with an anticoagulant coated syringe and centrifuged to separate plasma which was stored at − 18 °C (Lemons et al. 2012). Scale samples were stored in 70% ethanol. All samples were bought back to the Centre for Ecological Sciences, IISc, Bangalore, and dried in a hot air oven at 50 °C for 72–96 h. Dried samples were then homogenised using a scraper or mortar and pestle. Scale samples were lipid extracted (Bligh and Dyer 1959; Post et al. 2007) and analysed with Isotope Ratio Mass Spectroscopy at the Centre for Earth Sciences, IISc, Bangalore.

Sampling fisheries catch

We determined the composition of catch from gillnets and trawl nets by random sampling of landings at Malvan (Mini 2014). Small, mechanised boats employing gillnets were sampled in the morning, between 5 and 9 am, when they landed their catch. Trawler catch was sampled at the landing centre in the evening. We recorded the identity of the specimens to the lowest taxonomic unit (Family, Genus, or species), failing which they were recorded as unidentified. We recorded the sample weight, the total weight of the catch, fishing effort and the depth of fishing for each fishing trip that was sampled (similar to "Fisheries-dependent sampling for sea snakes and fishing effort").

Analysis

Calculating fishing effort and geocoding fishing trips

Using structured interviews, we determined effort per boat trip as the product of number of days fished, the number of times the net was set or hauled in each fishing day and the duration of each set or haul. We used average haul durations from trawl nets where multiple hauls were carried out on each trip. We used a two-step method to estimate the location of fishing from each boat trip. We first geocoded landmark locations from Google Maps API using the 'mutate_geocode' function in the ggmap package in R Ver. 3.5.3 (R Core Team 2014). We then compared the geocoded locations along with depth of fishing from landing surveys to the General Bathymetric Chart of the Oceans (GEBCO) bathymetric database using custom matching functions and the 'fuzzy_inner_join' function in the 'fuzzyjoin' package (R 3.5.3).

The extent of occurrence of fishing events was then converted into a raster grid with a cell size of 10 km^2 using the 'extent' function in package 'sp' and the 'raster' function in the 'raster' package. We removed grid cells that overlapped with the mainland. The total fishing extent was divided into 702 cells (27 rows by 26 columns). Effort from each boat trip occurring in a cell was then summed to determine the fishing intensity in that cell over the sampling period (Stelzenmüller et al. 2008).

Determining sea snake distribution and habitat niche

We calculated the catch per unit effort (CPUE) of each species of sea snake caught during each boat trip as the number of sea snakes caught during a given boat trip divided by fishing effort (haul-h^{-1}, calculated as in "Calculating fishing effort and geocoding fishing trips"). The location of each boat trip was then geocoded and assigned to a cell in a grid. CPUE for each species was then summed for each cell in the grid. We calculated the species spatial extent as the sum of areas of all cells in which it occurred (i.e., where CPUE of species was greater than zero). We calculated percentage overlap in sea snake distribution as the number of cells in which both species occurred divided by the total spatial

extent of both species. We calculated the mean depth of each cell (cell depth) in the raster grid using the GEBCO database. The mean cell depth of raster grid cells in which a species of sea snake occurred was used as a measure of habitat preference. Standard deviation of cell depths was used as a measure of niche width and plasticity. We tested the difference in depth preference between sea snake species using a *t* test.

Determining sea snake diet and trophic niche

We analysed prey preference by sea snake species using the Index of Relative Importance (IRI) (Pinkas et al. 1971). We used diversity (Shannon's index) of prey families found in gut as a measure of trophic niche breadth. We used a measure of similarity in composition (Morisita–Horn index) of prey families to estimate trophic niche overlap (Schoener 1974). Diversity and composition of prey families were computed using the 'Diversity' and 'SimilarityPair' functions respectively in the 'SpadeR' package in R 4.0.1 (Chao et al. 2016). We used a Permutative Multivariate Analysis Of Variance (PERMANOVA, function 'adonis2' in package 'vegan') to test differences in prey composition between sea snake species (2012 Anderson and Walsh 2013).

Determining sea snake isotopic niche overlap using stable isotope analysis

We fitted a multivariate normal (MVN) model to estimate the bivariate mean and variance of carbon and nitrogen stable isotope ratios of sea snake tissues. MVN models were run using a Bayesian framework with 20 k iterations and a 10 k burn in using the 'siberMVN' function from the 'SIBER' package. We computed standard ellipses from posterior means and variance from the MVN model using the 'siberEllipses' function. We used standard ellipse area (SEA) as a measure of overall isotopic niche width and variation to compare across sea snake species. Difference in SEA among species was calculated as P (SEA of *H. curtus* > SEA for *H. schistosus*) for 10 k posterior ellipses. We sampled and plotted ten random posterior standard ellipses to visualise sea snake isotopic niches. Overlap between paired posterior ellipses was computed from isotope ratios of plasma and scale tissue using the 'bayesian.overlap' function. We used the mean and standard deviation overlap of 10 k posterior standard ellipses as a measure of isotopic niche overlap (Newsome et al. 2007; Jackson et al. 2011).

Quantifying trophic overlap with fisheries

We calculated the total biomass of various fish, mollusc and crustacean families in each catch sample as well as the total sample weight. We calculated the proportion of prey of each

sea snake species in each catch sample as measure of trophic overlap. We tested the difference in overlap across sea snake species and fisheries catch using Student's *t* tests.

Quantifying the effect of fisheries on isotopic niche

Sea snakes sampled for stable isotopes were assigned to a raster grid cell by geocoding and rasterising the boat trip in which they were caught (as in "Calculating fishing effort and geocoding fishing trips"). We tested the effect of fishing intensity on carbon and nitrogen isotope ratios of plasma sampled from each sea snake species using generalised linear models. We classified each cell in the raster grid as high and low fishing intensity zones using hierarchical clustering based on the centroid of each cell, the fishing intensity of gillnets and the fishing intensity of trawl nets in each cell. We then computed standard ellipses for each species in each fishing intensity zone and calculated their isotopic niche width (SEA_b) for both scale and plasma tissue samples (Jackson et al. 2011). We compared isotopic niche width of each species across fishing intensity zones as $P(SEA_{high} > SEA_{low})$ (Layman et al. 2007).

The data used for this manuscript and code for analysis are available at https://github.com/cheesesnakes/sea-snake-resource-use.

Results

Comparison of H. schistosus and H. curtus resource use

Habitat use and distribution

We sampled 179 *Hydrophis curtus* and 605 *H. schistosus* from bycatch in trawl nets (92.75 haul h) and gillnets (270.56 haul h). *Hydrophis curtus* (0.16 ± 1.22 CPUE in each grid cell) was found in 540 km² (54 grid cells) and *H. schistosus* (0.60 ± 4.43 CPUE) was found in an area of 620 km² (62 grid cells) (Fig. 1), with 33.33% spatial overlap with each other. *Hydrophis curtus* (mean depth = 28.55 ± 12.10 m) was caught in deeper waters than *H. schistosus* (mean depth = 17.67 ± 10.64 m, $T_{92} = 5.1$, Cohen's $d = 0.95$, $p = 1.4 \times 10^{-6}$).

Diet and trophic niche

A total of 93 *H. schistosus* (22 dead and 71 live specimens) and 36 *H. curtus* (19 dead and 17 live specimens) were found with some gut content present. Eight sea snakes had more than one prey specimen present in their guts. Visual gut content analysis showed a total of 26 prey species (40.31% unidentified) from 17 families (29.45%
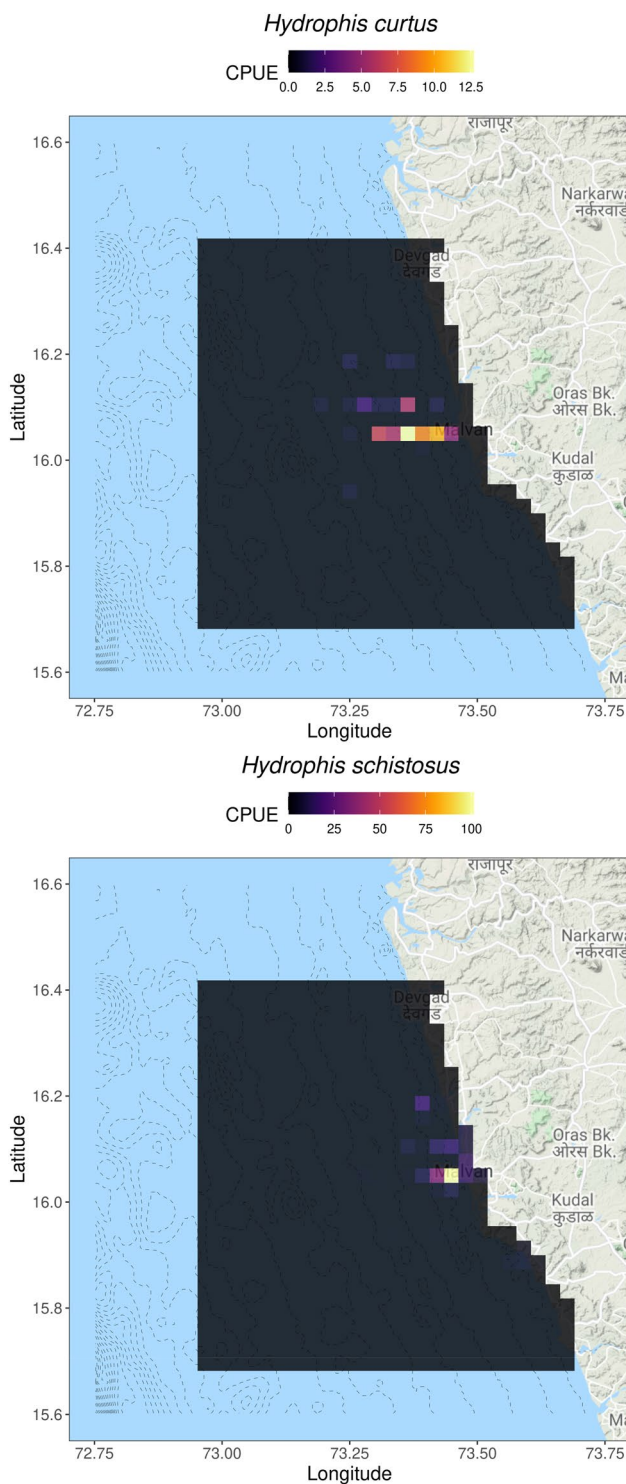
Fig. 1 Distribution and depth use by sea snakes in the near shore waters of Sindhudurg, Maharashtra based on fisheries dependent data. Black dashed lines indicate 10 m depth contours
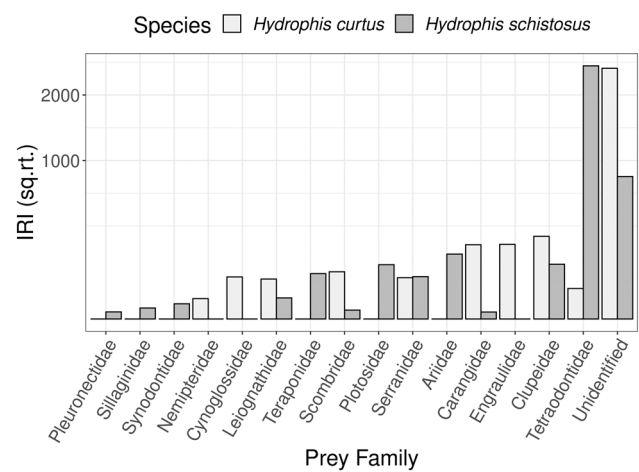

**Fig. 2** Index of relative importance (IRI, square root transformed) (Pinkas et al. 1970) of prey families in sea snake diet

(Shannon diversity $= 6.42 \pm 0.97$(SE)). Both species preyed on six common prey families (Morisita—Horn overlap $= 0.27 \pm 0.09$(SE)). However, we found that prey composition differed significantly among species (PER-MANOVA, $R^2 = 0.05$, $F_{71} = 3.77$, $p = 0.001$). *H. schistosus* showed a preference for fish from family Tetraodontidae (IRI $= 2554.8$), which comprised 34.24% of its diet, followed by Ariidae (IRI $= 168.15$), Clupeidae (IRI $= 119.63$) and Plotosidae (IRI $= 117.61$) which together comprised 19.4% of its diet. We did not observe any diet preferences among *H. curtus*. *Hydrophis schistosus* fed on prey with a greater maximum width (3.46 ± 1.17 cm) than *H. curtus* (2.76 ± 0.76 cm, $T_{29} = 2.38$, Cohen's $d = 0.64$, $p < 0.05$).

Isotopic niche

We analysed a total of 63 *H. curtus* tissue samples (28 plasma and 35 scales) and 120 *H. schistosus* tissue samples (68 plasma and 52 scales). Carbon isotope values were more depleted for *H. curtus* than *H. schistosus*; similarly, nitrogen isotope ratios were enriched slightly in *H. schistosus* compared to *H. curtus* for both tissues. However, the difference in nitrogen ratios was only significant for plasma (Table 1). *Hydrophis curtus* (Plasma: $SEA_b = 1.81 \pm 0.38$, Scales: $SEA_b = 3.23 \pm 0.64$) had a smaller isotopic niche than *H. schisotus* (Plasma: $SEA_b = 2.51 \pm 0.36$, Scales: $SEA_b = 4.64 \pm 0.69$) based on both plasma ($P(SEA_{H.\ schistosus} > SEA_{H.\ curtus}) = 0.9$) and scale ($P(SEA_{H.\ schistosus} > SEA_{H.\ curtus}) = 0.93$) samples (Fig. 3). Overlap of standard ellipses computed from isotopic ratios was lower for plasma (0.42 ± 0.05) than for scales (0.61 ± 0.1).

unidentified, Fig. 2). *Hydrophis curtus* preyed on a total of nine fish families (Shannon diversity $= 8.07 \pm 1.3$(SE)) compared to 12 prey families preyed on by *H. schistosus*

Table 1 Summary and comparison of isotope ratios of plasma and scales from *Hydrophis curtus* and *H. schistosus*

Isotope	*Hydrophis curtus*	*Hydrophis schistosus*	*T*	d.f	*P*	Cohen's *d*
Plasma						
δC^{13}	− 16.98 ± 1.08	− 16.74 ± 0.92	− 0.966	41	0.33	0.24
δN^{15}	13.92 ± 0.76	14.73 ± 1.25	− 3.36	74	0.0005	0.72
Scales						
δC^{13}	− 14.68 ± 0.99	− 14.52 ± 1.29	− 0636	80	0.52	0.13
δN^{15}	14.44 ± 1.02	14.69 ± 1.18	− 0.968	65	0.33	0.21

Fig. 3 Bayesian ellipses in isotopic space describing difference in niche width and resource use between *Hydrophis curtus* and *H. schistosus*
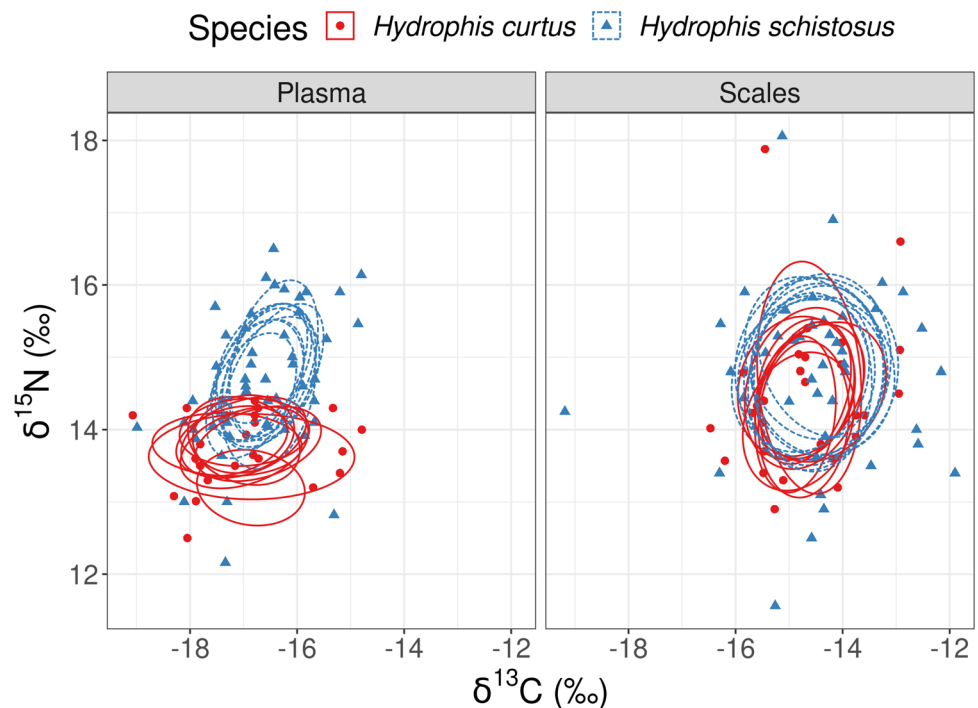
Resource use in relation to varying fishing intensity

Resource overlap

We sampled a total of 38 gillnet trips (35.41 haul h) and 140 trawler trips (434.65 haul h) to characterise catch composition from each gear. Weight of catch landed was 252.94 ± 265.59 kgs per fishing trip. Fisheries caught a total 48 families of fish, crustaceans, and molluscs. *Hydrophis curtus* prey families (richness = 9, 73.56%) formed a significantly higher proportion of trawler catch than *H. schistosus* prey (richness = 10, 48.42%, $T = 7.02$, Cohen's $d = 0.88$, $p < < 0.05$). Both species had similar prey overlap with gillnet catch (richness$_{HC}$ = 7, richness$_{HS}$ = 7, $T = 0.04$, $p = 0.96$, Cohen's $d = 0.009$, Fig. 4).

Effects on isotopic niche width

We sampled a total of 175 gillnet trips and 104 trawler trips to determine fishing intensity and spatial extent in

the near shore waters of Sindhudurg. The sampled fishing trips covered a total of 1290 km^2 (129 grid cells) with a mean intensity of 7.28 ± 9.42 haul h per grid cell (10 km^2) (Fig. 5).

We geocoded 39 *H. curtus* samples (16 plasma and 23 scales) and 77 *H. schistosus* samples (40 plasma and 37 scales). Fishing intensity had little effect on $\delta^{15}N$ and $\delta^{13}C$ ratios of scales and plasma for both species (see supplementary materials A). Mean plasma isotopic niche widths of *H. curtus* and *H. schistosus* were similar in areas with high (*H. curtus*: SEA$_b$ = 1.78 ± 0.68, *H. schistosus*: SEA$_b$ = 2.69 ± 0.54) and low (*H. curtus*: SEA$_b$ = 1.65 ± 0.77, *H. schistosus*: SEA$_b$ = 2.33 ± 0.66) fishing intensity (*H. curtus*: P(SEA$_{high}$ > SEA$_{low}$) = 0.58, *H. schistosus*: P(SEA$_{high}$ > SEA$_{low}$) = 0.69). However, isotopic niche widths computed from scale samples were larger (*H. curtus*: P(SEA$_{high}$ > SEA$_{low}$) = 0.99, *H. schistosus*: P(SEA$_{high}$ > SEA$_{low}$) = 0.96) in areas of high
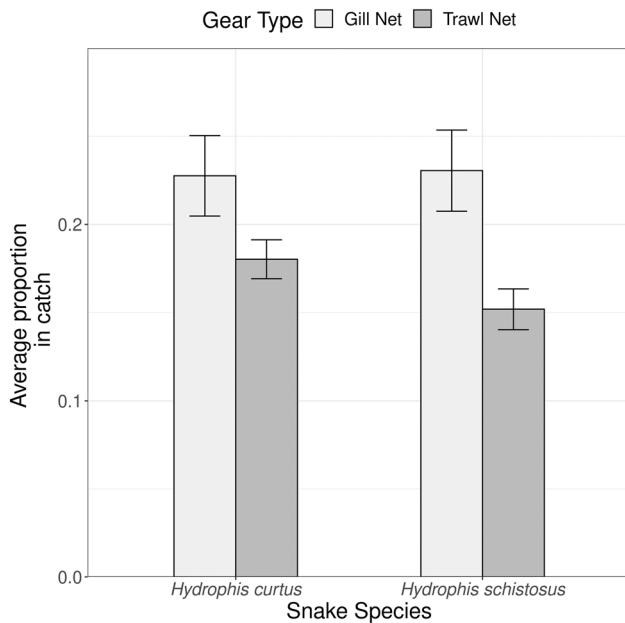
Fig. 4 Average proportion of sea snake prey families in gillnet and trawler catch. Bars indicate standard error
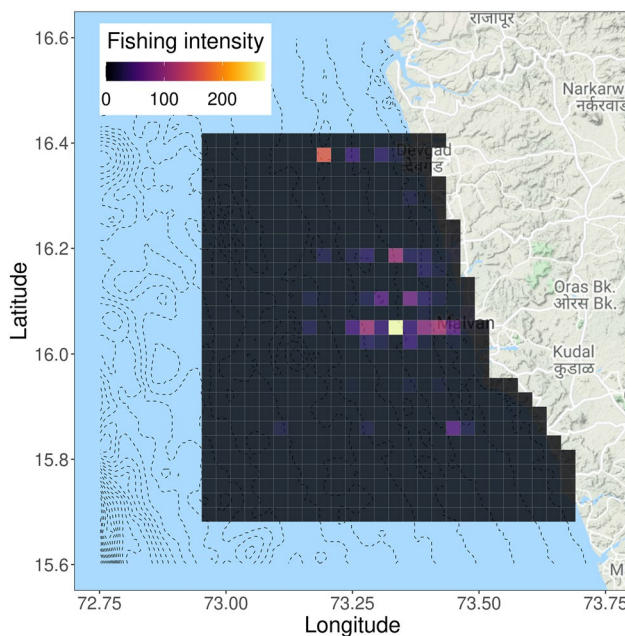

Fig. 5 Distribution of fishing intensity of trawl nets and gillnets operating from Malvan, Maharashtra. Black lines indicate 10 m depth contours

fishing intensity (*H. curtus*: $SEA_b = 3.21 \pm 0.95$, *H. schistosus*: $SEA_b = 6.69 \pm 1.62$) than in areas with low fishing intensity (*H. curtus*: $SEA_b = 1.17 \pm 0.4$, *H. schistosus*: $SEA_b = 3.69 \pm 0.95$, Fig. 6).

Discussion

We compared the resource use strategies and interaction with fisheries of two sympatric sea snake species on the west coast of India. Our findings suggest that they had distinct trophic and habitat niches which were also reflected in their isotopic niches (Figs. 1, 2 and 3). *Hydrophis curtus* showed greater resource overlap with trawler catch than *H. schistosus* (Fig. 4). We found that the isotopic niche width of both species increased along a fishing gradient and that the effect was amplified over longer time periods (Fig. 6).

### Habitat use by sea snakes and spatial overlap with fisheries

Hydrophis curtus was encountered in deeper waters than *H. schistosus* (Fig. 1). The carbon isotope ratios of both plasma and scales were relatively depleted in *H. curtus* indicating a greater proportion of carbon in its diet comes from offshore habitats (Wunder 2012). Fishing effort is also concentrated in areas where *H. curtus* forage (Figs. 1 and 5). *Hydrophis schistosus* on the other hand prefers near shore areas. Differences in habitat use between these species may result in varying spatial overlap with different fishing gears. This may create differential risk of lethal and sub-lethal effects of fisheries for both these species.

As we relied on fisheries dependent methods for our sampling, we were unable to determine the true level of spatial overlap between sea snakes and fisheries. Thus, it is difficult to determine to what degree spatial overlap with fisheries affects each sea snake species. Rao et al. (2021) showed that sea snakes suffer greater mortality in trawler bycatch than gillnets in the Konkan region. Greater overlap with fisheries may indicate greater risk for *H. curtus*. Udyawer et al. (2016) suggested that *H. curtus* juveniles may seek areas of lower fishing intensity as refuges, indicating possible altered behaviour. This difference in adult and juvenile habitat use may also reflect in their isotopic niches.

Sea snake diet, competition and fisheries catch

Diet and foraging strategies also differ among these species. *Hydrophis curtus* is a generalist who likely uses a sit and wait strategy in the deeper water column whereas *H. schistosus* is a specialist which cruises benthic habitats in search of prey (Voris and Voris 1983; Lobo et al. 2005). Interestingly, Voris and Voris (1983) report that *H. schistosus* primarily fed on fish from the family Ariidae, with Tetraodontidae forming a smaller but still significant proportion of its diet. This is in contrast with our findings (Fig. 3) and may suggest geographic variability in prey preferences. The lower prey

Fig. 6 Violin plots depicting the effect of fishing intensity on plasma and scale isotopic niche width of *Hydrophis schistosus* and *H. curtus*
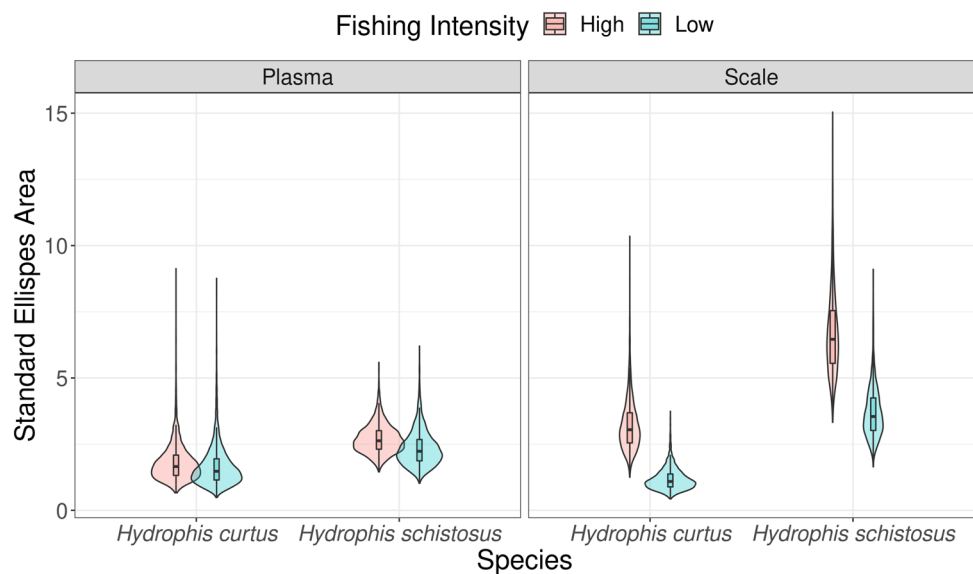
family richness reported in our study compared to previous studies is likely due to differences in sample size (see supplementary materials D).

We found that *H. curtus* feeds at lower trophic levels compared to *H. schistosus* based on their prey preference and depleted nitrogen values (Fig. 3). However, without an isotopic baseline, it is difficult to conclusively infer trophic preferences among these species. Our results, along with previous studies, also suggest that *H. schistosus* is more plastic (flexible) as far as diet and trophic niche are concerned (Voris et al. 1978). However, it is difficult to explain why *H. curtus* exhibits a wider trophic niche than congeneric species throughout its range (Voris and Voris 1983).

Despite being a known trophic generalist, we found that *H. curtus* had a smaller isotopic niche than *H. schistosus* (Fig. 3) (Lemen and Voris 1981). In addition, there was limited overlap in isotopic space between these two species, indicating distinct resource pools and /or habitats. The difference in trophic niche between *H. curtus* and *H. schistosus* may also be attributed to prey sizes selectivity due to differences in body size (Brischoux and Lillywhite 2013). Head and jaw morphologies are limiting factors for feeding, consequently larger snakes can take larger prey (Shine 1991). This limitation, combined with a diversity of foraging strategies drive evolution among sea snakes (Sherratt et al. 2018; Brischoux et al. 2011).

While resource use strategies differ among *H. curtus* and *H. schistosus*, we found a significant overlap in fisheries catch and diet of both species (Fig. 4). Gears such as trawl nets are more efficient at gathering large quantities of fish and thus may pose a greater threat in terms of competition for dietary resources than gillnets (Dineshbabu et al. 2010). *Hydrophis curtus* shows a greater trophic overlap with trawl fisheries than *H. schistosus*, possibly due to its generalist feeding strategy. Fry et al. (2001) found that *H. curtus* diets in the Gulf of Carpentaria, Australia overlapped with prawn trawler discards and observed opportunistic feeding by some individuals. In addition, they found that *H. curtus* gut content comprised a higher proportion of squid (~65%) in areas open to trawling whereas bony fish made up a majority of *H. curtus* gut content in areas closed to trawling. Lobo et al. (2005) reported many commercially important families such as Clupeidae, Cynoglossidae and Trichiuridae in the diet of *H. curtus* along the Goa coast, located ~80 km from our primary sampling site. We found similar overlap of prey species with trawl fisheries in our study that may put *H. curtus* at greater risk (Fig. 2).

The effect of fisheries on isotopic niche and resource use by sea snakes

Fishing intensity had a limited effect on δC^{13} and δN^{15} values of both *H. schistosus* and *H. curtus*. However, both species displayed a larger (2×) isotopic niche width in areas with high fishing intensity based on scale tissue samples, indicating a possible shift and expansion in resource use (Fig. 6). Human presence and anthropogenic disturbance can have far ranging effects beyond the removal of organisms from wild populations. These sub-lethal effects manifest themselves as changes in behaviour of animals because of varied perception of fear and risk (Srinivasan 2019). We hypothesise that the presence of fisheries may have effects beyond that of mortality and may result in changing resource use patterns of mesopredators such as sea snakes. These changes may propagate through coastal food webs through trait mediated species interactions (Schmitz et al. 2004; Hawlena and Schmitz 2010).

Isotopic niche width based on plasma samples also showed a similar trend, however, with a much smaller magnitude (Fig. 6). Plasma has shorter metabolic turnover rate than scales and thus represents short-term resource use (Reich et al. 2008). The difference in isotopic niche width across time scales of assimilation may indicate movement in a landscape of varying fishing intensity because of individual specialisation (Bearhop et al. 2004). This may also indicate niche expansion or plasticity in resource use in these populations (Layman et al. 2007). It must be noted, however, that this change in resource use may not necessarily be the result of fishing pressure but could be the result of a combination of environmental and anthropogenic pressures (DeMaster et al. 2006).

Fishing fleets have been expanding their trophic and spatial ranges to offset stock declines (Bhathal and Pauly 2008; Mashjoor et al. 2018). This phenomenon may increase the interaction of fisheries with vulnerable species that previously had not encountered fisheries in these areas of expansion. Increased overlap with fisheries may pose a twofold effect in the form of resource depletion as well as mortality from bycatch (Milton 2001; Rao et al. 2021).

Caveats and future directions

We relied heavily on fisheries dependent methods in the current study. While these methods are cost effective, we were unable to comprehensibly survey areas along the coast where fisheries do not operate such as estuaries or deeper waters (> 80 m). In addition, the use of interview data to infer spatial coverage may also have a margin of error. The use of stomach content analysis to infer diet composition can also be biased (Newsome et al. 2007). While stable isotopes provide a robust alternative to inferring resource use, these inferences must also be interpreted with caution (Hette-Tronquart 2019; Petta et al. 2020). We believe the use of multiple complementary methods however, adds weight of our inferences presented here. While we have described the resource use patterns of two mesopredators in relation to anthropogenic disturbance, we cannot definitively attribute these differences to fishing intensity. Future studies may benefit from testing similar hypotheses with control sites such as Marine Protected Areas. However, control sites that are entirely free from anthropogenic interference but similar in other respects are hard to find.

Conclusions

Sea snake populations have changed in relative abundance in the Konkan region over the past 2 decades (Rao et al 2021). Our findings suggest that fishing pressure may change resource use patterns in sea snakes with varying effects on different species. In addition, *H. curtus* may be more vulnerable to fishing pressure than *H. schistosus* due to differences in their resource use strategies. While both *H. curtus* and *H. schistosus* are protected under the Wildlife Protection Act (1972) in India, they are still listed as Least Concern in the IUCN red list of species. Similarly, most sea snakes are listed as data deficient (IUCN 2017). We believe there is an urgent need for studies highlighting the effects of anthropogenic pressures on near shore marine fauna and to inform associated management action.

Unregulated fishing has already resulted in the depletion of top predators in near shore marine areas (Myers et al. 2007; Steneck 2012). The effects of fishing pressure on mesopredators may have further cascading effects on lower trophic levels that are targets for these fisheries. Thus, unregulated fishing may threaten entire food webs through not just excessive harvests, but trait-mediated trophic effects. Studies such as ours highlight the need for dynamic spatial management of near shore marine areas that considers more than just mortality due to bycatch but also associated effects of fisheries that may not be readily apparent to ensure the health of these ecosystems and the livelihoods of the fishers who depend on them.

Declarations

Informed consent We acquired informed consent from all individual human participants in this study (namely fishers) and have published the data on condition of anonymity.

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