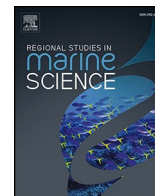




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Diet composition and variation in four commonly landed and threatened shark species in Maharashtra, India

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ABSTRACT

The diets of *Carcharhinus limbatus*, *Scoliodon laticaudus*, *Chiloscyllium arabicum* and *Ch. Griesum* from the west coast of India were investigated. We compared trophic resource use and overlap across and within benthic and pelagic habitat guilds, between the two sympatric species belonging to family Hemiscylliidae, and between the life stages of *S. laticaudus*. It was observed that there was a significant difference in the diet composition of benthic and pelagic shark species. There was no difference in the diet of the two sympatric *Chiloscyllium* species. *S. laticaudus* showed an ontogenetic dietary niche shift from an invertebrate-rich to an ichthyophagous diet. Specifically, *C. limbatus* showed an ichthyophagous diet while *S. laticaudus* showed a diet consisting of both benthic and pelagic prey. *C. arabicum*, *C. griesum*, and *S. laticaudus* were less dependent on teleosts and displayed similar diet composition. The study also found that several of the prey species were commercially important fish species caught in the fisheries of Malvan. Thus a change in the relative abundance of either prey or predators due to fishing pressure could influence coastal food webs, leading to impacts both on ecosystems and fisheries.

1. Introduction

Elasmobranch stand as prominent predators in marine ecosystems, exerting a crucial influence on prey populations through predation (Wetherbee and Cortés, 2012). The theory of resource partitioning is often linked to competitive or cooperative interactions. This concept suggests that spatial or temporal partitioning can enhance tolerance for niche overlap, potentially alleviating competition pressures among coexisting species (Root, 1967; Schlosser, 1982).

Comprehending the ecological significance of a species within an ecosystem is heavily reliant on a thorough understanding of its trophic relationships (Braga et al., 2012). An illustration of this principle is evident in a species' feeding ecology, which serves as valuable information for investigations related to resource partitioning, competition, energy transfer, and the dynamics of food webs (Pimm, 2002; Navia et al., 2010; Bornatowski et al., 2014). The exploration of these complex approaches depends on fundamental dietary descriptions and so are affected by the lack of diet composition data. Therefore, the comprehensive understanding of trophic interactions and the positions of large predators within a food web is imperative for elucidating the dynamics of marine communities and discerning the impactful roles that sharks

play within trophic network compartments (Lucifora et al., 2009; Heithaus et al., 2013).

There is substantial data on the diet of different elasmobranch species. They are often opportunistic predators with a wide trophic spectrum; specifically, oceanic elasmobranchs feed on squid and larger fishes (Hegde et al. 2014), whereas coastal and benthic species feed on crustaceans, molluscs, and smaller fishes (Carrasson et al., 1992; Simpfendorfer, 1998; Hegde et al. 2014). Research on trophic relationships among sympatric species of elasmobranchs is scarce and the results have varied across different studies (Ellis et al. 1996; Orlov, 2003; Bethea et al. 2004), probably due to the differing environmental and stress factors experienced by the species. In the case of sympatric predatory species, identification of their trophic interactions and overlaps in resource use is important for the effective management of co-occurring populations (Pikitch et al. 2004). Given their importance as apex predators, an understanding of ecological processes is necessary to gain insight about their role in the food web. Resource use and partitioning is often associated with competitive or facilitative interactions and helps to predict spatial or temporal partitioning. This knowledge can be important for understanding and managing species and ecosystems (Valls et al. 2011; Hegde et al. 2014).

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The feeding ecology of elasmobranch species along the coast of India is poorly known. The species selected for this project included the spadenose shark (*Scoliodon laticaudus*) and the common blacktip shark (*Carcharhinus limbatus*), categorized as Near Threatened and Vulnerable, while the grey bamboo and Arabian carpet sharks (*Chiloscyllium griesum* and *Chiloscyllium arabicum* respectively) are categorized as Near Threatened in the IUCN Red List. Here, we aimed to study the differences in diet within and between commonly occurring shark species in Malvan, Maharashtra. Specifically, we aimed to (1) examine the differences in the feeding ecology of benthic *Chiloscyllium* sp. with respect to the pelagic *S. laticaudus* and *C. limbatus*, (2) study the difference in the two sympatric species, *Ch. griesum* and *Ch. arabicum*, and (3) explore the ontogenetic dietary shift in *Scoliodon laticaudus*.

2. Materials and methods

2.1. Study area

Malvan is a coastal town situated in the Sindhudurg district of Maharashtra, bordering Goa. At this location, the catch is landed and sold by fishing boats owned by fishermen from various communities throughout the Malvan region. Trawlers are part of a multi-species fishery that pursues a variety of species, such as pomfret (*Pampus* sp.), mackerel (*Rastrelliger kanagartha*), and other pelagic fish using a pelagic net or prawns, crabs, and demersal fish using a benthic net (i.e., bottom trawl net). Trawl fishing is permitted from August to May; however, the government imposes a seasonal ban in June and July to protect breeding fish (Narayanakumar et al. 2017). Elasmobranchs are regularly caught, especially in trawlers, although they are also caught in gillnets and artisanal fisheries. Most of the capture is kept and sold for the meat, which is salted, dried, and consumed locally. Sharks are more profitable than the rays, but overall, elasmobranchs are considered low-value goods (Gupta et al. 2020).

2.2. Data collection

2.2.1. Sampling

We sampled sharks caught as bycatch in fisheries and landed in Malvan from February–April 2022 and January–February 2023. We sampled boats when they landed their catch; mornings (7–10 am) for gillnetters and evenings (5 pm to 8 pm) for trawlers. The individuals sampled were marked using a paper clip and morphometric measurements were taken. Body weight, total length, sex, sexual maturity were recorded. Once a marked shark was purchased by a customer, it was followed till the cleaning station where the stomachs were collected in an airtight container and transported to the field station.

Chiloscyllium arabicum was morphologically differentiated from *Chiloscyllium griesum* on the presence of a ridge on each side of body, free rear tips of dorsal fins attenuated which is absent in the latter (Fischer and Bianchi, 1984). The maturity stage of each *Scoliodon laticaudus* was recorded using the following protocol: umbilical scars were used to identify neonates; juvenile females lacked ovaries and juvenile males had uncalcified claspers; and adult females had developed ovaries/gravid and adult males had hardened, calcified claspers (Carrier et al. 2012).

2.2.2. Visual gut content analysis

The presence of gut content was measured based on whether it was full, partially full, or empty. The weight of the stomach was also recorded before dissection. After dissection, the prey were identified to the nearest taxonomic unit (family), failing which they were recorded as unidentified. A score for the prey's stage of digestion was recorded on a scale of 1–5 (1 being intact and 5 being completely digested) (Espinoza et al. 2012; Dsouza et al. 2021). The number and weight of the prey specimens were also recorded.

2.3. Data analysis

Data from 2022 and 2023 were combined for the analysis, as they represented the same season with similar catch (Kottillil et al. 2023). A cumulative prey curve was employed to assess the validity of the sample size used to examine each species' diet (Ferry and Cailliet, 1996). If a visual asymptote was achieved by the curves, the sample size was deemed sufficient (Magurran, 2004). An asymptote was reached only for *S. laticaudus* species indicating that sufficient stomachs were examined to fully describe their diets. This does not affect our inference regarding differences in diets as the most commonly consumed prey were captured for all shark species.

The Effective Number of Species (ENS) was calculated for the four species of sharks to compare prey diversity (Jost, 2006; Cao and Hawkins, 2019). Diets were quantified using three indices: percent by number (%N), percent by weight (%W), and percent by frequency of occurrence (%F). The numerical occurrence (%N) is the number of prey items in a particular prey group given as a proportion of the overall number of prey items; the gravimetric occurrence (%W) is the mass of prey items in a certain prey group expressed as a percentage of total prey mass; and the frequency of occurrence (%F) is calculated as the proportion of all stomachs that contain a specific prey group. The index of relative importance (IRI) was also calculated as $IRI = \%F (\%N + \%W)$ (Pinkas et al., 1971). To calculate the index of relative importance on a percentage basis, the IRI for each prey type was divided by the total IRI for all prey items (%IRI; Cortés, 1997).

2.3.1. Across species and within species comparison

Non-parametric multivariate analysis of variance (PERMANOVA) using Bray–Curtis distances was used to assess the difference in species composition between the target groups of (i) pelagic and benthic sharks, (ii) two sympatric species of benthic bamboo sharks, and (iii) three size classes of *Scoliodon laticaudus*. If differences were found, analyses of percentage of similarity (SIMPER; Clarke and Gorley, 2015) were used to estimate the contribution of each prey category to the differences in diets. The analyses were performed using PRIMER7 software package (PRIMER-E Ltd; <http://www.primere.com/>). Taxa identified as food items were subjected to non-metric multidimensional scaling (nMDS) ordination using a Bray–Curtis dissimilarity matrix based on the presence/absence of taxa for the three objectives. All graphics and statistics were produced using R (version 2.14.0; R Development Core Team, 2011).

3. Results

Of a total of 356 specimens examined, we were able to collect gut samples for 258 specimens of *S. laticaudus* (132), *C. limbatus* (37), *Ch. arabicum* (44) and *Ch. griesum* (45) across the two seasons (Fig. 1). *S. laticaudus* ranged in size from 25.8 to 69.9 cm L_{ST} (mean \pm S.D. 46.87 \pm 13.02 cm); *C. limbatus* from 55.2 to 115.1 cm L_{ST} (73.73 \pm 7.08 cm); *Ch. arabicum* from 60.7 to 69.9 cm L_{ST} (60.7 \pm 2.77 cm); and *Ch. griesum* from 60.7 to 69.9 cm L_{ST} (73.83 \pm 7.86 cm). A total of 28 prey groups were identified to the family level, including fourteen (ENS=8.95), ten (ENS=5.93), eleven (ENS=5) and nine (ENS=8.21), prey families for *S. laticaudus*, *C. limbatus*, *Ch. arabicum* and *Ch. griesum* and, respectively.

The IRI values of *S. laticaudus* show that cephalopods constitute a majority of the diet (40.73% IRI) followed by prawns (36.93% IRI) and solefishes (5.82% IRI) (Table S1). For *C. limbatus*, mackerels dominated the diet (31.69% IRI) with cephalopods (27.63% IRI) and mantis shrimps (14.85% IRI) forming secondary and tertiary prey groups (Table S2). The two carpetshark species had a similar order of prey preference. *Ch. arabicum* diet was dominated by cephalopods (41.76% IRI), solefish (31.54% IRI), mantis shrimps (10.96% IRI) and swimming crabs (10.00% IRI) (Table S3); *Ch. griesum* was similar with cephalopods (46.31% IRI), solefish (17.01% IRI), and prawns (16.81% IRI) dominating the diet (Table S4).

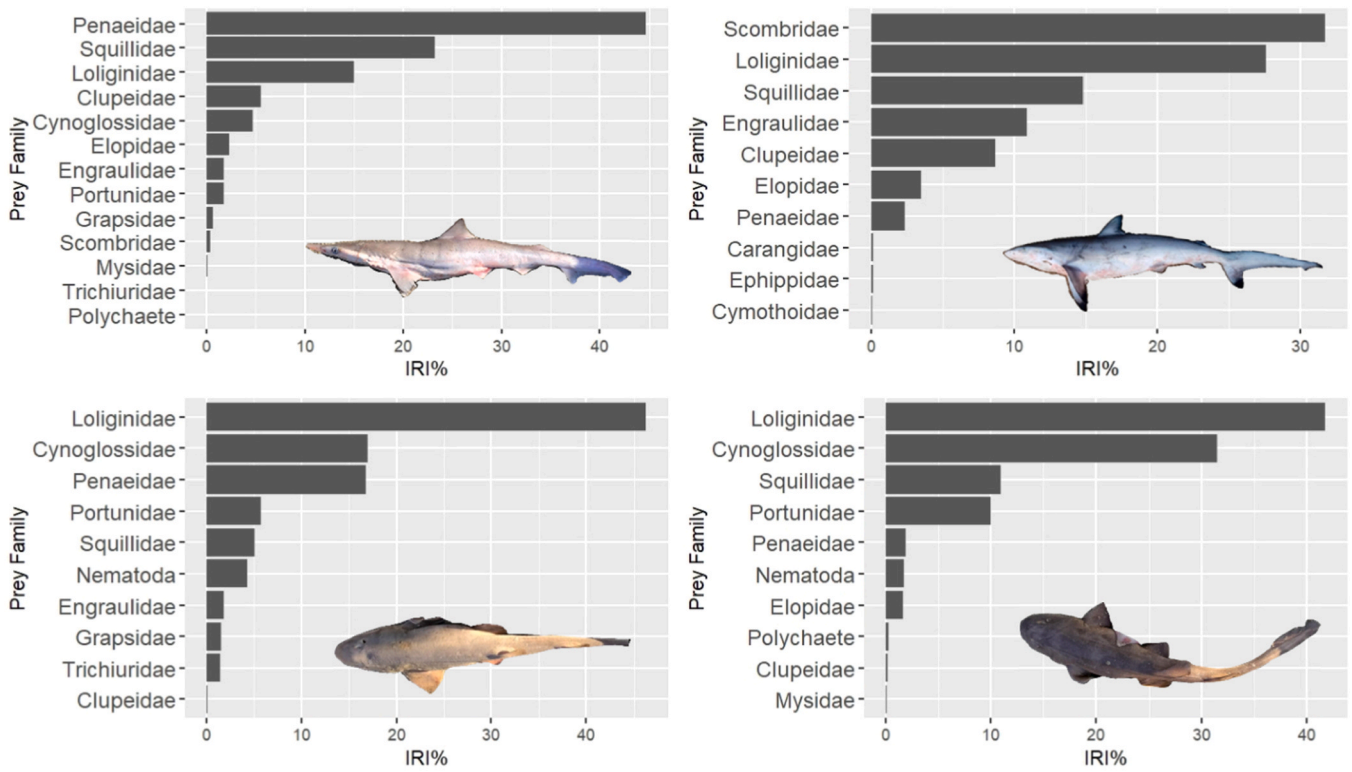


Fig. 1. Index of relative importance (IRI%) (Pinkas et al. 1970) of prey families in four species of sharks (Clockwise from left to right): (*Scoliodon laticaudus*, *Carcharhinus limbatus*, *Chiloscyllium arabicum*, *Chiloscyllium griseum*).

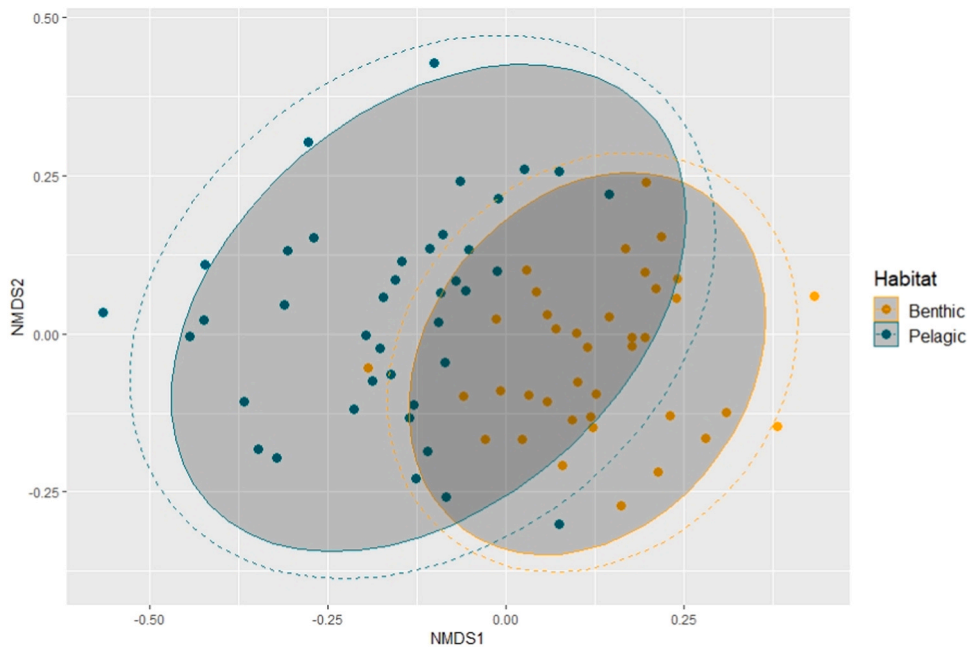


Fig. 2. Nonmetric multidimensional scaling plot of the presence/absence of prey families for benthic and pelagic species (stress=0.13).

3.1. Effect of habitat on diet

Differences in diet composition between benthic and pelagic shark species (benthic, n=64 and pelagic, n=67) were observed (PERMANOVA $r^2 = 0.11$, $p < 0.05$). SIMPER analysis indicated an average dissimilarity of 82.65% between benthic and pelagic species. Prey from Indian squids (*loliginidae*) (13.26%), shrimps (*penaeidae*) (12.96%),

mantis shrimp (*squillidae*) (10.49%), swimming crabs (*portunidae*) (8.81%), and tongue sole-fish (*cynoglossidae*) (8.02%) were most important in discriminating between the diets of benthic and pelagic species. Squid, mantis shrimps, prawns, tongue sole-fish and swimming crabs were most important in grouping benthic elasmobranchs. Indian oil mackerels, king mackerels, squids, shrimps, anchovies, prawns, ladyfish were most important in grouping pelagic elasmobranchs. The

nMDS ordination plot of dietary data revealed clusters with a very small overlap in the diet of the benthic and pelagic species (Fig. 3), which confirms the SIMPER results.

3.2. Differences in diet between sympatric species

No difference was observed in the diet composition between the two species of carpetsharks (*Ch. arabicum* and *Ch. griesum*) (PERMANOVA $R^2 = 0.02082$, $p > 0.05$). Since there was no difference in diet, SIMPER analysis was not conducted. nMDS ordination plot revealed the two clusters with overlapping areas showing a lack of difference in the diets of the sympatric species (Fig. 4).

3.3. Changes in diet with ontogeny

Changes in diet composition between three life stages of *Scoliodon laticaudus* were observed (neonates, $n=43$, juveniles, $n=44$ and adults, $n=45$) (PERMANOVA $r^2 = 0.14$, $p < 0.05$). SIMPER analysis indicated an average dissimilarity of 67.06% between neonates and juveniles, 78.75% between juveniles and adults, and 81.28% between neonates and adults. Indian squid (19.24%), penaeid shrimps (18.71%), opossum shrimp (15.52%), mantis shrimp (12.3%), and nematodes (10.05%) were most important in discriminating between the diets of neonates and juveniles. Penaeid shrimps (14.12%), Indian squid (12.76%), tongue-sole fish (11.4%), and opossum shrimp (10.66%) differentiated neonate and adults. Mantis shrimps (16.98%), Indian squid (15.73%), and tongue-sole fish (12.48%) differentiated juveniles and adults (Table S5). Penaeid shrimps, squids and opossum shrimp were most important in the diet of neonates, while penaeid shrimps and Indian squid were most important for juveniles and tongue-sole fish, squids, mantis shrimps and ladyfish were most important for adults (SIMPER).

4. Discussion

We compared the composition of and variation in the diet of four commonly landed shark species in the coastal waters of Malvan on the west coast of India. We found clear evidence of resource partitioning based on habitat selection. There was no difference in the diet composition of the two sympatric carpetshark species indicating possible interspecific interaction of the species for shared resources. An

ontogenetic shift in diet of *Scoliodon laticaudus* was observed, where the neonate diet was dominated by epibenthic crustaceans and the adult diet was dominated with teleost fishes.

4.1. Effect of habitat on diet

The findings suggested a clear distinction in the diets between benthic and pelagic sharks despite occupying similar trophic levels. Smaller crustaceans and teleosts were the most dominant groups noted in the diet of *S. laticaudus* across different locations (Fofandi et al., 2013; Osmany et al., 2018; Lim et al., 2023). Our findings showed that mantis shrimps, prawns, cephalopods and a very small representation of teleosts formed their diet. *C. limbatus* diet from other parts of the world identified teleosts as the most important prey (Castro, 1996; Barry, 2002; Tavares, 2008). It was also noted that a small number of crustaceans, cephalopod beaks were also a part of their diet (Castro, 1996; Barry, 2002; Gaitán-Espitia and López-Peña, 2008). We observed a similar pattern in the diet of *C. limbatus* which majorly consumed teleosts and a small percentage of their diet were cephalopods and crustaceans. The two carpetshark species preferred crustaceans followed by cephalopods and benthic teleosts. This differs from dietary studies of *C. griseum* which had teleosts as the dominant prey (Devadoss, 1986; Hegde et al., 2014). This variation in the diet composition between locations can be owed to both prey and predator species diversity (Heithaus et al., 2013; Lim et al., 2019). The low degree of diet overlap between pelagic and benthic groups can be attributed to the availability of a wide array of prey items and the difference in habitat which resulted in resource partitioning between these species (Burrell, 1992). These habitat differences also influence certain morphological adaptations like mouth morphology, dentition and feeding behaviour which then affects their diets and results in differences between the two groups (Scrimgeour and Winterbourn, 1987; Motta and Wilga, 2001). The observed spatial variations likely resulted from differences in the local prey types. Our study could not investigate the seasonality of prey availability due to the constraints of the limited sampling season.

4.2. Differences in diet between sympatric species

Diet composition studies on carpetsharks species suggest that they show a preference for cephalopods (squids), crustaceans, polychaetes,

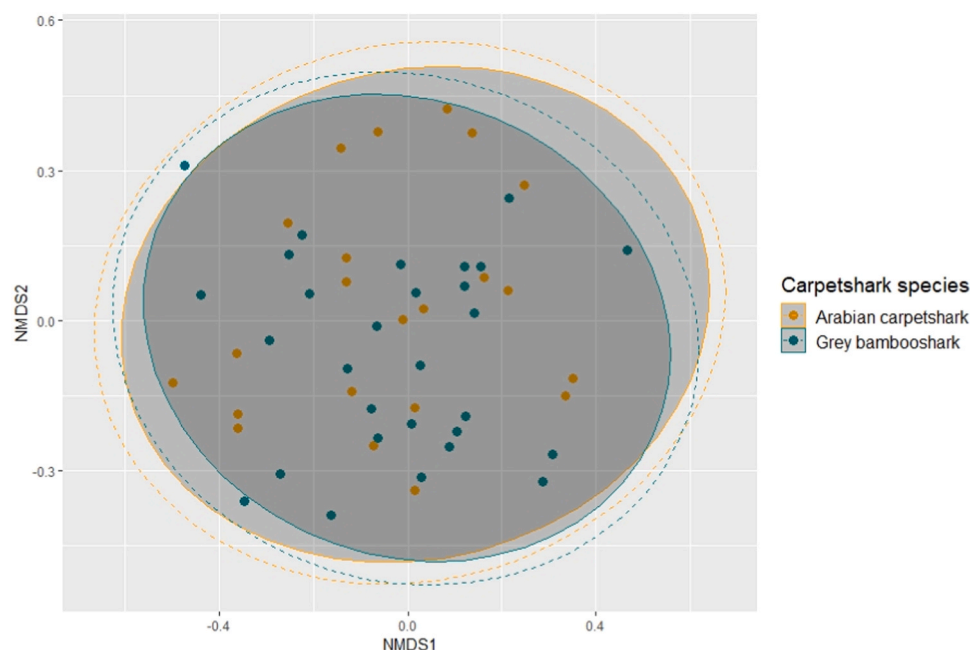


Fig. 3. Nonmetric multidimensional scaling plot of the presence/absence of prey families for Arabian carpetshark and grey bambooshark (stress=0.15).

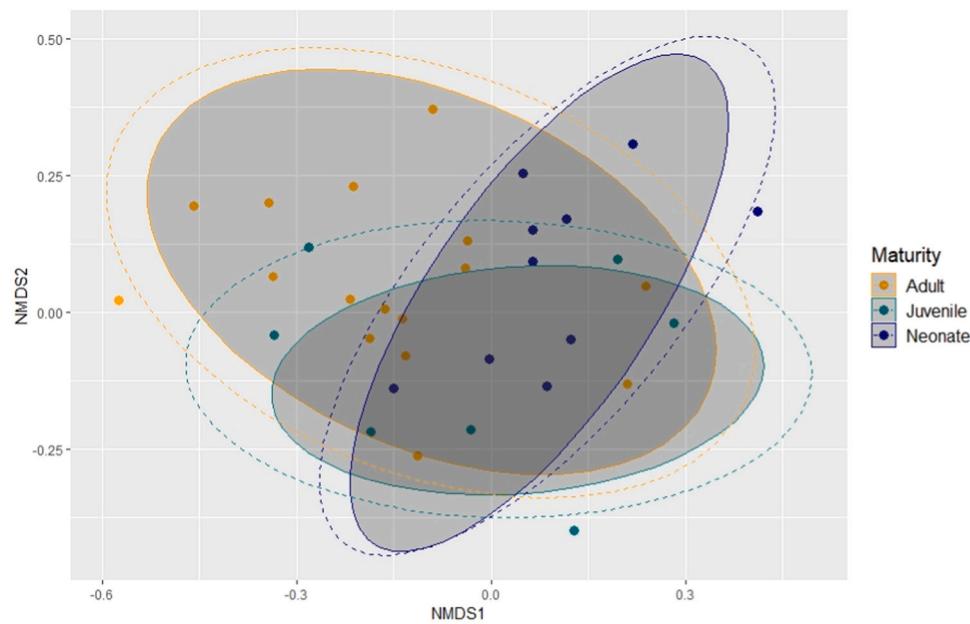


Fig. 4. Nonmetric multidimensional scaling plot of the presence/absence of prey families for the three life stages of *Scoliodon laticaudus* (stress=0.097).

and some teleosts (Nur-Farhana et al. 2013; Liu et al. 2020; Yogi et al. 2022; Lim et al., 2023). The Arabic carpetshark and the grey bamboo shark also share a similar morphology and feeding behavior. Both species have flattened bodies and broad heads that are well-suited for bottom-dwelling and ambush-style predation (Walker, 2014). They also have small, pointed teeth that are adapted for capturing and crushing hard-shelled prey such as crabs and mollusks. The diet overlap between the two species of carpetshark was expected since these species were frequently caught together, hinting at a spatial niche overlap. It is known that both species inhabit benthic waters (Moore, 2015; Vander-Wright et al. 2020) and therefore probably share similar feeding areas. The next step would be to study the extent of interspecific competition for the limited resources with respect to space and resource sharing or behavioural changes to avoid interactions with each other in those spaces. There was a significant amount of unidentified tissue and skeletal bones in the gut of carpet sharks. This could be explained by their ability to survive at least 1–3 hours out of water, leading to a much more digested stomach content (Kottillil et al., 2022).

4.3. Changes in diet with ontogeny

Diet comparisons between life stages of *Scoliodon laticaudus* revealed clear ontogenetic dietary shifts. Crustaceans (mainly shrimps, crabs and stomatopods) dominated the diet of immature individuals, while adults had a higher proportion of teleosts. Other studies indicate that juveniles mostly feed on epibenthic crustacean and slow-moving organisms whereas adults feed on benthic and pelagic teleosts (Abdurahiman et al., 2010; Hegde et al. 2014). Ontogenetic variation in shark diet is also well known with a tendency to ingest larger and more mobile animals with increasing size (Bethea et al. 2006; Hegde et al. 2014). In general, carnivorous fishes become more ichthyophagous with size and age (Renones et al. 2002). Dietary change with increasing size or maturity stage is considered to be a common strategy in elasmobranchs to reduce intraspecific competition (Lowe et al., 1996). Ontogenetic dietary changes in prey diversity and prey size may occur because: (1) larger elasmobranchs can feed on larger prey due to increased gape size, (2) many elasmobranchs exhibit size or sexual segregation, therefore immature and mature individuals may use different foraging sites to reduce their degree of overlap and (3) larger elasmobranchs may be faster and more efficient predators, thus allowing them to capture faster

moving or higher energy prey (Lowe et al., 1996; Platell & Potter, 2001; White et al., 2004).

4.4. Significance of elasmobranch diet composition studies

These species are high trophic level predators in these waters and face immense fishing pressure with incidental catch being a major issue (Gupta et al., 2020; Kottillil et al. 2023). Historical evidence suggests that overfishing can lead to the collapse of marine ecosystems (Jackson et al., 2001) such as along the West Coast of Australia where the removal of the top predators such as sharks was shown to have an additive effect on pre-existing anthropogenic effects on the coral reefs (Ruppert et al., 2013). Fishing activities have been linked with declines in shark populations and proliferation of smaller, mesopredators on the study reefs, consistent with the phenomenon of “mesopredator release” (Courchamp et al., 1999; Stevens et al., 2000; Ritchie and Johnson, 2009). In this case, an increased number of mid-level predators – such as snappers – led to a reduction in the number of herbivores such as parrotfishes.

Shark fisheries in India show a decline in the number and size of sharks captured compared to previous decades (Karnad et al., 2020). Fishers also reported a decline in the total number of adult large-bodied sharks, while the landings of small-bodied sharks and juveniles of large-bodied species have increased (Kizhakudan et al., 2015; Jabado et al., 2018). Smaller-bodied mesopredators typically take over when larger shallow-water elasmobranchs disappear due to overfishing. Malvan is currently exhibiting patterns similar to the shift in the community structure in the North Sea (Rogers & Ellis, 2000) and Southeast Asia (Lam and Sadovy de Mitcheson, 2011). Here, the only abundant species caught are *S. laticaudus*, *Chiloscyllium* spp., and *B. walga*, indicating a shifting community structure with reduced capture of large-bodied species (Kottillil et al. 2023).

Elasmobranchs, as apex predators within marine ecosystems, are susceptible to bottom-up pressure, especially when their prey species overlap with those targeted by fisheries. We found a qualitative overlap in the prey of elasmobranchs and humans, indicating potential competition for resources. Additionally, similar dietary overlaps have been reported in the diet of two sympatric sea snakes, *Hydrophis curtus* and *Hydrophis schistosus*, suggesting that fishing pressure might change resource use patterns in sea snakes along the west coast of India (Dsouza et al., 2021). Fishing vessels have begun to expand their trophic and

geographic ranges to compensate for stock declines (Bhathal and Pauly, 2008), potentially leading to increased interactions with previously unaffected vulnerable species. This expansion of resource overlap with fisheries may have two consequences: resource depletion and increased bycatch risk (Brewer et al., 2006; Rao et al. 2021; Dsouza et al. 2021). This study provides a first step towards an understanding of top-down and bottom-up impacts on marine ecosystems in Malvan. It is important to understand the trophic web and to determine the trophic position of predators to study the cascading effect of anthropogenic disturbance.

5. Conclusion

This study highlights the importance of studying the feeding ecology of sharks and its implications for their conservation and management. Our analysis of the diets of multiple shark species reveals significant overlap in the prey items consumed by these predators. This overlapping diet suggests that these sharks compete for similar resources in their shared ecosystems. However, it is important to note that our study also revealed species-specific variations in diet, indicating that these sharks have evolved unique feeding strategies to suit their individual niches. The dietary analysis also provided valuable insights into the resource overlap between fisheries and the diet of several shark species. The results suggest that some shark species could be vulnerable due to their reliance on similar prey targeted by commercial and recreational fisheries. Future research should continue to explore the complexities of shark feeding ecology, considering the potential effects of environmental factors and human activities on their diets. Such research will provide valuable information for the development of effective conservation and management strategies for these important and iconic marine predators.

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CRedit authorship contribution statement

Kartik Shanker: Writing – review & editing, Supervision, Conceptualization. **Shawn Dsouza:** Writing – review & editing, Methodology, Formal analysis, Conceptualization. **Garima Bora:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization.

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.

Data availability

I have mentioned my github folder in the manuscript

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.rsma.2024.103531.

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