Feeding Ecology of Elasmobranch Species along the Visakhapatnam Coast, India

A Thesis

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by

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Certificate

This is to certify that this dissertation entitled **Feeding Ecology of Elasmobranch Species along the Visakhapatnam Coast, India** towards the partial fulfilment of the BS-MS dual degree programme at the Indian Institute of Science Education and Research, Pune represents work carried out by **Avanthika Prasad** at the Indian Institute of Science Education and Research, Pune, under the supervision of **Prof. Kartik Shanker**, Centre for Ecological Sciences, Indian Institute of Science during the academic year 2024-2025.

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Declaration

I hereby declare that the matter embodied in the report entitled **Feeding Ecology of Elasmobranch Species along the Visakhapatnam Coast, India** are the results of the work carried out by me at the Department of Biology, Indian Institute of Science Education and Research, Pune, and the Centre for Ecological Sciences, Indian Institute of Science, under the supervision of **Prof. Kartik Shanker**, Centre for Ecological Sciences, Indian Institute of Science, and the same has not been submitted elsewhere for any other degree.

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Abstract

Overfishing is a major threat to Indian elasmobranch populations. The reduction in their numbers leads to significant top-down ecological consequences, disrupting marine ecosystems. Therefore, understanding the marine food web dynamics is essential. This study investigates the feeding ecology and trophic interactions of elasmobranchs, including bigeye houndsharks (*Iago omanensis*), longtail butterfly rays (*Gymnura poecilura*), stripenose guitarfish (*Acroteriobatus variegatus*), whitespotted whiprays (*Maculabatis gerrardi*) and mobulid rays along the Visakhapatnam coast. We used stomach content analysis (SCA) and stable isotope analysis (SIA) to investigate: (i) the effect of habitat on diet, and (ii) dietary differences between species. *G. poecilura* and *I. omanensis* exhibited piscivorous diets, with *I. omanensis* showing greater prey diversity. In contrast, *A. variegatus* and *M. gerrardi* majorly consisted of crustaceans, indicating lower dependence on teleosts. Overall, benthic species (*A. variegatus*, *G. poecilura*, and *M. gerrardi*) showed distinct diet differences from pelagic species (*I. omanensis*), minimizing niche overlap. Similarly, SIA revealed the benthic species, *G. poecilura* and *M. gerrardi*, were enriched in ^{13}C while the pelagic species, mobulids and *I. omanensis*, were depleted in ^{13}C, consistent with their expectations based on their feeding habitats. δ^{15}N values highlighted significant differences in trophic levels: mobulids had low δ^{15}N values, aligning with their planktivorous diet, whereas *G. poecilura* had high δ^{15}N values, indicating its role as a predator. This study valuable insights into the feeding ecology of elasmobranchs and their role in the western Bay of Bengal. Further research on temporal variation, resource partitioning, and ecological roles are required to support conservation and management efforts.

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Part I

Introduction

Chapter 1

Introduction

1.1 The role of elasmobranchs in marine ecosystems

Elasmobranchs are a subclass of cartilaginous fishes that includes sharks, rays, skates, and sawfish, and have played a significant evolutionary and ecological role in marine environments for over 400 million years. These species are integral to maintaining the balance of oceanic ecosystems due to their diverse ecological niches and trophic interactions (Stein et al., 2018). They occupy various trophic levels within marine food webs, from apex predators to mesopredators and even filter feeders.

Elasmobranchs occupy different trophic positions in marine food webs, ranging from apex predators to mesopredators and filter feeders. The trophic roles depend largely on species and body size. Large sharks substantially influence prey populations, maintaining the balance of marine ecosystems. The great white shark (*Carcharodon carcharias*), an apex predator, exerts top-down control over prey populations by preying on mesopredators. They help regulate prey abundance and maintain food web stability. For example, studies along the U.S. eastern seaboard have shown that a decline in large-bodied shark populations led to an increase in small-bodied species, such as skates and rays. This resulted in the disruption of benthic communities and impacted shellfish populations (Myers et al., 2007).

In Shark Bay, Western Australia, tiger sharks (*Galeocerdo cuvier*) influence dugong and sea turtle foraging by forcing them to shift from nutrient-rich seagrass rhizomes in low-risk conditions to grazing on less nutritious leaves when shark presence is high. This prevents overgrazing and supports seagrass ecosystem health (Heithaus et al., 2008). Similarly, in the Gulf of Mexico, the decline of large shark populations correlated with a surge in pelagic stingray (*Pteroplatytrygon violacea*) populations, leading to increased predation on commercially important fish species (Ward and Myers, 2005). Conversely, filter-feeding species like the whale shark (*Rhincodon typus*) and oceanic manta ray (*Mobula birostris*) occupy lower trophic levels as they consume plankton and small fish, influencing nutrient cycling and plankton dynamics.

Beyond their roles as predators and filter feeders, elasmobranchs (particularly batoids) provide essential ecosystem services through their foraging activities. Thrush et al. demonstrated that rays play a crucial role in sediment turnover, which enhances habitat complexity and nutrient cycling. On New Zealand's intertidal sandflats, eagle rays (*Myliobatis tenuicaudatus*) reworked 700 to 800 square meters of sediment in just 70 days, enhancing habitat complexity and increasing organic matter availability for benthic organisms (Thrush et al., 1991). In Guinea-Bissau's Bijagós Archipelago, predator exclusion experiments showed that sediment erosion rates decreased by 43% without benthic rays. In comparison, sedimentation rates increased by 17%, resulting in changes in species composition with a rise in Capitellidae worms and a greater biomass of Malacostraca (Nauta et al., 2024). In the Brisbane Water estuary, Australia, rays excavated over 57.6 tonnes of sediment daily, facilitating nutrient cycling and influencing the spatial distribution of benthic invertebrates (Grew et al., 2024).

Elasmobranchs can also facilitate feeding opportunities for other marine species. For example, rays such as the bat ray (*Myliobatis californica*) and round stingray (*Urobatis halleri*) eject hidden prey from sediments, which are then consumed by sand dabs (*Citharichthys stigmaeus*) (VanBlaricom, 1982). On coral reefs, sharks and rays frequently visit cleaning stations where smaller fish remove ectoparasites, enhancing their health while benefiting cleaner species with food sources (Sazima and Moura, 2000). Additionally, cownose rays (*Rhinoptera bonasus*) fragmented seagrass beds in the Chesapeake Bay, creating patchy habitats that improved juvenile crab survival rates by reducing predator densities (Hovel and Lipcius, 2001). They also act as nutrient vectors by transporting nutrients across different habitats. Grey reef sharks (*Carcharhinus amblyrhynchos*) contributed significantly to nitrogen transfer from pelagic environments to reef habitats, supporting primary productivity and ecosystem stability (Williams et al., 2018). The deposition of large shark carcasses provides organic material that support microbial and invertebrate communities, enhancing benthic productivity (Heithaus et al., 2022). Furthermore, stingray feeding pits accumulate organic matter, facilitating faster remineralization processes and supporting colonization by amphipods and other invertebrates (VanBlaricom, 1982).

The foraging activities of benthic rays influence nutrient cycling and species interactions, resulting in significant habitat changes. Blue-spotted maskrays (*Neotrygon kuhlii*) disturb sediment layers while foraging, creating pits that influence sediment distribution and oxygenation. These disturbances promote the recolonization of benthic invertebrates and enhance habitat complexity, supporting diverse benthic communities (Warry et al., 2009). Stingrays, including the blackspotted whipray (*Himantura astra*) and coach whipray (*Himantura uarnak*), create feeding pits while foraging in shallow sandflats. This bioturbation increases sediment turnover, creating microhabitats that harbor various benthic organisms and promote biodiversity in the lagoon ecosystems (O'Shea et al., 2013). Similarly, in Bahia La Choya, Mexico, batoids reworked extensive sediment areas to a depth of 20 cm, creating dynamic habitats that fostered biodiversity by enabling the persistence of early colonizing species (Lynn-Myrick and Flessa, 1996). The loss of bioturbators like rays would disrupt sediment processes, reducing nutrient cycling and habitat complexity.

1.2 Impact of loss of elasmobranchs in marine ecosystems

Despite their ecological importance, elasmobranchs possess life history traits that render them particularly vulnerable to overexploitation. Traits such as low fecundity and late maturity make them susceptible to population declines caused by overfishing and habitat degradation at rates higher than many other vertebrate groups.

One of the most significant consequences of elasmobranch declines is the phenomenon of "mesopredator release". Here, the reduction of apex predator populations, such as sharks, increases smaller predator populations due to reduced predation pressure. This shift can disrupt the balance of prey communities, leading to the overexploitation of certain species and the decline of others (Dulvy et al., 2014). Elasmobranchs, particularly rays, also function as bioturbators, disturbing sediments and influencing nutrient cycling. Their decline can disrupt these processes, impacting the productivity of benthic communities and the overall ecosystem. Heithaus et al. discusses the complex role of elasmobranchs in nutrient flow, highlighting the potential for both increases and decreases depending on the specific trophic interactions within the ecosystem. While the impact of elasmobranch declines on nutrient flow is complex and requires further research, the potential for disruption is clear. Heithaus et al. notes that the potential nutrient input from juvenile shark mortality is similar to that of salmon carcasses in freshwater systems (Heithaus et al., 2008).

Overfishing, particularly targeted fishing for commercially valuable species, is a primary driver of elasmobranch declines (Jabado and Spaet, 2017). The Arabian Sea serves as an example, where targeted ray fishing has led to population declines and even localized extinctions of some species (Jabado, 2018). There is also a lack of fisheries data, especially for bycatch (Dulvy et al., 2008). This lack of data hinders effective management initiatives and can lead to undocumented biomass removal, further exacerbating population declines. Venugopal and Kumar highlights this issue in the Indian context, where many ray species caught as bycatch are poorly documented and classified as “Data Deficient” by the IUCN, while commercially important species are often already threatened (Venugopal and Kumar, 2020).

To address the far-reaching consequences of their decline, comprehensive conservation strategies that consider the complex ecological roles of these species are required. Understanding the trophic roles of elasmobranchs, including their feeding ecology, is essential to develop ecosystem-based management approaches (Espinoza et al., 2015). Given the documented declines in top predators (Myers and Worm, 2003; Dulvy et al., 2014), understanding the trophic connections of predators becomes important for comprehending food web dynamics (Heithaus et al., 2008).

1.3 Feeding ecology studies

The separation in food resource use is a key aspect of this coexistence among elasmobranch species (Platell and Potter, 2001; Papastamatiou et al., 2006; Heithaus et al., 2013). Several factors influence elasmobranch diets, including body size (ontogenetic shifts due to changes in morphology or metabolic needs), spatial and seasonal distribution (Mollet et al., 2002; Clarke et al., 2014), and sex. Therefore, detailed knowledge of these factors is essential for accurately characterizing feeding ecology. Addressing this gap in India is essential for advancing our understanding of elasmobranch ecology and informing conservation strategies since the feeding ecology of elasmobranchs remains largely understudied in India, with less than 10% of species investigated in this regard (Bornatowski et al., 2023).

Typically, the diets of sharks and batoids consist primarily of teleosts (bony fishes), followed by crustaceans and cephalopods (Bornatowski et al., 2023). Benthic species tend to consume more crustaceans and other invertebrates, while teleosts are the most common prey for pelagic sharks and rays (Wetherbee and Cortés, 2004; Martinho et al., 2012; Bora et al., 2024). Ontogenetic dietary shifts are common, with juveniles consuming smaller prey like teleosts, crustaceans, and cephalopods, while adults of larger species may incorporate elasmobranchs, reptiles, or even mammals into their diets (Bornatowski et al., 2023). These dietary patterns highlight the adaptability of elasmobranchs and their ability to exploit a wide range of prey resources, which underscores their importance in influencing trophic dynamics in marine ecosystems.

Several methods are employed in elasmobranch feeding ecology studies. Stomach content analysis (SCA) is a traditional method involving the collection and identification of stomach contents (Hyslop, 1980; Cortés, 1999; Ebert and Bizzarro, 2007). Morphological identification of prey items is the most common approach (Barnett et al., 2010). Various quantitative methods are used to analyze stomach contents, including numerical counts, frequency of occurrence, and prey volume. The Index of Relative Importance (%IRI) is a composite measure that incorporates these variables into a single metric (Cortés, 1999). However, factors like feeding approach, prey preference and gastric evacuation rate can also influence the results of SCA (Ahlbeck et al., 2012).

Stable isotope analysis (SIA) is another valuable tool used to infer diet and trophic relationships (Bucking et al., 2015). SIA involves measuring isotope ratios and comparing them to standards. This method has become increasingly common in elasmobranch research (Bucking et al., 2015) and can provide insights into trophic level positions using long-term integrated dietary information (Hussey et al., 2011). Isotopes of carbon (δ^{13}C) and nitrogen (δ^{15}N) are particularly useful for tracking movements between habitats and examining trophic relationships, respectively (Post, 2002; Hussey et al., 2011). Trophic levels can also be determined by analyzing stable nitrogen isotopes. This approach relies on the ratio of ^{15}N to ^{14}N (δ^{15}N), as consumers exhibit an increase in ^{15}N relative to their prey. Consequently, the δ^{15}N value of an organism reflects its trophic position in relation to primary consumers within the ecosystem (Cabana and Rasmussen, 1996). Likewise, the δ^{13}C values of consumers offer insights into energy sources (Boutton, 1991) and can help determine feeding locations. This is because δ^{13}C values tend to be less negative (indicating greater ^{13}C enrichment) in coastal or benthic food webs compared to pelagic ones (Borrell et al., 2011). This difference arises because benthic plants, such as seagrass and macroalgae, use bicarbonates from seawater as their carbon source for photosynthesis, while pelagic producers, like phytoplankton, use dissolved CO_2, which has a lighter (more negative) carbon signature (Fry and Sherr, 1984; France, 1995; Hemminga and Mateo, 1996). Analyzing both δ^{15}N and δ^{13}C allows researchers to identify dietary preferences and map food web connections for elasmobranch species (Borrell et al., 2011). As elasmobranch populations continue to face threats from overfishing, habitat degradation, and climate change, understanding their feeding ecology is essential for understanding their ecological contributions and ensuring the health and stability of marine ecosystems.

1.4 Impact of habitat on diet

The limiting similarity principle proposes that coexisting species must diverge in their resource use to avoid exceeding a threshold of ecological similarity, which would otherwise make coexistence unsustainable (MacArthur and Levins, 1967). Such divergence in foraging niche components helps reduce competition and promotes species coexistence (Pianka, 1974). According to ecological theory, coexisting species reduce competition by partitioning resources such as food, habitat, and time (Heithaus et al., 2013; Knickle and Rose, 2013). The foraging niche, a critical aspect of a species' ecological niche, can be divided into temporal, spatial, and trophic components (Spitz et al., 2011). In fish communities, dietary partitioning is a common strategy for niche segregation (Knickle and Rose, 2013). As top predators, elasmobranchs often partition resources through differences in spatial habitat use or prey selection, minimizing competition among species that occupy similar trophic levels.

In sympatric species, dietary divergence is a common strategy to minimize niche overlap and competition. For example, Knickle and Rose examined the feeding habits of two co-occurring gadid species, Atlantic cod (*Gadus morhua*) and Greenland cod (*Gadus ogac*). They showed minimal dietary overlap, with *G. morhua* consuming more pelagic prey (e.g., hyperiid amphipods and fish) and *G. ogac* preferring benthic prey (e.g., polychaetes and fish) (Knickle and Rose, 2013). Similarly, Teixeira et al. investigated trophic interactions among three sympatric dolphin species in southern Brazil. While Guiana dolphins (*Sotalia guianensis*) and bottlenose dolphins (*Tursiops truncatus gephyreus*) primarily consumed demersal prey, franciscana dolphins (*Pontoporia blainvillei*) fed on pelagic prey, resulting in lower niche overlap (Teixeira et al., 2021).

Resource partitioning is also evident in elasmobranchs. Albo-Puigserver et al. studied three coexisting chondrichthyans in the northwestern Mediterranean: the blackmouth catshark (*Galeus melastomus*), velvet belly lanternshark (*Etmopterus spinax*), and rabbitfish (*Chimaera monstrosa*). Each species exhibited distinct trophic niches, with *G. melastomus* consuming cephalopods, *E. spinax* preying on shrimps, and *C. monstrosa* feeding on crabs (Albo-Puigserver et al., 2015). Similarly, Yick et al. observed trophic partitioning in two sympatric batoid species, *Urolophus cruciatus* and *Narcine tasmaniensis*, in southeast Australia. While both species primarily consumed benthic invertebrates, *U. cruciatus* specialized in small crustaceans, whereas *N. tasmaniensis* preferred polychaetes. These studies collectively demonstrate that sympatric species partition dietary resources to minimize competition and promote coexistence (Yick et al., 2011).

In allopatric species, habitat separation reduces direct competition, allowing for independent evolution and dietary specialization. For instance, Carbla et al. found that allopatric species exhibited wider and more stable niche widths compared to sympatric species, which showed narrower niches due to resource partitioning. The broader dietary niche of allopatric species can be attributed to reduced competition from similar species. However, allopatric species may use different habitats, leading to differences in prey types, and therefore smaller trophic niche overlap (Hayata et al., 2021).

Davis et al. reported lower dietary overlap between allopatric populations of red snapper (*Lutjanus campechanus*) and vermilion snapper (*Rhomboplites aurorubens*) compared to sympatric populations (Davis et al., 2015). Additionally, Robertson and Gaines observed that surgeonfish species in allopatry exhibited reduced overlap in both habitat use and diet, suggesting that habitat separation drives dietary divergence (Robertson and Gaines, 1986).

Habitat type significantly influences dietary composition, particularly in elasmobranchs. Benthic species tend to consume more crustaceans and cephalopods, while pelagic species rely heavily on teleosts. For example, Bora et al. found that benthic shark species, such as *Chiloscyllium arabicum* and *Chiloscyllium griseum*, primarily fed on crustaceans and cephalopods, whereas pelagic species like *Carcharhinus limbatus* consumed predominantly teleosts (Bora et al., 2024). Similarly, Lucifora et al. reported that sand tiger sharks, which inhabit epipelagic and mesopelagic zones, fed mainly on teleosts and elasmobranchs, with larger individuals consuming more benthic prey (Lucifora et al., 2009).

Ebert and Bizzarro noted that benthic skate species primarily consumed decapods, fishes, amphipods, and polychaetes (Ebert and Bizzarro, 2007). In contrast, Afonso et al. found that pelagic elasmobranchs in the Colombian Eastern Tropical Pacific primarily consumed teleosts (Afonso et al., 2022). These patterns highlight the strong influence of habitat on dietary preferences, with benthic species relying more on crustaceans and pelagic species favoring teleosts.

1.5 Objectives

In India, there is limited research on the patterns of resource partitioning among marine predators in various habitats. Such data are crucial for understanding food web dynamics and developing ecosystem-based fisheries management plans. This study investigated the feeding ecology and trophic interactions of elasmobranchs, including bigeye houndsharks (*Iago omanensis*), longtail butterfly rays (*Gymnura poecilura*), stripenose guitarfish (*Acroteriobatus variegatus*), whitespotted whiprays (*Maculabatis gerrardi*) and mobulid rays along the understudied Visakhapatnam coast in the western Bay of Bengal. Diet and trophic niche were assessed using stomach content analysis (SCA) and stable isotope analysis (SIA) to understand (i) the effect of habitat on diet and (ii) dietary differences between species.

It was hypothesised that (i) elasmobranch species would exhibit distinct dietary compositions, reflecting prey availability and habitat preferences; (ii) benthic species would show a higher reliance on crustaceans and benthic prey, while pelagic species would predominantly consume teleosts, indicating habitat-driven dietary partitioning; and (iii) SIA would reveal distinct isotopic niches among species, with benthic species showing enriched δ^{13}C values due to their reliance on benthic prey, while pelagic species would exhibit depleted δ^{13}C values, reflecting their pelagic feeding habits.

Part II

Materials and Methods

Chapter 2

Materials and Methods

2.1 Study area

The coastal stretch of Visakhapatnam (17°44’N, 83°23’E) in Andhra Pradesh was chosen for this study due to its high faunal diversity and limited prior research. This biodiverse region, with a continental shelf extending about 35 km into the Bay of Bengal, is a crucial area for mechanized fishing. Despite its ecological significance, few studies have focused on the area’s ichthyofauna (Sujatha, 1995; Sujatha, 1996; Kandra et al., 2010; Das et al., 2013; Rao et al., 2013). Unfortunately, many species of chondrichthyans on the Visakhapatnam coast are at risk due to overfishing, habitat degradation, and pollution (Roy and Chakrabarti, 2020).

2.2 Gut content sampling

Elasmobranch species caught as bycatch in fisheries and landed in the Visakhapatnam fishing harbor from June to October 2024 were sampled. The landed individuals were identified, and morphometric measurements were taken. Body weight, total length, sex, and sexual maturity were recorded. The individuals were taken to the cleaning station, where they were dissected. The maturity stage of each species was recorded following established criteria. The umbilical scar was used to identify neonates (Yokota and Lessa, 2006). Individuals with absent ovaries for females and uncalcified claspers for males (Stehmann, 2002) were classified as juveniles. The individuals with developed ovaries/gravid in females (Tyabji et al., 2020)

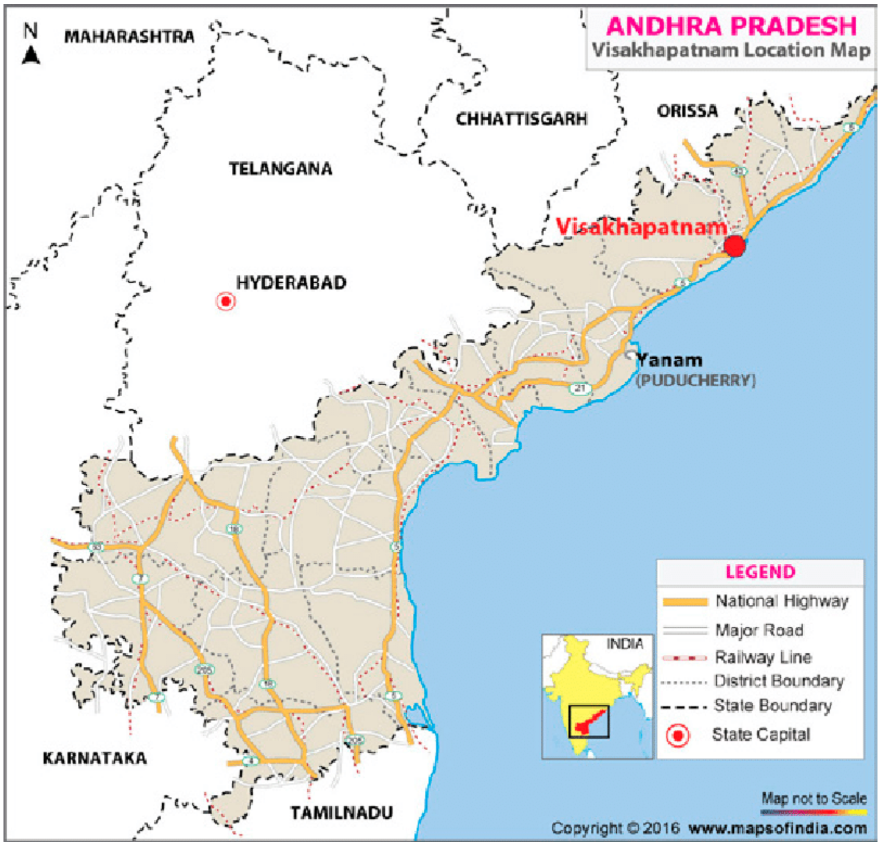

Figure 2.1: Locator map of sampling location. Sampling location at Vishakapatnam, Andhra Pradesh. (Source: mapsofindia.com)

and hardened, calcified claspers in males were considered adults.

2.3 Visual gut content analysis

Stomachs were collected and assessed for fullness visually, with a score assigned ranging from 1 (nearly empty) to 5 (fully distended). The stomach weight was recorded prior to dissection. Prey items were identified to the lowest possible taxonomic level after dissection. A digestion stage score, ranging from 1 (intact) to 5 (completely digested), was recorded for each prey item (Bora et al., 2024). Additionally, the number and weight of each prey specimen were documented. To ensure adequate sample sizes, the cumulative prey curve was used; if the curve reached a visual asymptote, the sample size was considered sufficient (Magurran, 2004). The Index of Relative Importance (IRI) was calculated to assess prey preference by elasmobranch species:

$$\mathrm{IRI} = (\%\mathrm{N} + \%\mathrm{W})(\%\mathrm{F}_o),$$

where %N is the percentage of a given prey type by number, %W is the percentage of prey type by weight, and $\%\mathrm{F}_o$ is the frequency of occurrence of each prey type (Bora et al., 2024). The relative abundance of prey species was then analyzed by calculating IRI%:

$$\mathrm{IRI}\% = \frac{\mathrm{IRI}}{\sum \mathrm{IRI}} \times 100.$$

Five prey categories were considered to calculate standardized diet compositions and trophic levels of sharks (Table 2.1).

Trophic levels (TL_k) were then calculated for each species (k) as follows:

$$TL_k = 1 + \left(\sum_{j=1}^{n} P_j \times TL_j \right)$$

where P_j is the proportion of each prey category, TL_j is the trophic level of each prey category j, and n is the total number of preys. Trophic level (TL) of prey categories was taken from (Cortés, 1999).

Table 2.1: Trophic levels of prey categories from Cortés (1999) used to calculate the trophic levels of elasmobranch species.

Group code	Taxa included	Trophic level
FISH	Class Actinopterygii	3.24
CEPH	Class Cephalopoda	3.2
CR	Order Decapoda	2.52
POLY	Class Polychaeta	2.5
MOL	Phylum Mollusca (excluding Cephalopoda)	2.1

2.4 Stable isotope analysis

Muscle tissue samples (approximately 1 g) were collected from the ventral musculature of the elasmobranchs. The samples were rinsed with distilled water, stored in falcon tubes, and frozen at $-20°\text{C}$ until further analysis (Espinoza et al., 2015). In the laboratory, lipid extraction was carried out by placing the samples in glass scintillation vials with 10 ml of petroleum ether (PE), followed by sonication for 15 minutes. This procedure was repeated for a second rinse. For urea extraction, the samples were rinsed with 10 ml of deionized water (DIW) and sonicated for 15 minutes, with the process repeated twice. The samples were then oven-dried at 60°C for 48 hours and ground into a fine powder for subsequent analysis. The stable isotope ratios of $^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$ were determined using the isotope ratio mass spectrometer facility at IISER, Pune. These ratios were expressed in δ notation according to the equation:

$$\delta \mathrm{X} = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000\,(‰),$$

where R_{sample} is the ratio of the heavy to light isotope in the sample, and R_{standard} is the corresponding ratio in the reference standard (Kim and Koch, 2011).

2.5 Statistical analysis

Permutational Multivariate Analysis of Variance (PERMANOVA; 1000 permutations) based on the Bray–Curtis dissimilarity matrix was used to test for differences in diet composition among elasmobranch species. To evaluate the effect of habitat, pelagic species (bigeye houndsharks, bull sharks, mobulids, hammerhead sharks) were compared to benthic species (stripenose guitarfish, longtail butterfly rays, Indian blue-spotted maskray, cownose ray, whitespotted whiprays, Bennett's stingray). Additionally, species-specific differences were tested among bigeye houndsharks, stripenose guitarfish, longtail butterfly rays, and whitespotted whiprays. Effects were considered significant at $p < 0.05$. Univariate analysis of variance (ANOVA) was conducted separately for both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ isotopes, followed by multiple comparisons based on Tukey's HSD post hoc test. These analyses were done using the `vegan` library in R statistical package v.4.4.2.

Part III

Results and Discussion

Chapter 3

Results

3.1 Sample collection

We were able to collect gut samples of 145 individuals – 34 longtail butterfly rays (*Gymnura poecilura*), 31 whitespotted whiprays (*Maculabatis gerrardi*), 31 bigeye houndsharks (*Iago omanensis*), 22 mobulids, 10 stripenose guitarfishes (*Acroteriobatus variegatus*), 8 bull sharks (*Carcharhinus leucas*), 5 Indian bluespotted maskrays (*Neotrygon kuhlii*), 2 Bennett's stingrays (*Hemitrygon bennetti*), 1 cownose ray (*Rhinoptera bonasus*) and 1 hammerhead shark gut samples. A total of 14 prey groups were identified to family level, 1 to infraorder level, 1 to infraclass and 1 to class level.

3.2 Diet composition

20 identifiable prey remains were recorded in 18 guts of houndsharks (*Iago omanensis*). Their diet mainly consisted of teleosts (72.84% IRI), specifically Engraulidae, which was the primary contributor. Shrimps of the family Penaeidae were another important prey, contributing to 18.71% of IRI. Cephalopods and stomatopods (Parasquillidae) were infrequent prey, contributing 0.8% IRI and 0.75% IRI, respectively (Figure 3.1 (A)). The diet of longtail butterfly rays (*Gymnura poecilura*) was analyzed based on 8 identifiable prey remains found in 8 stomachs. Teleosts dominated the diet, contributing 93.27% of the IRI, with Mugilidae being the primary component at 90.82% IRI. Gastropods (Chilodontidae) and cephalopods were infrequent prey, accounting for 2.14% and 2.05% IRI, respectively (Figure 3.1 (C)). The

diet of stripenose guitarfish (*Acroteriobatus variegatus*) was analyzed based on 9 identifiable prey remains found in 8 stomachs. Their diet exclusively consisted of shrimps (Penaeidae) (Figure 3.1 (D)). The diet of whitespotted whiprays (*Maculabatis gerrardi*) was analyzed based on 19 identifiable prey remains found in 15 stomachs. Their diet primarily consisted of crustaceans (91.72% IRI) and polychaetes, specifically those of the family Capitellidae (5.57% IRI). Teleost fishes were infrequent prey, contributing only 1.63% IRI (Figure 3.1 (B)).

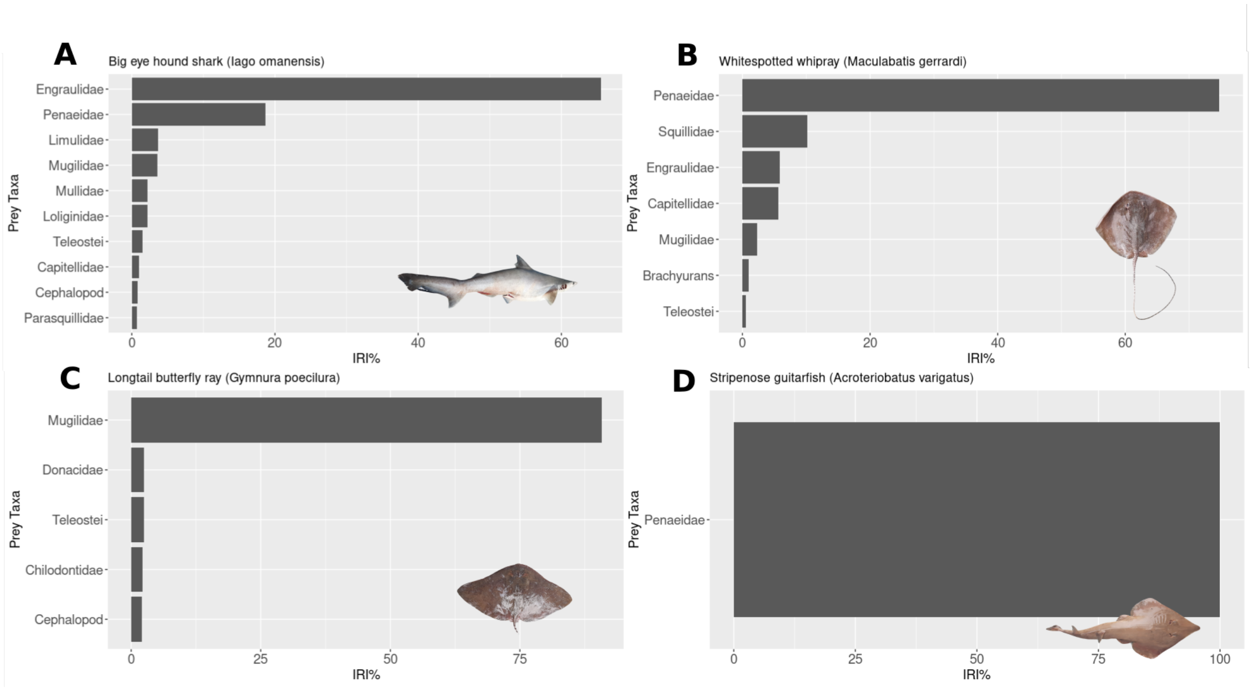

Figure 3.1: Diet Composition of Elasmobranch Species. (A) Diet composition of bigeye hound shark (*Iago omanensis*). (B) Diet composition of whitespotted whipray (*Maculabatis gerrardi*) (C) Diet composition of longtail butterfly ray (*Gymnura poecilura*) (D) Diet composition of stripenose guitarfish (*Acroteriobatus variegatus*).

3.3 Trophic level

The trophic levels of 49 individuals were examined across 4 species of elasmobranchs. They were calculated based on prey species trophic levels from Cortés, 1999, given in Table 2.1. *I. omanensis*, *A. variegatus*, *G. poecilura*, and *M. gerrardi* had trophic levels greater than four and were tertiary consumers (TL>4) (Table 3.1). The trophic levels ranged from 4.02 for *A. variegatus* to 4.72 in *M. gerrardi.*

Table 3.1: Trophic levels of elasmobranchs species.

Species	**Trophic level**	**n**
M. gerrardi	4.72	15
I. omanensis	4.27	18
G. poecilura	4.09	8
A. variegatus	4.02	8

3.4 Dietary variation across habitats

Significant differences between the diets of benthic (*A. variegatus*, *G. poecilura*, *M. gerrardi*, *H. bennettii*, *N. indica*, *Rhinoptera* spp.) and pelagic (*I. omanensis*, *C. leucas*, *M. birostris*, *S. lewini*) elasmobranch species (benthic, $n = 36$ and pelagic, $n = 24$) were observed (PERMANOVA; R^2 value $= 0.09$, $p < 0.05$).

3.5 Dietary differences across species

We also observed differences in diet composition among and between benthic and pelagic species. Among benthic sympatric species, *A. variegatus* and *G. poecilura* (PERMANOVA; R^2 value $= 0.38$, $p < 0.05$) and *M. gerrardi* and *G. poecilura* (PERMANOVA; R^2 value $= 0.24$, $p < 0.05$), showed a significant difference in their diet composition. *I. omanensis* and *G. poecilura* (PERMANOVA; R^2 value $= 0.11$, $p < 0.05$), *M. gerrardi* and *I. omanensis* (PERMANOVA; R^2 value $= 0.11$, $p < 0.05$), and *A. variegatus* and *I. omanensis* (PERMANOVA; R^2 value $= 0.14$, $p < 0.05$), showed significant differences in their diet composition.

3.6 Dietary changes from SIA

The isotopic values were measured from tissue samples for 62 elasmobranchs across 4 different groups (mobulids, *I. omanensis*, *M. gerrardi*, *G. poecilura*). The δ^{13}C values ranged from -18.3 (for mobulids) to -15.9 (for *M. gerrardi*). Intraspecific variability in δ^{13}C was sometimes high (Table 3.2), as for *I. omanensis* ($n = 16$; s.d. $= 0.85$) and *M. gerrardi* ($n = 15$; s.d. $= 0.73$). Comparison of the data among all elasmobranch species revealed significant differences in δ^{13}C (ANOVA; $F = 49.23$, $p < 0.001$). The δ^{13}C values of mobulids were significantly lower than those of *I. omanensis*, *M. gerrardi* and *G. poecilura* (Tukey's HSD test; $p < 0.001$). The δ^{13}C values of *I. omanensis* were also significantly lower than those of *M. gerrardi* and *G. poecilura* and higher than in mobulids (Tukey's HSD test; $p < 0.05$). *M. gerrardi* and *G. poecilura* did not show significant differences (Table 3.2).

The δ^{15}N values ranged from 10.4 (for *G. poecilura*) to 8.14 (for mobulids). Similar levels of intraspecific variability were found: the maximum δ^{15}N s.d. was 1.14 for *I. omanensis*, and the minimum was 0.84 for *G. poecilura*. Comparison of the data among all elasmobranch species revealed significant differences in δ^{15}N (ANOVA; $F = 13.31$, $p < 0.001$). The δ^{15}N values of *G. poecilura* were significantly higher than those of mobulids, *I. omanensis* and *M. gerrardi* (Tukey's HSD test; $p < 0.05$). δ^{15}N values of other species were indistinguishable (Table 3.2).

Table 3.2: The number of fish analyzed and isotope values for each species sampled, along with the results from the ANOVA for significant differences between species' means. Species sharing at least one letter in common indicate no significant difference (Tukey's test, p < 0.05).

Species	**n**	**δ^{13}C**			**δ^{15}N**		
		Mean	**s.d.**	**Significant difference**	**Mean**	**s.d.**	**Significant difference**
Mobulidae	15	-18.3	0.32	b	8.14	1.06	a
Iago omanensis	16	-16.5	0.85	c	8.99	1.14	a
Maculabatis gerrardi	15	-15.9	0.73	a	8.92	0.93	a
Gymnura poecilura	16	-16.0	0.37	a	10.4	0.84	b

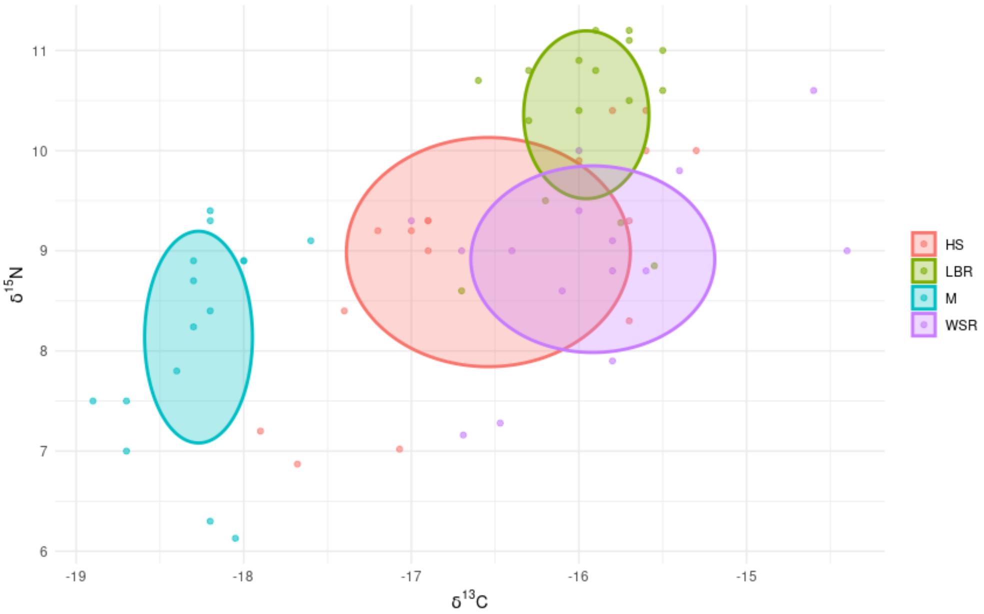

Figure 3.2: Isotopic Niche of Elasmobranch Species. Standard deviation ellipse areas for *I. omanensis* (HS), *G. poecilura* (LBR), mobulids (M) and *M. gerrardi* (WSR).

Chapter 4

Discussion

This study investigates the feeding ecology and trophic interactions of commonly landed elasmobranchs along the central eastern coast of India. Stomach content analysis revealed distinct dietary differences between benthic and pelagic species, minimizing dietary niche overlap. Significant differences in diet were also observed between sympatric and allopatric species. Benthic species primarily consumed crustaceans, whereas pelagic species predominantly fed on teleosts. Similarly, isotope analysis revealed that benthic species were enriched in δ^{13}C while pelagic species were depleted in δ^{13}C. Additionally, δ^{15}N values highlighted significant differences in trophic levels across elasmobranch species.

4.1 Diet composition and trophic level

4.1.1 Diet Composition and trophic level of *I. omanensis*

The predominance of teleosts in the diet of *Iago omanensis* aligns with findings from previous studies. Rastgoo et al., 2019 reported that teleosts constituted 80% IRI in the stomachs of *I. omanensis* from the Oman Sea, while cephalopods and crustaceans (including stomatopods) were also significant prey groups. Similarly, Waller and Baranes, 1994 observed that teleosts comprised 42% of IRI in *I. omanensis* from the Red Sea, with cephalopods and benthopelagic fishes also playing important roles. Earlier studies by Nair and Appukuttan, 1973 and Baranes, 1982 further corroborate the importance of cephalopods, stomatopods, and other crustaceans in the diet of this species in regions such as the Gulf of Eilat and deep-water habitats.

The dietary patterns of *I. omanensis* are consistent with those of other triakid sharks. For example, Cortés, 1999 noted that teleosts, crustaceans, and cephalopods are the primary prey for many *Mustelus* species, often exceeding 70% of their diet. Crustaceans have also been documented as a preferred prey group for *Mustelus* species in the western Mediterranean (Morte et al., 1997) and eastern Adriatic Sea (Jardas and Klančnik, 2007), which is the second most abundant prey taxa found in the bigeye houndshark. These findings suggest that *I. omanensis* share a similar dietary niche with other members of the family Triakidae.

Dietary studies indicate that *I. omanensis* has an overall trophic level of 4.4 (Rastgoo et al., 2019), which is consistent with our findings, where the trophic level was measured at 4.27 (Table 3.1), reinforcing its role as a top predator. The elevated trophic level of *I. omanensis* (TL > 4) places it as a tertiary consumer, a category shared by other sharks and certain batoids (Rastgoo and Navarro, 2017). Additionally, this trophic level surpasses that of other genera within its family (Cortés, 1999).

These findings suggest that *I. omanensis* is a significant predator of teleosts and crustaceans in deep-water ecosystems. The dominance and variety of teleosts in its diet highlight its active predatory behaviour, while the inclusion of crustaceans indicates a bottom-dwelling foraging strategy. This reinforces its role as a crucial predator in the bathypelagic ecosystem of the western Bay of Bengal, helping to regulate prey populations and influence overall ecosystem dynamics.

4.1.2 Diet Composition and trophic level of *G. poecilura*

Other studies support the abundance of teleosts in the diet of *G. poecilura*. For example, Jhu-Xhing Leung et al., 2023 reported that teleosts constituted 94.4% IRI in the stomachs of *G. poecilura* from Malaysia, while crustaceans and polychaetes were also significant prey groups. Similarly, Muktha Menon et al., 2020 observed that teleosts made up 80.9% of IRI in *G. poecilura* from the Bay of Bengal. These findings align with broader patterns observed in Gymnurid rays, where teleosts are the dominant prey, often exceeding 90% IRI in stomach contents (Jacobsen et al., 2009; Yokota et al., 2013; Jargowsky et al., 2019; Muktha et al., 2020). However, some variation exists among species; for instance, *G. altavela* exhibits a diet dominated by crustaceans, followed by teleosts (Capapé, 1986).

In this study, the trophic level of *G. poecilura* was measured at 4.09 (Table 3.1), which is lower than that of the shark *I. omanensis* and the benthic ray *M. gerradi.* This difference aligns with the general trend that sharks tend to occupy higher trophic levels than rays (Cortés, 1999). Butterfly rays, belonging to the family Gymnuridae, are classified as tertiary consumers with trophic levels exceeding 4 (Jacobsen and Bennett, 2013; Rastgoo et al., 2016). These rays are ambush predators that utilize an intermittent feeding strategy, preying on relatively large prey in small numbers. Their ability to stun large prey before ingestion, achieved by delivering physical blows with their pectoral fins, facilitates this feeding behavior (Muktha Menon et al., 2020).

By stunning their prey, ambush predators such as *G. poecilura* can efficiently capture, handle, and ingest large prey items, particularly teleosts, which explains the high proportion of teleosts in their diet and their elevated trophic level (Figure 1(C)). Cluster analysis further supports this feeding strategy by grouping Gymnuridae with the majority of Torpedinoidei in the FISH trophic guild, indicating a diet dominated by fish (Jacobsen and Bennett, 2013). These specialized feeding strategies contribute to the high trophic level of *G. poecilura* (4.05), comparable to that of most shark families.

The Indo-West Pacific region, including the Bay of Bengal, harbors the highest species diversity of butterfly rays (Yokota and White, 2016). Despite their ecological significance, gymnurids remain understudied. One exception is the work of Muktha Menon et al., 2020 in the western Bay of Bengal, which identified size-based variations in feeding strategies and prey selection among *G. poecilura.* Recently, the IUCN Red List reassessed the conservation status of *G. poecilura*, upgrading it from Near Threatened to Vulnerable due to overfishing and population declines over the past several decades. These threats emphasize the need for further research on the ecology and biology of Gymnuridae to support conservation efforts. Given their high degree of feeding specialization and role as apex predators, understanding the dietary habits of *G. poecilura* is critical for assessing its ecological function and vulnerability to environmental changes.

4.1.3 Diet Composition and trophic level of *M. gerrardi*

The predominance of crustaceans in the diet of *M. gerrardi* aligns with findings from other studies. Rastgoo et al., 2018 reported that crustaceans accounted for 71.96% of the Index of Relative Importance (IRI) in the stomach contents of *M. gerrardi* from the Oman Sea, with teleosts and polychaetes also contributing significantly. This crustacean-based diet is common among other stingray species, including those of the genus *Himantura* in Australian waters (O'Shea et al., 2013). Similarly, various dasyatid species have been found to primarily consume polychaetes (O'Shea et al., 2013). Kleinertz et al., 2022 also identified crustaceans as the dominant prey in *M. gerrardi* from Indonesia, while Aghajari Khazaei et al., 2023 reported that bivalves, worms, and crustaceans formed the primary dietary components of this species in Hormozgan Province, Iran.

The diet composition of *M. gerrardi* primarily consists of crustaceans, with teleosts and stomatopods also serving as important prey items. The high proportion of crustaceans in its diet suggests that *M. gerrardi* is a specialized active predator foraging on the seafloor (Rastgoo et al., 2018). In this study, *M. gerrardi* was found to have a high trophic level of 4.27, classifying it as a tertiary consumer and highlighting its role as an important top predator in the western Bay of Bengal food web. While sharks typically occupy higher trophic levels than rays (Cortés, 1999), this study reveals that *M. gerrardi* exhibits a slightly higher trophic level despite its primary reliance on crustaceans. This finding provides a baseline description of the species' trophic ecology. However, further studies across different seasons are necessary to obtain a more precise estimation of its feeding habits and trophic level, as well as to understand potential temporal variations in its diet.

M. gerrardi is an ecologically significant species within the family Dasyatidae. Roul et al., 2021 noted that it ranked second in species catch analysis along the Odisha coast in 2020, indicating its considerable biomass and importance in local fisheries. This stingray inhabits demersal shallow waters, typically found on soft substrates at depths of up to 60 meters (Last and Compagno, 1999). Despite its ecological relevance, information on the feeding habits and trophic level of *M. gerrardi* remains scarce.

4.1.4 Diet Composition and Trophic Level of *A. variegatus*

A. variegatus, a critically endangered species endemic to the eastern coast of India and Sri Lanka, belongs to the family Rhinobatidae, which is known to primarily feed on benthic invertebrates and small fishes. This aligns with our findings, as shrimps were the sole prey item identified in the diet of *A. variegatus*.

Similar dietary patterns have been documented in other members of the Rhinobatidae family. Lara-Mendoza et al., 2015 found that the diet of the speckled guitarfish (*Rhinobatos glaucostigma*) in Magdalena Bay was predominantly composed of shrimps (%IPSIR = 43.47), amphipods (%IPSIR = 18.89), and crabs (%IPSIR = 18.07). Likewise, Bornatowski et al., 2010 reported that *Rhinobatos percellens* primarily consumed Decapoda (69%) and Teleostei (22%), as determined by the Alimentary Index (IAi). Notably, polychaetes, which are frequently found in the diets of other benthic fishes, were scarcely represented in the diet of *R. percellens*, a pattern that aligns with our findings for *A. variegatus*.

In this study, the trophic level of *A. variegatus* was measured at 4.01 (Table 3.1), the lowest among the four species analyzed. Although this value surpasses 4, categorizing it as a tertiary consumer, it remains the lowest among the studied elasmobranchs. This suggests that *A. variegatus* occupies a position between secondary and tertiary consumers, resembling other guitarfishes, which are generally classified as secondary consumers. Previous research on the Rhinobatidae family has reported trophic levels (TL) ranging from 3.6 to 4.2 based on stable-isotope analysis, with an average TL of approximately 3.72, reinforcing their classification as secondary consumers inhabiting soft-bottom environments (Blanco-Parra et al., 2012), a pattern reflected in their diet composition (Figure 3.1 (D)).

Lara-Mendoza et al., 2015 further observed that *Rhinobatos glaucostigma* (family: Rhinobatidae) predominantly feeds on benthic crustaceans, a finding consistent with the present study. This highlights a specialized and active foraging strategy similar to that of many other guitarfishes (Lara-Mendoza et al., 2015). These findings underscore the specialized feeding ecology of *A. variegatus* and its reliance on shrimp as a primary food source. Given its critically endangered status, understanding its dietary habits and ecological role is essential for informing conservation efforts.

4.2 Dietary variation across habitats

Differences in diet composition were observed between benthic and pelagic elasmobranch species despite all being tertiary consumers. *Iago omanensis*, a bathypelagic species (Pearce et al., 2023), primarily consumes teleosts, followed by shrimps, with cephalopods and stomatopods appearing in lesser proportions. Similarly, other pelagic species such as, the bull shark (*Carcharhinus leucas*) (Rigby et al., 2021) and mobulids was found to exclusively consume teleosts, while hammerhead sharks (*Sphyrna lewini*) was found to feed on cephalopods.

Among benthic species, crustaceans form the dominant prey. *Maculabatis gerrardi*, *Acroteriobatus variegatus*, *Hemitrygon bennettii*, *Neotrygon indica* and *Rhinoptera spp.* primarily consume crustaceans such as shrimps and stomatopods. However, *Gymnura poecilura*, despite being a benthic species, exhibits a teleost-heavy diet. This exception may be attributed to its unique 'stun prior to ingestion' feeding strategy using its pectoral fins. Overall, benthic species tend to have a crustacean-dominated diet, while pelagic species predominantly consume teleosts.

The difference in diet composition between benthic and pelagic species is primarily driven by the availability of prey in their respective habitats. Pelagic species, such as *I. omanensis*, have access to a wider variety of teleosts in open waters, whereas benthic species are more specialized in preying on soft-bottom-dwelling crustaceans. Although both *I. omanensis* (pelagic) and *G. poecilura* (benthic) exhibit teleost-heavy diets, the former preys on four families of teleosts, while the latter feeds on only two families of teleosts. This disparity reflects the broader availability of teleosts in pelagic environments compared to benthic habitats.

Feeding strategies and morphological adaptations further contribute to this low dietary overlap and facilitate resource partitioning across habitats. For example, bull sharks employ various hunting techniques, such as ambush, bump-and-bite, and fast chases, aided by their muscular bodies, powerful jaws, and specialized teeth that allow them to capture and consume a wide range of prey, including fish, rays, sea turtles, and even other sharks. In contrast, the flattened, rhomboid disc and short, slender tail of Gymnurid rays, combined with their slightly arched mouths and bands of small teeth, are well-suited for feeding on bottom-dwelling organisms. Similarly, the shovel-shaped body and elongated snout of guitarfishes (Rhinobatidae family) enable them to probe sediments and capture hidden prey efficiently (Fellows, 2016). These morphological and behavioral adaptations explain the observed differences in diet across habitats.

4.3 Dietary differences across species

Gymnura poecilura exhibits a significant difference from other benthic species due to its teleost-heavy diet, contrasting with the crustacean-dominated diets of *Acroteriobatus variegatus* and *Maculabatis gerrardi*. Specifically, *G. poecilura* displays a piscivorous diet, with teleosts contributing 93.27% of the IRI (Figure 1 (C)). This sets it apart from the crustacean-heavy diets of *A. variegatus* and *M. gerrardi*.

In butterfly rays, stomach content analyses frequently reveal a single, large prey item ingested head-first, indicating a specialized feeding strategy (Jacobsen et al., 2009; Yokota et al., 2013). Conversely, members of the Rhinobatidae family, such as guitarfishes, typically remain partially buried in sand or mud, adopting a sit-and-wait strategy to capture crustaceans and small fish. They utilize their elongated snouts to pin down prey before suction-feeding, a behavior that accounts for their crustacean-dominated diet. Similarly, *M. gerrardi* exhibits a dietary specialization for shrimp, as illustrated by its stomach content composition (Figure 1 (B)). These findings suggest that resource partitioning among benthic species sharing the same habitat is facilitated by distinct feeding strategies and prey selection.

Comparing the diet composition of benthic and pelagic species, the pelagic species *Iago omanensis* differs from benthic species such as *G. poecilura* and *M. gerrardi* due to its teleost-heavy diet. While both *G. poecilura* and *I. omanensis* primarily consume teleosts, *G. poecilura* predominantly feeds on the Mugilidae family, whereas *I. omanensis* preys on a wider variety of teleost families, including Engraulidae, Mugilidae, and Mullidae, albeit in smaller proportions (Figure 1 (A)).

This pattern is supported by the high diversity of teleosts found in pelagic ecosystems, which is driven by the dynamic nature, resource availability, spatial complexity, and migratory behaviors of these habitats (Froese and Pauly, 2023; Worm and Tittensor, 2011). Pelagic ecosystems offer a wider range of prey types (e.g., plankton, small fish, and cephalopods) and greater opportunities for niche partitioning, leading to higher teleost diversity. In contrast, demersal ecosystems are more resource-limited, with species often specializing in specific prey types, such as crustaceans and polychaetes (Longhurst, 2007).

This distinction is further highlighted by the whitespotted whipray (*M. gerrardi*), which specializes in feeding on shrimps (Figure 1 (B)), underscoring the distinct dietary preferences between pelagic and benthic species. These findings suggest that pelagic species, such as *I. omanensis*, tend to have a more diverse teleost-heavy diet, while benthic species exhibit specialized morphologies and feeding strategies that align with their crustacean-dominated diets. These differences emphasize the ecological role of *I. omanensis* as an active predator and a dominant pelagic species, reflecting the broader patterns of resource partitioning and habitat specialization in marine ecosystems.

4.4 Dietary changes from SIA

Based on their δ^{13}C values (Table 3.2), Mobulidae (-18.3 ± 0.32) is identified as the most pelagic or epipelagic species. This conclusion aligns with the known ecology of Mobulids, which are highly mobile, epipelagic rays that primarily feed on zooplankton using specialized gill-raker apparatus (Couturier et al., 2012). Their reliance on pelagic zooplankton leads to the depletion of heavy carbon isotopes, as pelagic feeding is typically associated with lighter carbon isotope values (Davenport and Bax, 2002; Hobson et al., 2002). Furthermore, the narrow range of isotopic niches observed in Mobulids (Figure 3.2) reflects their specialized feeding behavior on pelagic prey. In Mobulidae, the mean carbon isotope values for juveniles (-18.3) were comparable to those of adults (-18.2), though slightly higher. This suggests that juveniles may exhibit slightly more benthic feeding tendencies than adults. However, their primary feeding grounds remain similar, which is also concluded by Stewart et al., 2017 in *Mobula birostris*. The nitrogen isotope values for Mobulidae also provide insights into their trophic ecology. The δ^{15}N values for Mobulidae (8.14 ± 1.06) are the lowest among the four elasmobranchs studied, consistent with their planktivorous diet, which occupies lower trophic levels. Interestingly, the mean nitrogen isotope value for juveniles (8.46) was higher than that of adults (7.85), which contrasts with the general trend of a positive relationship between body size and trophic level in filter-feeding elasmobranchs (Borrell et al., 2011). This shift could be attributed to the opportunistic or less specialized feeding behavior of juvenile Mobulids, which gradually become more specialized plankton feeders as they grow into adults.

The bigeye houndshark (*I. omanensis*) exhibits a broad range of δ^{13}C values (-16.5 ± 0.85), with the measured average value indicating a depletion in heavy carbon isotopes, suggesting that *I. omanensis* primarily feeds on pelagic resources. However, this deep-sea shark also shows high interspecies variability, which is consistent with its bathypelagic nature. As an active predator, it can exploit pelagic and deep-sea benthic resources, leading to *I. omanensis* having a larger isotopic niche (Pearce et al., 2023; Rastgoo and Navarro, 2017). This broad feeding range is further reflected in its diverse diet composition, which includes a wide variety of teleosts and crustaceans (Figure 3.1 (A)). In *I. omanensis*, the mean carbon isotope value for juveniles (-17.1) was lower than that of adults (-16.0). This pattern is logical, as juveniles tend to inhabit coastal habitats and migrate to deeper waters as they mature, leading to the enrichment of ^{13}C in adults. This ontogenetic shift in habitat use contributes to the high variability in prey items consumed by adults. Similarly, the mean δ^{15}N value for *I. omanensis* was 8.99 ± 1.14, with juveniles (8.57) exhibiting lower nitrogen isotope values than adults (9.4). This trend aligns with the general behavior of sharks, which are often opportunistic feeders during their juvenile stages and transition to more active predation as adults, allowing them to feed at higher trophic levels. This ontogenetic shift in feeding behavior is consistent with findings by Espinoza et al., 2015, who observed that larger demersal sharks feed at higher trophic levels than smaller individuals, reflecting changes in isotopic niche space as they grow.

The benthic species, the longtail butterfly ray (*G. poecilura*), exhibits enrichment in ^{13}C, with a mean value of -16.0 ± 0.37 and a narrow isotopic niche range (Figure 3.2). This enrichment in heavy carbon isotopes indicates that *G. poecilura* primarily feeds on benthic resources, consistent with its habitat as a demersal species. Members of the Gymnuridae family, including *G. poecilura*, are commonly found in sandy and muddy bottoms of tropical seas and are frequently caught in bottom trawl nets (Yokota et al., 2013). Previous studies have also shown that *G. poecilura* specializes in feeding on demersal teleosts with relatively low dietary diversity (Yokota et al., 2013; Muktha Menon et al., 2020; Jhu-Xhing Leung et al., 2023; Jacobsen and Bennett, 2013). For δ^{15}N values, the longtail butterfly ray exhibits a mean nitrogen isotope value of 10.4 ± 0.84, reflecting its high trophic level. The mean carbon isotope values for juveniles (-16.0) were comparable to those of adults (-15.9), suggesting similar feeding habitats across life stages. However, the mean nitrogen isotope value for *G. poecilura* was the highest among the four elasmobranchs studied, consistent with its specialized teleost diet (Figure 3.1 (C)). Interestingly, juveniles (10.6) had higher nitrogen isotope values than adults (10.1). According to Muktha Menon et al., 2020, smaller individuals of *G. poecilura* primarily feed on fish, consuming medium-sized prey in smaller quantities. In contrast, larger individuals either consume large-sized fish in smaller numbers or feed on small-sized fish and shrimp in larger quantities. This difference in feeding behavior may explain why juveniles, which primarily consume fish, occupy a higher trophic level than adults, who have a more varied diet.

The whitespotted whipray (*M. gerrardi*), a benthic species, exhibits a mean value of -15.9 ± 0.73 with a slightly broader range of δ^{13}C values (Figure 3.2) compared to the longtail butterfly ray and has the highest δ^{13}C value among the four elasmobranch species studied, indicating a stronger reliance on benthic resources. This is supported by its diet composition (Table 3.2), which reveals a predominance of crustaceans, such as shrimps and mantis shrimps, typical of soft-bottom habitats. In *M. gerrardi*, the mean carbon isotope value for juveniles (-16.1) is lower than that of adults (-15.8). This pattern is consistent with the ontogenetic habitat shift observed in many elasmobranchs, where juveniles inhabit coastal areas and migrate to deeper waters as they mature. This shift leads to the enrichment of ^{13}C values in adults and contributes to the greater variability in prey items consumed by larger individuals.

For δ^{15}N values, the whitespotted whipray exhibits a value of 8.92 ± 0.93. The mean nitrogen isotope value for juveniles (9.05) is higher than that of adults (8.8). Although Rastgoo et al., 2018 states that positive association between trophic level and body size is common in elasmobranchs since larger individuals often exhibit a broader trophic spectrum and actively predate higher up the food chain. This shift could be attributed to the opportunistic or less specialized feeding behavior of juvenile individuals, which gradually become more specialized crustacean feeders as they grow into adults.

A comparison of the data among all elasmobranch species revealed significant differences in δ^{13}C values (ANOVA; $F = 49.23$, $p < 0.001$). Specifically, the δ^{13}C values of Mobulids were significantly lower than those of *I. omanensis*, *M. gerrardi*, and *G. poecilura* (Tukey's HSD test, $p < 0.001$). This reflects the distinct feeding ecology of planktivorous pelagic Mobulids compared to the benthic species *M. gerrardi* and *G. poecilura*, which primarily feed on benthic crustaceans and teleosts, respectively. The reliance of Mobulids on pelagic zooplankton, which is depleted in heavy carbon isotopes, results in significantly lower δ^{13}C values than the benthic species, as evidenced by their diet composition (Figure 3.1 (B,C)).

The δ^{13}C values of *I. omanensis* were significantly lower than those of *M. gerrardi* and *G. poecilura* but higher than those of Mobulids (Tukey's HSD test, $p < 0.05$). Although both *I. omanensis* and Mobulids are pelagic species, *I. omanensis* exhibits significantly higher enrichment of heavy carbon compared to Mobulids. This difference can be attributed to the specialized pelagic feeding behavior of Mobulids, which results in their lower δ^{13}C values. Consistent with stomach content data, both *G. poecilura* and *I. omanensis* primarily consume teleosts. However, *I. omanensis* displays a more pronounced pelagic signature than *G. poecilura* (Table 3.2). This suggests that while both species occupy similar trophic levels (i.e., feeding on teleosts), *I. omanensis* preferentially feeds on more pelagic teleosts, aligning with its bathypelagic nature (Pearce et al., 2023). In contrast, the reliance of *I. omanensis* on teleosts, as opposed to the crustacean-dominated diet of *M. gerrardi*, results in significantly lower δ^{13}C values compared to this benthic species (Figure 3.1 (B)). Interestingly, no significant differences were observed between the δ^{13}C values of *M. gerrardi* and *G. poecilura*. This indicates that, despite their distinct feeding behaviors as revealed by stomach content analysis, these sympatric species share similar long-term dietary sources.

Comparison of the data among all elasmobranch species revealed significant differences in δ^{15}N values (ANOVA; $F = 13.31$, p-value < 0.001). Specifically, the δ^{15}N values of *G. poecilura* were significantly higher than those of Mobulids, *M. gerrardi*, and *I. omanensis* (Tukey's HSD test, $p < 0.05$). In contrast, the δ^{15}N values of the other species were indistinguishable from each other (Table 3.2). The higher δ^{15}N values of *G. poecilura* reflect its higher trophic level compared to Mobulids, as *G. poecilura* specializes in feeding on benthic teleosts, which occupy a higher trophic level than the planktivorous diet of Mobulids. Although both *M. gerrardi* and *G. poecilura* are benthic species, the reliance of *G. poecilura* on teleosts, as opposed to the crustacean-dominated diet of *M. gerrardi*, results in significantly lower δ^{15}N values compared to *G. poecilura* (Figure 3.1 (B)). Similarly, *G. poecilura* exhibits a higher trophic level than *I. omanensis*. While stomach content analysis suggests that *I. omanensis* and *G. poecilura* have similar trophic levels (Table 3.2), stable isotope analysis provides long-term dietary information, revealing that *G. poecilura* occupies a higher trophic level over time. This is likely due to its specialized teleost diet and intermittent feeding strategy (Muktha Menon et al., 2020), which contrasts with the broader trophic spectrum of *I. omanensis*. These findings highlight the importance of integrating both stomach content and stable isotope analyses to fully understand the trophic ecology of elasmobranch species.

Chapter 5

Conclusion

Research on resource partitioning and ecological roles of elasmobranchs is critical for conservation and management efforts, given their declining populations. This study analyzed the diets of multiple elasmobranch species and revealed significant differences in prey items across habitats, indicating dietary niche segregation. Such partitioning occurs not only along habitat axes but also in dietary preferences, suggesting that species adapt to exploit available resources efficiently. These adaptations lead to specialization in prey types, reducing trophic niche overlap and enabling them to evolve in response to distinct environmental conditions with unique resource bases. Additionally, this study highlights species-specific dietary variations, indicating that these elasmobranchs have evolved specialized feeding strategies or behaviours to occupy specific niches. Further research is needed to investigate temporal dynamics in elasmobranch feeding ecology and understand anthropogenic impacts to inform effective conservation strategies for these ecologically vital marine predators.

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Appendix

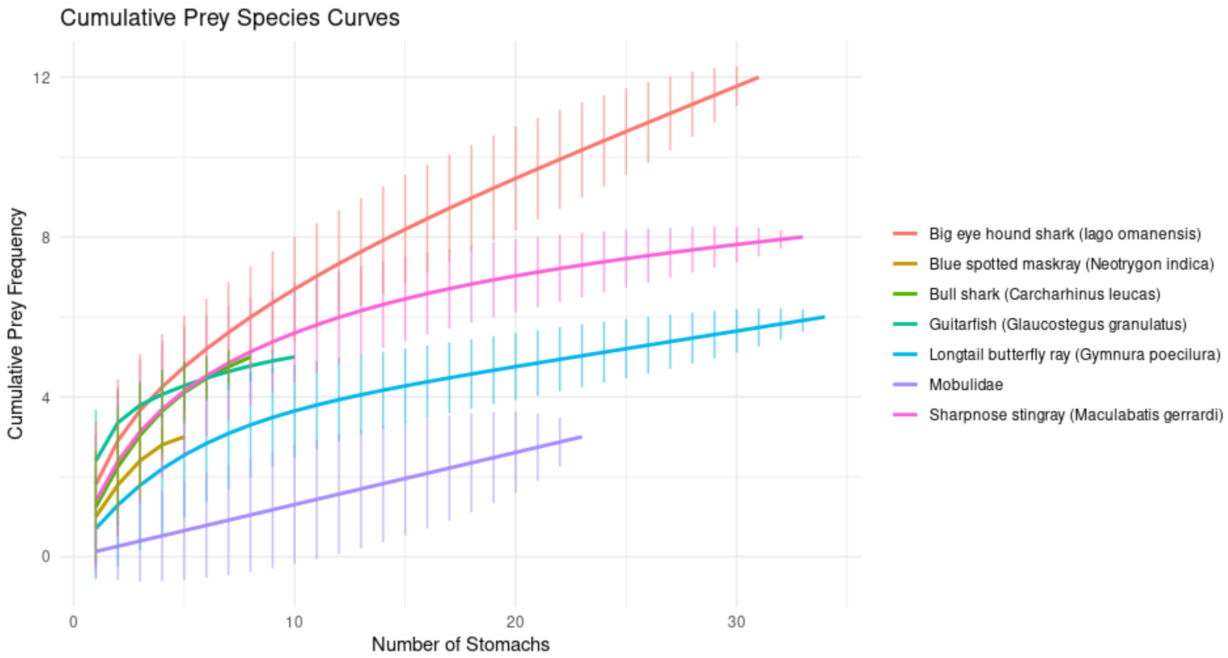

Figure A.1: Cumulative Prey Species Curves of Elasmobranch Species. Cumulative prey curves have been plotted with all taxa identified at the family level. The curves for longtail butterfly ray, sharpnose stingray, bigeye hound shark and guitarfishes were close to reaching an asymptote. This suggests that the most common prey species were likely captured for these species with sufficient stomach counts.

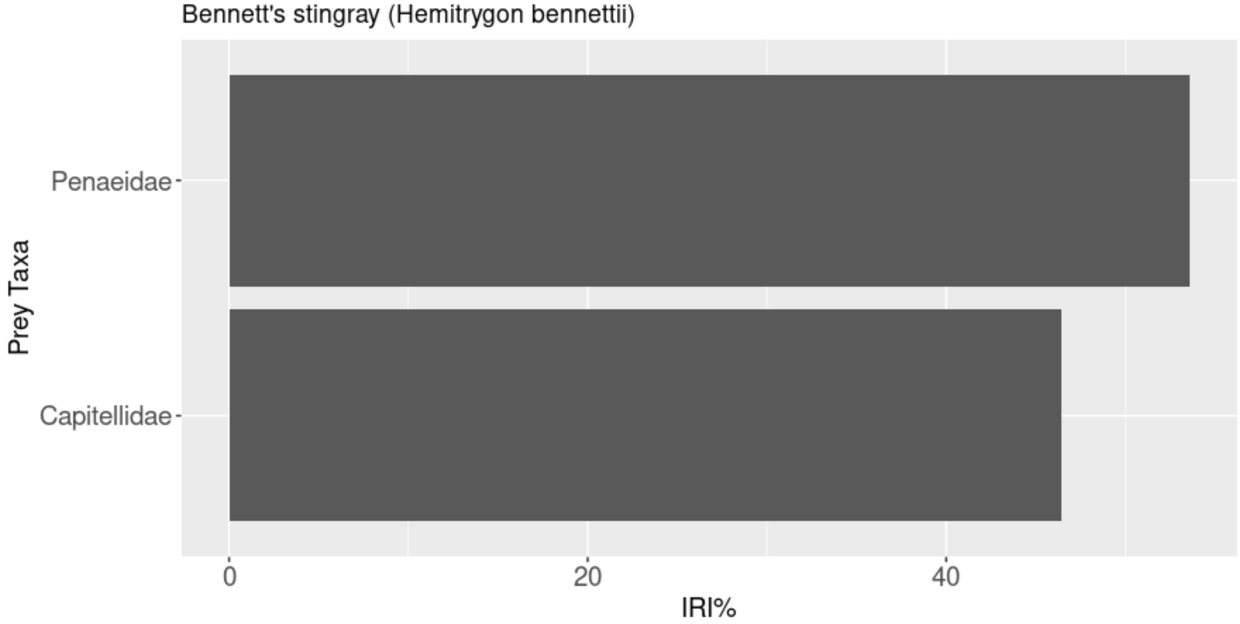

Figure A.2: Diet Composition of Bennett's Stingray (*Hemitrygon bennetti*)

Table A.1: Diet composition of stripenose guitarfish (*Acroteriobatus variegatus*), showing the frequency of occurrence (%F), weight contribution (%W), numerical abundance (%N), index of relative importance (IRI), and percentage IRI (%IRI) for each prey taxon.

Prey taxa	%F	%W	%N	IRI	%IRI
Peneidae	100.00	100.00	100.00	20000.00	100.00

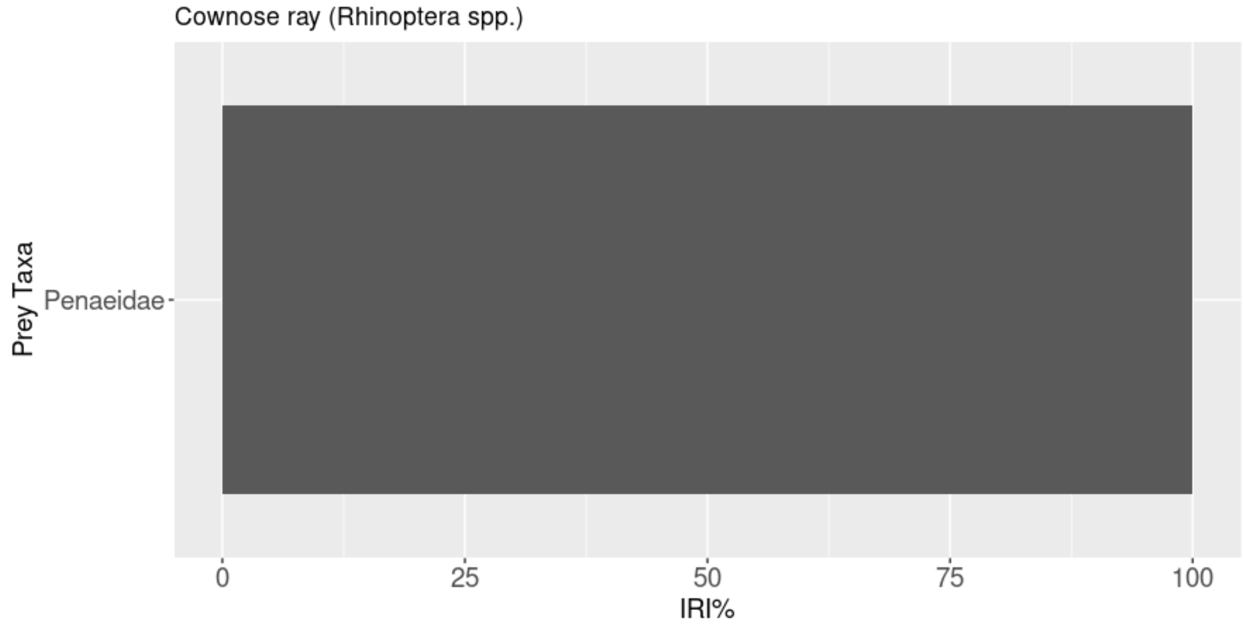

Figure A.3: Diet Composition of Cownose Ray (*Rhinoptera spp.*)

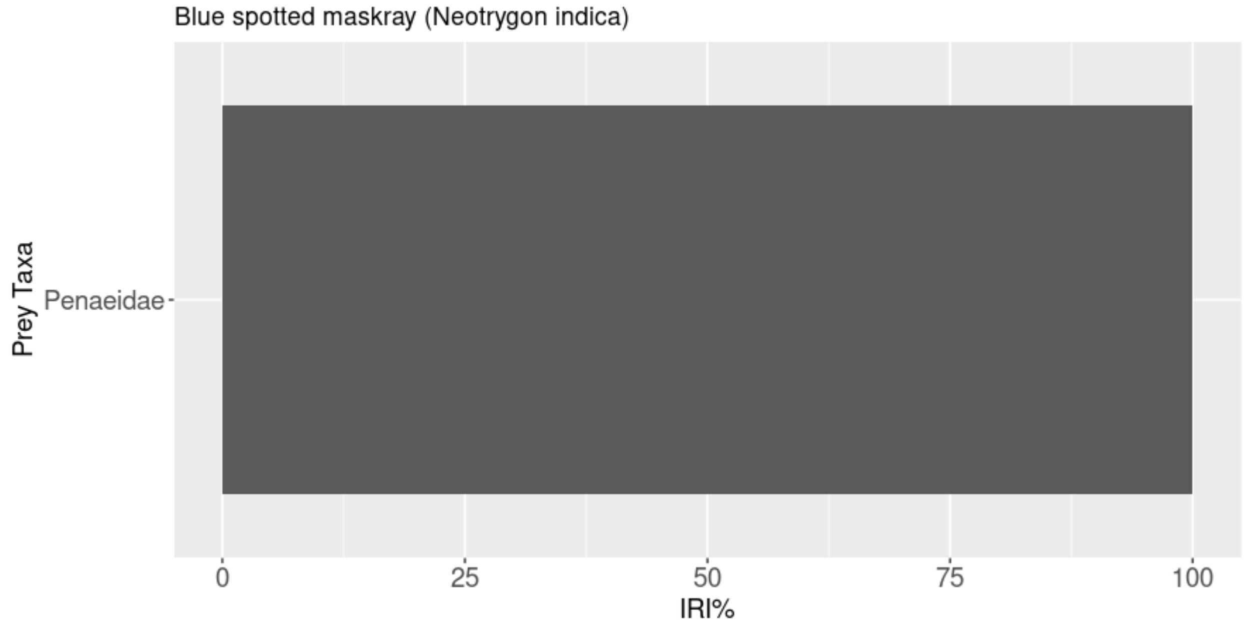

Figure A.4: Diet Composition of Indian Blue-spotted maskray (*Neotrygon indica*)

Table A.2: Diet composition of longtail butterfly ray (*Gymnura poecilura*), showing the frequency of occurrence (%F), weight contribution (%W), numerical abundance (%N), index of relative importance (IRI), and percentage IRI (%IRI) for each prey taxon.

Prey taxa	**%F**	**%W**	**%N**	**IRI**	**%IRI**
Mugilidae	50.00	92.46	50.00	7123.16	90.83
Donacidae	12.50	3.43	12.50	199.07	2.54
Teleostei	12.50	2.84	12.50	191.79	2.45
Chilodontidae	12.50	0.92	12.50	167.81	2.14
Cephalopod	12.50	0.34	12.50	160.53	2.05

Table A.3: Diet composition of Bennett's stingray (*Hemitrygon bennetti*), showing the frequency of occurrence (%F), weight contribution (%W), numerical abundance (%N), index of relative importance (IRI), and percentage IRI (%IRI) for each prey taxon.

Prey taxa	**%F**	**%W**	**%N**	**IRI**	**%IRI**
Peneidae	50.00	57.11	50.00	5355.36	53.55
Capitellidae	50.00	42.89	50.00	4644.64	46.45

Table A.4: Diet composition of bigeye hound shark (*Iago omanensis*), showing the frequency of occurrence (%F), weight contribution (%W), numerical abundance (%N), index of relative importance (IRI), and percentage IRI (%IRI) for each prey taxon.

Prey taxa	**%F**	**%W**	**%N**	**IRI**	**%IRI**
Engraulidae	38.89	31.87	35.00	2600.53	65.49
Peneidae	22.22	13.44	20.00	743.17	18.71
Limulidae	11.11	3.25	10.00	147.21	3.71
Mugilidae	5.56	20.84	5.00	143.54	3.61
Mullidae	5.56	11.05	5.00	89.18	2.25
Loliginidae	5.56	10.60	5.00	86.69	2.18
Teleostei	5.56	5.77	5.00	59.83	1.51
Capitellidae	5.56	2.05	5.00	39.19	0.99
Cephalopod	5.56	0.75	5.00	31.93	0.80
Parasquillidae	5.56	0.37	5.00	29.85	0.75

Table A.5: Diet composition of whitespotted stingray (*Maculabatis gerrardi*), showing the frequency of occurrence (%F), weight contribution (%W), numerical abundance (%N), index of relative importance (IRI), and percentage IRI (%IRI) for each prey taxon.

Prey taxa	**%F**	**%W**	**%N**	**IRI**	**%IRI**
Peneidae	71.43	29.29	47.62	5493.37	74.70
Squillidae	28.57	7.15	19.05	748.48	10.18
Engraulidae	14.29	20.55	9.52	429.58	5.84
Capitellidae	14.29	19.13	9.52	409.41	5.57
Mugilidae	7.14	18.35	4.76	165.11	2.25
Brachyurans	7.14	5.23	4.76	71.35	0.97
Teleostei	7.14	0.30	4.76	36.16	0.49

Table A.6: Diet composition of blue-spotted maskray (*Neotrygon indica*), showing the frequency of occurrence (%F), weight contribution (%W), numerical abundance (%N), index of relative importance (IRI), and percentage IRI (%IRI) for each prey taxon.

Prey taxa	**%F**	**%W**	**%N**	**IRI**	**%IRI**
Peneidae	100.00	100.00	100.00	20000.00	100.00

Table A.7: Diet composition of cownose ray (*Rhinoptera spp.*), showing the frequency of occurrence (%F), weight contribution (%W), numerical abundance (%N), index of relative importance (IRI), and percentage IRI (%IRI) for each prey taxon.

Prey taxa	**%F**	**%W**	**%N**	**IRI**	**%IRI**
Peneidae	100.00	100.00	100.00	20000.00	100.00

Table A.8: PERMANOVA results.

Variable	**R^2-value**	**p-value**
Among differing depths (benthic, n=36 and pelagic, n=24)	0.08677	0.004**
Among benthic sympatric species (*G. poecilura*, n=8 vs *A. variegatus*, n=8)	0.37964	0.002**
Among benthic sympatric species (*G. poecilura*, n=8 vs *M. gerrardi*, n=15)	0.24469	0.001***
Among allopatric species (*I. omanensis*, n=18 vs *G. poecilura*, n=8)	0.11441	0.004**
Among allopatric species (*I. omanensis*, n=18 vs *M. gerrardi*, n=15)	0.11193	0.015*
Among allopatric species (*I. omanensis*, n=18 vs *A. variegatus*, n=8)	0.13694	0.017*