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Diet composition of data-limited marlins (Istiophoridae) in the Northwest Atlantic

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Abstract

Knowledge of the dietary composition of Atlantic marlins, especially for recently acknowledged species such as roundscale spearfish (*Tetrapturus georgii*), is limited, as sample access is constrained by international quotas and intermittent landing rates. A series of annual offshore recreational fishing tournaments target Atlantic blue marlin (*Makaira nigricans*), white marlin (*Kajikia albida*) and roundscale spearfish on their seasonal foraging grounds in the South and Mid-Atlantic Bight. Through this network of tournaments and recreational anglers, we collected stomachs from Atlantic blue marlin ($n = 32$), white marlin ($n = 35$) and roundscale spearfish ($n = 44$) from 2018 to 2020 to investigate general diet composition. Stomach content analysis and DNA barcoding identified a total of 16 prey families across the three focal species, but the majority of prey weight (%W) was from two families (Scombridae and Ommastrephidae). Blue marlin and roundscale spearfish were predominantly piscivorous (99.0 and 80.6%W fishes, respectively), whereas white marlin mainly consumed cephalopods (80%W). The contribution of Scombridae was highest for blue marlin (94.6%W), intermediate for roundscale spearfish (51.7%W) and lowest for white marlin (11%W), with an inverse pattern of relative contribution for Ommastrephidae (0.9, 16.1 and 73.9%W, respectively). Roundscale spearfish and white marlin, despite having a near identical morphology, had diets composed of different prey types in our sample. These dietary data, from three epipelagic apex predators, provide important information for wider ecosystem-based studies, including in relation to the Mackerel, Squid and Butterfish Fishery Management Plan overseen by the Mid-Atlantic Fishery Management Council.

KEYWORDS
highly migratory species, istiophoridae, ommastrephidae, scombridae, trophic interactions

1 | INTRODUCTION

Marlins are apex predators that occupy temperate and tropical pelagic waters throughout the Atlantic, where they are target and by-catch species of various recreational and commercial fisheries (Lynch et al., 2011). In the western North Atlantic Ocean, marlin fisheries interact mainly with Atlantic blue marlin (*Makaira nigricans*, Lacepède, 1802), white marlin (*Kajikia albida*, Poey, 1860) and roundscale spearfish (*Tetrapturus* georgii, Lowe, 1841). Recreational tournaments primarily target blue and white marlin (Ehrhardt & Fitchett, 2016; Venizelos et al.,

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2003), whereas roundscale spearfish are also landed but have historically been misidentified as white marlin (Anon., 2019b). Atlantic marlin species are also caught in commercial longline and purse seine fisheries (Beerkircher et al., 2009; Karnauskas et al., 2013; Lauretta et al., 2012; Ramos-Cartelle et al., 2019).

Atlantic marlins utilize large-scale oceanographic currents and water masses (e.g., the Gulf Stream) to migrate within suitable environmental conditions in search of favourable foraging or spawning habitats (Andrzejaczek et al., 2023; Braun et al., 2015; Dutton, 2010). Atlantic blue marlin and white marlin generally inhabit tropical and subtropical waters, spending the majority of time in the epipelagic zone (Goodyear et al., 2008; Horodysky et al., 2007; Kraus & Rooker, 2007), but both species make occasional vertical descents >200 m, to temperatures as low as 12°C for short intervals (Freitas et al., 2022; Vaudo et al., 2017). Habitat data for roundscale spearfish are limited, but their distribution is presumed to be similar to white marlin due to frequent capture in fisheries targeting white marlin (Beerkircher et al., 2009). In addition, electronic tagging data showed similar depth distributions for co-occurring white marlin and roundscale spearfish with both species occupying surface waters <10 m (Loose, 2014).

Foraging patterns have been investigated previously for Atlantic blue marlin and white marlin, whereas published data on roundscale spearfish are limited. Blue and white marlin diets consist largely of pelagic schooling fishes and squids, particularly of the families Scombridae and Ommastrephidae (Logan et al., 2013; Rudershausen et al., 2010; Vaske-Jr et al., 2011). Published dietary data for roundscale spearfish are very limited, but it is known to predate on cephalopods, which were found in 55.6% of specimens ($n = 9$) sampled in the Mid-Atlantic Bight (Staudinger et al., 2013), as well as fishes (Hildebrand, 2022; $n = 2$).

Diet data of marlins and other highly migratory top predator species can inform Ecosystem-Based Fisheries Management (EBFM; Pikitch et al., 2004) as well as ecosystem models [e.g., Ecopath (Christensen et al., 2015)]. Regional fisheries management in the United States has recognized the importance of accounting for trophic complexity through a more holistic EBFM approach furthering the importance of diet studies (Arkema et al., 2006; Long et al., 2015). Inclusion of diet data in ecosystem models can also allow for further assessments of food web responses to different environmental or fishery management scenarios (e.g., Kitchell et al., 1999).

Although some marlin fisheries provide access to stomach samples, the limited dietary data available restrict the development of detailed ecosystem models, which can in turn inform EBFM. International regulations limit the United States to landing 250 Atlantic marlins annually, (Anon., 2019a), and a strong catch and release ethic (Pine III et al., 2008) limits the annual number of marlins retained. Additionally, Atlantic marlins caught as by-catch in US commercial fisheries cannot be landed and are discarded at sea, further limiting access to biological samples. Moreover, historical datasets for white marlin and roundscale spearfish are often conflated and earlier white marlin studies are assumed to contain an unknown proportion of roundscale spearfish, masking potential differences between these predators (Anon., 2019b).

We obtained stomach samples of Atlantic blue marlin, white marlin and roundscale spearfish from fishing tournaments targeting marlins in the Mid-Atlantic Bight region of the United States to address data gaps in the trophic ecology of these recreationally important billfish species. The aim of the present study was to provide new dietary data for marlin species in the Northwest Atlantic, as these data can inform regulatory specifications in fishery management plans for prey species as seen with the Mid-Atlantic Fishery Management Council's Mackerel, Squid, and Butterfish Fishery Management Plan.

2 | METHODS

2.1 | Stomach collection

Atlantic blue marlin, white marlin and roundscale spearfish stomachs were collected during the spring and summer of 2018–2020. Stomachs were collected from the White Marlin Open (Ocean City, Maryland), the Mid-Atlantic Tournament (Cape May, New Jersey) and the Big Rock Tournament (Morehead City, North Carolina; Figure 1). Additional stomach samples ($n = 10$) were collected opportunistically from fishery partners who participated in the recreational rod and reel marlin fishery and retained marlins outside of the tournaments. Typical fishing practices include surface troll gear along the continental shelf break and warm water eddies initiating from the Gulf Stream. Stomachs were collected after weigh-in and inspection by the weigh master, and when appropriate, permission was obtained from the landing vessel. Fish species was recorded and lower jaw fork length (LJFL) to the nearest centimetre was measured using a tape measure following the curvature of the body. Stomachs were then cut away from the intestinal mass, placed in individual plastic bags to ensure separation and put on ice. Stomachs from the White Marlin Open ($n = 3$, blue marlin; $n = 15$, roundscale spearfish; $n = 10$, white marlin) and the Mid-Atlantic ($n = 8$, blue marlin; $n = 26$, roundscale spearfish; $n = 24$, white marlin) were stored frozen at −20°C, whereas Big Rock stomachs ($n = 15$, blue marlin) remained unfrozen.

2.2 | Stomach content analysis

Each stomach was thawed completely before dissection. The stomach was then cut along the median plane to expose the contents which were then emptied over a fine mesh sieve (≤500 μm). While over the fine mesh sieve, the emptied stomach and any contents, were gently rinsed with unfiltered tap water to ensure all contents were in the sieve. Contents were laid on a work surface (e.g., cutting board) with a stomach identification tag. A photo of all contents was taken for future reference and to ensure contents were not double counted.

Prey items were identified to the lowest identifiable taxonomic classification using morphological characteristics (Campana, 2004; Clarke, 1986). Individual whole prey items were weighed to the nearest gram, whereas prey digested beyond identification were separated by class (e.g., teleost, cephalopod) and an aggregate weight (g) was

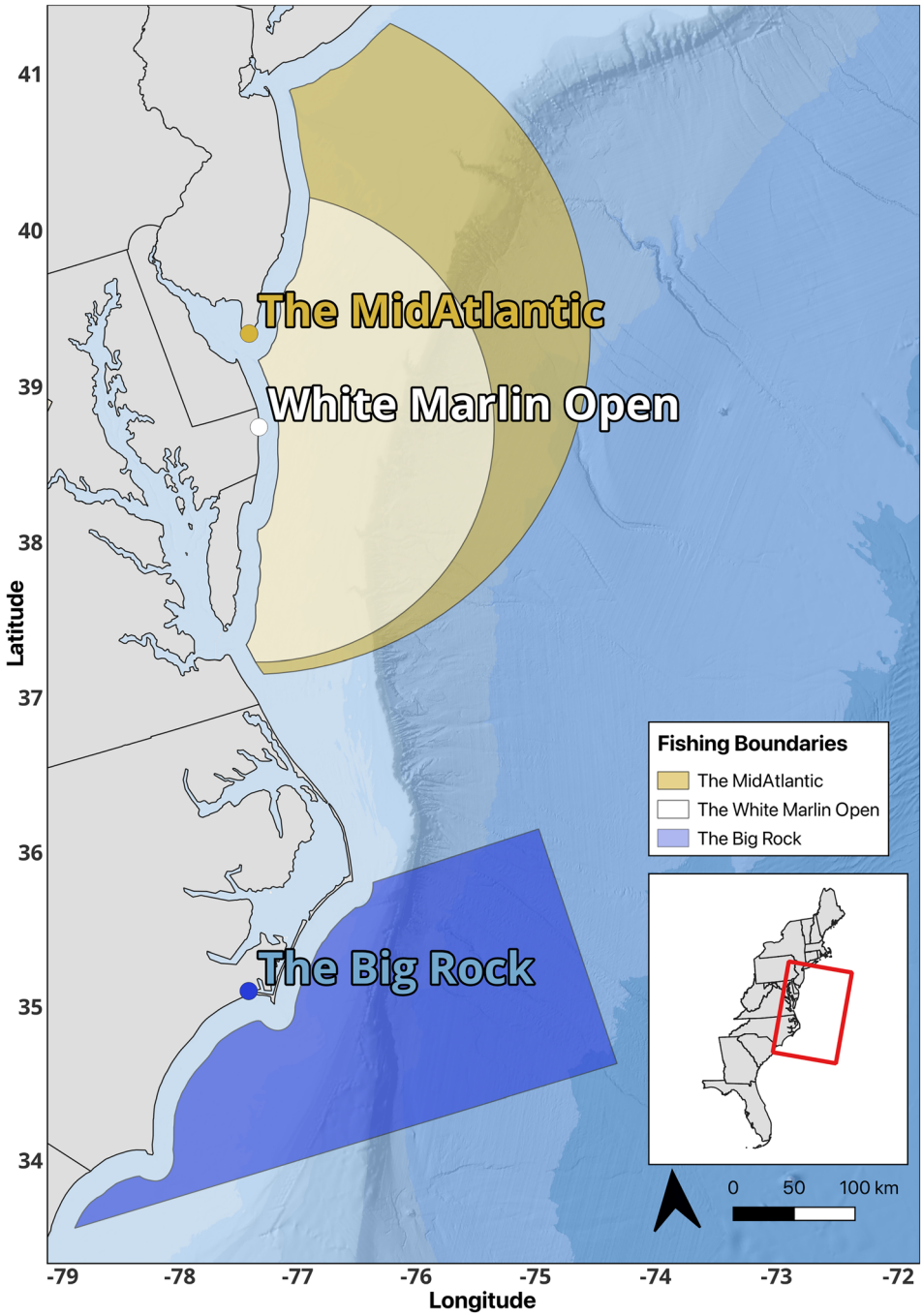


FIGURE 1 Locations of the three fishing tournaments where stomach samples were collected from 2018 to 2020. Fishing boundaries represent reasonable assumptions on where stomachs were collected based on official tournament regulated boundaries for the three tournaments. The eastern boundary for the Big Rock tournament was assumed to be 100 nautical miles from shore based on the reasonable offshore capability of fishing vessels and time limit imposed by the tournaments (Dr. Golet, personal communication, September 2025).

taken. Otoliths or beaks from prey that could not be visually identified were removed and compared against reference keys (Campana, 2004; Clarke, 1986). Cleaned dry otoliths were archived in labelled vials, whereas cephalopod beaks were stored in 95% ethanol. Stomach contents identified as fishing bait (rigged or cut baits) were noted and subjected to the above procedure, but were subsequently removed from further analyses.

Prey items that were highly digested with no identifiable hard parts were sent for genetic barcoding to allow for species-specific identification, and in some cases genetic barcoding was used to confirm identifications based on morphology. A 5 × 5 × 5 mm sample of innermost muscle tissue was taken from the prey to reduce potential cross-contamination with genetic material in the stomach and placed in a tissue-preservative filled vial (RNAlater; Life Technologies Corporation, 2011). DNA was extracted from each sample using commercially available kits following the manufacturer's protocol (QIAGEN Corporation, Maryland, USA) and then stored frozen at −80°C. Aliquots of isolated DNA were amplified using the polymerase chain reaction (PCR) and initially targeted a fragment of the COI locus using the LoboF1 and LoboR1 primers and conditions described in Lobo et al. (2013). The presence and quality of amplified DNA were confirmed by 1.5% agarose gel electrophoresis with ethidium bromide staining. Samples that demonstrated poor amplification and/or sequencing products with the COI locus were reamplified with the

'universal' 16s primers (16sar and 16sbr, Palumbi, 1996). Some DNA extractions were repeated (several times) after multiple failed amplifications that yielded no discernible product. However, in no instance did re-extraction yield positive results. Sequencing, sequence editing and barcoding approaches followed methods described in Helgoe et al. (2020).

2.3 | Dietary metrics

Percent weight (%W), mean proportion by weight (%MW), frequency of occurrence (%FO), mean proportion by number (MN%), proportion by number (%N), total number of individual prey (N) and Prey-Specific Index of Relative Importance (%PSIRI) were calculated for each family and respective higher level of classification (Brown et al., 2012; Logan et al., 2021). Partial prey items, either identified or unidentified, were not included in proportion by number calculations. Percentages are additive to their respective taxonomic classification (higher classification or family). The equation for mean proportion by weight (%MW) and number (%MN) is as follows:

$$MA_i = \frac{1}{P}\sum_{j=1}^{p}\left(\frac{A_{ij}}{\sum_{i=1}^{Q} A_{ij}}\right)$$

where MA_i is mean abundance either by weight or number for prey item i, in the total number of non-empty stomachs, P. A_{ij} is the abundance of prey item i in stomach sample j and Q is the total number of prey items. Proportion by number and weight, %N and %W, respectively, were calculated using the following formula:

$$A_i = \frac{A_{ij}}{\sum_{i=1}^{Q} A_{ij}}$$

Frequency of occurrence was calculated for each family and higher classification as follows:

$$FO_i = \frac{J_i}{P}$$

where J_i is the number of stomachs that contain prey item i. Prey Specific Index of Relative Importance (%PSIRI) was also calculated as a robust measure of relative importance between prey items (for reasoning behind %PSIRI see Brown et al., 2012). %PSIRI was calculated as:

$$\%\text{PSIRI} = \frac{\%FOi\, x\, (\%PNi + \%PWi)}{2}$$

where *%PNi* and *%PWi* are the prey specific abundance by number and weight, respectively. These indices were calculated as:

$$\%PA_i = \frac{\sum_{j=1}^{n} \%A_{ij}}{n_i}$$

where A_{ij} is the abundance in weight of prey item i in stomach j, n_i is the number of stomachs that contain prey item i and n is the total number of stomachs overall. %PSIRI gives a value of relative importance for prey values represented as a percentage.

2.4 | Data analysis

Cumulative prey curves were generated using the iNEXT package (Chao et al., 2014; Hsieh et al., 2016) in R (R Core Team, 2023) to determine if the sample sizes collected were adequate to reflect total dietary prey species richness. Prey curves were generated with both species and family level specificity, and curves were extrapolated to double the number of stomachs for all three marlin species to investigate when prey species richness may be met.

To assess differences in diet composition between roundscale spearfish and white marlin, a principal coordinate analysis (PCoA) was performed with the vegan package (Oksanen et al., 2026) in R (R Core Team, 2023) on both prey counts and weights. PCoA is a robust measure of ecological distance between groups and reprojects the original dataset as a distance matrix in multidimensional space leading to a representation of relative proximity in Euclidean space (Faith et al., 1987). Prey items were grouped to the family level, except for crustaceans which remained Crustacea due to the lack of species-level identification. Unknown teleosts and unknown cephalopods were removed from the dataset for this analysis to eliminate potential instances of identified species being double counted as a distinct unidentified category. Bray–Curtis dissimilarity matrices were calculated for count and weight-based diet compositions (Faith et al., 1987). PCoA was then performed to visualize any patterns in dissimilarity among individuals and plotted on the first two principal axes with 75% confidence ellipses for roundscale spearfish and white marlin. To test differences observed in the PCoA plot, a permutational multivariate analysis of variance (PERMANOVA) was performed with 999 permutations and the Bray–Curtis distances (Anderson, 2017). Significance was assessed to $p = 0.05$. As a PERMANOVA is sensitive to within predator species variation, a dispersion test was applied to check for homogeneity of multivariate dispersion.

3 | RESULTS

Contents were observed in 95% of sampled stomachs (i.e., 106 of 111) with 787 individual prey items identified across the three marlin species (Table 1). Total stomach contents included 18 unique families, which were organized into three higher taxonomic classifications (Tables 2–4). Genetic barcoding enabled the identification of 122 prey items, providing a higher resolution of the diet for these three marlin species. Despite this documented diversity, species-specific cumulative prey curves did not reach an asymptote at the study sample size for any marlin species (Figure 2). When prey were grouped into taxonomic families, roundscale spearfish and blue marlin curves approached asymptotic diversity while white marlin did not. Extrapolated curves estimate increases in prey diversity of one, nine and eight

TABLE 1 Summary of sampling efforts for Atlantic marlin stomachs.

Species	WMO	MA	BR	Other	Total	LJFL (cm)	Weight (kg)
Atlantic blue marlin	3	8	15	6	32	281.2 ± 22.3 (246.4–360.7)	221.6 ± 50.6 (127.6–370)
Roundscale spearfish	15	26	0	3	44	178.2 ± 19.6 (141.3–281.9)	28.8 ± 2.7 (22.7–33.6)
White marlin	10	24	0	1	35	173.6 ± 7.7 (158.8–209.6)	30 ± 3.1 (23.1–37.6)
Total	28	58	15	10	111		

Note: Samples were sourced from the White Marlin Open (WMO), the Mid-Atlantic (MA) and the Big Rock (BR) tournaments. Miscellaneous (Other) stomach samples were collected opportunistically from colleagues or fishery partners. Mean lower jaw fork lengths (LJFLs) and mean weights for each sampling period are listed with ± associated standard deviation. The range of each measurement is included in parentheses under the mean and standard deviation.

TABLE 2 Atlantic blue marlin (*Makaira nigricans*) stomach contributions by family and by higher prey classifications (bold).

Higher classification	Family	*N*	*N* (%)	MN (%)	W (%)	MW (%)	FO (%)	%PSIRI
All cephalopods		**9**	**7.4**	**6 (17.9)**	**1.0**	**4.3 (18.2)**	**20.7**	**5.1**
	Ommastrephidae	2	1.6	1.4 (5.2)	0.9	4 (16.7)	6.9	2.7
	Unidentified Cephalopods	7	5.8	4.5 (13.6)	0.1	0.3 (1.4)	17.2	2.4
All crustaceans		**1**	**0.8**	**0.7 (3.6)**	**0.0**	**0 (0)**	**3.5**	**0.3**
	Unidentified crustacean	1	0.8	0.7 (3.6)	0.0	0 (0)	3.5	0.3
All fishes		**111**	**91.7**	**93.3 (9)**	**99.0**	**95.7 (5.3)**	**96.6**	**94.5**
	Scombridae	86	71.1	75.9 (23.5)	94.6	81.5 (18.9)	86.2	78.7
	Tetraodontidae	2	1.6	0.7 (3.6)	0.2	0.4 (2.3)	3.5	0.6
	Unidentified Teleosts	23	19.0	16.7 (27.5)	4.2	13.8 (27.5)	34.5	15.3

Note: Columns are organized as number of prey (*N*), percent number (%*N*), mean percent by number [%MN(SD)], percent weight (%W), mean percent by weight [%MW(SD)], mean proportion by weight [%MW(SD)], frequency of occurrence (%FO) and Prey Specific Index of Relative Importance (%PSIRI).

species and one, ten and one taxonomic families if stomach samples were doubled for blue marlin, white marlin and roundscale spearfish, respectively (Figure 2). The contrast between the two roundscale spearfish curves is a result of six prey species belonging to Scombridae and two species belonging to Carangidae aggregating the overall diversity from 20 species to only 13 families.

Scombridae and Ommastrephidae were the dominant prey families overall, but relative dietary contributions differed among marlin species (Figure 3). Scombridae was most prevalent in blue marlin samples (86.2%FO), intermediate in roundscale spearfish (74.4%FO) and secondary in white marlin (12.1%FO; Tables 2–4). Ommastrephidae prevalence showed the opposite trend; its contribution ranged from minor in blue marlin (6.9%FO), to intermediate (46.5%FO) and high (51.5%FO) in roundscale spearfish and white marlin, respectively (Tables 2–4).

Blue marlin diet was dominated by fishes, which were found in 96.6% of stomachs and contributed on average 95.7% of each stomach's total prey weight (Table 2). Within fishes, Scombridae was the most important prey family and consisted mainly of bullet tunas (*Auxis rochei* and *Auxis* spp.; 52.1%N) and Atlantic mackerel (*Scomber scombrus; 3.3%N*) (Table S1). Cephalopods were the second most important group, but only contributed 1.0% of the total weight of prey. Ommastrephidae occurred in a relatively high percentage of stomach samples (20.7%), due to a higher prevalence of loose beaks compared to whole prey items.

Fishes were a dominant prey group for roundscale spearfish, but to a lesser extent than blue marlin (Table 3). Fish prey comprised 80.6% of prey weight and 70.8% of prey items. Scombridae was the main prey family and included six species (Table S2). Cephalopods were the next most prevalent group accounting for 19.4%W and found in 83.7% of stomachs. The majority of cephalopod prey items observed were loose beaks rather than whole prey. Unidentified cephalopods occurred in 69.8% of stomachs but contributed only 5.8%MW, similar to the trend observed with blue marlin. Ommastrephidae, most commonly *Illex* spp., was the main identifiable cephalopod family (Table S2).

Although the stomach contents of blue marlin and roundscale spearfish were similar, white marlin exhibited a higher prevalence of cephalopod prey compared to fishes (Figure 3). Cephalopods comprised 80% of the weight and 70.6% of the number of prey in white marlin stomachs. Cephalopod prey was dominated by Ommastrephidae (exclusively *Illex* spp.; Table S3), which accounted for 73.9% of prey weight, while being found in 51.5% of stomachs, the highest frequency of occurrence among positively identified prey families. Fishes

TABLE 3 Roundscale spearfish (*Tetrapturus georgii*) stomach contributions by family and by higher prey classifications (bold).

Higher classification	Family	*N*	*N* (%)	MN (%)	W (%)	MW (%)	FO (%)	%PSIRI
All cephalopods		**140**	**28.6**	**27.1 (22.8)**	**19.4**	**20 (27)**	**83.7**	**23.5**
	Histioteuthidae	2	0.4	0.4 (1.9)	0.0	0 (0)	4.7	0.2
	Ommastrephidae	87	17.8	15 (21.4)	16.1	14.2 (24.4)	46.5	14.6
	Unidentified cephalopods	51	10.4	11.7 (10)	3.3	5.8 (11)	69.8	8.7
All crustaceans		**3**	**0.6**	**1.6 (6.8)**	**0.0**	**0 (0.1)**	**4.7**	**0.8**
	Unidentified crustacean	3	0.6	1.6 (6.8)	0.0	0 (0.1)	4.7	0.8
All fishes		**346**	**70.8**	**71.3 (23.8)**	**80.6**	**80 (25.4)**	**97.7**	**75.7**
	Alepisauridae	4	0.8	0.7 (2.7)	1.7	3.4 (15.3)	7.0	2.0
	Ariommatidae	2	0.4	0.3 (2)	0.3	0.5 (3)	2.3	0.4
	Carangidae	12	2.5	2.2 (6.5)	3.3	3.6 (11.6)	13.9	2.9
	Coryphaenidae	7	1.4	0.7 (2.6)	3.0	3 (11.2)	7.0	1.9
	Hemiramphidae	5	1.0	1.1 (3.1)	1.1	2 (6.1)	11.6	1.6
	Luvaridae	2	0.4	0.2 (1.1)	0.1	0.1 (0.4)	4.7	0.2
	Monacanthidae	1	0.2	0.3 (1.9)	0.0	0.1 (0.7)	2.3	0.2
	Myctophidae	21	4.3	3.8 (11.2)	1.2	3.7 (13.7)	20.9	3.8
	Nomeidae	3	0.6	0.4 (1.7)	0.1	0.1 (0.5)	4.7	0.2
	Scombridae	146	29.9	29.1 (18.2)	51.7	40.9 (23)	74.4	35.0
	Sternoptychidae	2	0.4	0.5 (2.5)	0.2	1.1 (6.4)	4.7	0.8
	Unidentified teleosts	141	28.8	32.1 (19.7)	17.8	21.5 (21.7)	90.7	26.8

Note: Columns are organized as number of prey (*N*), percent number (%*N*), mean percent by number [%MN(SD)], percent weight (%W), mean percent by weight [%MW(SD)], mean proportion by weight [%MW(SD)], frequency of occurrence (%FO) and Prey Specific Index of Relative Importance (%PSIRI).

TABLE 4 White marlin (*Kajikia albida*) stomach contributions by family and by higher prey classifications.

Higher classification	Family	*N*	*N* (%)	MN (%)	W (%)	MW (%)	FO (%)	%PSIRI
All cephalopods		**125**	**70.6**	**61.5 (30.3)**	**80.0**	**60.9 (34.3)**	**78.8**	**61.2**
	Argonautidae	2	1.1	1.5 (8.4)	0.1	1.7 (9.5)	3.0	1.6
	Ommastrephidae	78	44.1	32.3 (30.7)	73.9	39 (34.9)	51.5	35.7
	Unidentified Cephalopods	45	25.4	27.7 (27.1)	6.0	20.2 (30.5)	72.7	24.0
All crustaceans		**4**	**2.3**	**2 (11.2)**	**0.0**	**0.3 (1.4)**	**3.0**	**1.1**
	Unidentified crustacean	4	2.3	2 (11.2)	0.0	0.3 (1.4)	3.0	1.1
All fishes		**48**	**27.1**	**36.5 (33.2)**	**20.0**	**38.8 (36.5)**	**57.6**	**37.6**
	Belonidae	1	0.6	0.6 (3.4)	0.2	0.8 (4.6)	3.0	0.7
	Carangidae	2	1.1	1.5 (8.4)	0.6	2.9 (16.1)	3.0	2.2
	Echeneidae	1	0.6	1.5 (8.4)	0.9	2.6 (14.4)	3.0	2.0
	Gempylidae	3	1.7	0.7 (3.6)	1.6	0.3 (1.8)	3.0	0.5
	Hemiramphidae	3	1.7	2.2 (8.7)	1.8	3.9 (14.4)	9.1	3.1
	Scombridae	13	7.3	7.4 (20.6)	11.0	9.8 (25)	12.1	8.6
	Unidentified teleosts	25	14.1	22.6 (30.2)	3.8	18.6 (32.3)	42.4	20.6

Note: Columns are organized as number of prey (*N*), percent number (%*N*), mean percent by number [%MN(SD)], percent weight (%W), mean percent by weight [%MW(SD)], mean proportion by weight [%MW(SD)], frequency of occurrence (%FO) and Prey Specific Index of Relative Importance (%PSIRI).

accounted for 20% of prey weight and were found in 57.6% of stomachs. Scombridae was the main fish prey family, which included the only Atlantic chub mackerel (*Scomber colias*) in our marlin diet dataset (1.1%N) (Table S3).

A PERMANOVA showed that white marlin and roundscale spearfish diet samples were significantly different for both prey family weight and count contributions ($p = 0.001$). A dispersion test signified that variation within the roundscale spearfish and white marlin diet

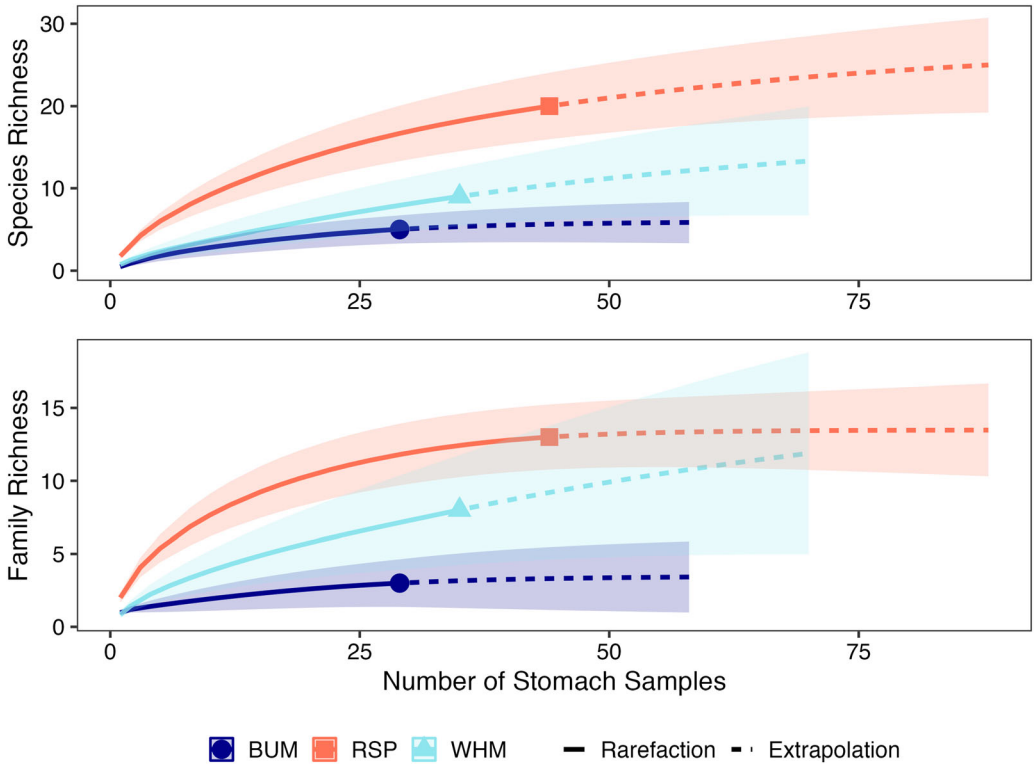


FIGURE 2 Cumulative prey richness curves for Atlantic blue marlin (*Makaira nigricans*), white marlin (*Kajikia albida*) and roundscale spearfish (*Tetrapturus georgii*). Mean prey diversity is identified to species (top) and family (bottom) specificity with shaded 95% confidence intervals for roundscale spearfish (RSP), white marlin (WHM) and blue marlin (BUM). Observed sample size (solid line) was extrapolated to double the size (dashed line) to estimate the asymptotic prey diversity for each predator species.

was not driving the significant difference between predator species with a *p*-value of 0.5 and 0.3 for prey number and weight, respectively. PCo1 and PCo2 collectively explained 53.4% and 40.5% of the variance in the data for counts and weights, respectively (Figure 4).

4 | DISCUSSION

The foraging preferences inferred from this study were consistent with existing literature and represent dietary trends for specialized apex predators narrowly adapted to feed on pelagic schooling squids and fishes (Logan et al., 2013; Rudershausen et al., 2010; Vaske-Jr et al., 2011). Scombridae and Ommastrephidae, the two main prey families for the three sampled marlin species, have significant ecological and economic value, serving as both abundant intermediate and higher trophic level food web components as well as focal species in fisheries globally (FAO, 2022; Rodhouse et al., 2014; Seto et al., 2023).

Blue marlin diet was dominated by scombrid prey, almost exclusively *Auxis* spp., a trend seen in ocean systems globally (Abitia-Cardenas et al., 1999; Baker, 1966; Brock, 1984; Erdman, 1962; Krumholz & DeSylva, 1958; Rudershausen et al., 2010; Shimose et al., 2006). As *Auxis* spp. are not assessed stocks, little is known about their abundance in the Mid-Atlantic Bight (J. Beaty and J. Hadley, personal communication, October 2024), but they are an important prey source for blue marlin and other large pelagic fish predators (Rudershausen et al., 2010). Citing this importance to highly migratory species, the South Atlantic Fishery Management Council (SAFMC) included *Auxis* spp. as an ecosystem component to the Dolphin and Wahoo Fishery Management Plan (SAFMC, 2020). Unlike *Auxis* spp., Atlantic mackerel, the second most prevalent prey item for blue marlin, is an assessed stock with assessments from this period (2018 and 2022), indicating that spawning stock biomass was at historically low levels (Northeast Fisheries Science Center, 2018; Van Beveren et al., 2023). Atlantic mackerel undergo migrations to Georges Bank and the Gulf of Maine during the summer season (Radlinski et al., 2013), so the lower contribution of this prey species relative to *Auxis* spp. may be due to limited spatiotemporal overlap on Mid-Atlantic Bight foraging grounds.

To the best of our knowledge, this study represents the largest stomach content analysis (SCA) reported for roundscale spearfish to date and has expanded our prior knowledge of this species diet. A small sample ($n = 9$) of roundscale spearfish stomachs from Mid-Atlantic Bight fishing tournaments was previously analysed with a specific focus only on cephalopod diet, which accounted for 12.8% mass and 55.6% frequency of occurrence (Staudinger et al., 2013). Two roundscale spearfish stomachs analysed from longline fisheries in the South Atlantic Bight mainly contained teleost prey (95.8%W), primarily of the family Tetraodontidae (68.9%W) (Hildebrand, 2022). In our study, roundscale spearfish diet was the most diverse of the three

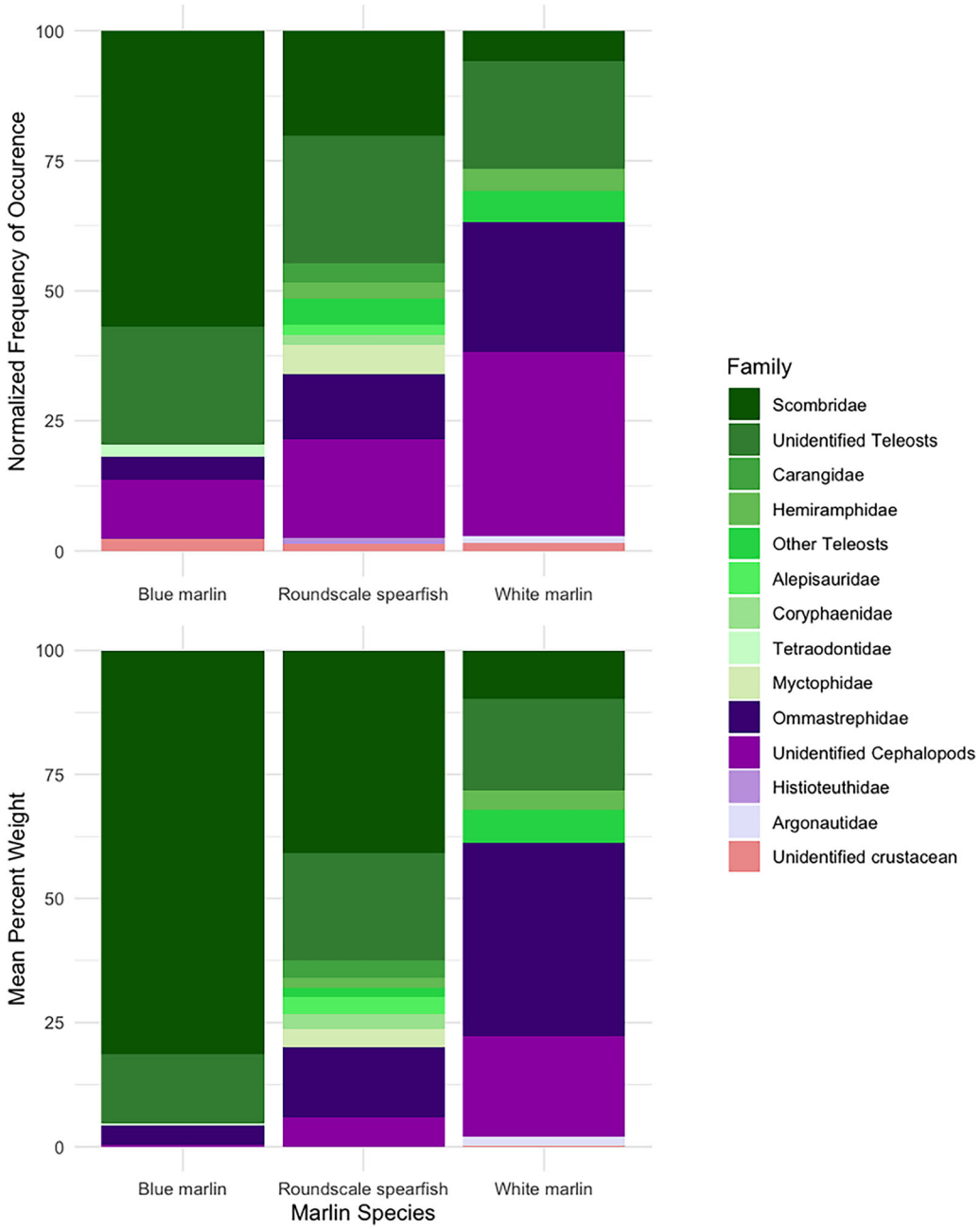


FIGURE 3 Dietary contributions by taxonomic family for Atlantic blue marlin (*Makaira nigricans*), white marlin (*Kajikia albida*) and roundscale spearfish (*Tetrapturus georgii*). Frequency of occurrence was proportionally normalized on a 0–100 scale to be comparable between species. Prey items are colour-coded by higher classification, with fish prey shades of green, cephalopod prey shades of purple and crustacean prey shades of red. To aid readability, any fish prey with a %MW <3 and %FO <5 were lumped into 'Other Teleosts'. For white marlin, 'Other Teleosts' included Belonidae, Carangidae, Echeneidae and Gempylidae. For roundscale spearfish, 'Other Teleosts' included Ariommatidae, Monacanthidae, Nomeidae, Sternoptychidae and Luvaridae.

Atlantic marlins but, like the other two marlin species, ommastrephid and scombrid prey were the dominant prey families, setting foundational inferences on the diet composition of roundscale spearfish. Compared to fish prey, cephalopod prey contributed a relatively small amount of prey weight for roundscale spearfish despite its high occurrence, which could be due to differences in digestion rates as a result of prey characteristics or timing of ingestion (Hilton et al., 1998; Olson & Boggs, 1986).

White marlin diet differed from the other two Atlantic marlins in this study, but was consistent with prior literature (Hildebrand, 2022; Pinheiro et al., 2010). Differences in contributions of Ommastrephidae between Atlantic marlins may be a result of precise locality of capture (Brock, 1984), timing of capture (Hilton et al., 1998), vertical behaviour (da Silva et al., 2019) or fishing tactics (Wilson et al., 2015). Ommastrephidae, notably *Illex* spp., exhibit vertical diel migrations to feed near the surface at night (Hendrickson & Holmes, 2004) where

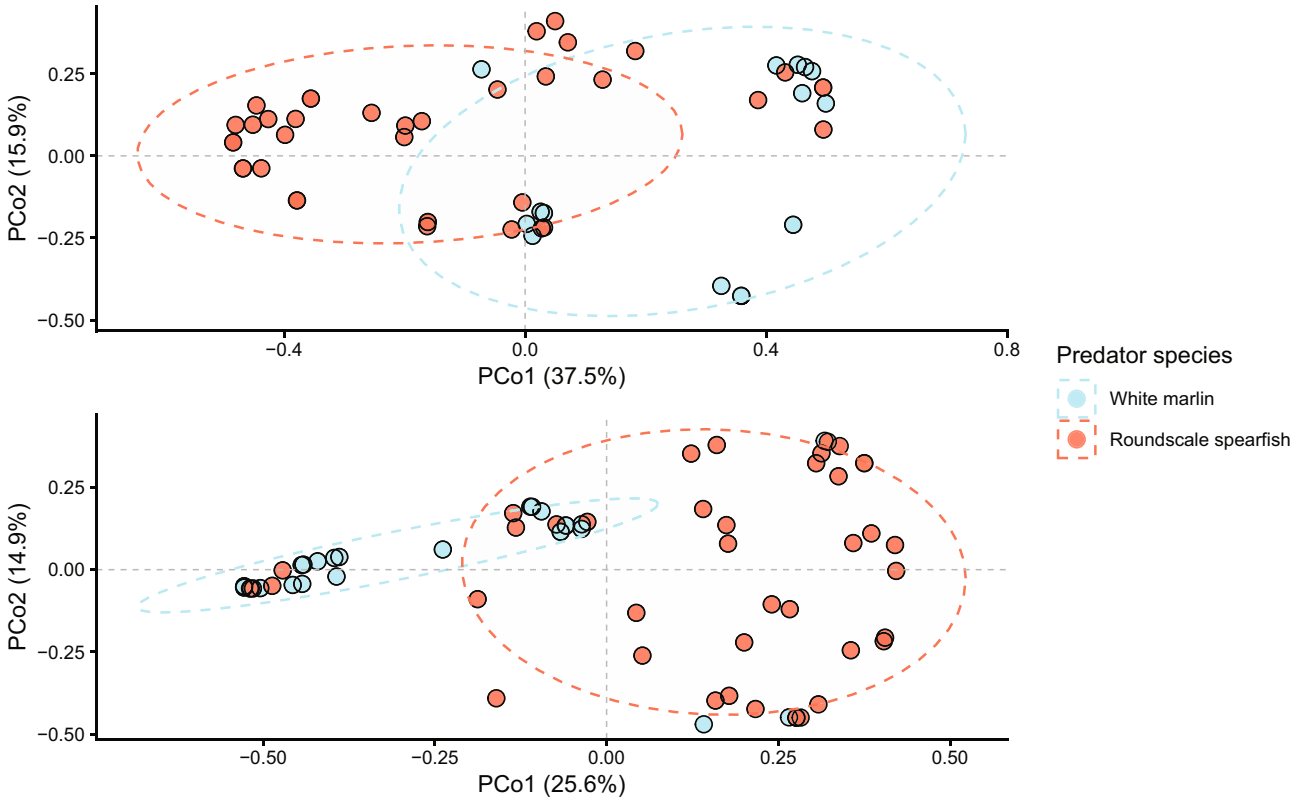


FIGURE 4 Principal coordinate analysis (PCoA) plots for white marlin (*Kajikia albida*) and roundscale spearfish (*Tetrapturus georgii*) diet by prey family count (top) and weight (bottom) contributions. Each point represents an individual stomach, and ellipses represent the 75% confidence interval for the respective predator species. Percentages in parentheses along each axis represent the amount of variation explained by that principal coordinate.

white marlin spend the majority of their time (Hoolihan et al., 2015). These diel migrations create a temporal mismatch between tournament fishing hours and when white marlin may ingest the majority of Ommastrephidae prey, allowing for substantial digestion before capture (Amorim et al., 2009; De Sylva & Davis, 1963). Such offsets can help explain the large quantity of cephalopod beaks found in the stomachs of white marlin, and to a lesser extent roundscale spearfish.

Genetic differences between roundscale spearfish and white marlin using biological tissues were first observed in 2006, but unknown proportions of roundscale spearfish are present in catch data and biological tissue samples previously attributed to white marlin (Shivji et al., 2006). Due to this integration in historical datasets, roundscale spearfish is included in the white marlin stock assessment (Anon., 2019b). The white marlin and roundscale spearfish samples presented here suggest differences in foraging preferences. Differences in diet may be the result of distinct behaviour patterns or localized abundance of potential prey (Dill, 1983). The current stock delineation within the white marlin assessment may not be appropriate if the dynamics of a behaviourally distinct species are intertwined (Anon., 2019b). Accurate identification of these two species in fisheries sampling moving forward is essential as evolving management practices increasingly require tailored approaches to effectively assess and monitor these distinct populations, and to inform managers.

As top predators, marlins have trophic interactions with smaller pelagic species (fishes and squid) and dietary overlap with other larger predatory epipelagic fishes, including tunas (Rudershausen et al., 2010). Hence, they can be important in food web structure (Bornatowski et al., 2018; Kitchell et al., 1999; Kitchell et al., 2006). Such trophic interactions are an important consideration within EBFM, as shown by the Mid-Atlantic Fishery Management Council incorporating marlin diet data alongside similar studies on tunas and other predators to inform the implementation of a commercial fishery for Atlantic chub mackerel. Atlantic chub mackerel was added to the Mackerel, Squid, and Butterfish Fishery Management Plan in 2020 (NOAA, 2020), with recent landings remaining low and current management regulations deemed appropriate (Mid-Atlantic Fishery Management Council, 2023). Although white marlin was found to predate on Atlantic chub mackerel, it was only a small proportion of the diet. Nevertheless, a range of other scombrids (as well as squid) were found to be important in the diets of all three marlins. As such, Atlantic chub mackerel could be included in future ecosystem models for the epipelagic fish assemblage of the eastern coast of the United States.

5 | POTENTIAL CAVEATS

Recreational fishing tournaments provide the only aggregated sampling efforts for Atlantic marlins making them the primary source of biological samples used to answer questions relating to life history,

foraging ecology and genetic characterization. This opportunistic sampling in a limited fishery creates a challenge when seeking to collect a sufficient number of samples to examine dietary trends over space and time. As visualized by Figure 2, species-specific dominance within stomachs is likely influenced by the local abundance of prey at the time and place of sampling (Brock, 1984), particularly for environmentally responsive and seasonally variable species such as squids (Luckhurst, 2017). This may make it difficult to use diet data restricted by sample size as a proxy for relative abundance of prey items. Prey abundance questions become important when considering common Atlantic marlin prey items in the Scombridae and Ommastrephidae families, given they are among the most widely distributed and exploited species assemblages (FAO, 2022).

Despite the inherent challenges in drawing definitive conclusions about the general composition of Atlantic marlin diets, annual stomach sampling at recreational fishing tournaments remains an important tool for understanding foraging ecology and facilitating its inclusion as an ecosystem consideration within EBFM (Han et al., 2020; Hyslop, 1980). Consistent sampling in time and space can provide valuable insights into potential shifts in forage abundance over that same scale, acknowledging that these individuals may only represent the segment of the population exploited by the fishery that is sampled (Baker et al., 2024).

6 | NEXT STEPS

To fully characterize the diets of these three species, stomach collection efforts should continue and expand to help encompass a broader spatial and temporal range. The need for a larger sample is evident both in the literature and in Figure 2 of this study. As a complement to SCA, bulk and compound specific stable isotope analyses could be performed on non-lethal samples (e.g., muscle biopsy, fin clip) and researchers may partner with fishers to aggregate samples. Stable isotope analysis has already shown promise in studying marlins globally and can be useful for determining trophic position and foraging areas (Chang et al., 2019; Guillemin et al., 2022; Logan & Lutcavage, 2013; Young et al., 2018).

Morphologically similar species have the capacity to exhibit distinct behavioural patterns (Robinson et al., 1993), and further trophic analyses are recommended to better understand dietary overlap of roundscale spearfish and white marlin. Beyond trophic studies, we recommend further investigation into developmental, genetic and behavioural characterization of white marlin and roundscale spearfish to ensure that effective management measures are in place.

AUTHOR CONTRIBUTIONS

J.D.: Investigation, formal analysis, writing; J.L.: Conceptualization, formal analysis, writing; R.A.: Methodology, investigation; Z.W.: Methodology, investigation; I.S.: Methodology, investigation; B.M.: Methodology, investigation; L.K.: Conceptualization; J.Q.: Methodology, investigation; W.G.: Conceptualization, methodology, writing. All authors read and approved the final manuscript.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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