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Comparative feeding strategies of yellowfin tuna around St Helena and adjacent seamounts of the South Atlantic Ocean

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Abstract

Yellowfin tuna are the mainstay of the traditional tuna fisheries in St Helena waters, but there is limited knowledge of their ecology and feeding behaviour in the area. In this study yellowfin tuna stomach contents were used to assess spatio-temporal changes in feeding strategy and consider the role of tuna in the local ecosystem. Comparisons of the feeding spectra of yellowfin tuna between inshore regions of St Helena and oceanic seamounts demonstrated that in both areas the species was largely piscivorous. In inshore waters yellowfin consumed more neritic fauna, including significant numbers of crab megalopa, whereas around seamounts the diet included a greater diversity of epi- and mesopelagic fish and squids. The most important fish prey species in inshore waters was the St Helena butterflyfish *Chaetodon sanctahelenae*, and around seamounts was the pufferfish *Lagocephalus lagocephalus*. Results indicate that the diet spectrum of yellowfin tuna in St Helena waters is relatively similar to those of conspecifics living in waters with relatively low productivity, with strategies indicative of food-poor ecosystems. The availability of coastal fauna may make areas around islands and seamounts more attractive for feeding aggregations of yellowfin tuna, compared to the open ocean. The relatively unselective feeding of yellowfin tuna means that stomachs can provide valuable data on the species diversity, particularly in remote areas with limited opportunities for dedicated research expeditions.

KEYWORDS
diet, seamounts, St Helena, *Thunnus albacares*, tuna

1 | INTRODUCTION

With annual catches of over 5 million tonnes (FAO, 2019a), tuna are one of the most important marine resources on the planet and are estimated to contribute at least $ 42 billion to the global economy (Macfadyen, 2016). Despite their importance, there are still significant gaps in our understanding of the ecology of this key group.

Yellowfin tuna (*Thunnus albacares*) is one of the more widespread and abundant of the tuna, being found in the tropical and subtropical parts of all the oceans (Carpenter & De Angelis, 2016b; Collette & Nauen, 1983). Yellowfin landings averaged 1.4 million tonnes per annum between 2013 and 2017, representing the second highest landings of any tuna species and accounting for about a quarter of the total catch of all tuna combined (FAO, 2019a, b). Their distribution in the upper 200 – 300 m, mostly above 100 m (Hoolihan et al., 2014; Josse et al., 1998; Weng et al., 2009), also allows them to exploit the biomass of juvenile fish and crustaceans in coastal areas, including foraging on fish dispersed from coastal reefs (Bertrand et al., 2002). They are known to forage at the surface and in the sound scattering layer during both day and night, opportunistically and unselectively (Josse et al., 1998; Moteki et al., 2001; Poitier et al., 2007; Silva et al., 2019; Weng et al., 2009), which allows them to profit from diel vertical migrations of both epi- and mesopelagic fauna. Therefore, understanding the diet of yellowfin tuna is impossible without covering all seasons and different grounds within the same area of interest. Furthermore, their non-selective feeding behaviour might provide a means of sampling epi-pelagic and mesopelagic communities in remote regions where possibilities of research sampling is limited. Previous studies of tuna have also used diet data to assess seasonal and diurnal changes in feeding behaviour; including in bluefin (Battaglia et al., 2013; Olafsdottir et al., 2016) and albacore (Williams et al., 2015) tuna.

St Helena is a small, isolated island in the middle of the South Atlantic Ocean, situated approximately 1290 km from the nearest island (Ascension) and 1870 km from the nearest mainland, Angola. It is surrounded by a shallow shelf which rapidly descends to abyssal depths, but the 200 nautical mile exclusive economic zone also includes two large seamounts that extend to within 100 m of the surface. Whilst St Helena waters are not an important area for industrial scale tuna fisheries, the island has a long history of artisanal fishing which provides an important source of protein to the island's population (Collins, 2017; Edwards, 1990). The fishery uses traditional pole and line fishing methods to target tuna and wahoo, with yellowfin tuna as the mainstay of the inshore fishery. Recent tagging work has indicated that immature yellowfin tuna have a long-term residency in St Helena waters (Collins, 2017; Wright et al., 2019) as has been shown for Pacific Ocean populations and around Ascension Island (Edwards & Sulak, 2006; Richardson et al., 2018).

The aim of this paper is to shed some light on tuna diet in the previously unexplored waters around St Helena, establish its position in the trophic web, and it's utilisation of coastal versus oceanic prey. This study is also an opportunity to enhance our knowledge on the local biodiversity of epi- and upper mesopelagic waters.

2 | MATERIAL AND METHODS

Tuna stomachs were collected between November 2016 and April 2019 in inshore waters of St Helena (usually within 5 miles of the coast) and the nearby seamounts of Cardno and Bonaparte (Figure 1) as part of the UK Government's Blue Belt Programme. The Cardno Seamount (12°54.00' S, 6°03.00' W) is approximately 180 nautical miles (nm) to the north of St Helena and rises to 77 m below the sea surface. Bonaparte Seamount (15°38.40' S, 6°58.20' W) is around 80 nm to the west of St Helena with the seamount plateau being 105 m below the sea surface.

Tuna were caught by vessels from the commercial pole and line fishery of St Helena, where fishermen normally "chum" the water around the boat to provoke feeding frenzies using both cut and live bait (locally caught *Decapterus* spp. or mackerel, *Scomber colias*). Therefore, all representatives of these genera, found in tuna stomachs that did not have any sign of digestion, were considered to be bait and were excluded from calculations. Stomachs containing only bait were considered to be empty. Fish were measured as the straight fork length (FL) to the nearest cm below.

A total of 215 stomachs of yellowfin tuna (57-185 cm, mean 100 cm FL) (Figure 2) were frozen for investigation in the lab, of which 197 were full, or partially full and contained natural food (other than bait).

All items were identified to the lowest possible taxonomic level, counted, weighed to within 0.5 g, and measured to within 1 mm when possible. To describe the prey size, the total length of prey was used rather than standard measurements (such carapace length in crustaceans and mantle length in cephalopods). Knowledge of the relative prey size might help understand the ecological factors defining ontogenetic changes in feeding spectra other than food availability.

Some single amphipods and crab megalopa that could not be accurately weighed (due to limitations of the scales available on St Helena), were arbitrarily given the wet weight of 0.5 g each, as derived from larger samples of the same groups of species. Unweighed squid beaks and fish otoliths were arbitrarily given the wet weight of 0.1 g, as derived from random samples of preserved materials. Thus, the prey individual wet weight ranged from 0.1 to 517 g (mean = 49 g).

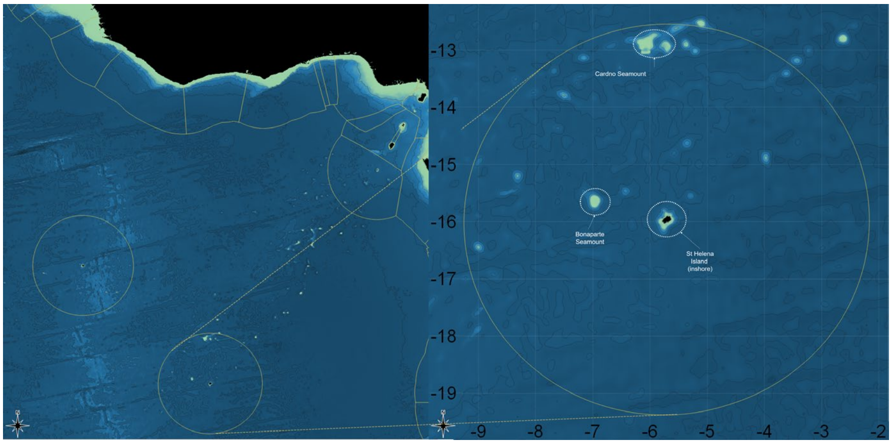


FIGURE 1 Map of the sampled area

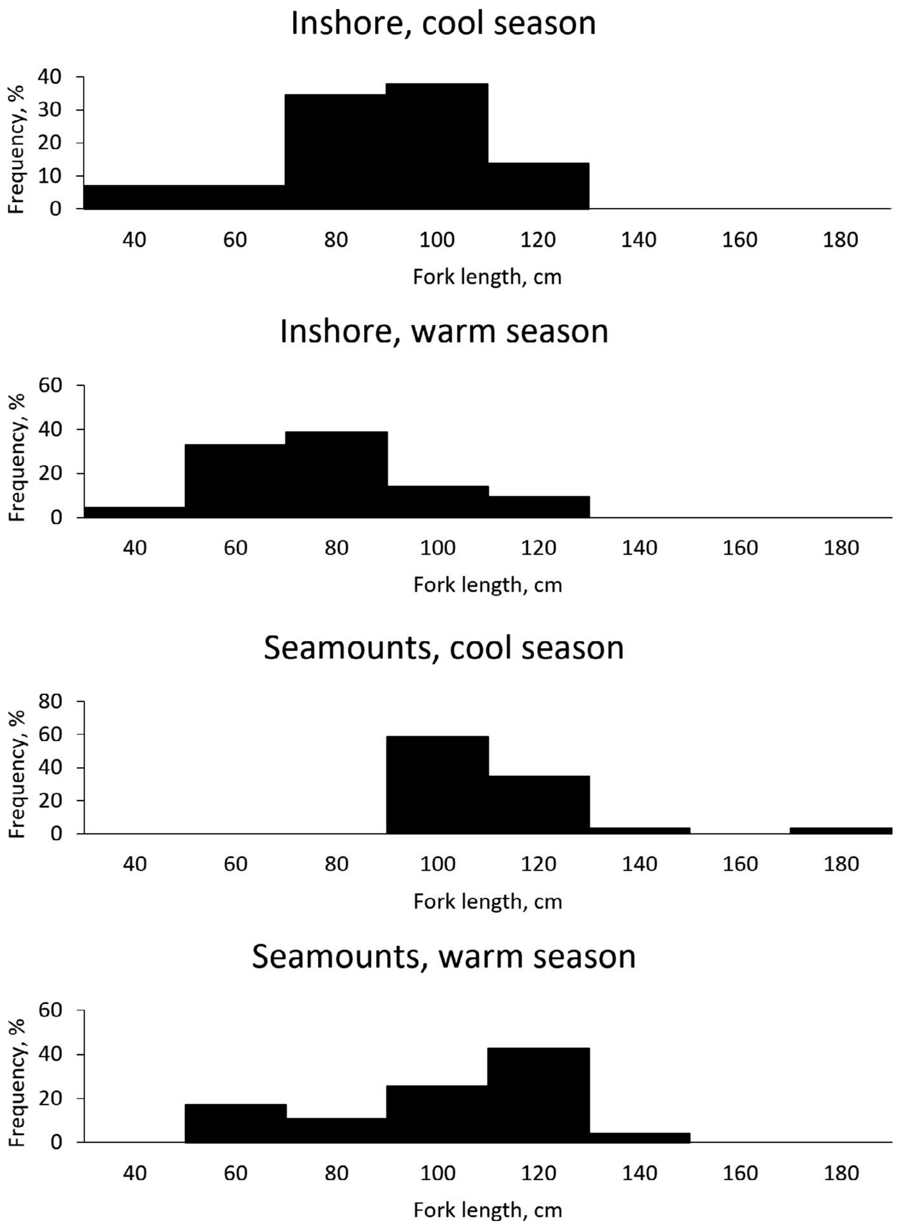


FIGURE 2 Length-frequencies distribution of the sampled yellowfin tuna

The calendar year was split into two seasons: warm (December - May) and cool (June – November) as the highest water temperatures around St Helena are recorded from January to March (Feistel et al., 2003).

All prey was segregated into "coastal" and "oceanic" species using ecological features (Carpenter & De Angelis, 2014). Coastal species encompass fish and invertebrates normally occurring in close proximity to the shore, and ecologically related to the bottom. Due to the steepness of the island slopes they may descend to 200-400 m and many of them also occur on shallow tops of seamounts. Oceanic species include fish and invertebrates of the open ocean not associated with the seafloor, being either "epipelagic" (e.g. flying fish, paper nautilus, hyperiid amphipods) or "deep-sea" - mesopelagic to nycto-epipelagic (ommastrephid and enoploteuthid squids, shrimps, myctophids). Where the species ecology did not fit exactly into one of these categories, or the species was not identified precisely, the third category – "undefined" was used.

For each season and area, the prey importance was estimated as percentage in numbers (%N), percentage in weight (%W), frequency of occurrence (%FO), and the prey-specific index of relative importance, PSIRI (Brown et al., 2012) was calculated as:

$$\text{PSIRI} = \left(\%\text{PN}_i + \%\text{PW}_i\right) * \%\text{FO}_i/2, \text{where}$$

$$\%\text{PN}_i = \%\text{N}_i/\%\text{FO}_i \text{and} \%\text{PW}_i = \%\text{W}_i/\%\text{FO}_i$$

Confidence intervals as quantiles for bootstrapped estimates of %N, %O %W and PSIRI were calculated using 10,000 iterations of data with R-package Boot (Bootstrap functions) ver. 1.3-23 in R v. 3.3.3 (R Core Team, 2016).

Efficiency of the sampling was tested using the prey cumulative curve. It was based on the assumption that an asymptote is achieved when the slope of the line generated from the mean values of the last four endpoints is not statistically different from zero (Bizarro et al., 2007). These endpoints were estimated as well as the total possible number of tuna prey predicted using R package *vegan* "Ordination methods, diversity analysis and other functions for community and vegetation ecologists" (https://cran.r-project.org/web/packages/vegan/index.html).

Experimental animals were not used in the study and stomachs were sampled from dead fish obtained from commercial fishermen before marketing. Therefore, animal welfare laws, guidelines and policies are not applicable to this project. No fish were collected as a part of faunal surveys or killed specifically for this particular research. All work conforms to UK legislation under the Animals (Scientific Procedures) Act 1986 Amendment Regulations (SI 2012/3039).

3 | RESULTS

A total of 125 stomachs collected from inshore waters contained 1,553 natural prey items, 55 stomachs from Cardno Seamount contained 990 natural prey items, and 17 stomachs from Bonaparte Seamount contained 93 natural prey items.

3.1 | Prey composition

The prey species cumulative curve (Figure 3) in yellowfin tuna was approaching an asymptote. The predicted number of detected taxa by the time the last four stomachs were analysed was estimated as 92.08 ± 1.15, 92.31 ± 0.99, 92.54 ± 0.80 and 92.77 ± 0.56 so were not statistically different, though the slope of resulting line was different from zero ($P < 0.01$). The total number of taxa on which tuna potentially might be preying was estimated as 138.77 ± 8.56 (Jackknife estimator) or 112.43 ± 4.82 (Bootstrapping).

Yellowfin tuna forage on a variety of organisms, with the relative size of the prey ranging from ~ 1% to> 30% of the predator length (Figure 4). Crustaceans were 1-3% of the predator FL, cephalopods were 2-20% of the predator FL and fish were 1-37% of the predator FL. The relative size of prey decreased with increase in tuna FL ($r=-0.493$, $p < 0.0001$ in fish; $r=-0.455$, $p = 0.006$ in cephalopods). Absolute size of the prey did not correlate with the predator length ($t = -0.50095$, $P = 0.6172$).

Smaller tuna consumed a higher proportion of crustaceans by numbers (Figure 5). In respect of percentage by weight, the crustaceans' role varied between 0.8 and 4.8% in the different size groups. The contribution of cephalopods did not exhibit any obvious trend. The role of fish increased with tuna size in terms of numbers and they were the most important items in terms of weight in all size groups.

3.2 | Yellowfin tuna caught inshore

In the coastal waters of St Helena fish was the most important prey, particularly in the warm season (Table 1, Figure 6). It represented 80-95% by weight occurring in 85-100% of stomachs, though small deep-sea shrimps (Acanthephyridae, Oplophoridae, Benthesicymidae) were important in the cool season.

The most common (in terms of numbers and occurrence) fish prey items were coastal species such as St Helena butterfly fish, *Chaetodon sanctahelenae* and scad, *Decapterus* spp. which represented the bulk of the diet in the warm season. The pufferfish, *L. lagocephalus* and chub mackerel, *Scomber colias* were also important prey items. In terms of crustaceans, the tuna consumed decapod megalopa in the warm season, particularly those of crabs, as well as different adult oceanic shrimps: Acanthephyridae, Oplophoridae and Benthesicymidae. The nycto-epipelagic ommastrephid *Hyaloteuthis pelagica* and epipelagic octopus *Argonauta* spp. represented the bulk of the cephalopods in the tuna diet and were also more important in the warm season. Therefore, the prey was represented by mixture of both coastal and oceanic species.

3.3 | Yellowfin tuna caught on seamounts

The diet of tuna on seamounts consisted primarily of fish (~90% by weight, occurring in 85-95% of stomachs) with invertebrates making up a small portion of the diet by weight (Table 2, Figure 6).

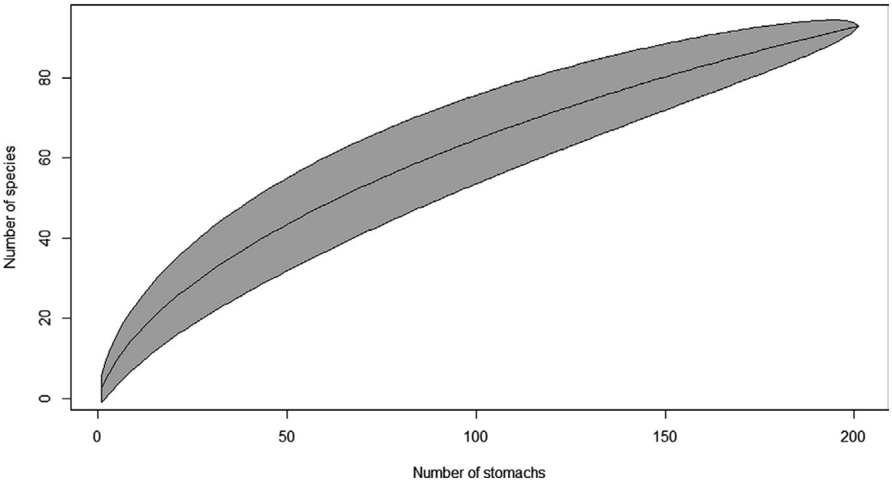


FIGURE 3 Accumulation curve of tuna prey

FIGURE 4 Relative size of tuna prey

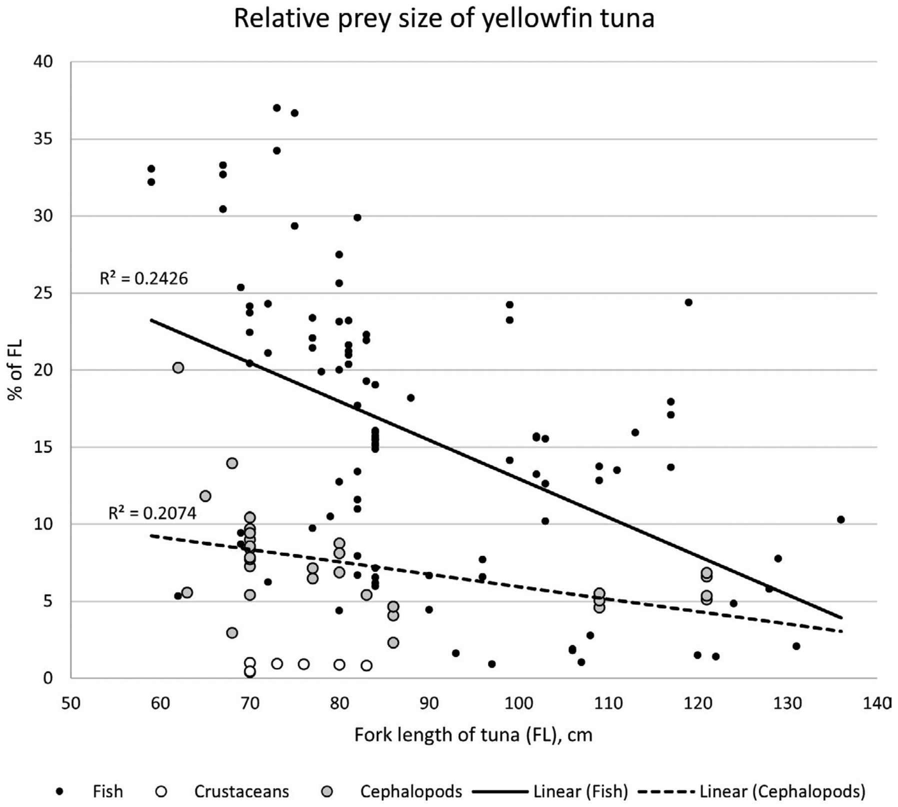
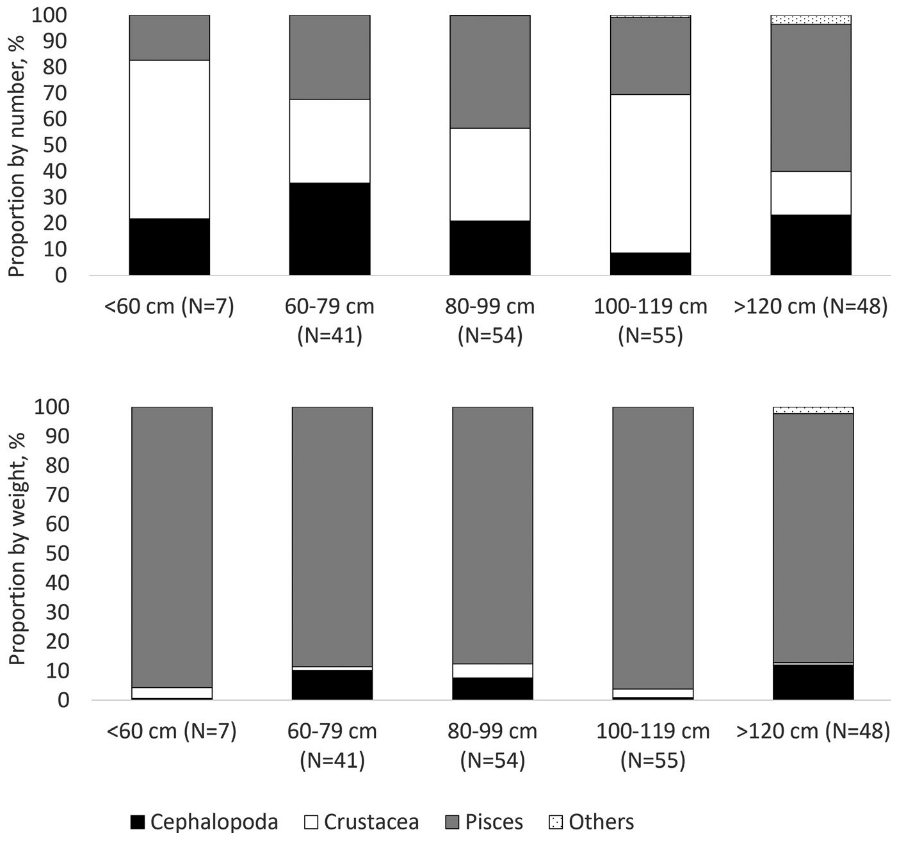


FIGURE 5 Prey species composition in tuna of the different size



The most important fish prey item was the oceanic epipelagic pufferfish, *L. lagocephalus*, particularly in the cool season. During this period the puffer was a staple food, whereas some other oceanic epipelagic fish like flying fish and seahorses were consumed occasionally. In the warm season tuna feeding was less specialised, with tuna preying on a variety of different fish, mostly on pufferfish (both oceanic *L. lagocephalus* and the more neritic species, *Sphoeroides pachygaster*), scad, chub mackerel and flying fishes.

TABLE 1 Stomach contents of yellowfin tuna in inshore waters at St Helena in warm ($n = 95$) and cool ($n = 22$) season. Confidence intervals in brackets. Range types: O-oceanic, C- coastal, U-undefined

	Prey	Range type	cool season				warm season			
			%N	%W	%O	%PSIRI	%N	%W	%O	%PSIRI
Mollusca										
Cephalopoda										
Octopoda										
Argonautidae	*Argonauta* sp.	O	1.44	0.08	9.09	0.76	3.82	0.55	21.05	2.185
Ctenoglossa		O					0.12	0.01	1.05	0.065
Tremoctopodidae	*Tremoctopus violaceus*	O	0.13	0.04	4.55	0.085	1.48	0.01	1.05	0.745
Octopoda unident.		U					1.11	0.01	2.11	0.56
Teuthida: Oegopsida										
Cranchiidae	*Helicocranchia pfefferi*	O	0.13	0.04	4.55	0.085				
	Leachia atlantica	O	1.83	0.54	40.91	1.185				
	Liocranchia reinhardti	O	0.13	0.04	4.55	0.085				
	Cranchiidae unident	O	0.13	0.04	4.55	0.085				
Ommastrephidae	*Hyaloteuthis pelagica*	O	0.13	0.04	4.55	0.085	2.96	3.41	23.16	3.185
	Sthenoteuthis pteropus	O					0.74	0.72	6.32	0.73
	Ommastrephidae unident.	O					0.99	0.50	5.26	0.745
Onychoteuthidae	*Onychoteuthis prolata*	O					0.12	0.01	1.05	0.065
Thysanoteuthidae	*Thysanoteuthis rhombus*	O					0.25	0.27	2.11	0.26
Oegopsida unident.		O	4.31	<0.01	4.55	2.16	4.68	0.20	11.58	2.44
Cephalopoda unident.		O	2.75	0.04	9.09	1.395	1.97	0.11	7.37	1.04
Total Cephalopoda			**10.98 (2.12-22.19)**	**0.87 (0.08-2.25)**	**36.36 (14.81- 48.15)**	**5.925**	**18.23 (2.48-22.19)**	**5.80 (1.67-10.63)**	**48.42 (43.88- 64.29**	**12.015**
Crustacea										
Mysida										
Mysidae	*Mysidopsis* sp.	O	<0.01	0.04	4.55	0.02				
	Mysidae unident.	U					0.12	0.01	1.05	0.065
Amphipoda										
Hyperiidae	*Anchylomera blossevillei*	O					0.37	0.01	2.11	0.19
	Eupronoe minuta	O	3.14	<0.01	4.55	1.575	0.12	0.00	1.05	0.06
	Parapronoe campbelli	O					0.74	0.02	3.16	0.38
	Parapronoe crustulum	O					9.36	0.19	2.11	4.775
	Parapronoe sp.	O					0.25	0.01	1.05	0.13

(Continues)

TABLE 1 (Continued)

			cool season				warm season			
	Prey	Range type	%N	%W	%O	%PSIRI	%N	%W	%O	%PSIRI
	Phrosina semilunata	O	0.26	<0.01	4.55	0.135				
	Platyscelus ovoides	O					0.37	0.01	1.05	0.19
	Hyperiidae unident.	O					1.11	0.01	1.05	0.56
Amphipoda unident.		U	0.13	<0.01	4.55	0.07	0.37	0.02	2.11	0.195
Decapoda										
Grapsidae	Grapsidae megalopa	C					3.08	0.06	7.37	1.57
Oplophoridae	Oplophoridae unident.	O	<0.01	0.04	4.55	0.02				
Palinuridae	*Palinurus echinatus* puerulus	C					0.12	<0.01	1.05	0.06
	Palinurus echinatus phyllosoma	C					<0.01	1.05	0.13	
Sergestidae	Sergestidae unident	O					0.86	0.04	2.11	0.45
Acanthephyridae	*Acanthephyra pelagica*	O	0.52	0.71	18.18	0.615				
Decapoda megalopa		U	0.92	0.02	4.55	0.47	10.34	0.16	13.68	5.25
Decapoda unident.		U	75.69	17.32	18.18	46.505	10.10	0.21	30.53	5.155
Stomatopoda										
Pseudosquillidae	*Pseudosquillisma oculata*	C	0.52	0.04	4.55	0.28	0.25	0.01	1.05	0.13
Crustacea unident		U					0.62	0.01	1.05	0.315
Total Crustacea			**78.04 7.31-100**	**18.13 1.15-39.46**	**54.55 25.93-62.96**	**49.69**	**38.30 (19.63-64.27)**	**0.75 (0.44-1.19)**	**45.26 (28.57-48.95)**	**19.525**
Acanthuridae	*Acanthurus bahianus*	C					0.12	0.01	1.05	0.065
Berycidae	*Beryx splendens*	O					0.12	0.46	1.05	0.29
Carangidae	*D.macarellus*	C					1.72	6.17	14.74	3.945
	D.muroadsi	C					0.37	1.26	3.16	0.815
	D.punctatus	C					0.86	6.45	7.37	3.655
	Decapterus sp.	C	1.44	2.82	22.73	2.13	1.35	4.91	7.37	3.13
	Carangidae unident.	C					0.25	0.01	1.05	0.13
Caristiidae	Caristiidae unident.	O	0.78	4.01	4.55	2.395				
Centrolophidae	Centrolophidae unident.	O					0.12	0.01	1.05	0.065
Chaetodontidae	*Chaetodon sanctaehelenae*	C					7.39	8.63	32.63	8.01

(Continues)

TABLE 1 (Continued)

	Prey	Range type	cool season				warm season			
			%N	%W	%O	%PSIRI	%N	%W	%O	%PSIRI
Diodontidae	*Diodon* sp.	C					0.12	0.01	1.05	0.065
Diretmidae	*Diretmichthys parini*	O	0.13	0.04	4.55	0.085	0.37	0.22	2.11	0.295
Echeneidae	*Remora* sp.	O	0.39	0.88	13.64	0.635	0.86	0.33	7.37	0.595
Emmelichthydae	*Emmelichthys ruber*	C					0.62	0.70	2.11	0.66
Epigonidae	*Epigonus* sp.	O	0.26	1.25	4.55	0.755	0.37	0.01	2.11	0.19
Exocoetidae	*Cheilopogon* sp.	O					0.12	0.01	1.05	0.065
Gempylidae	*Gempylus serpens*	O	0.26	2.50	4.55	1.38				
Gonostomatidae	*Gonostoma* sp.	O					7.88	0.53	1.05	4.205
Sternoptychidae	*Argyropelecus/Sternoptyx* spp.	O	0.13	0.04	4.55	0.085				
Lophiiformes unident.		O	0.13	0.13	4.55	0.13				
Myctophidae	*Diaphus* sp.	O					0.25	0.01	1.05	0.13
	Lampanyctus sp.	O					0.37	0.01	1.05	0.19
	Lampichthys procerus	O					0.12	0.01	1.05	0.065
	Myctophum nitidulum	O					0.25	0.01	1.05	0.13
Paralepididae	*Lestidiops* sp.	O					0.12	0.01	1.05	0.065
Pomacentridae	*Adudefduf saxatilis*	C					0.12	0.84	1.05	0.48
	Pomacentridae unident.	C	0.13	0.08	4.55	0.105				
Scombridae	*Katsuwonus pelamis*	O					0.25	7.77	2.11	4.01
	Scomber colias	C	0.39	10.22	13.64	5.305	0.37	8.69	3.16	4.53
Sparidae	Sparidae unident.	C	0.65	10.43	13.64	5.54				
Stomiidae	Stomiidae unident.	O					0.12	0.18	1.05	0.15
Syngnathidae	*Hippocampus* sp	C	0.13	0.02	4.55	0.075	3.08	0.45	4.21	1.765
Tetraodonidae	*Lagocephalus lagocephalus*	O					2.09	9.04	8.42	5.565
Tetraodontidae	*Sphoeroides pachygaster*	C					0.25	1.79	2.11	1.02
Zenionidae	*Zenion hololepis*	C					0.12	0.01	1.05	0.065
Pisces unidet		U	4.58	48.57	90.91	26.575	13.18	34.93	55.79	24.055
Total Pisces			**9.41** 6.27-13.1	**80.99** 42.97-100	**100.00** 70.4 - 100	**45.19**	**43.35** (29.88-62.80)	**93.44** (60.49-100)	**84.21** (73.47-88.78)	**68.395**
Unidentified							**0.12** **(0-0.85)**	**0.01** **0-0.026**	**1.05** **(0-7.14)**	**0.065**

Invertebrates were of low importance, the most common of them being the ommastrephid squid *H. pelagica* (Table 2).

Deep-sea food did not play a major role in yellowfin tuna diet at seamounts with only the occasional appearance of *Beryx splendens* or mesopelagic squids. Coastal species (like butterfly fish or surgeon fish) were absent.

4 | DISCUSSION

Existing data on the yellowfin tuna diet at St Helena are restricted to the information obtained during studies of fish fauna at Bonaparte Seamount, which included investigation of stomach contents of longline-captured yellowfin tuna. Among the listed fish species there were hatchetfishes *Sternoptyx diaphana* and *S. pseudobscura*, anglerfish *Cryptopsarus couesii*, fangtooth *Anoplogaster cornuta*, suckerfish *Remora remora*, and inshore serranid *Holanthias fronticinctus*, known only from St Helena shelf, which represented about 20% of tuna diet (Edwards, 1993). Unfortunately, neither the full list of fish species found in tuna stomachs, nor information about cephalopods and crustaceans are available. Identification of *H. fronticinctus* in tuna diet from this seamount also remains unconfirmed (Caprenter & de Angelis, 2016b).

4.1 | Diet composition and its variability

The data from this study is consistent with other studies of yellowfin tuna diet in indicating that yellowfin tuna are relatively non-selective, opportunistic feeders and consume a broad range of available prey (Borodulina, 1981; Josse et al., 1998; Moteki et al., 2001; Poitier et al., 2007). The specific diet composition of adult yellowfin tuna is thus very variable throughout the species range with region and habitat, as well as temperature and productivity (Kuhnert et al., 2012). Although not a major fishing region, there is evidence that yellowfin tuna remain resident in St Helena waters for extended periods (Wright et al., 2019), which is thought to be due to the elevated levels of productivity associated with the island and seamounts (White et al., 2007). Our study demonstrates that yellowfin prey on both coastal and oceanic prey. The availability of coastal prey in addition to oceanic species may be an important factor in keeping juvenile fish around the island and seamounts.

As a consequence of their opportunistic and non-selective feeding strategy, yellowfin tuna diet is likely influenced by prey availability in the different habitats rather than prey selection and therefore might be locally similar to that of other non-selective large predators (Ruderhausen et al., 2010). Hence, in the different oceanic areas the yellowfin diet might be dominated either by crustaceans, or by fish or by cephalopods.

4.2 | Role of crustaceans

Yellowfin tuna in St Helena waters exhibited a high level of crustacean consumption in inshore waters, but not at seamounts where they played a minor role in the diet throughout the year. In the cool season, in inshore waters, crustacean importance (principally of deep-sea shrimps) exceeded that of fish (Table 1). In summer, crustaceans were still important (%PSIRI ~ 20) but were mostly represented by other, likely seasonally available, groups such as larval decapods (megalopa) as well as relatively abundant hyperiid amphipods. The megalopa may be the larvae of shallow water taxa, hence they may be present at high densities in the vicinity of the island; alternately they may be aggregated by local hydrographic conditions.

The finding of a crustacean dominated diet is not unusual and has even been reported in large fish (mean tuna FL of 120 cm), such as in winter off Sri Lanka where the diet is dominated by a swimming portunid crab *Charybdis smithii* (Dassanayake et al., 2008). *Charybdis smithii* is an ecologically important species, which forms pelagic swarms that are an important part of the diet of several large pelagic species and hence represent a crucial seasonal trophic link in the open ocean ecosystem of the western Indian Ocean (Couwelaar et al., 1997; Romanov et al., 2009). A very similar seasonal situation, with a strong predomination of this species (64% by numbers, 55% by weight), was found north of the Seychelles (Potier et al., 2007). In summer the diet changes with small tuna of the genus *Auxis*, rather than pelagic crabs, the most important prey for yellowfin (Maldeniya,). Annual predominance of crustacean in the diet of yellowfin tuna was found in the Eastern tropical Pacific with another pelagic crab (Romanov et al., 2009) – a galatheid *Pleuroncodes planipes* representing 54% of food by weight and 49% by numbers; the second by importance was the squid *Dosidicus gigas* with fish playing a very small role in the diet (Alatorre-Ramirez et al., 2017).

4.3 | Role of fish

Fish was the most important prey of yellowfin tuna at the seamounts accounting for ~ 80 %PSRI (Table 2) and its diversity varied seasonally. In the cool season, around a half of the fish prey was represented by oceanic pufferfish *Lagocephalus lagocephalus*. During the warmer season it was substituted by another pufferfish – *Sphoeroides pachygaster*. Pufferfish are well known to be an important food for tuna (Carpenter & de Angelis, 2016b) and the switch from one species to another probably reflected seasonal shifts in species ranges. Inshore fishes were absent in the diet and occasional seahorses that theoretically might fit into this category probably drifted in there with drifting *Sargassum* spp. seaweeds so were effectively oceanic. The rest of the fish prey was represented by diverse epi-end mesopelagic fish.

In the inshore waters of St Helena fish dominated the diet in the warm season and was of similar importance to crustacea in the cool season. Proximity to shoreline provided an opportunity for tuna to prey on a range of neritic taxa including butterfly fish and small pelagics of the Carangidae and Scombridae families whilst also consuming more oceanic species, such as pufferfish.

A mixture of both inshore and oceanic (epi- and mesopelagic) fish in varying proportions represent the bulk of yellowfin tuna diet in many areas, but may be biased by greater sampling effort in coastal regions.

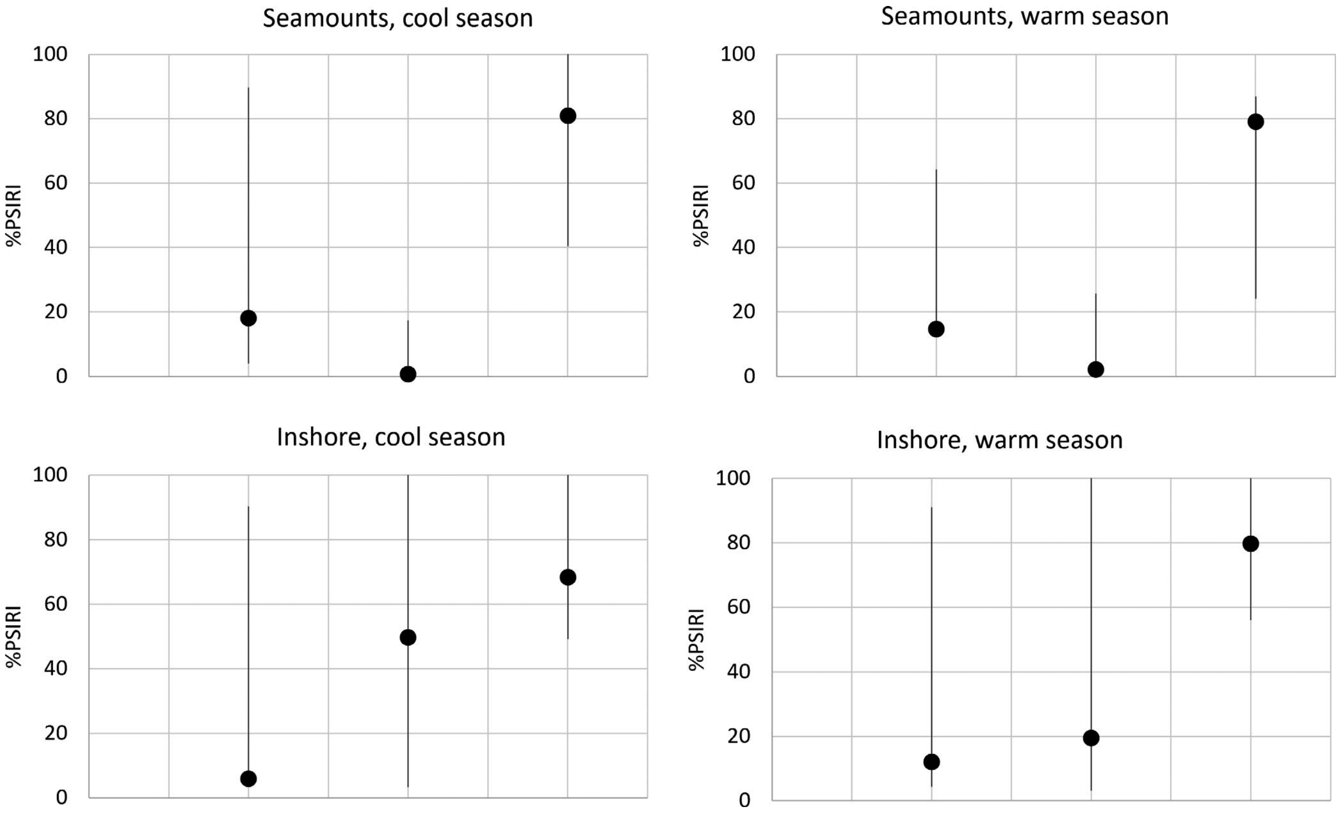


FIGURE 6 Importance of the different prey in yellowfin tuna diet

For example, ecologically diverse fish occurred in 60-90% of stomachs and represented some 60-99% of food by weight in waters of Angola and Congo, in the equatorial zone of the Indian Ocean (Kornilova, 1980) as well as along the western and central tropical Pacific (Allain, 2004; Bertrand et al., 2002; Dragovich & Potthoff, 1972).

Mesopelagic fish are reported to be the most important food source in open waters of the equatorial Atlantic (10–20° W, 0–5° N) where a single species, *Vinciguerria nimbaria*, accounted for 82% by number and 71% in volume of the prey (Marchal & Lebourge, 1996; Ménard & Marchal, 2003).

Inshore, coastal fish predominated (53% by weight) in the diet of yellowfin tuna off the east coast of India with the rest represented mostly by purpleback flying squid *Sthenoteuthis oualaniensis* and swimming crabs (Rohit et al., 2010). A similar situation with predominance of the aforementioned two species and coastal fish (though to a lesser extent) was found off western coasts of India (Varghesi & Somvanshi, 2016).

Further offshore, epi-pelagic, oceanic species are likely to be the main prey. This ecological group, including flying fishes and scombrids represented ~ 90% of food by weight in yellowfin tuna in June off the east coasts of the USA (Ruderhousen et al., 2010) and all year round at remote South Atlantic archipelago of St Peter and St Paul, Brazil (Vaske et al., 2003) with a minor role of mesopelagic fauna and crustaceans.

In general, tuna stomachs contained species whose presence in St Helenian waters was either already known or presumed based on the species occurrence in adjacent areas with the same oceanographic properties (see Carpenter & De Angelis, 2014). However, a fish of family Caristiidae that cannot be allocated to any of described species was found in the stomach of yellowfin tuna captured at Cardno Seamount and has been kept for further studies. Seahorses occasionally occurred in stomachs and were tentatively identified as slender or longsnout seahorse, *Hippocampus reidi*, that occurs in the Western tropical Atlantic including the Sargasso Sea (Froese & Pauly, 2019) and may have been brought into the area with Sargassum spp. weeds. Seahorses have been reported in shallow water around the island by divers, but the specific identification of these is not known (Brown, 2014).

4.4 | Role of cephalopods

Cephalopod molluscs (6-18 %PSRI) did not play a major role in yellowfin tuna diet around St Helena. This may be a consequence of low abundance of large epi-pelagic ommastrephid squids that might be important part of the diet elsewhere (e.g. Alatorre-Ramirez et al., 2017; Kaymaram et al., 2000; Rohit et al., 2010). Most of the cephalopod prey around St Helena was represented by mesopelagic squids. The epipelagic octopod *Argonauta* spp. was also very common in the diet at both St Helena and the seamounts and it also occurs in yellowfin diets in other tropical seas (e.g. Alatorre-Ramirez et al., 2017; Allain, 2004; Dragovich & Pothoff, 1972; Ruderhausen et al., 2010).

Cephalopods also can dominate the diet of yellowfin tuna in some regions, such as in the Gulf of Mexico with inshore and

TABLE 2 Stomach contents of yellowfin tuna on Cardno and Bonaparte seamounts in warm ($n = 42$) and cool ($n = 25$) season. Confidence intervals in brackets

			cool season				warm season			
	Prey	**Range type**	**%N**	**%W**	**%O**	**PSIRI**	**%N**	**%W**	**%O**	**PSIRI**
Mollusca										
Cephalopoda										
Octopoda										
Argonautidae	*Argonauta* sp.	O	0.90	0.01	4.00	0.455	0.16	0.01	2.38	0.087
	Octopoda unident.	U	0.90	0.13	4.00	0.515	0.16	0.01	2.38	0.087
Teuthida: Oegopsida										
Ancistrocheiridae	*Ancistrocheirus lesuerii*	O					0.16	0.08	2.38	0.122
Cranchiidae	*Taonius* sp B. (Voss)	O	0.45	0.01	4.00	0.23				
	Cranchiidae unident.	O	1.35	0.22	4.00	0.785	0.16	0.01	2.38	0.087
Enoploteuthidae	*Enoploteuthis anapsis*	O					0.16	0.03	2.38	0.097
Lycoteuthidae	*Lycoteuthis lorigera*	O	1.80	0.01	4.00	0.905	0.16	0.03	2.38	0.097
Ommastrephidae	*Hyaloteuthis pelagica*	O	7.66	0.01	4.00	3.835	8.31	1.42	33.33	4.865
	Sthenoteuthis pteropus	O					0.16	0.91	2.38	0.537
	Ommastrephidae unident.	O	0.45	8.13	4.00	4.29	1.47	0.04	7.14	0.755
Onychoteuthidae	*Onychoteuthis prolata*	O					0.16	0.08	2.38	0.122
	Onychoteuthidae	O					0.16	0.01	2.38	0.087
Oegopsida unident.		O	2.70	0.67	4.00	1.685	7.49	2.27	38.10	4.88
Cephalopoda unident.		O	10.81	0.00	4.00	5.405	4.40	1.44	21.43	2.92
Total Cephalopoda			**27.03 (10.81-49.55)**	**9.20 (0.27-25.83)**	**32 (16.11-44.52)**	**18.12**	**23.13 (14.09-38.88)**	**6.35 (3.38-9.99)**	**61.9 (46.51-74.42)**	**14.74**
Crustacea										
Amphipoda										
Hyperiidae	*Phrosina* sp.	O					0.16	0.00	2.38	0.087
Euphausiacea										
Euphausiidae	*Thysanopoda* sp.	O					0.33	0.08	2.38	0.205

(Continues)

TABLE 2 (Continued)

	Prey	Range type	cool season				warm season			
			%N	%W	%O	PSIRI	%N	%W	%O	PSIRI
Decapoda										
Pasiphaeidae	*Pasiphaea* sp.	O					0.16	0.08	2.38	0.122
	Decapod megalopa	U	0.90	0.01	4.00	0.455	1.30	0.08	14.29	0.69
	Decapoda unident.	U					1.95	0.19	9.52	1.07
	Crustacea unident.	U	0.45	0.02	4.00	0.235				
Total Crustacea			**1.35 (0-3.60)**	**0.03 (0-0.11)**	**8.00**	**0.69**	**3.91 (1.70-7.13)**	**0.44 (0.20-1.02)**	**28.57 (16.28-41.86)**	**2.175**
Thaliacea										
Pyrosomidae	*Pyrosoma* sp	O	**0.45 (0-1.35)**	**0.02 (0-0.06)**	**4 (1.51-6.32)**	**0.235**				
Pisces										
Osteichthyes										
Argentinidae	*Glossanodon* sp.	O					3.09	0.03	4.76	1.56
Berycidae	*Beryx splendens*	O	3.15	2.23	8.00	2.69				
Caproidae	*Antigonia capros*	C					0.65	1.46	1.055	1.055
Cariistiidae	Caristiidae unident.	O					1.95	0.03	2.38	0.99
Chlorophtalmidae	*Chlorophtalmus agassizi*	O					1.47	0.03	4.76	0.75
Emmelichthyidae	*Emmelichthys ruber*	C					0.33	0.23	4.76	0.28
Exocoetidae	*Cheilopogon* sp.	O					0.16	0.01	2.38	0.087
	Exocoetidae undent.	O	0.45	1.02	4.00	0.735	1.14	2.40	9.52	1.77
Epigonidae	*Epigonus* sp.	O					0.33	0.01	2.38	0.17
Hemiramphidae	*Oxyporhamphus micropterus*	O					1.14	0.01	2.38	2.76
Myctophidae	*Lampadena luminosa*	O					0.16	0.01	2.38	0.087
Nomeidae	*Cubiceps* sp.						0.16	0.69	2.38	0.427
Scombridae	*Scomber colias*	C					0.33	2.58	4.76	1.455
Stomiidae	*Neonesthes capensis*	O					0.16	0.01	2.38	0.087
Syngnathidae	*Hippocampus* sp.	C	0.45	0.02	4.00	0.235	0.16	0.01	2.38	0.087

(Continues)

TABLE 2 (Continued)

	Prey	Range type	cool season %N	cool season %W	cool season %O	cool season PSIRI	warm season %N	warm season %W	warm season %O	warm season PSIRI
Tetraodontidae	*Lagocephalus lagocephalus*	O	22.07	58.17	100.00	40.12	0.98	2.57	9.52	1.775
	Sphoeroides pachygaster	C					0.98	4.34	2.38	12.66
Trachuridae	*Decapterus* sp.	C					0.33	3.95	4.76	2.14
Trichiuridae	*Aphanopus intermedius*	O					4.72	6.85	7.14	5.785
Zenionidae	*Zenion hololepis*						1.31	0.04	7.14	0.675
Pisces unident.		U	45.05	29.30	92.00	37.175	48.21	64.99	100.00	45.6
Total Pisces			**71.17** **(34.23-100)**	**90.75** **(56.38-100)**	**92.00** **(72.41-96.55)**	**80.955**	**67.77** **(44.14-90.32)**	**90.28** **(50.41-100)**	**85.71** **(74.42-95.35)**	**79.025**
Unidentified							**5.05**	**2.90**	**9.52**	**3.975**

epi-pelagic fish being of slightly lower importance (Manooch III & Mason, 1983). Even stronger cephalopod predominance was found in offshore (depth> 200 m) upper slope waters of south Brazil, where fish (nearly all mesopelagic) and crustaceans occurred only occasionally and in relatively low numbers. The most important prey were squids which represented 86% food by weight and 40% by numbers. Such high consumption of cephalopods was found also in other tuna, swordfish and sharks sampled in the same area (Gorni et al., 2013). Another area where yellowfin tuna is preying mostly on cephalopods is the Oman Sea where the species forages on *Sthenoteuthis oualaniensis* (Kaymaram et al., 2000).

5 | CONCLUSION

The diet spectrum of the yellowfin tuna off St Helena (Tables 1, 2) is characterised by predominance of piscivory all year round, both close to the island and on remote seamounts. This type of the diet is characterised by the use of all available resources – inshore (as butterfly fish), epipelagic (as flying fishes) and mesopelagic (cephalopods) and tuna consume food of very diverse size: from small larval crustaceans to fish attaining a quarter of tuna length. This strategy may be a trait of remote oceanic ecosystems, with very diverse types of available food. In such areas, tuna aggregate around small islands and seamounts where oceanic circulation provides both high pelagic productivity that fuels higher trophic levels (White et al., 2007) and retention area for eggs and larvae of fish and invertebrates reproducing there in shallow waters (Genin & Dower,). Yellowfin tuna might remain foraging in these remote productive spots up to 104 days (Ascension Is.) and 277 days (St Helena) as was shown by tagging studies (Richardson et al., 2018; Wright et al., 2019).

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CONFLICT OF INTERESTS

There is no any potential source of conflict of interest that authors are aware of.

DATA AVAILABILITY STATEMENT

Research data are not shared.

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