Trophic ecology and stable isotope niche space of tuna, billfishes and sharks in New Zealand waters

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ABSTRACT

Context. Highly migratory species (HMS), such as tuna, billfishes and sharks, are a major component of the top predator guild in oceanic ecosystems, but the trophic relationships of many populations remain poorly understood. **Aims.** This study aimed to characterise the trophic ecology and habitat use of 10 HMS collected from two subtropical oceanic regions around Aotearoa–New Zealand. **Methods.** We examined stable isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) in muscle tissue of HMS considering differences in capture location and body size. **Key results.** Three trophic groups were distinguished: (1) swordfish, (2) tuna and *Lamna nasus* (porbeagle) in northern New Zealand and (3) marlins and other pelagic sharks. Despite stable isotope overlap among taxonomically similar species, subtle differences in foraging strategies likely contribute to variation in ecological roles. Trophic position estimates revealed that HMS occupy high trophic levels, though these estimates may be influenced by variations in $\delta^{15}N$ baseline. Stable isotope analysis indicated consistent trophic relationships across the two investigated oceanic regions, with evidence of ontogenetic shifts in resources use in some species. **Conclusions.** Stable isotope ratios varied widely among HMS, suggesting exploitation of diverse foraging habitats and extensive migration. **Implications.** These data highlight the diverse trophic roles of HMS and emphasise their significance in structuring marine food webs and ecosystem functioning.

Keywords: billfishes, $\delta^{13}C$, $\delta^{15}N$, ecosystem function, foraging ecology, highly migratory species, New Zealand, sharks, trophic position, tunas.

Introduction

Highly migratory species (HMS), in the context of fish include tuna, billfishes and sharks. These organisms occupy a high trophic position (TP) in the food web and therefore perform important ecological roles in marine ecosystems, principally mediated through their foraging behaviour, i.e. movements and diet. These species can exert strong controls on prey populations and community structure through both consumptive and non-consumptive activities, and also stimulate bottom-up processes through the translocation of nutrients within and across ecosystems (Roff *et al.* 2016; Williams *et al.* 2018). As such, the removal of these species can elicit trophic cascades and ecosystem-state shifts, potentially weakening ecosystem resilience (Bornatowski *et al.* 2018; Dedman *et al.* 2024). Due to overexploitation from both targeted and incidental capture, many HMS have undergone population decline over the last 50 years (Pacoureau *et al.* 2021; Juan-Jordá *et al.* 2022). Additionally, HMS are influenced by large-scale ocean circulation and localised mesoscale phenomena (i.e. eddies, fronts and cyclonic circulations; Pinti *et al.* 2025). Variation in these oceanographic features can significantly alter the availability of prey resources (Arostegui *et al.* 2022), critical habitat (Adams *et al.* 2016) and migration corridors essential for HMS (Pagniello *et al.* 2023). Climate-induced alterations in oceanic circulation and mesoscale features may thus exacerbate or mitigate the effects of environmental variability on HMS, ultimately shaping species' responses to global change (Erauskin-Extramiana *et al.* 2019; Braun *et al.* 2023). Therefore, studies on trophic ecology and movements of HMS are useful to assess

the impact of oceanographic and human factors on marine fishery resources, and provide important baseline information to assist in ecosystem-based fisheries management (Trenkel *et al.* 2014).

Access to wide-ranging and often migratory prey populations challenges our ability to fully understand the trophic dynamics of HMS. Several approaches have been used to investigate the trophic ecology of HMS, including stomach content (Shimose *et al.* 2010; Battaglia *et al.* 2013), fatty acid (Peng *et al.* 2013; Pethybridge *et al.* 2014) and stable isotope analyses (Estrada *et al.* 2005; Carlisle *et al.* 2012), and habitat modelling (Arrizabalaga *et al.* 2015; De Wysiecki *et al.* 2020). Over the last 40 years, the application of naturally occurring stable isotope methods has grown exponentially (Newsome *et al.* 2010; Shipley and Matich 2020). This advancement is in part due to non-lethal means of sampling to study resource use and trophic dynamics of threatened or difficult to study species (Hussey *et al.* 2012). The stable isotope ratios of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) of a consumer, hereafter expressed as $\delta^{13}C$ and $\delta^{15}N$ respectively, can be related to animal diets in a predictable manner (Vander Zanden and Rasmussen 1999; Bearhop *et al.* 2004; Fry 2006). Carbon stable isotope ratios are used to trace the basal source of carbon supporting a consumer within a food web, where sources are isotopically distinct such as coastal *v.* offshore and benthic *v.* pelagic end-members (Fry and Sherr 1984; Rounick and Winterbourn 1986; France and Peters 1997). In comparison, $\delta^{15}N$ is indicative of TP (DeNiro and Epstein 1978; Peterson and Fry 1987), due to a relatively predictable trophic discrimination factor of ~3.4‰ (Zanden and Rasmussen 2001; Post 2002).

Aotearoa–New Zealand is an archipelago comprising two major islands and ~700 offshore islands and islets. The New Zealand 200-nautical mile (~370.4-km) Exclusive Economic Zone (EEZ) extends over most of the submerged sub-continent and significant areas of the surrounding deeper ocean basins, making it among the world's largest EEZs with a total area of 4,083,744 km^2 (Migiro 2018). The New Zealand marine environment is thus large, oceanographically diverse and highly productive, supporting fisheries and other ecosystem services that generate important social and economic benefits to New Zealand (MacDiarmid *et al.* 2013; Cryer *et al.* 2016). The HMS are key components of New Zealand's marine megafauna assemblage, including tropical and temperate tuna, billfishes and pelagic sharks (Roberts *et al.* 2023). Some are seasonally abundant during the austral spring and summer months (Mckenzie 1964), whereas others use New Zealand waters as a long-term nursery ground for juvenile growth, e.g. shortfin mako (*Isurus oxyrinchus*) and smooth hammerhead (*Sphyrna zygaena*) (Francis 2016*a*; Francis *et al.* 2019). Since HMS spend a portion of their life cycle in New Zealand waters, we are only able to capture ecological data on specific stages of their life history. Within New Zealand's EEZ, tuna fisheries (i.e. bigeye tuna, *Thunnus obesus*, and southern bluefin tuna, *Thunnus maccoyii*) commonly interact

with HMS as target or as bycatch species (Francis *et al.* 2001; Griggs *et al.* 2024).

Few studies have attempted to investigate patterns of resource use for New Zealand HMS and limited information exists on interspecies comparisons using stable isotopes. Horn *et al.* (2013) conducted stomach content analysis on several HMS species in New Zealand waters, revealing that their diets predominantly comprised mesopelagic fishes and cephalopods, but there were slight differences in the proportions of these prey items among the species. Although stomach content studies yield information on dietary diversity, they may not be representative of diet over longer timescales and across the geographic range of HMS (Cortés 1997; Hussey *et al.* 2011). By contrast, stable isotope analysis provides long-term integrated dietary information that can be used to examine broader dietary changes (Fisk *et al.* 2002), niche breath and niche overlap (Jackson *et al.* 2011), TP (Hussey *et al.* 2014*a*, 2014*b*) and the identification of migration routes (Trueman *et al.* 2012; Hoffman 2016). In this context, using carbon and nitrogen stable isotope data collected from muscle tissues, the objectives of this study were to (1) determine potential long-distance migration movements of HMS across the south-west Pacific Ocean, (2) examine trophic interactions and niche overlap among 10 HMS coexisting in New Zealand waters and (3) assess variations in their trophic roles, considering differences in capture locations and body size. Consequently, this study aimed to provide new insights into the ecological role of these large predators.

Materials and methods

Study region

New Zealand has a relatively small land area, but when accounting for offshore islands, its latitudinal range is extensive (~30–55°S, Fig. 1), and the oceans that surround it encompass a diverse range of environmental conditions (Heath 1985; Chiswell *et al.* 2015). In New Zealand, the Subtropical Front (STF) defines the boundary between warm, Subtropical Water (STW) and the cold, less saline Subantarctic water (SAW) masses (Chiswell *et al.* 2015). The nominal position of the STF is at 44°S (Uddstrom and Oien 1999), although it is perhaps best regarded as a frontal zone in the southern Tasman Sea, after which it is diverted southwards around southern New Zealand before its extension along eastern South Island (Smith *et al.* 2013) and reformation as a broad frontal zone on Chatham Rise (Sutton 2001). New Zealand's marine productivity varies significantly based on the proximity to these different water masses and can be divided into four descriptive oceanic regions: Chatham Rise (STF east of New Zealand), Tasman Sea (TAS, STW and STF west of New Zealand), STW (northern New Zealand) and SAW (southern New Zealand, Pinkerton *et al.* 2023). New Zealand STW and SAW water masses are generally classified as
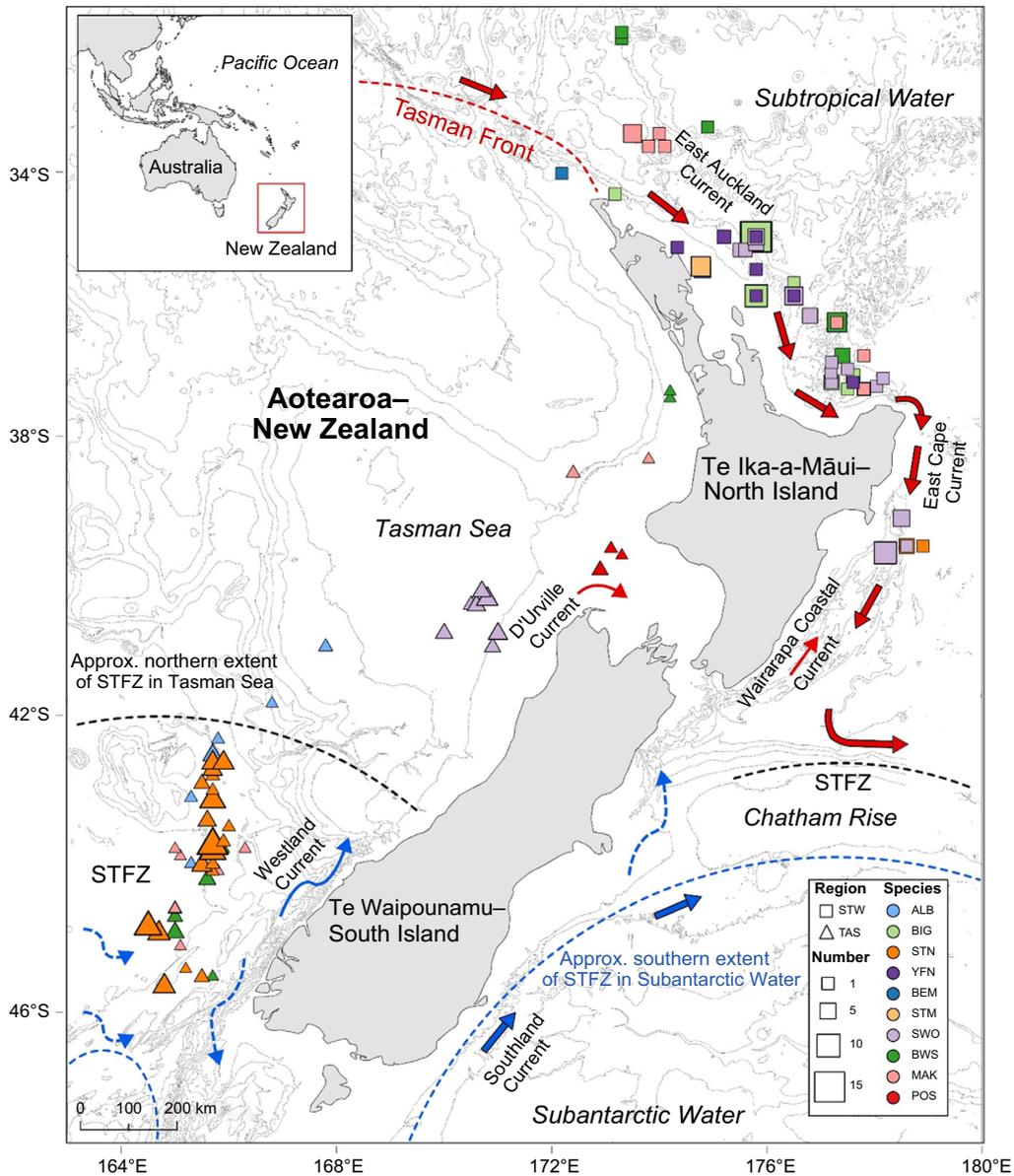
Fig. 1. Distribution of highly migratory species (HMS) samples collected throughout New Zealand waters during 2013–15. Key oceanographic features of regional water masses, fronts (Tasman Front, Subtropical Frontal Zone-STFZ) and associated mean currents (adapted from Chiswell *et al.* 2015) are shown to illustrate the dynamic circulation influencing HMS distributions. Species are abbreviated as in Table 1 and colour coded according to the legend. Regions of collection are indicated by squares (Subtropical water, STW) and triangles (Tasman Sea, TAS). Dotted blue lines represent unnamed current flows.

oligotrophic with low macronutrients and productivity compared to higher productivity waters of the STF, especially over Chatham Rise where surface waters are typically classified as mesotrophic (Pinkerton *et al.* 2023). The TAS ecogeographical province is bordered by the STF in the south and the Tasman Front in the north and is characterised by dynamic mesoscale processes and strong winds, resulting in physically distinctive subsurface 'central water' that sits just below the STW in the central Tasman Sea (Longhurst 2010;

Chiswell *et al.* 2015). Geographical variability in stable isotope ratios of primary producers, driven by differences in trophic conditions across oceanic regions, have been shown to propagate through the food web, and are reflected in the stable isotopes of top predators (Magozzi *et al.* 2017; Bird *et al.* 2018). Therefore, delineating the regional differences in stable isotope ratios of HMS is essential for interpreting the ecological dynamics within New Zealand's marine environment.

Data collection and processing

A total of 443 muscle samples from four species of tuna – albacore (*Thunnus alalunga*), bigeye tuna, southern bluefin tuna, yellowfin tuna (*Thunnus albacares*); three species of billfish – blue marlin (*Makaira mazara*), striped marlin (*Tetrapturus audax*) and swordfish (*Xiphias gladius*); and three species of pelagic shark – blue shark (*Prionace glauca*), shortfin mako and porbeagle (*Lamna nasus*) were collected in the New Zealand EEZ during 2013–15 (Fig. 1, Table 1). Species were sampled from the STW and TAS regions, with some species occurring in both regions, whereas others were sampled exclusively in one (Fig. 1, Table 1). The HMS were mostly collected from pelagic longline vessels through the Ministry for Primary Industries Fisheries Observer Program. A set of instructions was prepared for observers on how to sample HMS muscle tissue. Observers recorded species name, fish length (fork length, FL, cm), date and catch location (latitude and longitude). Supplementary muscle tissues of HMS were provided from recreational fishers following the same protocols. In addition to fish sample collection, particulate organic matter (POM) was obtained from surface waters on various R/V *Tangaroa* voyages around New Zealand during 2006–18. Seawater samples were filtered at low vacuum through pre-combusted, glass fibre filters, acidified with 0.4 N of sulfuric acid and rinsed with 0.2-μm filtered seawater. All samples were shipped to the New Zealand Institute for Earth Science Ltd (Earth Sciences New Zealand, formerly National Institute for Water and Atmospheric Research Ltd) in Wellington and kept frozen at −20°C until further analyses.

Pelagic shark muscle tissue samples were rinsed with deionised water to address the stable isotope bias of urea (Kim and Koch 2012). All frozen muscle tissue and POM samples were thawed and dried in an oven at 50°C for 48 h and then ground into a homogeneous powder using a mortar and pestle. Ground samples were weighed (0.5–1 mg) into tin capsules. Carbon and nitrogen stable isotope ratios were determined using a continuous flow stable isotope ratio mass spectrometer coupled to an elemental analyser, at Earth Sciences New Zealand's Environmental and Ecological Stable Isotope Analytical Facility (Bury *et al.* 2024, see text S6 in their supplementary material for method details). Repeat analysis of National Institute of Standards and Technology and laboratory standards produced data accurate to within 0.25‰ and a precision of better than 0.25‰ for $\delta^{13}C$ and $\delta^{15}N$ respectively. The stable isotope composition is reported in the conventional delta (δ) per mille notation (‰), relative to Vienna Pee Dee Belemnite ($\delta^{13}C$) and atmospheric N_2 ($\delta^{15}N$).

Lipid synthesis strongly discriminates against the ^{13}C stable isotope (DeNiro and Epstein 1977, 1978) producing lower $\delta^{13}C$ in lipids compared to protein and carbohydrates (Rounick and Winterbourn 1986; Ricca *et al.* 2007;

Table 1. Summary metadata table for highly migratory species sampled around New Zealand.

Species	Code	Capture region	Number of samples	Mean size ±1 s.d. (FL, cm)	Range size (FL, cm)	Mean $\delta^{13}C$ ± s.d. (‰)	Mean $\delta^{15}N$ ± s.d. (‰)	Cluster (Fig. 2)	Hypervolume size (‰²)	Mean TP ± s.d.
Albacore (*Thunnus alalunga*)	ALB	STW	6	88.3 ± 21.3	75–131	−19.03 ± 0.60	12.82 ± 1.03	TG2	13.32	3.11 ± 0.36
		TAS	28	78.4 ± 12.5	41–103	−18.30 ± 0.61	12.76 ± 0.55	TG2	3.29	3.07 ± 0.19
Bigeye tuna (*Thunnus obesus*)	BIG	STW	45	137.3 ± 21.6	57–173	−18.80 ± 1.36	12.79 ± 1.47	TG2	21.48	3.11 ± 0.46
Southern bluefin tuna (*Thunnus maccoyii*)	STN	STW	10	139.9 ± 16.0	117–172	−19.57 ± 1.83	13.08 ± 0.43	TG2	16.88	3.18 ± 0.15
		TAS	165	149.1 ± 17.9	102–192	−18.28 ± 2.08	11.22 ± 1.28	TG2	47.80	2.61 ± 0.39
Yellowfin tuna (*Thunnus albacares*)	YFN	STW	8	129.6 ± 20.2	96–154	−19.12 ± 1.48	11.94 ± 0.98	TG2	31.81	2.81 ± 0.30
Blue marlin (*Makaira mazara*)	BEM	STW	6	277.7 ± 18.2	254–309	−17.10 ± 0.21	14.48 ± 0.38	TG3	1.67	3.71 ± 0.16
Striped marlin (*Tetrapturus audax*)	STM	STW	7	207.0 ± 35.6	132–236	−17.78 ± 0.49	14.19 ± 1.33	TG3	13.66	3.63 ± 0.51
Swordfish (*Xiphias gladius*)	SWO	STW	40	164.6 ± 37.2	113–296	−21.30 ± 2.21	11.09 ± 3.34	TG1	106.12	2.72 ± 0.90
		TAS	47	175.4 ± 39.6	96–280	−20.50 ± 1.71	11.80 ± 2.90	TG1	86.11	2.87 ± 0.82
Blue shark (*Prionace glauca*)	BWS	STW	14	145.6 ± 48.1	66–245	−17.63 ± 0.62	13.37 ± 0.52	TG3	7.07	3.28 ± 0.18
		TAS	28	122.4 ± 35.3	69–187	−18.16 ± 0.40	15.17 ± 1.33	TG3	12.28	4.06 ± 0.58
Shortfin mako (*Isurus oxyrinchus*)	MAK	STW	14	164.6 ± 53.9	71–249	−17.22 ± 0.66	14.86 ± 0.83	TG3	14.81	3.77 ± 0.38
		TAS	11	184.5 ± 37.3	97–245	−16.77 ± 1.38	15.16 ± 1.60	TG3	44.66	4.09 ± 0.77
Porbeagle (*Lamna nasus*)	POS	STW	4	82.0 ± 8.0	73–96	−18.99 ± 1.21	11.91 ± 1.44	TG2	33.19	2.82 ± 0.43
		TAS	10	184.5 ± 32.3	70–219	−18.47 ± 0.53	15.10 ± 2.53	TG3	28.59	4.11 ± 0.87

Stable isotope values are displayed as mean (±1 standard deviation, s.d.), STW, Subtropical water; TAS, Tasman Sea; FL, fork length; TP, trophic position.

Logan *et al.* 2008). For this study, lipids were not routinely extracted from HMS samples; instead, a correction factor developed for tropical Pacific tuna (Graham 2007) was applied to all HMS samples which had a C:N in excess of 3.5 (i.e. bigeye, southern bluefin and yellowfin tuna, and blue and striped marlins). Swordfish had very high C:N, ranging within 3.19–53.33, indicative of very high lipid content, for which the Graham (2007) correction factor was not applicable. Therefore, a subset ($n = 20$) of swordfish samples was sent to Earth Sciences New Zealand in Hamilton for lipid extraction (Bury *et al.* 2024, see text S6 in their supplementary material for method details) to generate a swordfish-specific $\delta^{13}C$ lipid correction to eliminate lipid-content bias of $\delta^{13}C$ for the remaining samples. For nitrogen stable isotopes, bulk non-corrected $\delta^{15}N$ was reported for all HMS samples.

Data analysis

Inter-species variations

Statistical analyses were performed using *RStudio* (ver. 4.2.764, Posit Software, PBC, Boston, MA, USA, see https://posit. co/products/open-source/rstudio/), based on the statistical computing language *R* (ver. 4.1.0, R Foundation for Statistical Computing, Vienna, Austria, see https://www.r-project.org/). Assumptions regarding normality and homogeneity of variance were not met following Shapiro–Wilk and *F* tests. Non-parametric tests were consequently used for further statistical analysis. Species were placed into three trophic groups (TG1–3) using Ward's hierarchical clustering analysis of mean $\delta^{13}C$ and $\delta^{15}N$ for each species (Ward and Hook 1963). To investigate differences among trophic groups obtained with Ward's method, a non-parametric multivariate analysis of variance (NPMANOVA; Anderson 2001) was performed using $\delta^{13}C$ and $\delta^{15}N$ of each species, followed by Wilcoxon (*W*) signed-rank test. To determine the trophic niche size and overlap among species, $\delta^{13}C$ and $\delta^{15}N$ were used to create hypervolumes representing each species' multidimensional trophic niche. Specifically, the *hypervolume* package (ver. 3.1.4, see https://cran.r-project.org/package=hypervolume; Blonder *et al.* 2014; Blonder 2018) was used to seed Gaussian kernel density estimations, generating a cloud of points along $\delta^{13}C$ and $\delta^{15}N$ axes for each species. Each hypervolume included 95% of the total probability density (quantile threshold = 0.05, Blonder *et al.* 2014). The size of each hypervolume was calculated, representing the relative breadth of each species' trophic niche. The degree of overlap between each pair of species' hypervolumes (trophic niches) was determined using the Sørensen overlap index (proportion overlapping, Blonder *et al.* 2014).

Trophic position

The TP of individual species was estimated from $\delta^{15}N$ following the scaled $\delta^{15}N$ framework approach based on a dietary $\delta^{15}N$-dependent model (Hussey *et al.* 2014a, 2014b). Relative TP was calculated as follows:

$$TP = \frac{\log\ (\delta^{15}N_{lim} - \delta^{15}N_{base}) - \log\ (\delta^{15}N_{lim} - \delta^{15}N_{TP})}{k} + TP_{base}$$

where $\delta^{15}N_{lim}$ is the saturating stable isotope limit as TP increases, $\delta^{15}N_{base}$ is the nitrogen stable isotope ratio of the baseline group in the food wed, $\delta^{15}N_{TP}$ is the nitrogen stable isotope ratio of each HMS individual, TP_{base} is the TP of the baseline group and k is the rate at which $\delta^{15}N_{TP}$ approaches $\delta^{15}N_{lim}$ per TP step. The $\delta^{15}N_{lim}$ and k of 21.93 and 0.14 respectively, were retrieved from a meta-analysis of experimental stable isotope data (Hussey *et al.* 2014a, 2014b). According to previous studies, the species used for estimating $\delta^{15}N_{base}$ should come from the same habitat as the consumer (Hussey *et al.* 2014a, 2014b). However, since HMS are known to migrate and forage across large areas, this complicates the assignment of a single, regional baseline both within New Zealand waters and across the south-west Pacific Ocean. Therefore, TP was calculated for each individual of each species using a New Zealand-wide baseline value, defined as the average $\delta^{15}N$ of POM representing the base of the food web in HMS sampling regions ($\delta^{15}N_{base} = 6.74 \pm 4.66‰$). Mean baseline $\delta^{15}N$ of POM was obtained from St John Glew *et al.* (2021) for TAS and from S. Nodder (Earth Sciences New Zealand, unpubl. data) for STW. These samples were collected during the same timeframe as the HMS samples. We used a TP_{base} of 1.5 to take into account that there are not only primary producers in POM (Lorrain *et al.* 2015).

Assumptions regarding normality and homogeneity of variance were not met for TP following Shapiro–Wilk and *F* tests. To analyse the differences of TP between and within groups determined by clustering analysis, Kruskal–Wallis (H) rank tests were performed on the TP data followed by *post hoc* comparison using the *W* signed-rank test.

Geographic and size-related variation

Geographic and size-related variation in basal source of carbon ($\delta^{13}C$) and relative TP ($\delta^{15}N$) were investigated using linear regressions. Cook's test was used to identify outliers. Each regression model slope was tested to determine if it deviated significantly from a slope of zero. Additionally, residuals were assessed for linear fits to ensure the appropriateness of the model and to ensure accurate predictions.

Results

Six of the ten species were collected in both STW and TAS regions (albacore, southern bluefin tuna, swordfish, blue shark, shortfin mako and porbeagle) whereas bigeye and yellowfin tuna, blue marlin and striped marlin were only collected in STW (Fig. 1, Table 1). Among tuna species, albacore from TAS ($n = 28$) had the smallest average size at 78.4 ± 12.5 cm FL (range 41–103 cm), whereas southern bluefin tuna from TAS ($n = 165$) had the largest average

size 149.1 ± 17.9 cm FL (range 102–192 cm, Table 1). Billfish species had larger average sizes than other taxa, with blue marlin ($n = 6$) and striped marlin ($n = 7$) displaying the highest average sizes among all species collected (mean ± s.d. = 277.7 ± 18.2 and 207.0 ± 35.0 cm FL respectively, Table 1). Shark species displayed moderate to high variability in size, with average size ranging from 82.0 ± 8.0 cm FL for porbeagle to 184.5 ± 37.3 cm FL for shortfin mako. Many shark individuals had small size categories, suggesting the prevalence of juveniles (Francis 2015, 2016*b*; Francis and Ó Maolagáin 2016). Overall, the data highlight distinctions in size distributions of individuals sampled across species, with billfish generally exhibiting the largest average sizes, followed by pelagic shark and tuna species.

Interspecies and regional variations

Species were classified into three distinct trophic groups (Fig. 2) with significant differences in mean stable isotope ratios (NPMANOVA, $F_{1,441} = 129.57$, $P < 0.001$). Trophic group δ^{13}C was significantly different, with TG3 having the highest δ^{13}C, followed by TG2 and TG1 (W tests, $P < 0.05$ for all tests, Supplementary Table S1). The TG3 had significantly higher δ^{15}N than TG1 and TG2 (W tests, $P < 0.05$ for all tests, Table S1) but no difference was observed between TG1 and TG2 (W test, $P = 0.36$, Table S1). Significant differences in

stable isotope ratios were observed for TG2 and TG3 (NPMANOVA, $F_{6,259} = 6.1895$, NPMANOVA, $F_{6,83} = 4.5129$, for TG2 and TG3 respectively, $P < 0.001$ for all tests) but not for TG1 (NPMANOVA, $F_{1,85} = 1.81$, $P = 0.17$).

Cluster analysis revealed that species from different regions were grouped into the same trophic groups, but intra-trophic group variations in stable isotope ratios related to regional differences were observed (Fig. 2, Table 1). Cluster TG1 (δ^{13}C = −20.87 ± 1.98‰ and δ^{15}N = 11.47 ± 3.11‰) included swordfish, characterised by the lowest δ^{13}C and a wide range of δ^{15}N (Fig. 2, Table 1). Cluster TG2 (δ^{13}C = −18.47 ± 1.82‰ and δ^{15}N = 11.79 ± 1.43‰) included all four tuna species and porbeagle from STW (Fig. 2, Table 1). Albacore and bigeye tuna from STW had significantly higher δ^{13}C than albacore and southern bluefin tuna from TAS respectively (W = 23 and 2557 respectively, both $P < 0.05$, Table S1). Southern bluefin tuna from TAS exhibited significantly lower δ^{15}N than all TG2 species, except for yellowfin tuna and porbeagle from STW (W = 398 and 428 respectively, both $P > 0.05$, Table S1). Southern bluefin tuna from STW showed significantly higher δ^{15}N than yellowfin tuna from the same region (W = 72, $P < 0.05$). The TG3, which included billfishes and pelagic sharks, except for porbeagle from STW (from TG2), were characterised by some of the highest δ^{13}C (−17.70 ± 0.87‰) and δ^{15}N (14.71 ± 1.47‰,

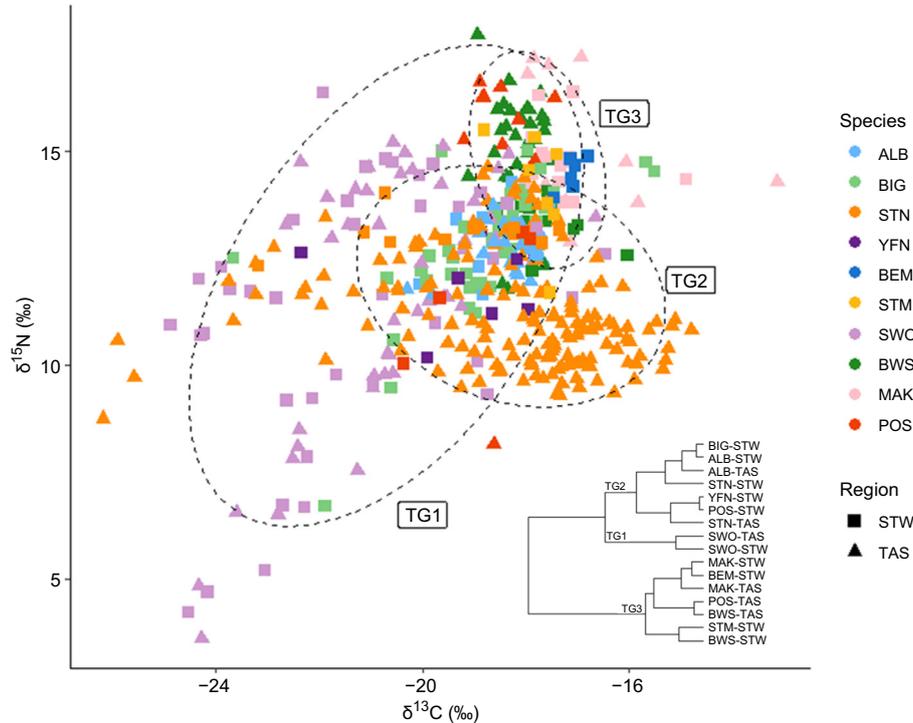**Fig. 2.** Biplot of δ^{13}C and δ^{15}N values for highly migratory species collected in New Zealand waters. Large ovals show trophic groups (TG1–3) from cluster analysis. Inset shows a dendrogram of cluster analysis; each node represents an individual species within a specific capture region. Species are abbreviated as in Table 1 and colour coded according to the legend. Regions of collection are indicated by squares (Subtropical water, STW) and triangles (Tasman Sea, TAS).

Fig. 2, Table 1). Blue shark and porbeagle from TAS had significantly lower δ^{13}C than all other species in TG3 (W tests, all $P < 0.05$, Table S1) but were not significantly different from each other (W = 198, $P = 0.08$, Table S1). Blue marlin from STW had significantly higher δ^{13}C than striped marlin and blue shark from the same region (W = 40 and 69 respectively, both $P < 0.05$, Table S1). Blue shark from STW exhibited significantly lower δ^{15}N than all TG3 species, with the exception of striped marlin from the same region (W = 22, $P = 0.10$, Table S1). Blue marlin had lower δ^{15}N than blue shark and porbeagle from TAS (W = 82 and 8 respectively, both $P < 0.05$, Table S1).

Hypervolume-based trophic niche size ranged from 1.67‰^{2} for blue marlin to 106.12‰^{2} for swordfish (Fig. 3, Table 1). Overall, high stable isotope niche space overlap occurred among species of the same trophic group, independent of regional differences (i.e. TG1–3, Fig. 3, Supplementary Fig. S1). For example, for TG1, swordfish from STW and TAS displayed the highest overlap (77.79%, Fig. 3, Fig. S1). Within TG2, species exhibited considerable overlap, particularly between albacore and bigeye tuna from STW (71.88%) and southern bluefin tuna from TAS and yellowfin tuna from STW (73.73%, Fig. 3, Fig. S1). In TG3, stable isotope niche space overlap exhibited high variability from 6.69% (blue marlin STW *v.* shortfin mako TAS) to 67.05% (striped marlin STW *v.* blue shark TAS, Fig. 3, Fig. S1). Stable isotope niche space overlap was generally low between species from different trophic groups, and for some species pairs was nearly absent, such as for albacore tuna and blue marlin from STW (2.79%, Fig. 3, Fig. S1).

Trophic position

The TP significantly differed among trophic groups (H = 137, $P < 0.0001$, Fig. 4). The TP of TG3 differed from TG1 and TG2 (W = 1123 and 1672 respectively, both $P < 0.001$), but there was no significant difference in TP between TG1 and TG2 (W = 12304, $P = 0.29$, Fig. 4). The TG3 had the highest mean TP (3.85 ± 0.62) followed by TG1 (2.80 ± 0.84) and TG2 (2.78 ± 0.62, Fig. 4). There was no difference in TP across oceanic regions for swordfish (H = 0.81, $P = 0.37$). Within TG2, there were significant differences in TP (H = 79.90, $P < 0.0001$) with southern bluefin tuna from TAS having significantly lower TP than all species in TG2 except yellowfin tuna and porbeagle from STW (W = 398 and 428 respectively, both $P > 0.05$). Southern bluefin tuna from STW also had significantly higher TP than yellowfin tuna from the same oceanic region (W = 72, $P < 0.05$). The TP among species differed significantly within TG3 (H = 3.392, $P < 0.0001$), with blue shark from STW showing lower TP than all TG3 species apart from striped marlin from the same region (W = 22, $P = 0.72$). Additionally, blue marlin from STW exhibited lower TP than blue shark from TAS and porbeagle from TAS (W = 31 and 8 respectively, both $P < 0.05$).
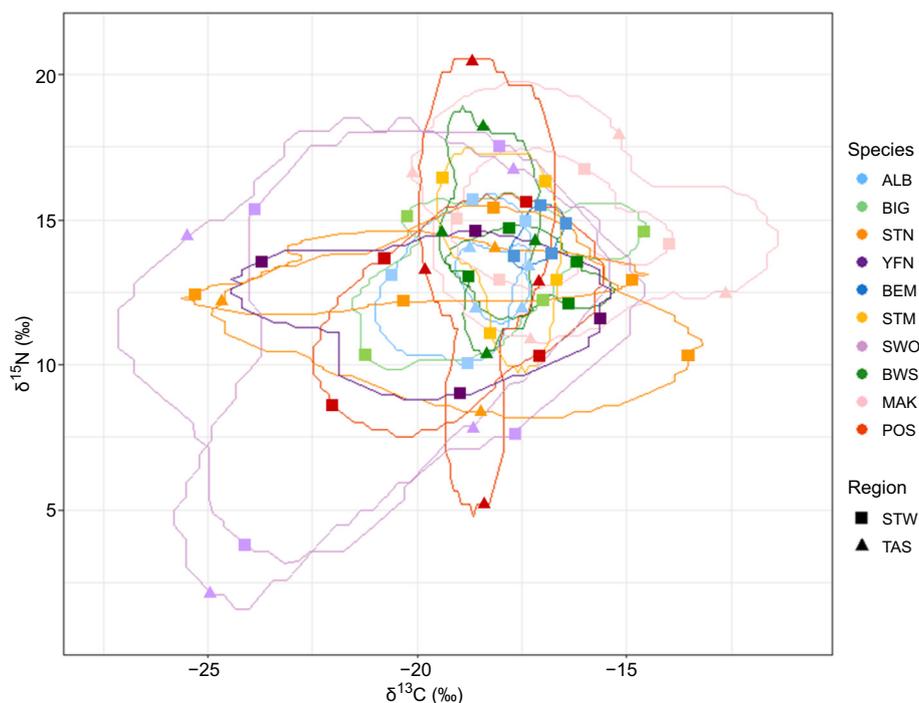

Fig. 3. Trophic niche hypervolumes for highly migratory species collected in New Zealand waters. Species are abbreviated as in Table 1 and colour coded according to the legend. Regions of collection are indicated by squares (Subtropical water, STW) and triangles (Tasman Sea, TAS).
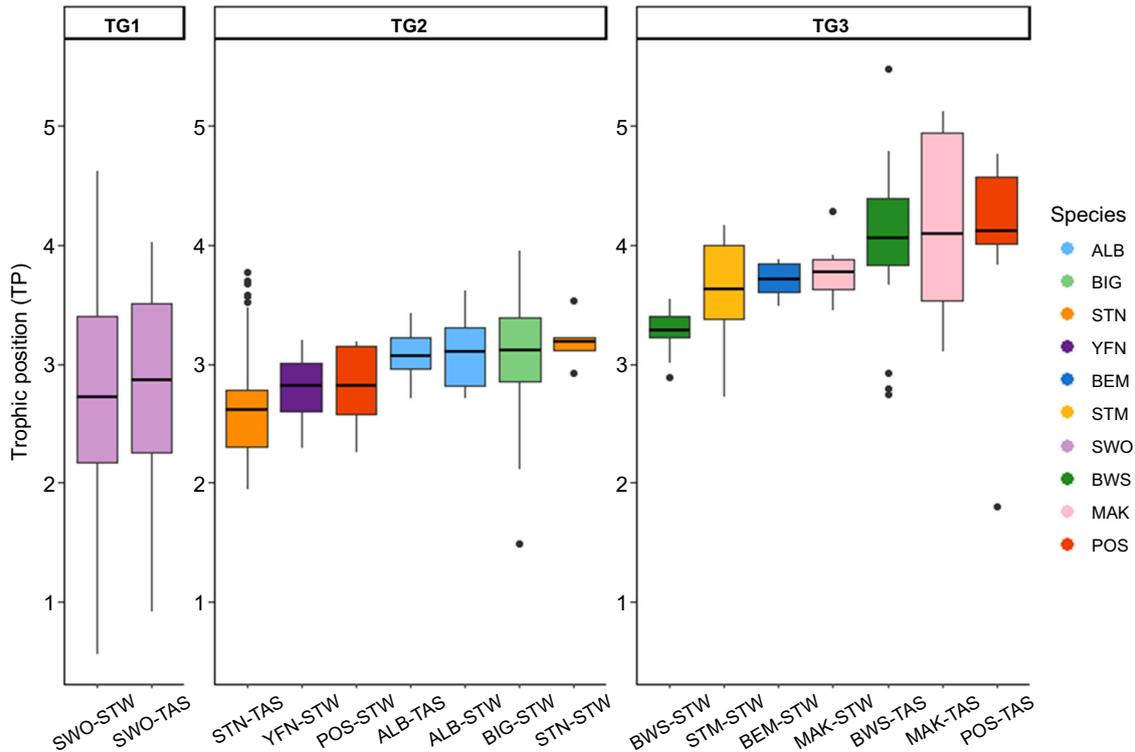
Fig. 4. Trophic position of highly migratory species collected in New Zealand waters following the scaled $\Delta^{15}N$ framework approach based on a dietary $\delta^{15}N$ value-dependent model (Hussey *et al.* 2014a, 2014b). Trophic group (TG) number corresponds to the trophic groups determined by cluster analysis (see Fig. 2). Species are abbreviated as in Table 1 and colour coded according to the legend. STW and TAS indicate collection regions: subtropical water and the Tasman Sea respectively. The black middle line of boxplots represents the mean trophic position of each species and black points indicate outliers.

Size-related variation

Albacore from TAS had a positive and significant relationship between size and $\delta^{13}C$ (Table S2 and Fig. S2). Four species – albacore and swordfish from TAS and bigeye tuna and blue shark from STW – showed a significant relationship between size and $\delta^{15}N$ (Table S2 and Fig. S2). Albacore showed a negative relationship between size and $\delta^{15}N$, with smaller individuals having higher $\delta^{15}N$ than larger individuals (Table S2 and Fig. S2). By contrast, larger bigeye tuna, swordfish and blue shark exhibited higher $\delta^{15}N$ compared to smaller individuals (Table S2 and Fig. S2).

Discussion

The findings of the present study suggest that a group of 10 HMS, which co-occur in New Zealand waters for at least part of the year, exhibited a broad range of resource-use strategies likely connecting ecosystems across substantial spatial and temporal scales. Inherent variability in stable isotope ratios at both the community and species levels reflected species-specific foraging behaviours and migration routes. However, considering the limited sample sizes from some species

(i.e. yellowfin tuna and blue and striped marlin) and the restriction of other species to a single life stage (i.e. albacore and shark species) results should be interpreted cautiously, as they may not fully capture variation in diet or habitat use within these species.

Foraging habitats

The first aim of this study was to determine potential long-distance migration movements of 10 HMS across the south-west Pacific Ocean, with a second aim of examining their trophic interactions and niche overlap. The broad range of stable isotope ratios obtained indicates that the studied species likely exploit multiple basal carbon and nitrogen sources. This heterogeneity is likely attributable to the highly mobile and wide-ranging nature of HMS, which traverse large areas over short periods of time (which are often shorter than the integration timeframe of the tissue types being analysed). Muscle samples used in this study have a slow tissue turnover rate (on the order of many months) and therefore represent an integrated diet over that time period (which is also integrated over the migration route relating to that timeframe). This can result in variable stable isotope ratios among individuals with similar diets sampled in similar locations (Trueman *et al.* 2012;

Richert *et al.* 2015), presenting problems in assigning a feeding area to an individual based on their stable isotopes. Accurate interpretation of stable isotopes in HMS sampled around New Zealand therefore requires contextualisation within the stable isotope landscape of the south-west Pacific Ocean, while accounting for each species' migratory pathways and habitat use.

In the south-west Pacific Ocean, the $\delta^{13}C$ gradient in POM is well-defined, with values ~−16‰ at the Equator, gradually decreasing to −32‰ along the Antarctic shelf (Tagliabue and Bopp 2008; Verwega *et al.* 2021). Poleward of 40°S, $\delta^{13}C$ exhibits minimal longitudinal variation (Magozzi *et al.* 2017; St John Glew *et al.* 2021), though notable variability occurs near south-east Australia (−27 to −16‰) and around New Zealand (−32 to −19‰; Graham and Bury 2019). Tropical waters, extending from 10°N to 10°S, are isotopically homogeneous, with higher $\delta^{13}C$ from −19‰ to −16‰ near Papua New Guinea (Graham and Bury 2019). Compared to $\delta^{13}C$, the nitrogen baseline in the south-west Pacific Ocean remains poorly defined, with relatively few studies available (Houssard *et al.* 2017; St John Glew *et al.* 2021). Low $\delta^{15}N$ (−1 to 2‰) occurs east of Australia (10–25°S), increasing eastward to 11.1‰ in the South Pacific Subtropical Gyre (Houssard *et al.* 2017). Higher $\delta^{15}N$ is also observed near landmasses such as New Zealand and southern Tasmania (St John Glew *et al.* 2021). In addition to geographic variations, depth-related gradients in $\delta^{13}C$ and $\delta^{15}N$ have also been observed in POM, with deeper samples showing lower $\delta^{13}C$ (Griffith *et al.* 2012; Cavagna *et al.* 2013; Close *et al.* 2014) and higher $\delta^{15}N$ relative to shallow-water counterparts (Hannides *et al.* 2009; Hannides *et al.* 2013; Gloeckler *et al.* 2018).

Stable isotope data from HMS around New Zealand highlighted diverse feeding strategies and migration patterns for these species, with differences in stable isotope niche space likely driven by species-specific foraging behaviours and migration routes. Swordfish exhibited the broadest stable isotope niche space, spanning a wide range of $\delta^{13}C$ and $\delta^{15}N$. This spread likely reflects their extensive lateral movements across the south-west Pacific Ocean, with seasonal migrations between tropical spawning regions and temperate foraging grounds (Holdsworth *et al.* 2010; Evans *et al.* 2014). Swordfish also exhibit a broad vertical distribution, which can influence $\delta^{13}C$ and $\delta^{15}N$ through depth-related baseline shifts if feeding occurs during dives (Logan and Lutcavage 2013). Given our results, a mixed influence of these two observations seems plausible, particularly as low $\delta^{13}C$ was observed with both low $\delta^{15}N$ (i.e. potentially reflecting feeding in tropical regions) and high $\delta^{15}N$ (i.e. potentially reflecting diving foraging behaviour, see Fig. 2). A large sample size ($n = 87$) may have also increased the likelihood of capturing a wider range of feeding strategies and migratory behaviours compared to other studied HMS with low sample sizes (e.g. marlin species).

Tuna species also exhibited diverse stable isotope patterns, likely reflecting their seasonal abundance around New Zealand (Mckenzie 1964). Southern bluefin tuna showed substantial $\delta^{13}C$ variability, consistent with known seasonal migration routes between the Great Australian Bight, the Indian Ocean and waters around New Zealand (Patterson *et al.* 2008; Patterson *et al.* 2018). However, some individuals of this species (likely non-spawners) are known to remain year-round in the Tasman Sea (Evans *et al.* 2012), which may account for the observed similarities in stable isotope ratios among certain individuals in this study. Albacore and bigeye tuna showed less variation in $\delta^{13}C$ compared to southern bluefin tuna. Tagging studies in the Coral Sea indicated that bigeye tuna mostly remain within 1800 km of release sites, with juveniles resident year-round (Gunn *et al.* 2005). Parasite data from albacore caught around New Zealand suggest that juvenile albacore move south to New Zealand from the tropics and do not return until the onset of sexual maturity (Jones 1991). The lower variability in $\delta^{13}C$ in albacore and bigeye tuna, along with the small mean size of albacore sampled, may indicate localised feeding strategies in the Tasman Sea near New Zealand's South Island.

Marlins and sharks occupied the most constrained stable isotope niche spaces of all trophic groups studied. Their stable isotope ratios were generally limited to low $\delta^{13}C$ and elevated $\delta^{15}N$, suggesting localised, higher trophic foraging within New Zealand's waters. Marlins and sharks sampled in this study likely exhibited residency sufficient to reflect localised feeding strategies. Striped marlin tagged off the New Zealand coast have been observed to move offshore following release, usually heading north or north-east (Holdsworth *et al.* 2009; Sippel *et al.* 2011). Blue shark, shortfin mako and porbeagle exhibited similar but more restricted movements, generally remaining close to, or entirely within, waters north of New Zealand, with juveniles showing prolonged site fidelity to coastal and shelf-edge habitats (Francis *et al.* 2015, 2019; Elliott *et al.* 2022). Therefore, it is possible that marlins and sharks forage in the same region (i.e. warmer water to the north of New Zealand) for discrete temporal periods, a pattern likely reflected in their stable isotope ratios.

Ecological role

Variation in estimated TP was considerable (0.55–5.48), with most species feeding across multiple trophic levels, suggesting individual differences in trophic interactions. This is consistent with the variability in basal carbon and nitrogen sources discussed earlier, with differences observed both within New Zealand waters and across the broader south-west Pacific Ocean. For the species studied, TP were similar to other studies using stable isotope methods (Kiszka *et al.* 2015; Li *et al.* 2016; Chandelier *et al.* 2023) and were also comparable to studies using stomach content analysis (Cortés 1999). Results from this study showed that, around New Zealand, HMS occupy high trophic levels. Overall, pelagic sharks had the highest TP (3.83 ± 0.68) followed by billfishes (2.91 ± 0.85) and tuna (2.78 ± 0.45), consistent with the

evaluation of the diets of HMS in New Zealand waters (Horn *et al.* 2013).

Swordfish and tuna had similar estimated mean TP (2.80 ± 0.85 and 2.78 ± 0.45 respectively), but were lower than marlin and pelagic shark species, indicating the former group were secondary consumers. In New Zealand, the diet of swordfish is composed of approximately three-quarters fish, primarily large mesopelagic species, with the remainder comprising squid, leading to an elevated TP (Horn *et al.* 2013). Therefore, it is surprising that swordfish exhibited relatively low estimated TP in this study. Similar to swordfish, southern bluefin tuna exhibited considerable variations in their TP compared to other tuna species. An inherent problem with assigning a discrete baseline organism to estimate stable isotope-based TP is the potential for temporal and spatial variations in trophic baseline stable isotopes. When examining TP of predators, especially for HMS, residency and movement across multiple regions makes assignment to a particular food web problematic and inappropriate, a known caveat of stable isotope food web analysis of migratory species (Post 2002; Hussey *et al.* 2014a, 2014b). In this study, individuals feeding across multiple diverse food webs over the timeframe that stable isotope ratios are incorporated into muscle tissue (months to years) have certainly influenced TP estimations. This effect is likely to be pronounced in swordfish and southern bluefin tuna, which had large variations in stable isotope ratios, leading to a potential mismatch for certain individuals between their actual TP and those estimated from local baseline stable isotope ratios. This observation highlights the importance of considering individual species' migratory patterns and the variability in stable isotope baselines across the regions where those organisms have been feeding when interpreting TP of HMS.

Future studies should aim to track HMS to establish their migratory trajectories and likely feeding locations and measure synoptic regional and seasonal δ^{15}N baselines to more accurately assess the TP of these species. Adding compound-specific stable isotope analysis (CSIA) of nitrogen in amino acids to such studies would also enable more accurate TP to be calculated, as a consumer sample contains 'source' and 'trophic' amino acids (McClelland and Montoya 2002; Hannides *et al.* 2009), allowing for the simultaneous determination of both the stable isotopic composition of primary producers and the consumer's TP (Popp *et al.* 2007; Olson *et al.* 2010). Unfortunately, utilisation of CSIA methods was outside the financial scope and timing of this study.

Relatively similar bulk stable isotope ratios and a high degree of overlap among tuna suggested that they fulfil similar trophic roles across their distribution in New Zealand waters. Although similar TP and stable isotope ratios among tuna might indicate foraging on similar TP prey or foraging in similar habitats, species-specific trophic strategies and behavioural differences could also contribute to differentiation in their ecological roles and potentially reduce competition. For example Young *et al.* (2010) suggested that diet overlap and

potential resource competition between yellowfin and bigeye tuna is minimised by differences in depth distributions, with yellowfin tuna feeding in shallower waters (~100 m) compared to bigeye tuna (~200 m). Supporting these observations, Horn *et al.* (2013) reported the presence of deep-dwelling prey items such as crab and crayfish in the diets of bigeye tuna, but their absence in the diet of yellowfin tuna. In this study, yellowfin tuna exhibited a lower TP (2.81 ± 0.30) than bigeye tuna (3.11 ± 0.46), consistent with the deeper foraging habitats of big-eye tuna, as δ^{15}N of tuna muscle tissue (and by extension the TP) increases with depth (Lorrain *et al.* 2015; Houssard *et al.* 2017). Additionally, bigeye tuna forage at similar depths to albacore but feed day and night, whereas albacore feed mainly in the daytime (Young *et al.* 2010). In this study, albacore and bigeye tuna from STW had comparable mean TP (3.11 ± 0.36 and 3.11 ± 0.46 respectively), consistent with their overlapping foraging depth ranges but differing temporal feeding behaviours, differences that cannot be discerned through stable isotope analysis. Porbeagle from STW, which exhibit a low TP (2.82 ± 0.43) were grouped with the tuna species. Most porbeagle from STW were young-of-the-year (YOY) based on total length (Francis 2015) likely contributing to their grouping with tuna species, as they may rely on lower TP prey. The clustering of YOY porbeagle with tuna species highlights the importance of considering ontogenetic factors and dietary shifts when interpreting trophic relationships in oceanic predators.

Marlin and pelagic shark species displayed significantly higher mean TP (3.85 ± 0.62) than the tuna and swordfish. However, significant differences in TP were observed among species within this trophic group. Overall, our results revealed that pelagic sharks fed at a higher TP than marlins (3.89 ± 0.64 and 3.66 ± 0.37 respectively) with these observations supported by stomach content analysis. The diets of blue shark, shortfin mako and porbeagle mainly comprise pelagic fish (e.g. Ray's bream, *Brama* sp.), cephalopods and occasionally smaller sharks and rays, with dietary composition also varying among these species (Horn *et al.* 2013). For example, the abundance of cephalopods is highest in blue shark (50.4%), followed by porbeagle (31.2%) and shortfin mako (10.1%, Horn *et al.* 2013). Comparatively, blue marlin are known to preferentially feed on scombrids and squid of highly varying size, whereas striped marlin rely largely on mid-sized schooling teleosts (Horn *et al.* 2013). Therefore, the clustering of marlins with pelagic sharks and the absence of significant differences in TP was surprising, as it suggests these species share similar ecological roles despite potential differences in foraging strategies.

Many shark individuals sampled were small, indicating a prevalence of juveniles (Francis 2015, 2016b; Francis and Ó Maolagáin 2016). In New Zealand waters, both pelagic shark species show ontogenetic changes in diet, with larger mesopelagic species becoming more abundant in the diet as the sharks grew, whereas smaller mesopelagic species decreased in abundance (Horn *et al.* 2013). Therefore, the smaller sized

categories of the sharks sampled during this study may have led to similar trophic interactions to those of blue marlin and striped marlin, as juvenile sharks display different dietary preferences and foraging strategies compared to adults. Additionally, the low sample size for blue and striped marlin ($n < 10$ individuals) may have limited the ability to fully capture their trophic dynamics, potentially influencing the robustness of comparisons with other species. It is also possible that stable isotope analysis may have not offered high enough resolution to discern trophic differences among these species in New Zealand waters. Indeed, if foraging in the same region and on similar phytoplankton-derived food webs, marlins and sharks would exhibit similar $\delta^{13}C$ (Bird *et al.* 2018), and possibly similar $\delta^{15}N$ depending on prey TP, even when feeding on different prey.

Several studies have demonstrated that $\delta^{13}C$ and $\delta^{15}N$ overestimate overlapping foraging areas by not reflecting the importance of coastal–oceanic gradients and foraging depths (Kiszka *et al.* 2015; Plumlee and Wells 2016; Curnick *et al.* 2019). In eastern Australia, similar to this study, blue and striped marlin had similar $\delta^{13}C$, suggesting little overall difference between the prey sources or food webs utilised by these two species (Guillemin *et al.* 2022). However, when using $\delta^{34}S$ as a third natural tracer the same study found that blue marlin had less coastal and benthic dietary influence than striped marlin (Guillemin *et al.* 2022). Similarly, in southern Baja California Sur, blue shark and shortfin mako had similar $\delta^{13}C$ and $\delta^{15}N$ but mercury levels in the sharks' tissues suggested that blue sharks forage in deeper waters than shortfin mako (Besnard *et al.* 2021). This complexity emphasises the need for further research integrating tracking device data, stomach content analysis, an array of stable isotope analyses ($\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$), CSIA of nitrogen in amino acids and trace metal analyses to provide insight into multiple dimensions of HMS ecology and to better understand the full range of their trophic roles in pelagic ecosystems.

Regional and ontogenetic variation

The third aim of this study was to assess variations in trophic roles of HMS, considering differences in capture locations and body size. Although intraspecific regional differences in $\delta^{13}C$ and $\delta^{15}N$ were observed for some species (albacore, southern bluefin tuna and blue shark) relatively low spatial variation in the stable isotope niche space and overlap among HMS suggest that these relationships are likely consistent across the two study regions (Shiffman *et al.* 2019). However, a robust interpretation of these patterns is difficult due to the variable sample sizes and the potential for HMS to traverse multiple oceanic regions. Additionally, whereas isoscapes are available on a global scale, these large-scale models and datasets often lack regional finer-scale spatial stable isotope variability specific to New Zealand to fully interpret stable isotope data for species of interest.

Assessing size-based differences in trophic interactions among HMS are crucial for a more comprehensive understanding of ecosystem function and to assess the ecological role of these organisms. In this study, bigeye tuna, swordfish and blue shark demonstrated ontogenetic shifts in diet, supporting the idea that larger individuals tend to consume higher TP prey (Grubbs 2010). However, it will be important to increase sampling of juvenile and mature adult fishes to fully test this hypothesis. Unlike other HMS, albacore collected in TAS had a negative correlation between $\delta^{15}N$ and size, but a positive correlation between $\delta^{13}C$ and size. Small individuals (FL < 80 cm) had the highest $\delta^{15}N$ and the lowest $\delta^{13}C$ compared to intermediate size fish (FL = 80–110 cm). As previously discussed, juvenile albacore migrate south to New Zealand from the tropics and do not return until the onset of sexual maturity (Jones 1991). Therefore, it is possible that the observed stable isotope patterns of lower $\delta^{15}N$ and higher $\delta^{13}C$ in larger individuals indicate habitat shifts that occur as albacore mature.

Conclusion

In this study, large variations in $\delta^{13}C$ and $\delta^{15}N$ and a high degree of stable isotope overlap were observed among 10 HMS captured in New Zealand waters. The high degree of overlap was particularly evident among taxonomically similar species (i.e. tuna, marlins and pelagic sharks), suggesting that these species share similar trophic roles, despite potential differences in other feeding attributes (e.g. water depths and time). Differences in stable isotope niche space indicated that some species had either high inter-individual variability or that some species rely on different basal sources from multiple regions. Overall, HMS occupy high TP, with some species exhibiting considerable variation in their TP. Together, these observations support the idea that HMS are a major component of the top predator guild in oceanic ecosystems, connecting spatially distinct habitats across large scales. Interpreting stable isotope ratios of HMS therefore requires careful considerations, including residency duration, migration route, tissue integration timeframes, stable isotope fractionation and baseline stable isotope sources across migration routes, which are not always available. Stable isotope analysis can thus be a powerful tool to examine the ecology and behaviour of HMS, particularly if combined with other complementary analytical methods; however, the study of organisms that potentially traverse and feed across oceanic basins will always provide interpretive challenges.

Supplementary material

Supplementary material can be accessed from the article page online.

Reference

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