

ORIGINAL ARTICLE



WILEY

Trait-based analyses reveal global patterns in diverse diets of albacore tuna (*Thunnus alalunga*)

Natasha A. Hardy¹ | Cindy Matuch² | Zachary Roote¹ | Iris George¹ | Barbara A. Muhling^{3,4} | Michael G. Jacox^{5,6} | Elliott L. Hazen^{4,5} | Steven J. Bograd^{3,5} | Larry B. Crowder⁷ | Stephanie J. Green¹

¹Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada

²University of California Santa Cruz, Santa Cruz, California, USA

³Institute of Marine Sciences, University of California Santa Cruz, Santa Cruz, California, USA

⁴NOAA Southwest Fisheries Science Center, La Jolla, California, USA

⁵NOAA Southwest Fisheries Science Center, Environmental Research Division, Monterey, California, USA

⁶NOAA Physical Sciences Laboratory, Boulder, Colorado, USA

⁷Hopkins Marine Station of Stanford University, Pacific Grove, California, USA

Correspondence

Natasha A. Hardy and Stephanie J. Green, Department of Biological Sciences, CW 422 Biological Sciences Building, University of Alberta, Edmonton, AB T6G 2E9, Canada.
Email: nahardy.wildlife@gmail.com and stephanie.green@ualberta.ca

Funding information

Marine Environmental Observation Prediction and Response Network, Grant/Award Number: 0052372; NOAA Climate and Fisheries Adaptation CAFA Program, Grant/Award Number: NA20OAR4310507; NOAA Coastal and Ocean Climate Application COCA Program, Grant/Award Number: NA17OAR4310268; Pew Charitable Trusts Lenfest Ocean Program, Grant/Award Number: 00032174

Abstract

Simplifying complex species interactions can facilitate tracking and predicting functional responses to ecological stressors. This is important for highly migratory pelagic predators, exploiting diverse prey fields as they respond to dynamic environments. We reconstructed the historical resource use of albacore tuna (*Thunnus alalunga*) globally from the 1900s to 2015 and confirmed highly biodiverse diets with 308 prey species, and an additional 238 taxa at coarser taxonomic resolution. We synthesised prey diversity into seven functional trait guilds using hierarchical divisive clustering algorithms as a function of four traits that describe habitat use and influence predator–prey encounter rates – prey habitat association vertically in the water column, horizontally along the coastal to pelagic gradient, seasonal and diel vertical migratory behaviour. We explored variability in historical composition of albacore diets across geographies based on species identity, individual trait information and functional trait guilds using a multi-matrix modelling framework. Taxonomic information remains important for trophic ecology, however, species-based diet composition in albacore tuna was highly variable across geographies and years sampled, making interpretation of these patterns difficult. By simplifying species identity into habitat-based traits, we highlight changes in prey resources consumed, such as the historical importance of near-surface epipelagic prey resources from coastal to oceanic habitats, and seasonally migrating continental shelf prey, with less frequent pulses of deeper water and demersal taxa. Trait information and trait guilds serve as useful classification frameworks for identifying functionally redundant food web linkages across biodiverse prey, and will prove useful in tracking predators' foraging responses to changing resource availability.

KEYWORDS

functional biogeography, highly migratory species, macro-ecology, pelagic predators, predator–prey interactions, tuna

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial](https://creativecommons.org/licenses/by-nc/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.

© 2023 The Authors. *Fish and Fisheries* published by John Wiley & Sons Ltd.

1 | INTRODUCTION

Stressors such as climate change and intensive fishing efforts (Casini et al., 2009; Poloczanska et al., 2016) are altering the distributions and composition of pelagic communities (Cheung et al., 2015; Hazen et al., 2013; Morley et al., 2018), causing widespread ecological change and undesirable ecosystem states (Molinos et al., 2016; Polovina et al., 2011). Altered pelagic ecosystems can lead to changes in fisheries production and uncertain economic futures (Bell et al., 2021; Blenckner et al., 2015; Cheung et al., 2010; Free et al., 2019). Within pelagic systems, highly migratory predators such as tunas and billfishes contribute to valuable and extensive international fisheries (Sala et al., 2018). These species evolved to migrate across ocean basin scales to exploit seasonal food resources for growth and warmer waters for reproduction (Mariani et al., 2016). However, anomalies and long-term changes in climate are producing mismatches among predator migration and the productivity of forage resources, with implications for fisheries productivity (Scheffers et al., 2016; Thackeray et al., 2010).

Accounting for trophic interactions is often the missing link to forecasting species redistributions under climate change (Green et al., 2022; Lan et al., 2021), especially for highly migratory marine species (Lehodey et al., 2010; Muhling et al., 2019). Marine species redistributions are typically predicted based on habitat use and changing physical oceanographic properties (Morley et al., 2018). Despite empirical relationships between the biomass of prey species and their prevalence in predator diets, efforts to model predator distributions in relation to the distribution of key prey are often plagued by the accuracy of prey distribution information (Muhling et al., 2019) and the number and functional redundancy of interacting species (Carroll et al., 2019; Link, 2007). These hurdles may be overcome by modelling functional ecological relationships using synthetic parameters, or traits (Green et al., 2022; Zakharova et al., 2019).

Trait-based approaches to modelling predator-prey interactions aim to simplify taxonomically complex interactions among hundreds of species by using functional ecological and non-taxonomic predictors for those relationships (Kjørboe et al., 2018; McGill et al., 2006). For example, the strength of predator-prey interactions can be modelled as a function of single or multiple individual prey trait variables influencing the predation process (Arrizabalaga-Escudero et al., 2019; Green et al., 2022). Additionally, grouping prey into 'guilds' is a common ecological practice of dimension or variable reduction (Parravicini et al., 2020; Pomerleau et al., 2015), based on shared traits describing similar trophic or other functional roles for those species (Gitay & Noble, 1997) in order to model complex species distribution and interactions. Notably, this practice is instrumental in designing diet matrices for ecosystem mass balance models or food web modelling (Hui, 2012). Functional and non-taxonomic predictors for species interactions position scientists to predict ecological outcomes in new contexts (Green et al., 2022; Kjørboe et al., 2018; McGill et al., 2006).

1.	INTRODUCTION	269
2.	METHODS	270
2.1	Historical diet data collation	270
2.2	Prey trait information	270
2.3	Prey life stage estimation	270
2.4	Trait-based analyses	272
2.4.1	Taxonomic and trait diversity in albacore diets	272
2.4.2	Albacore prey trait guilds	273
2.4.3	Trait-based and taxonomic diet variation	273
3.	RESULTS	275
3.1	Taxonomic and trait diversity in albacore diets	275
3.2	Albacore prey trait guilds	275
3.3	Historical trait-based albacore diet composition	275
4.	DISCUSSION	276
4.1	Synthesis of albacore diet diversity and historical trait relationships	276
4.2	Synthesis limitations and knowledge accessibility	278
5.	CONCLUSIONS	278
	AUTHOR CONTRIBUTIONS	279
	ACKNOWLEDGEMENTS	279
	CONFLICT OF INTEREST STATEMENT	279
	DATA AVAILABILITY STATEMENT	279
	REFERENCES	279

Functional trait-based approaches may be particularly useful for tunas because they have taxonomically broad diets (Duffy et al., 2017; Pethybridge et al., 2018) and continue to consume very small prey with increasing predator body size (Ménard et al., 2006; Portner et al., 2022; Romanov et al., 2020; Young et al., 2010). While these foraging properties make tunas salient indicator species to track changing prey communities and predator-prey interactions under climate change, they also make them excellent candidates for trait-based modelling to synthesise complex interactions with numerous prey species and to investigate evidence for selection for certain types of forage (Glaser, 2010; Valls et al., 2022). Previous diet analyses of yellowfin, bluefin, bigeye and albacore tunas revealed dietary shifts and niche partitioning across predator species and life stage, latitude and environmental drivers (Allain et al., 2012; Duffy et al., 2017; Nickels et al., 2023; Olson et al., 2016; Pethybridge et al., 2018; Portner et al., 2022; Valls et al., 2022; Young et al., 2015). Additionally, shifts in albacore distribution have previously been linked to prey availability (Pearcy, 1973). Many of these studies hypothesise about the role of traits in driving observed patterns and shifts.

However, the extent to which trait information could explicitly explain tuna foraging ecology across space and time, and to predict their resource use under changing environmental states remains poorly understood.

Using albacore (*Thunnus alalunga*) as a case study, we sought to move beyond descriptive diet analyses to identify non-taxonomic predictors for trophic relationships in highly migratory pelagic predators and commercially valuable species. Our synthesis aggregated historical data on albacore diets from published and grey literature dating from 1880 to 2020 globally. Our aims were threefold, to: (1) reconstruct historical resource use for albacore across geographies from published, aggregate, mean diet composition data; (2) use functional traits to distil diverse predator–prey interactions into key trait-based guilds; and (3) explore species-based and trait-based variability in the historical composition of albacore diets across the geographies sampled.

2 | METHODS

2.1 | Historical diet data collation

Our synthesis required quantitative data on adult or juvenile albacore diet composition obtained from stomach content analyses that identified consumed prey to species-level. To obtain these data, we compiled published and grey literature, research theses, and historical reports for albacore diets by searching bibliographic databases (Table S1) queried from 1900 until 2020 using diet analysis search terms and synonymous scientific names for albacore (*Thunnus alalunga*; Table S1). We also investigated diet reports cited within articles, which expanded our range to include several reports from the 1880s. Studies typically reported a mix of diet metrics (i.e. frequency of occurrence, numerical abundance and/or other metrics). However, except for frequency of occurrence data, few studies consistently reported on other metrics.

We obtained diet data from 26 studies that were suitable for meta-analysis (Table S2); this included 69 independent observations (i.e. by specific geographic location, region, year and/or season sampled) of adult and juvenile albacore diet composition from 1880 to 2015 and that were digitised and transcribed (Figure 1a; Table S3). Several reports presented aggregate diet information for multi-year sampling programs (Table S3) and for analyses in these cases, we used the last year of sampling completed. Albacore was typically collected either via scientific sampling programs (i.e. National Oceanic and Atmospheric Administration [NOAA], Centre National de la Recherche Scientifique [CNRS]) or in collaboration with commercial fishing operations (Bello, 1999; Glaser et al., 2015; Joubin & Rouie, 1918; Romanov et al., 2020), and using surface troll, pole-and-line, longline gear fished at specified depths (ranging from set at the surface down to over 500m in depth), or purse-seining gear (for meta-information on specific depth and sampling information for each study see Table S3).

2.2 | Prey trait information

For each prey species and life stage (i.e. larva, juvenile, adult) identified (Table S4), we collected information for four habitat use traits known to affect the likelihood of pelagic predators encountering and consuming prey (Green et al., 2019). These were: (i) vertical habitat use defined as position in the water column, and (ii) horizontal habitat association with respect to distance from the coast through to oceanic ecosystems, (iii) presence of diel vertical migration and (iv) presence of seasonal migration and/or seasonal aggregation behaviour (Table 1; Table S5). These trait data were extracted from a broader database of traits that inform predator–prey interactions for albacore (Gleiber et al., 2022, 2023). This database was created by using online repositories for species-level information, primarily FishBase (Froese & Pauly, 2020), SeaLifeBase (Palomares & Pauly, 2020), and the IUCN Red List of Threatened Species (IUCN, 2020), and by searching descriptive published literature for each species using Web of Science and Google Scholar (for detailed trait data collection methodology see Gleiber et al., 2022, 2023). We further describe how prey species' trait values were used and in some instances modified for analyses in Supporting Information: Appendix B. For example, two species primarily occur at bathypelagic depths and are classified as such in the pelagic species trait database (Gleiber et al., 2022, 2023). However, albacore do not occur beyond mesopelagic depths (Goñi et al., 2011; Nikolic et al., 2017; Williams et al., 2015), where these species are also secondarily known to occur, they were thus reclassified as mesopelagic for the purposes of inclusion in analyses for this study. Similarly, for analyses and due to low representation of certain trait-values, reef-associated and coastal prey species were combined into the 'coastal' category, and continental shelf and continental slope species were combined into 'continental shelf' (Table 1).

2.3 | Prey life stage estimation

Juvenile and adult albacore generally consume post-larval and juvenile prey life stages, as well as adults of some species (Allain et al., 2012; Muhling et al., 2019; Romanov et al., 2020). Given that traits could vary between life stages for many species and the requirement for our analyses to select one trait value per trait per species, we needed to select traits for the life stage most consumed by albacore predators for each prey species. Of the 308 identified prey species, 72 (23% of species) were reported with associated life stage information (Figure S1; Table S4). Albacore rarely consumed larvae, 11 species in total were reportedly consumed as larvae, however, six of these were consumed with <1% frequency of occurrence and % numerical abundance, and were much more commonly consumed as post-larvae or juveniles, thus only five of these 11 species were classified primarily consumed as larvae and with larval traits used for this analysis.

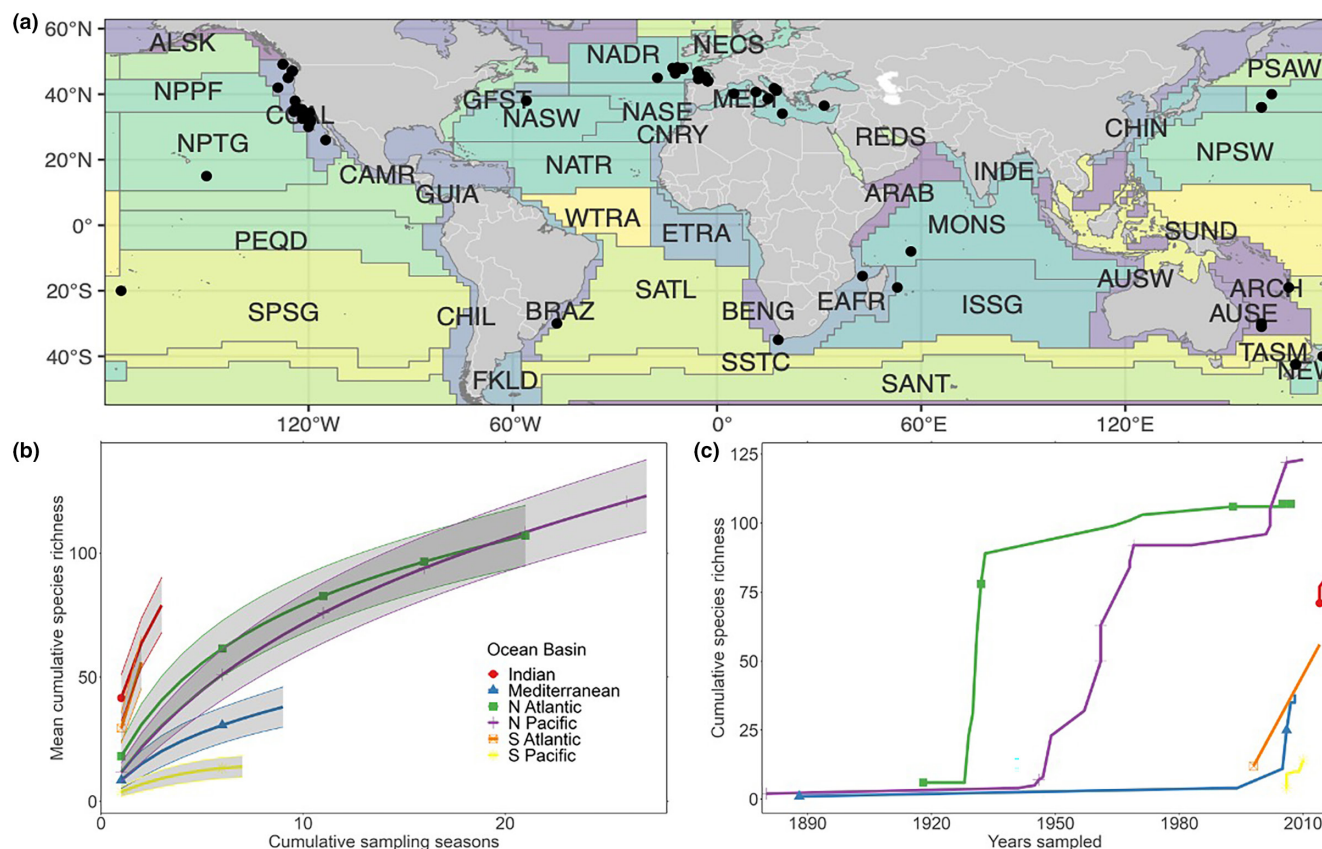


FIGURE 1 (a) Geographic distribution of published albacore diet papers, reports and grey literature from 1880 to 2020, including Longhurst biogeographical province codes (Reygondeau et al., 2013) to visualise biogeographic distribution of data. A total of 26 studies reported diet data for 69 individual sampling locations and 36 distinct sampling years. Of the 308 prey species in albacore tuna diets, we illustrate the: (b) mean species accumulation curve in relation to the number of seasons sampled in each ocean basin; and (c) step-wise species accumulation in relation to year and ocean basin sampled from the 1880's to 2015. Longhurst provinces were randomly coloured to enable better visualisation.

When specific information was not provided, it was necessary to estimate prey life stage from available information on the size and age class of either the predator or prey in each study (Figure S1; Table S4). For 15 species (~5%), prey length information was reported but not life stage. Reported total lengths ranged from 1.5 to 24.5 cm, and these prey species' life stages were therefore inferred relative to their known length at maturity (Figure S1; Table S4). There were 221 species (72%) identified in albacore diets without meta-information and assumed to be either juveniles or adults (Figure S1). Trait information was often similar between juvenile and adult life stages (Gleiber et al., 2022, 2023), thus for 127 of these species (41%), no further estimation of prey life stage was needed (Figure S1).

Trait information differed by at least one trait value and by life stage for remaining 94 prey species (31%); for example, these could include a benthic adult with a pelagic juvenile life stage (Figure S1). Here, the most plausible life stage consumed was then assessed on a case-by-case basis (described and annotated in Table S4). As albacore are epipelagic predators, the pelagic stage of these prey was most likely consumed, and albacore are more likely to consume smaller juvenile prey, for example, epipelagic juvenile hake (less than

10 cm and up to 20 cm length) than benthopelagic adult hake (~40–90 cm) (Bailey et al., 1982).

We corroborated these decisions based on calculated maxillary length (or 'gape limit') for the fork lengths (FL) of albacore sampled to determine whether adult prey could feasibly have been consumed from a published relationship between length and gape for closely related yellowfin tuna (Ménard et al., 2006; described in Supporting Information: Appendix C). Depending on the data reported, we used either a measured maximum albacore FL (51 species [16%]), or an estimated maximum FL for the population of albacore sampled for each study that did not measure or report albacore lengths sampled (43 species [14%]), as inputs to the equation (Figure S1) (Ménard et al., 2006). Albacore lengths were reported for 16 of 26 studies, and for 10 studies where albacore lengths were not reported, we coarsely matched gear-specific length data (range and mean FL) from relevant regional fisheries management organisations (ICCAT, 2020; ISC, 2006) to albacore diet studies by year and gear type used. We then estimated the likely life stage(s) sampled using region-specific age and growth curves, and sizes at maturity (described in detail for each study in Table S3). Further detail and resources used in estimating the

TABLE 1 Description of the four trait variables and values that influence the prey encounter phase of the predation process extracted from the Pelagic Species Trait Database (Gleiber et al., 2022).

Trait	Variable type	Definitions & relationships of traits for predator–prey interactions
Vertical habitat use	Categorical (demersal, epipelagic and mesopelagic)	Represents the water column position that prey resources primarily occupy. Demersal includes benthic taxa, and mesopelagic includes bathypelagic taxa
Horizontal habitat use	Categorical (coastal, continental shelf and oceanic)	Represents the typical position from coastal to offshore waters that prey resources primarily occupy. Coastal = coastal and reef associated; continental shelf = shelf and slope; oceanic = offshore taxa
Diel migration	Binary (yes/no)	Prey species, particularly at larval, young-of-year and juvenile life stages, evolved to undertake these diel migrations to avoid predation, however, visual predators in turn evolved to mirror these migrations and intercept prey at crepuscular hours. We include this trait for exploratory analyses and generation of hypotheses on how this may affect predator–prey interactions for albacore tuna
Seasonal migration	Binary (yes/no)	Represents whether prey species are seasonally abundant in the system, either in the form of seasonal spawning aggregations or seasonal migrations within the system, or local resident prey present at similar abundances year-round

Note: Described here are traits that corresponded to the most consumed prey life stage, and while species can occur elsewhere, this informs us of their main habitat use trait (Section 2.3). Note several modifications made to the data extracted with respect to selecting traits and prey life stages most commonly by albacore.

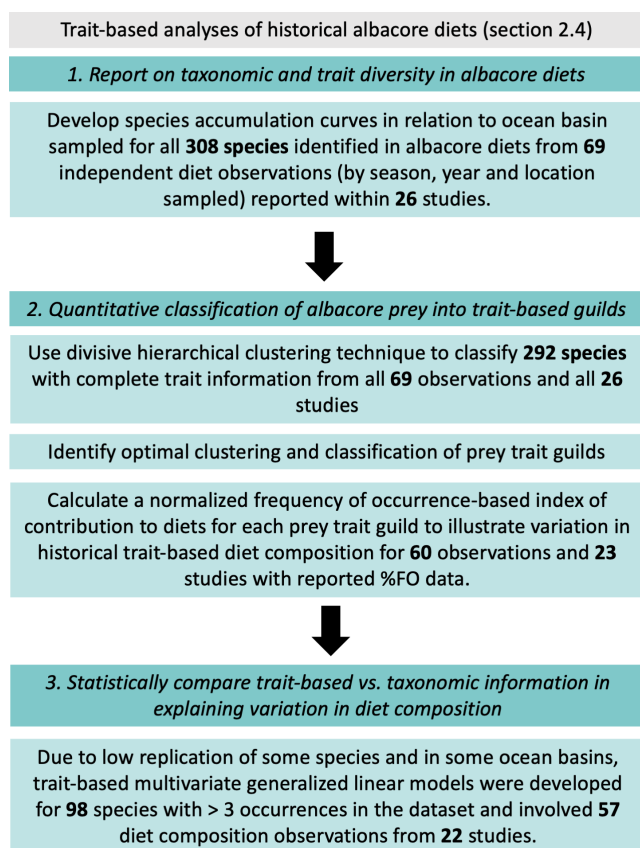


FIGURE 2 Flow chart of the workflow for statistical analyses of historical albacore diets.

mean and range in albacore lengths for a given study are further described in [Supporting Information: Appendix C](#).

Based on the results of a linear regression, there was no significant difference (p -value > .05) between the variances of mean, minimum and maximum FL for studies where these parameters were measured or where these parameters were estimated in this study

(Figure S2). This process of estimating albacore length information resulted in estimated gape limits of 6.4–11.5 cm across studies and locations sampled, and affected only 14% of decisions on prey life stage and selection of appropriate trait information, while providing useful meta-information for future studies aiming to investigate patterns in albacore diets (Figure S1). Overall, our synthesis uses the following prey life stages consumed by albacore: five larval life stages, 210 juveniles and 93 adults (Table S5).

2.4 | Trait-based analyses

The analytical workflow developed for this study is illustrated in Figure 2. All data manipulation, statistical analyses and graphical illustrations were performed in R (version 4.2.1) (R Core Team, 2022) and statistical routines and software packages used are described in reproducible detail herein. All graphical illustrations were produced in ggplot2 (v3.3.5) (Wickham, 2016).

2.4.1 | Taxonomic and trait diversity in albacore diets

To report on the historical taxonomic diversity of prey in albacore diets, species accumulation was calculated and plotted using *BiodiversityR* (version 2-14.1; Kindt & Coe, 2005) where the cumulative total number of species identified in albacore diets was calculated in relation to ocean basins and the year(s) sampled by each study. To report on the trait-based diversity of prey in relation to taxonomic diversity, species' phylogenetic information was extracted from the Open Tree of Life Data using the package *rotl* (version 3.0.12) (Michonneau et al., 2016) and parsed to a phylogenetic tree using *ape* (version 5.6-2) (Paradis & Schliep, 2019) and *stringr* (version 1.4.0) (Wickham, 2021) with integrated species-specific

TABLE 2 Model design, variables and matrices used in multi-matrix fourth corner analysis.

Diet data (L)	Trait variables (Q)	Geographic variable (R)	Model
Diet composition (SPP)	None	Ocean basin	Diet composition ~ ocean basin
	Q1 – Trait variables (Table 1, Figure 3a)		Diet composition ~ traits variables + ocean basin
	Q2 – Trait guilds (Figure 3b)		Diet composition ~ trait guilds + ocean basin

habitat use trait information (Table 1; Table S5) displayed using *ggtree* (v3.3.1.900) (Yu et al., 2017) to simultaneously visualise relationships across taxonomic and trait diversity.

2.4.2 | Albacore prey trait guilds

To simplify this large prey diversity, we aimed to quantitatively classify prey species into trait-based guilds (Figure 2). For the 292 prey species with complete trait information, key trait guilds were identified using a divisive hierarchical clustering algorithm (Anderberg, 1973; Legendre & Legendre, 1998). This was built on a Gower dissimilarity matrix for mixed variable types (here binomial and categorical) (Gower, 1971) to identify relational structure among albacore prey in relation to ecological trait data for the four habitat use variables: two binomial variables (seasonal and diel vertical migration) and two multi-level categorical variables (vertical and horizontal habitat use) (Table 1; Table S4) in *vegan* (v2.5-7) (Oksanen et al., 2020) and *cluster* (v2.1.2) (Maechler et al., 2021) and visualised using *dendextend* (v1.15.2) (Galili, 2015).

We used a consensus approach for validating cluster results and for optimising cluster selection and partition by assessing several stability and internal validation metrics (Table S6) (Brock et al., 2008). Specifically, we assessed: (1) inter-cluster variation – maximum separation of species between clusters – indicated by higher average distance between species clusters (Rousseeuw, 1987); (2) intra-cluster variance or minimum separation of species within clusters indicated by lower average distance within species clusters (Handl et al., 2005); (3) high silhouette width coefficient value and Dunn's Smith residuals (Dunn, 1974; Rousseeuw, 1987) representing optimal cluster compactness and separation qualities; and lastly, (4) optimal evenness or balance of cluster composition indicated by the number of species in each cluster (Legendre & Legendre, 1998). Trait values that influence a species' occupancy within a cluster were visualised using heat maps illustrating the importance of trait values to the composition of each cluster.

2.4.3 | Trait-based and taxonomic diet variation

Historical albacore diet composition across geographies was visualised using frequency of occurrence data from 23 studies that yielded 60 observations (independent years and locations sampled) of diet composition, because three studies in this dataset (nine observations) included presence only data and there were insufficient studies reporting numerical abundance ($n=13$ studies, 23 observations)

and mass-based ($n=10$ studies, 32 observations) information on prey contributions to diets. To visualise frequency-based contributions of prey trait guilds to albacore diets, we calculated a normalised index of contribution for each prey species relative to (i) the trait guild they were classified in and (ii) the sum of frequency of occurrence data within each observation per study. Of note, several species with incomplete trait information are therefore 'not classified' with trait guilds and are included in illustrations of diet composition.

For statistical modelling of trait-based variance in albacore diet composition across geographies, rare species that occurred once or twice in this dataset were removed. Due to overdispersion in frequency of occurrence data containing large variation in species composition values, and in order to meet model assumptions of normality, we used data on species presence/absence in diets, which was also the most consistently reported and translatable metric of contribution historically. Poorly sampled locations were excluded from further analyses (samples from South Pacific [$n=7$ observations], South Atlantic [$n=2$], and Indian [$n=3$] Oceans, altogether from four studies). We therefore compare the diet composition for albacore from sampling locations in the North Pacific ($n=27$, samples mainly come from the California Current System), North Atlantic ($n=21$, largely representing North Atlantic Drift), and Mediterranean Sea ($n=9$), providing us with 57 observations from 22 studies of albacore diet composition, and including 98 species.

We used a fourth-corner, model-based approach (Brown et al., 2014; Dray & Legendre, 2008), which builds on the generalised linear modelling (GLM) framework (Nelder & Wedderburn, 1972) to simultaneously test how the composition of albacore diets (L matrix of species presence/absence) differed as a function of two different types of explanatory variables: a geographic variable (R matrix, here containing locations sampled) and prey trait information (Q matrices), producing the trait-geographic interaction ($Q \times R$) or the fourth corner solution to a multi-matrix problem. We built three models to test the role of species identity (with no traits) or two types of trait information (individual trait values Q1 and trait guilds Q2), and geographic location (R) in explaining the presence of prey types (L) across the global data set (Table 2).

We used a binomial distribution for presence/absence data, analysed via logistic regression (with logit link function) using the *traitglm* function in the R package *mvabund* (version 4.1.12) (Wang et al., 2021). We included a species effect in models (i.e. a different intercept term for each species), akin to fitting a random effect variable to account for differences in absolute number of species occurrences (Brown et al., 2014; Wang et al., 2021). Additionally, models were fit with a LASSO penalty, specifying the fitting method as '*glm-1path*', using penalised likelihood to impose a constraint on estimates

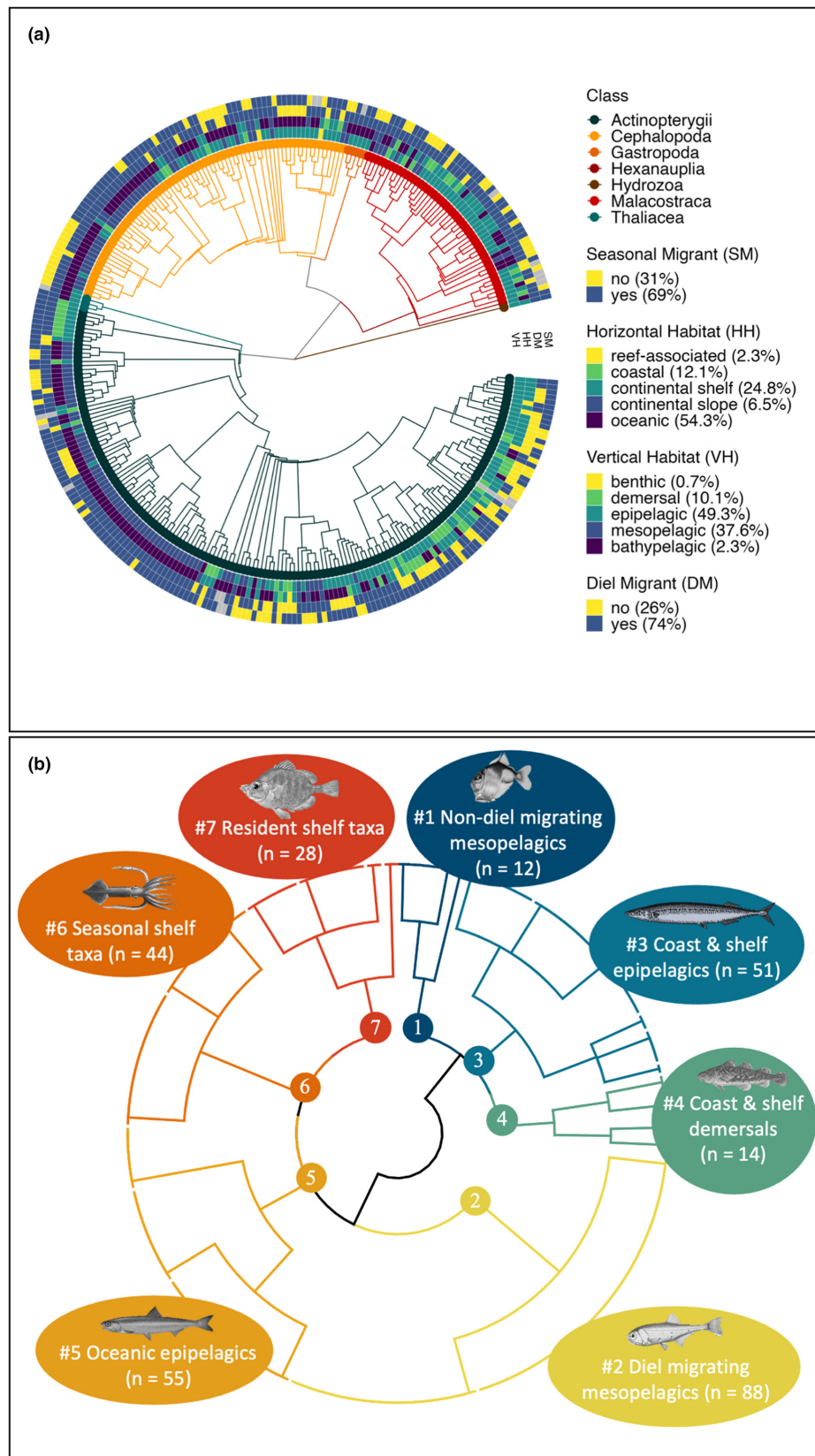


FIGURE 3 Diversity of (a) prey traits across phylogeny for 308 species (grey shading indicates no data available for a particular species and trait); and diversity quantitatively simplified to (b) radial cluster dendrogram of seven optimal albacore prey trait guilds generated by divisive hierarchical clustering for 292 species associated with complete trait information, overlaid description of the main trait values associated with each cluster (including the number of species within clusters). Traits included: vertical and horizontal habitat use, seasonal and diel vertical migration (available with trait guild information for each species in Table S5).

of model parameters (Brown et al., 2014; Hastie et al., 2009). This constraint shrinks coefficients to zero when not statistically significant, providing a combined approach for variable selection, *p*-value adjustment for multiple models and parameter estimation to evaluate the magnitude and significance of an explanatory variable (Hastie et al., 2009). Trait-geographic relationships for individual trait variables and constructed trait guilds were illustrated as heat maps indicating the interaction strength, and positive or negative correlation between trait information and geographies sampled. Model fit was assessed by plotting multivariate residuals against fitted values and plotting quantile–quantile (Q–Q) plots. Multivariate data were previously screened for broad trends using conditional boxplots (Zuur et al., 2010), for overdispersion and outliers by nMDS plots (Field et al., 1982) using *vegan*. All model assumptions were met.

3 | RESULTS

3.1 | Taxonomic and trait diversity in albacore diets

This synthesis revealed the large biodiversity of prey consumed by albacore globally (Figure 1) with 308 prey species, and 238 at coarser taxonomic resolution (Table S7). Prey species mainly hailed from seven classes representing 203 families in the total dataset including prey identified at coarser taxonomic resolution than species; ray-finned fishes (Actinopterygii, *n*=108 families of prey), cephalopods (*n*=29), and crustaceans (Malacostraca *n*=45, Hexanauplia *n*=6), and also including pelagic gastropods (*n*=6), salps (*n*=2) and one hydrozoan (Figure 3a). In addition to these classes, prey identified at finer taxonomic resolution included one appendicularian, one branchiopod and one elasmobranch (an unknown Squalidae species) (Table S7). Whilst the North Pacific, North Atlantic and the Mediterranean Sea received the greatest sampling effort and most of the albacore prey known to date were identified in these regions (Figure 1b,c). An unknown and potentially large diversity of prey remains to be identified in the South Pacific, South Atlantic, and Indian Oceans (as demonstrated by cumulative species richness curves, Figure 1b,c).

Individual traits varied across phylogeny and recurred across unrelated prey taxa (Figure 3a). The dominant habitat use trait values in the prey assemblage were those characteristic of pelagic and oceanic ecosystems, including epipelagic and mesopelagic vertical habitat use, oceanic and continental shelf horizontal habitat use, seasonal migration and aggregation behaviour, and diel vertical migration (Figure 3a).

3.2 | Albacore prey trait guilds

We obtained complete trait information for 292 prey species and these were optimally classified into seven trait guilds reflecting different combinations of four traits affecting predator–prey encounter processes, vertical and horizontal habitat use, seasonal migration and diel migration traits (Table 1, Figure 3; Supporting Information: Appendix D, Figure S4). The most species rich trait guild consisted of

diel migrating mesopelagics (trait guild 2), distinct from the least species rich non-diel migrating mesopelagics (1) (Figure 3b). The second and third most abundant groups included the oceanic (or 'offshore') epipelagics (5) and coastal and shelf epipelagics (3), followed by seasonal, continental shelf taxa (6) and resident continental shelf taxa (7) (Figure 3b). Finally, the second-rarest prey guild globally was that of the coastal and shelf demersal taxa (4) (Figure 3b). The hierarchical divisive clustering technique for seven optimal clusters performed well in grouping taxa that are also clustered based on their trait values in multivariate space (Figure S4).

3.3 | Historical trait-based albacore diet composition

Almost all trait guilds were observed in albacore diets in nearly all locations sampled (Figure 4). Albacore diet composition from the Mediterranean was characterised by consistent high reliance on seasonal shelf taxa, with differing temporal patterns of contribution to diets of resident shelf taxa, diel migrating mesopelagics and oceanic epipelagics at different points in time (Figure 4). Throughout the historical period assessed, North Atlantic samples were characterised by consistent high prevalence of samples containing seasonal shelf taxa (Figures 4 and 5). North Atlantic diet composition from the 1930's samples were characterised by a mix of most trait guilds. From 1968 however, North Atlantic diets varied mainly in contributions of the seasonal shelf taxa, coast and shelf epipelagics and oceanic epipelagics. These guilds and the diel migrating mesopelagics were also common in North Pacific diets, with greater relative contribution to diets of coast and shelf epipelagics and oceanic epipelagics than in other ocean basins (Figures 4 and 5). South Pacific samples were characterised by varying composition of oceanic epipelagics, non-diel migrating mesopelagics, seasonal and resident continental shelf species. Notably in this region, a relatively high contribution of unclassified species were observed in albacore diets lacking complete trait information. Indian Ocean observations were few, and diets included two sampling periods containing mixed composition of nearly all trait guilds, while one sampling period was dominated by coast and shelf epipelagics. Overall, non-diel migrating mesopelagics were primarily observed in diets prior to 1950's samples from the North Atlantic and in select years in the mid-2010s in the Indian Ocean and South Pacific. The coast and shelf demersals were the rarest group across geographies, observed primarily in North Pacific samples from 1946 and North Atlantic samples from 1957.

Underlying taxonomic variation in regional dietary signatures (Figure S5) was significantly explained by both trait information and trait guilds, particularly for samples from the North Pacific and the Mediterranean, although correlation coefficients for notable relationships ranged from 0.1 to 0.2 (Figure 5). The model built on individual trait information provides results on significance testing of each individual trait, while the model built on trait guilds assumes all traits used to build those guilds are of interest. It is useful to observe that the results of both models are congruent, and thus both approaches are likely interchangeable in this context.

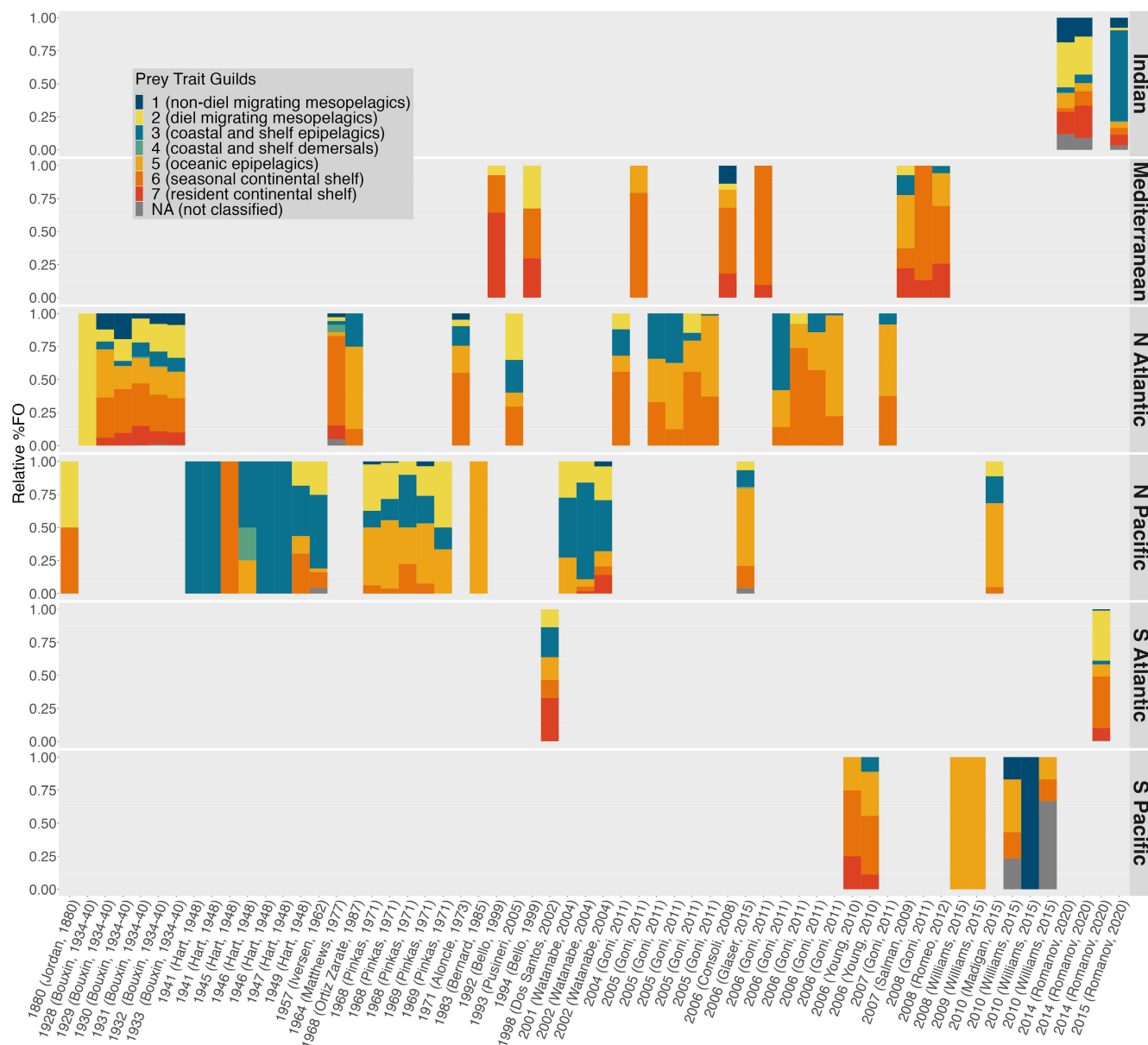


FIGURE 4 Composition of prey trait guilds within historical albacore diets (y axis; relative % frequency of occurrence [FO]) across locations and dates sampled from 1880 to 2015 (x axis; including first author and publication date information). Studies (x axis) are ordered by year from oldest on the left to most recent on the right. Diet composition is illustrated using a normalised metric of relative contribution to the total frequency of occurrence of all species within each trait guild, normalised for each replicate diet observation. Note that both samples from the 1880's only reported one or two prey items, and therefore, contain 100% of a trait guild, displayed here and not included in statistical analyses.

4 | DISCUSSION

4.1 | Synthesis of albacore diet diversity and historical trait relationships

We reconstructed historical resource use for albacore tuna (*Thunnus alalunga*) globally, highlighting biodiverse diets in this predator ($n=308$ prey identified to species, plus an additional 238 prey taxa identified to genus or higher). We quantitatively synthesised this large prey diversity into seven functional trait guilds using four sets of traits influencing predator–prey encounter rates: prey vertical and

horizontal habitat association, seasonal and diel vertical migration behaviour. Trait guilds included: diel migrating mesopelagics, non-diel migrating mesopelagics, oceanic epipelagics, coastal and shelf epipelagics, coastal and shelf demersal taxa, seasonal continental shelf and resident continental shelf taxa. Importantly, this study identifies both taxonomic and trait-based variability in diets of albacore tuna globally and identifies trait-based dietary signatures in albacore beyond taxonomic variability.

Our results indicate that both trait information and constructed functional trait guilds serve as useful classification tools for tracking large-scale shifts in albacore diets in time and space. Importantly,

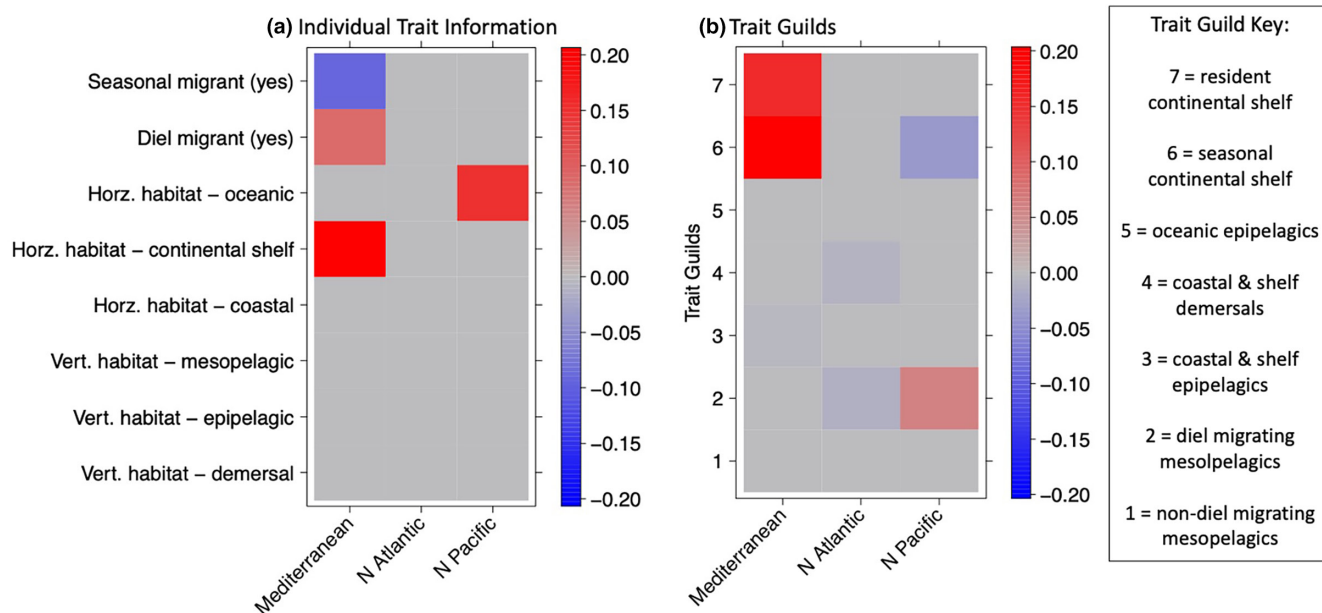


FIGURE 5 Correlation coefficients for the trait-geographic relationship modelled using the fourth corner solution for (a) individual trait information (Horz=horizontal habitat use, in relation to the coast; Vert=vertical habitat use, in relation to water column position), and (b) the trait guilds model and their interaction with the explanatory variable for ocean basin sampled. Coefficients for all trait values to geographic interactions are presented using a (GLM)-LASSO model (Brown et al., 2014). Significant trait-based relationships between albacore diet composition and geography sampled are coloured in relation to their correlation coefficient, the strength and direction of the relationship.

trait-based frameworks categorise or condense long lists of diverse prey and functionally redundant food web linkages (Link, 2007) into simpler and tractable groups based on ecological function, and rendering that diversity more interpretable, especially salient for highly migratory pelagic predators. Here, we display the results of two models: (1) built using individual trait information which provides results on significance testing of individual trait information when assessing individual trait importance is needed, and (2) built on trait guilds where the user has assessed that a functional grouping of traits is needed. While the results of both models, run simultaneously, supported each other, the individual trait information provided higher resolution information on specifically which levels of trait variables most explained variance in diet composition and for each ocean basin assessed in this meta-analysis. It is encouraging that the model built on trait guilds produced similar results, the foundation of which were individual traits, because this lends support to projects that have needed to simplify diversity in diet analyses through quantitatively or qualitatively clustering prey species into guilds (Parravicini et al., 2020; Pomerleau et al., 2015).

Traits have proven useful in describing albacore foraging dynamics in prior studies of tuna diets (Young et al., 2010). In the South Pacific, previous studies described albacore diets as largely consisting of mesopelagic and epipelagic prey, and to a lesser extent include surface migrating bathypelagic and coastal reef-associated taxa (Allain, 2005; Allain et al., 2012; Olson et al., 2016; Young et al., 2010). Albacore diets in the Indian Ocean have previously been characterised by a reliance on mixed epipelagic to mesopelagic resident prey stocks (Romanov et al., 2020). Our reanalysis of these

data within the global synthesis corroborated and extended these previous descriptive observations.

Trait information was rarely used in an explanatory capacity in the North Pacific, North Atlantic and Mediterranean. Most studies from the North Atlantic and Mediterranean, home to some of the earliest and most detailed investigations of albacore diets (especially from the 1930's; Bouxin & Legendre, 1936; Legendre, 1934, 1940), categorised the diets of albacore as 'specialised' (Consoli et al., 2008), of narrow trophic niche width (Teffer et al., 2015), and of short food chain length and low trophic adaptability (Pethybridge et al., 2018) compared to the longer food chain lengths and higher trophic complexity of Pacific tuna diets. Our re-analysis of the same data substantiates earlier observations and found that three trait guilds, based on habitat-use, accounted for a large proportion of diet composition observations from the North Atlantic and Mediterranean. Mediterranean samples were especially dominated by seasonal and resident continental shelf taxa. However, in the North Atlantic dominant prey trait guilds shifted over time, and the detailed taxonomic identification by Bouxin and Legendre in the 1930's revealed particularly trait-diverse diet composition. Trait guilds identified in samples from the North Atlantic and North Pacific were also more diverse than observed elsewhere, and included frequent consumption of and shifts between continental shelf, offshore to coastal, mesopelagic and epipelagic trait guilds.

Our study shows clear differences in trait-based diet composition across the years and locations sampled. It may be that the contribution to diets of individual species alternates and shifts across environmental gradients and inter-annual productivity cycles, whilst that of

trait guilds may be more stable and offer predictive insights (e.g. the productivity of mesopelagics and coastal to shelf epipelagics in relation to environmental shifts). Linkages between traits that describe prey habitat use and migratory behaviour, alongside prey taxonomy, to their contribution to predators provide important inference for spatial and temporal variability of forage for predators and may contribute to identification of foraging hotspots in large pelagic ecosystems.

We posit that investigating trait-based diet shifts in albacore will be a powerful framework for tracking foraging responses to environmental variability in conjunction with long-term monitoring programmes for diet data collection. As a first step towards this endeavour, we provide a systematic prey functional guild and categorisation system for reuse in albacore studies, and for many pelagic predators. This paper outlines a framework for updating and regenerating prey guilds ([Supporting Information](#)). We highlight that advances in multivariate statistical analyses can be leveraged to further link spatial and temporal relationships between complex phylogenetic and trait-based data on species consumed and environmental gradients (Brown et al., 2014; Ovaskainen et al., 2017). Further, Bayesian statistical tools can be used to provide greater inference where trait values are unknown and combined with machine learning algorithms for greater predictive power across disparate time-series data (Parravicini et al., 2020; Wisniewski et al., 2023).

4.2 | Synthesis limitations and knowledge accessibility

Investigating the extent to which varying consumption of trait guilds relates to environmental drivers and climate states will require further access to disaggregated diet data (i.e., prey from each individual predator) sampled consistently over time and space. Additionally a limitation of this study and recommendation of future work is to formally test the extent to which species taxonomic, phylogenetic and trait information explains variation in diet composition. In applying traits to analysing ecological interactions, it will be important to quantify the extent to which traits recur across unrelated taxa (i.e. phylogenetically conserved or not) (Ives & Helmus, 2011). Trait and phylogenetic information are likely not completely redundant and ideally should both be accounted for in modelling frameworks (Ovaskainen et al., 2017), as both provide different and useful information in characterising trophic interactions between albacore and their prey.

This meta-analysis highlights variable sampling of albacore tuna diets in space and time, with long gaps between studies ranging from a few years to over 50 years apart in some ocean basins. Historically, the North Pacific and Atlantic basins were the most studied and taxonomically diverse regions for albacore diet composition, with over 100 species of prey identified in each region, particularly in the productive upwelling system of the Northeast Pacific where most samples were taken in this basin (from 1942 to 2010). In contrast, Pethybridge et al. (2018) found decreased dietary diversity in the productive upwelling regions of the Southeast Pacific (from 2000 to 2015) and for which diet data for albacore were not available for this meta-analysis.

Additionally, sampled locations tended to be aggregated within biogeographic provinces of an ocean basin, such as the California Current System for the North Pacific and North Atlantic Drift for the North Atlantic. In most studies examined in this meta-analysis, samples were concentrated in either frontal, upwelling or offshore gyre zones, thus likely more indicative of regional-scale rather than basin-scale processes. We note that published or open-access historical data were sparse for the South Pacific, South Atlantic and Indian Oceans, where we expect the taxonomic and trait biodiversity of prey consumed could be larger than currently identified.

Large, disaggregated datasets are needed to further resolve resource use in highly migratory pelagic predators at both broad and finer spatial scales, including information on predator and prey sizes (e.g. lengths and widths). This information is critical to understanding ontogenic shifts in predator diets, as well as changes in forage and fisheries species productivity under changing climate states. An additional data need is that of consistent reporting of more informative metrics than frequency of occurrence, such as contribution to diets based on numerical abundance and biomass of prey consumed (Nickels et al., 2023). Indeed, several project-based, global-scale databases exist for the trophic ecology and resource use of albacore, yellowfin, bluefin and bigeye tunas (Bizzarro et al., 2022; Duffy et al., 2017; WCPFC, 2023; Young et al., 2015). The maintenance, expansion and collaborative accessibility of these datasets will enable the production of powerful and predictive models for tuna resource use under climate change. Critically, Young et al. (2015) note both a lack of long-term monitoring and inadequate sampling in some regions, and to that, we add that the availability of such data after collection is also a significant hurdle. Tewksbury et al. (2014) and Young et al. (2015) also highlight the ongoing need for international cooperation and collaboration on data.

Further, the need for sound design, maintenance and accessibility of large databases is echoed for species' trait information. Many such efforts are publicly available for some taxonomic groups and classes (Froese & Pauly, 2020; Palomares & Pauly, 2020). However, researchers often expend significant effort and personnel towards further processing data from these databases to fill knowledge gaps (Kim et al., 2018), as well as testing and creating synthetic classifications from species-level data. Knowledge on the underlying distribution of traits across environmental gradients is critical to their use as synthetic predictors in changing ecosystems (McGill et al., 2006), and thus trait-based functional groupings of species present us with powerful tools to examine linkages between species, functional responses, and environmental change (Kjørboe et al., 2018; McGill et al., 2006). This is a key knowledge gap in marine and freshwater ecosystems (Green et al., 2022).

5 | CONCLUSIONS

Syntheses of historic trophic interactions are crucial for establishing baselines in understudied systems and understanding how they may change. By digitising and reconstructing historical data

on albacore diet composition, we reveal a comprehensive taxonomic and trait-based portrait of the trophic plasticity of albacore, foundational to future analyses of variation in resource use under changing environmental and forage conditions. We condense bio-diverse diet composition of albacore by generating seven functional trait-based guilds of prey consumed, applicable beyond this work to classifying prey in albacore and other tunas. We highlight the utility of both functional trait guilds and prey trait information for synthesising variation in predator diets, which here significantly advanced our understanding of globally diverse and temporally variable albacore diets. Trait-based models revealed broad biogeographic signatures in albacore diets and corroborated known ecological differences between sampled geographies, warranting further development of trait-based analyses and investigation into the stability or flexibility of trait-based biogeographic resource use in highly migratory pelagic predators. Ultimately, further modelling applications that use trait information in predator diet analysis frameworks are needed for tracking forage species dynamics and predators' foraging responses to changing ecological states and resource variability.

AUTHOR CONTRIBUTIONS

NH led the design, data collection, analysis and writing. LC, SG and BM contributed to the framework and design of the meta-analysis. NH, SG, CM, IG and ZR co-developed data collection protocols. NH, CM, IG and ZR co-developed methods for data re-analysis and graphics. LC, SG, EH, SB and MJ acquired funding for and supervised this project, providing direct intellectual support and contributions from the conceptualization through to publication of the research. All authors contributed text and substantial revision to the final manuscript.

ACKNOWLEDGEMENTS

We are grateful to the Lenfest Ocean Program, and Pew Charitable Trust (GRANT 00032174), and MEOPAR (GRANT 0052372) for funding and regular support. Future Seas I and II (NOAA's Coastal and Ocean Climate Application COCA Program (NA17OAR4310268); NOAA's Climate and Fisheries Adaptation CAFA Program (NA20OAR4310507)). We sincerely thank Prof. David Warton in the School of Mathematics and Statistics at UNSW for support in multi-matrix modelling and use of *mvabund* R package. We thank Dr. Miram Gleiber, and all anonymous reviewers, for providing valuable feedback on manuscript drafts. We are especially grateful to innumerable scientists, fishermen, government-based ecosystem monitoring and data collection initiatives for over 100 years of historical data, collected, published, reported, archived, at least in aggregate form, and made available to us through many online requests to numerous libraries across the world. The authors sincerely thank three anonymous reviewers for their much needed attention to detail and significant improvements to drafts of the manuscript.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data and meta-information for global and historical albacore diet composition from digitised published and grey literature is publicly available through a CC BY 4.0 public-use licence with attribution to authors, and citable as follows: Hardy et al. (2023), "Replication Data for: Global synthesis of trait-based patterns in albacore tuna diets", <https://doi.org/10.5683/SP3/IDOYEN>, Borealis, V1, UNF:6:xsaxWtx/siWD1pjtPk2kOA== [fileUNF]. The code written to produce analyses and illustrations for this manuscript are publicly available through a CC BY 4.0 public-use licence with attribution to authors at this link: <https://github.com/CHANGE-Lab/albacore-diet-global.git>.

ORCID

Natasha A. Hardy  <https://orcid.org/0000-0002-9003-6204>

REFERENCES

- Allain, V. (2005). Diet of four tuna species of the Western and Central Pacific Ocean. *SPC Fisheries Newsletter*, 114.
- Allain, V., Fernandez, E., Hoyle, S. D., Caillot, S., Jurado-Molina, J., Andréfouët, S., & Nicol, S. J. (2012). Interaction between coastal and oceanic ecosystems of the Western and Central Pacific Ocean through predator-prey relationship studies. *PLoS One*, 7(5), e36701. <https://doi.org/10.1371/journal.pone.0036701>
- Anderberg, M. R. (1973). Chapter 6—Hierarchical clustering methods. In M. R. Anderberg (Ed.), *Cluster analysis for applications* (pp. 131–155). Academic Press. <https://doi.org/10.1016/B978-0-12-057650-0.50012-0>
- Arrizabalaga-Escudero, A., Merckx, T., García-Baquero, G., Wahlberg, N., Aizpurua, O., Garin, I., Goiti, U., & Aihartza, J. (2019). Trait-based functional dietary analysis provides a better insight into the foraging ecology of bats. *The Journal of Animal Ecology*, 88(10), 1587–1600. <https://doi.org/10.1111/1365-2656.13055>
- Bailey, K. M., Francis, R. C., & Stevens, P. R. (1982). *The life history and fishery of Pacific whiting, Merluccius productus*. CalCOFI Report, Vol. XXIII.
- Bell, J. D., Senina, I., Adams, T., Aumont, O., Calmettes, B., Clark, S., Dessert, M., Gehlen, M., Gorgues, T., Hampton, J., & Hanich, Q. (2021). Pathways to sustaining tuna-dependent Pacific Island economies during climate change. *Nature Sustainability*, 4(10), 900–910.
- Bello, G. (1999). Cephalopods in the diet of albacore, *Thunnus alalunga*, from the Adriatic Sea. *Journal of Molluscan Studies*, 65(2), 233–240. <https://doi.org/10.1093/mollus/65.2.233>
- Bizzarro, J. J., Curtis, K. A., Field, J., Santora, J. A., & Wells, B. (2022). *California Current Trophic Database*. NOAA ERDAP. <https://oceanview.pfeg.noaa.gov/cctd/>
- Blenckner, T., Llope, M., Möllmann, C., Voss, R., Quaas, M. F., Casini, M., Lindegren, M., Folke, C., & Chr. Stenseth, N. (2015). Climate and fishing steer ecosystem regeneration to uncertain economic futures. *Proceedings of the Royal Society B: Biological Sciences*, 282(1803), 20142809. <https://doi.org/10.1098/rspb.2014.2809>
- Bouxin, J., & Legendre, R. (1936). La faune pélagique de l'Atlantique au large du Golfe de Gascogne, recueillie dans des estomacs de Germons—Deuxième Partie: Céphalopodes. *Annales de l'Institut Océanographique*, 16(1), 1–102.
- Brock, G., Pihur, V., Datta, S., & Datta, S. (2008). CValid, an R package for cluster validation. *Journal of Statistical Software*, 25(4), 1–22. <https://doi.org/10.18637/jss.v025.i04>
- Brown, A. M., Warton, D. I., Andrew, N. R., Binns, M., Cassis, G., & Gibb, H. (2014). The fourth-corner solution – Using predictive models to understand how species traits interact with the environment.

- Methods in Ecology and Evolution*, 5(4), 344–352. <https://doi.org/10.1111/2041-210X.12163>
- Carroll, G., Holsman, K. K., Brodie, S., Thorson, J. T., Hazen, E. L., Bograd, S. J., Haltuch, M. A., Kotwicki, S., Samhouri, J., Spencer, P., Willis-Norton, E., & Selden, R. L. (2019). A review of methods for quantifying spatial predator–prey overlap. *Global Ecology and Biogeography*, 28(11), 1561–1577. <https://doi.org/10.1111/geb.12984>
- Casini, M., Hjelm, J., Molinero, J.-C., Lövgren, J., Cardinale, M., Bartolino, V., Belgrano, A., & Kornilovs, G. (2009). Trophic cascades promote threshold-like shifts in pelagic marine ecosystems. *Proceedings of the National Academy of Sciences*, 106(1), 197–202. <https://doi.org/10.1073/pnas.0806649105>
- Cheung, W. W. L., Brodeur, R. D., Okey, T. A., & Pauly, D. (2015). Projecting future changes in distributions of pelagic fish species of Northeast Pacific shelf seas. *Progress in Oceanography*, 130, 19–31. <https://doi.org/10.1016/j.pocean.2014.09.003>
- Cheung, W. W. L., Lam, V. W. Y., Sarmiento, J. L., Kearney, K., Watson, R., Zeller, D., & Pauly, D. (2010). Large-scale redistribution of maximum fisheries catch potential in the global ocean under climate change. *Global Change Biology*, 16(1), 24–35. <https://doi.org/10.1111/j.1365-2486.2009.01995.x>
- Consoli, P., Romeo, T., Battaglia, P., Castriota, L., Esposito, V., & Andaloro, F. (2008). Feeding habits of the albacore tuna *Thunnus alalunga* (Perciformes, Scombridae) from Central Mediterranean Sea. *Marine Biology*, 155(1), 113–120. <https://doi.org/10.1007/s00227-008-1012-1>
- Dray, S., & Legendre, P. (2008). Testing the species traits–environment relationships: The fourth-corner problem revisited. *Ecology*, 89(12), 3400–3412. <https://doi.org/10.1890/08-0349.1>
- Duffy, L. M., Kuhnert, P. M., Pethybridge, H. R., Young, J. W., Olson, R. J., Logan, J. M., Goñi, N., Romanov, E., Allain, V., Staudinger, M. D., Abecassis, M., Choy, C. A., Hobday, A. J., Simier, M., Galván-Magaña, F., Potier, M., & Ménard, F. (2017). Global trophic ecology of yellowfin, bigeye, and albacore tunas: Understanding predation on micronekton communities at ocean-basin scales. *Deep Sea Research Part II: Topical Studies in Oceanography*, 140, 55–73. <https://doi.org/10.1016/j.dsr2.2017.03.003>
- Dunn, J. C. (1974). Well-separated clusters and optimal fuzzy partitions. *Journal of Cybernetics*, 4(1), 95–104. <https://doi.org/10.1080/01969727408546059>
- Field, J. G., Clarke, K. R., & Warwick, R. M. (1982). A practical strategy for Analysing multispecies distribution patterns. *Marine Ecology Progress Series*, 8(1), 37–52.
- Free, C. M., Thorson, J. T., Pinsky, M. L., Oken, K. L., Wiedenmann, J., & Jensen, O. P. (2019). Impacts of historical warming on marine fisheries production. *Science*, 363(6430), 979–983. <https://doi.org/10.1126/science.aau1758>
- Froese, R., & Pauly, D. (2020). *FishBase*. World Wide Web electronic publication. www.fishbase.org
- Galili, T. (2015). Dendextend: An R package for visualizing, adjusting and comparing trees of hierarchical clustering. *Bioinformatics*, 31(22), 3718–3720. <https://doi.org/10.1093/bioinformatics/btv428>
- Gitay, H., & Noble, I. (1997). What are functional types and how should we seek them? In M. M. Smith, H. H. Shugart, & F. I. Woodward (Eds.), *Plant functional types*. Cambridge University Press.
- Glaser, S. (2010). Interdecadal variability in predator–prey interactions of juvenile North Pacific albacore in the California current system. *Marine Ecology Progress Series*, 414, 209–221. <https://doi.org/10.3354/meps08723>
- Glaser, S. M., Waechter, K. E., & Bransome, N. C. (2015). Through the stomach of a predator: Regional patterns of forage in the diet of albacore tuna in the California current system and metrics needed for ecosystem-based management. *Journal of Marine Systems*, 146, 38–49. <https://doi.org/10.1016/j.jmarsys.2014.07.019>
- Gleiber, M. R., Hardy, N. A., Roote, Z., Krug-Macleod, A. M., Morganson, C. J., Tandy, Z., George, I., Matuch, C., Brookson, C. B., Daly, E. A., Portner, E. J., Choy, C. A., Crowder, L. B., & Green, S. J. (2023). The pelagic species trait database: An open data resource to support trait-based ocean research. *Scientific Data*. <https://doi.org/10.1038/s41597-023-02689-9>
- Gleiber, M. R., Hardy, N. A., Roote, Z., Morganson, C. J., Krug-Macleod, A., George, I., Matuch, C., Brookson, C. B., Crowder, L. B., & Green, S. J. (2022). *Pelagic Species Trait Database* [Data set]. Scholars Portal Dataverse [In press]. <https://doi.org/10.5683/SP3/0YFJED>
- Goñi, N., Logan, J., Arrizabalaga, H., Jarry, M., & Lutcavage, M. (2011). Variability of albacore (*Thunnus alalunga*) diet in the Northeast Atlantic and Mediterranean Sea. *Marine Biology*, 10, 1057–1073.
- Gower, J. C. (1971). A general coefficient of similarity and some of its properties. *Biometrics*, 27(4), 857–871. <https://doi.org/10.2307/2528823>
- Green, S. J., Brookson, C. B., Hardy, N. A., & Crowder, L. B. (2022). Trait-based approaches to global change ecology: Moving from description to prediction. *Proceedings of the Royal Society B: Biological Sciences*, 289(1971), 20220071. <https://doi.org/10.1098/rspb.2022.0071>
- Green, S. J., Dilley, E. R., Benkwitt, C. E., Davis, A. C. D., Ingeman, K. E., Kindinger, T. L., Tuttle, L. J., & Hixon, M. A. (2019). Trait-mediated foraging drives patterns of selective predation by native and invasive coral-reef fishes. *Ecosphere*, 10(6), e02752. <https://doi.org/10.1002/ecs2.2752>
- Handl, J., Knowles, J., & Kell, D. B. (2005). Computational cluster validation in post-genomic data analysis. *Bioinformatics*, 21(15), 3201–3212. <https://doi.org/10.1093/bioinformatics/bti517>
- Hastie, T., Tibshirani, R., & Friedman, J. (2009). *The elements of statistical learning: Data mining, inference, and prediction* (2nd ed.). Springer Science & Business Media.
- Hazen, E. L., Jorgensen, S., Rykaczewski, R. R., Bograd, S. J., Foley, D. G., Jonsen, I. D., Shaffer, S. A., Dunne, J. P., Costa, D. P., Crowder, L. B., & Block, B. A. (2013). Predicted habitat shifts of Pacific top predators in a changing climate. *Nature Climate Change*, 3(3), 234–238. <https://doi.org/10.1038/nclimate1686>
- Hui, D. (2012). Food web: Concept and applications. *Nature Education Knowledge*, 3(12), 6.
- ICCAT. (2020). *Albacore (Thunnus alalunga) Task 2 size/weight frequencies from ICCAT (as of Jan/2021) for the period 1956–2019*. Public statistical databases. <https://www.iccat.int/en/accesingdb.html>
- ISC. (2006). *Report of the ISC – Albacore Working Group Stock Assessment Workshop*. National Research Institute of Far Seas Fisheries, Shimizu.
- IUCN. (2020). *The IUCN Red List of Threatened Species*. World Wide Web publication. <https://www.iucnredlist.org>
- Ives, A. R., & Helmus, M. R. (2011). Generalized linear mixed models for phylogenetic analyses of community structure. *Ecological Monographs*, 81(3), 511–525. <https://doi.org/10.1890/10-1264.1>
- Joubin, L., & Rouie, L. (1918). Observations sur la nourriture des Thons de l'Atlantique (Germo alalonga Gmelin). *Bulletin de l'Institut Océanographique de Monaco*, 348, 21–27.
- Kim, S. W., Blomberg, S. P., & Pandolfi, J. M. (2018). Transcending data gaps: A framework to reduce inferential errors in ecological analyses. *Ecology Letters*, 21(8), 1200–1210. <https://doi.org/10.1111/ele.13089>
- Kindt, R., & Coe, R. (2005). *Tree diversity analysis. A manual and software for common statistical methods for ecological and biodiversity studies*. World Agroforestry Centre (ICRAF), Nairobi, Kenya. <http://www.worldagroforestry.org/output/tree-diversity-analysis>
- Kjørboe, T., Visser, A., & Andersen, K. H. (2018). A trait-based approach to ocean ecology. *ICES Journal of Marine Science*, 75(6), 1849–1863. <https://doi.org/10.1093/icesjms/fsy090>
- Lan, K.-W., Wu, Y.-L., Chen, L.-C., Naimullah, M., & Lin, T.-H. (2021). Effects of climate change in marine ecosystems based on the spatiotemporal age structure of top predators: A case study of bigeye tuna in the Pacific Ocean. *Frontiers in Marine Science*, 8, 614594. <https://doi.org/10.3389/fmars.2021.614594>

- Legendre, P., & Legendre, L. (1998). *Numerical ecology: Developments in environmental modelling*.
- Legendre, R. (1934). La faune pélagique de l'Atlantique au large du Golfe de Gascogne, recueillie dans des estomacs de Germons—Première Partie: Poissons. *Annales de l'Institut Océanographique*, 14, 249–418.
- Legendre, R. (1940). La faune pélagique de l'Atlantique au large du Golfe de Gascogne, recueillie dans des estomacs de Germons—Troisième partie: Invertébrés (Céphalopodes exclus). *Annales de l'Institut Océanographique*, 16, 1–99.
- Lehodey, P., Murtugudde, R., & Senina, I. (2010). Bridging the gap from ocean models to population dynamics of large marine predators: A model of mid-trophic functional groups. *Progress in Oceanography*, 84(1–2), 69–84.
- Link, J. S. (2007). Underappreciated species in ecology: “Ugly fish” in the Northwest Atlantic Ocean. *Ecological Applications*, 17(7), 2037–2060. <https://doi.org/10.1890/06-1154.1>
- Maechler, M., Rousseeuw, P., Struyf, A., Hubert, M., & Hornik, K. (2021). cluster: Cluster Analysis Basics and Extensions. *R Package Version 2.1.2*. <https://CRAN.R-project.org/package=cluster>
- Mariani, P., Krivan, V., MacKenzie, B. R., & Mullon, C. (2016). The migration game in habitat network: The case of tuna. *Theoretical Ecology*, 9(2), 219–232. <https://doi.org/10.1007/s12080-015-0290-8>
- McGill, B. J., Enquist, B. J., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, 21(4), 178–185. <https://doi.org/10.1016/j.tree.2006.02.002>
- Ménard, F., Labruno, C., Shin, Y.-J., Asine, A. S., & Bard, F.-X. (2006). Opportunistic predation in tuna: A size-based approach. *Marine Ecology Progress Series*, 323, 223–231. <https://doi.org/10.3354/meps323223>
- Michonneau, F., Brown, J. W., & Winter, D. J. (2016). Rotl: An R package to interact with the open tree of life data. *Methods in Ecology and Evolution*, 7(12), 1476–1481. <https://doi.org/10.1111/2041-210X.12593>
- Molinos, J. G., Halpern, B. S., Schoeman, D. S., Brown, C. J., Kiessling, W., Moore, P. J., Pandolfi, J. M., Poloczanska, E. S., Richardson, A. J., & Burrows, M. T. (2016). Climate velocity and the future global redistribution of marine biodiversity. *Nature Climate Change*, 6(1), 83–88. <https://doi.org/10.1038/nclimate2769>
- Morley, J. W., Selden, R. L., Latour, R. J., Frölicher, T. L., Seagraves, R. J., & Pinsky, M. L. (2018). Projecting shifts in thermal habitat for 686 species on the north American continental shelf. *PLoS One*, 13(5), e0196127. <https://doi.org/10.1371/journal.pone.0196127>
- Muhling, B., Brodie, S., Snodgrass, O., Tommasi, D., & Jacox, M. (2019). Dynamic habitat use of albacore and their primary prey species in the California current system. *CalCOFI Reports*, 60, 15.
- Nelder, J. A., & Wedderburn, R. W. M. (1972). Generalized linear models. *Journal of the Royal Statistical Society: Series A (General)*, 135(3), 370–384. <https://doi.org/10.2307/2344614>
- Nickels, C., Portner, E. J., Snodgrass, O., Muhling, B. A., & Dewar, H. (2023). Juvenile albacore tuna (*Thunnus alalunga*) foraging ecology varies with environmental conditions in the California current large marine ecosystem. *Fisheries Oceanography*, 32, 431–447. <https://doi.org/10.1111/fog.12638>
- Nikolic, N., Morandeau, G., Hoarau, L., West, W., Arrizabalaga, H., Hoyle, S., Nicol, S. J., Bourjea, J., Puech, A., Farley, J. H., & Williams, A. J. (2017). Review of albacore tuna, *Thunnus alalunga*, biology, fisheries and management. *Reviews in Fish Biology and Fisheries*, 27, 775–810.
- Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E., & Wagner, H. (2020). *vegan: Community Ecology Package*. R package version 2.5-7. <https://cran.r-project.org/web/packages/vegan/vegan.pdf>
- Olson, R. J., Young, J. W., Ménard, F., Potier, M., Allain, V., Goñi, N., Logan, J. M., & Galván-Magaña, F. (2016). Bioenergetics, trophic ecology, and niche separation of tunas. In *Advances in marine biology* (Vol. 74, pp. 199–344). Academic Press.
- Ovaskainen, O., Tikhonov, G., Norberg, A., Blanchet, F. G., Duan, L., Dunson, D., Roslin, T., & Abrego, N. (2017). How to make more out of community data? A conceptual framework and its implementation as models and software. *Ecology Letters*, 20(5), 561–576. <https://doi.org/10.1111/ele.12757>
- Palomares, M., & Pauly, D. (2020). *SeaLifeBase*. World Wide Web electronic publication. www.sealifebase.org
- Paradis, E., & Schliep, K. (2019). Ape 5.0: An environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics*, 35(3), 526–528. <https://doi.org/10.1093/bioinformatics/bty633>
- Parravicini, V., Casey, J., Schiettekatte, N., Brandl, S., Pozas-Schacre, C., Carlot, J., Edgar, G., Graham, N., Harmelin-Vivien, M., Kulbicki, M., Strona, G., & Stuart-Smith, R. (2020). Delineating reef fish trophic guilds with global gut content data synthesis and phylogeny. *PLoS Biology*, 18, e3000702. <https://doi.org/10.1371/journal.pbio.3000702>
- Pearcy, W. G. (1973). Albacore oceanography off Oregon – 1970. *Fishery Bulletin*, 71, 489–504.
- Pethybridge, H., Choy, C. A., Logan, J. M., Allain, V., Lorrain, A., Bodin, N., Somes, C. J., Young, J., Ménard, F., Langlais, C., Duffy, L., Hobday, A. J., Kuhnert, P., Fry, B., Menkes, C., & Olson, R. J. (2018). A global meta-analysis of marine predator nitrogen stable isotopes: Relationships between trophic structure and environmental conditions. *Global Ecology and Biogeography*, 27(9), 1043–1055. <https://doi.org/10.1111/geb.12763>
- Poloczanska, E. S., Burrows, M. T., Brown, C. J., García Molinos, J., Halpern, B. S., Hoegh-Guldberg, O., Kappel, C. V., Moore, P. J., Richardson, A. J., Schoeman, D. S., & Sydeman, W. J. (2016). Responses of marine organisms to climate change across oceans. *Frontiers in Marine Science*, 3, 63. <https://doi.org/10.3389/fmars.2016.00062>
- Polovina, J. J., Dunne, J. P., Woodworth, P. A., & Howell, E. A. (2011). Projected expansion of the subtropical biome and contraction of the temperate and equatorial upwelling biomes in the North Pacific under global warming. *ICES Journal of Marine Science*, 68(6), 986–995. <https://doi.org/10.1093/icesjms/fsq198>
- Pomeroy, C., Sastri, A. R., & Beisner, B. E. (2015). Evaluation of functional trait diversity for marine zooplankton communities in the northeast subarctic Pacific Ocean. *Journal of Plankton Research*, 37(4), 712–726. <https://doi.org/10.1093/plankt/fbv045>
- Portner, E. J., Snodgrass, O., & Dewar, H. (2022). Pacific bluefin tuna, *Thunnus orientalis*, exhibits a flexible feeding ecology in the Southern California bight. *PLoS One*, 17(8), e0272048. <https://doi.org/10.1371/journal.pone.0272048>
- R Core Team. (2022). R: A language and environment for statistical computing, version 4.2.1. Vienna, Austria, R Foundation for Statistical Computing.
- Reygondeau, G., Longhurst, A., Martinez, E., Beaugrand, G., Antoine, D., & Maury, O. (2013). Dynamic biogeochemical provinces in the global ocean. *Global Biogeochemical Cycles*, 27(4), 1046–1058.
- Romanov, E. V., Nikolic, N., Dhurmea, Z., Bodin, N., Puech, A., Norman, S., Hollanda, S., Bourjea, J., West, W., & Potier, M. (2020). Trophic ecology of albacore tuna (*Thunnus alalunga*) in the western tropical Indian Ocean and adjacent waters. *Marine and Freshwater Research*, 71, 1517. <https://doi.org/10.1071/MF19332>
- Rousseeuw, P. J. (1987). Silhouettes: A graphical aid to the interpretation and validation of cluster analysis. *Journal of Computational and Applied Mathematics*, 20, 53–65. [https://doi.org/10.1016/0377-0427\(87\)90125-7](https://doi.org/10.1016/0377-0427(87)90125-7)
- Sala, E., Mayorga, J., Costello, C., Kroodsma, D., Palomares, M. L. D., Pauly, D., Sumaila, U. R., & Zeller, D. (2018). The economics of fishing the high seas. *Science Advances*, 4(6), eaat2504. <https://doi.org/10.1126/sciadv.aat2504>

- Scheffers, B. R., Meester, L. D., Bridge, T. C. L., Hoffmann, A. A., Pandolfi, J. M., Corlett, R. T., Butchart, S. H. M., Pearce-Kelly, P., Kovacs, K. M., Dudgeon, D., Pacifici, M., Rondinini, C., Foden, W. B., Martin, T. G., Mora, C., Bickford, D., & Watson, J. E. M. (2016). The broad footprint of climate change from genes to biomes to people. *Science*, 354(6313), aaf7671. <https://doi.org/10.1126/science.aaf7671>
- Teffer, A. K., Staudinger, M. D., & Juanes, F. (2015). Trophic niche overlap among dolphinfish and co-occurring tunas near the northern edge of their range in the western North Atlantic. *Marine Biology*, 162(9), 1823–1840. <https://doi.org/10.1007/s00227-015-2715-8>
- Tewksbury, J. J., Anderson, J. G. T., Bakker, J. D., Billo, T. J., Dunwiddie, P. W., Groom, M. J., Hampton, S. E., Herman, S. G., Levey, D. J., Machnicki, N. J., del Rio, C. M., Power, M. E., Rowell, K., Salomon, A. K., Stacey, L., Trombulak, S. C., & Wheeler, T. A. (2014). Natural history's place in science and society. *Bioscience*, 64(4), 300–310. <https://doi.org/10.1093/biosci/biu032>
- Thackeray, S. J., Sparks, T. H., Frederiksen, M., Burthe, S., Bacon, P. J., Bell, J. R., Botham, M. S., Brereton, T. M., Bright, P. W., Carvalho, L., Clutton-Brock, T., Dawson, A., Edwards, M., Elliott, J. M., Harrington, R., Johns, D., Jones, I. D., Jones, J. T., Leech, D. I., ... Wanless, S. (2010). Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. *Global Change Biology*, 16(12), 3304–3313. <https://doi.org/10.1111/j.1365-2486.2010.02165.x>
- Valls, M., Saber, S., Gómez, M. J., Reglero, P., & Mele, S. (2022). Diet and feeding behaviour of albacore *Thunnus alalunga* in the western Mediterranean Sea during the spawning period. *Journal of Fish Biology*, 100(1), 203–217. <https://doi.org/10.1111/jfb.14935>
- Wang, Y., Naumann, U., Eddelbuettel, D., Wilshire, J., & Warton, D. I. (2021). mvabund: Statistical Methods for Analysing Multivariate Abundance Data. *R Package Version 4.1.12*. <https://CRAN.R-project.org/package=mvabund>
- WCPFC. (2023). Pacific Marine Specimen Bank (Tuna Tissue Bank). World Wide Web electronic publication. www.spc.int/ofp/PacificSpecimenBank
- Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis* (v. 3.3.5).
- Wickham, H. (2021). *stringr: Simple, Consistent Wrappers for Common String Operations*. <http://stringr.tidyverse.org>, <https://github.com/tidyverse/stringr>
- Williams, A. J., Allain, V., Nicol, S. J., Evans, K. J., Hoyle, S. D., Dupoux, C., Vourey, E., & Dubosc, J. (2015). Vertical behavior and diet of albacore tuna (*Thunnus alalunga*) vary with latitude in the South Pacific Ocean. *Deep Sea Research Part II: Topical Studies in Oceanography*, 113, 154–169.
- Wisniewski, A. L., Nations, J. A., & Slater, G. J. (2023). Bayesian prediction of multivariate ecology from phenotypic data yields new insights into the diets of extant and extinct taxa. *The American Naturalist*, 202(2), 192–215.
- Young, J. W., Lansdell, M. J., Campbell, R. A., Cooper, S. P., Juanes, F., & Guest, M. A. (2010). Feeding ecology and niche segregation in oceanic top predators off eastern Australia. *Marine Biology*, 157(11), 2347–2368. <https://doi.org/10.1007/s00227-010-1500-y>
- Young, J. W., Olson, R. J., Ménard, F., Kuhnert, P. M., Duffy, L. M., Allain, V., Logan, J. M., Lorrain, A., Somes, C. J., Graham, B., Goñi, N., Pethybridge, H., Simier, M., Potier, M., Romanov, E., Pagendam, D., Hannides, C., & Choy, C. A. (2015). Setting the stage for a global-scale trophic analysis of marine top predators: A multi-workshop review. *Reviews in Fish Biology and Fisheries*, 25(1), 261–272. <https://doi.org/10.1007/s11160-014-9368-4>
- Yu, G., Smith, D. K., Zhu, H., Guan, Y., & Lam, T. T.-Y. (2017). Ggtree: An R package for visualization and annotation of phylogenetic trees with their covariates and other associated data. *Methods in Ecology and Evolution*, 8(1), 28–36. <https://doi.org/10.1111/2041-210X.12628>
- Zakharova, L., Meyer, K. M., & Seifan, M. (2019). Trait-based modelling in ecology: A review of two decades of research. *Ecological Modelling*, 407, 108703. <https://doi.org/10.1016/j.ecolmodel.2019.05.008>
- Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, 1(1), 3–14. <https://doi.org/10.1111/j.2041-210X.2009.00001.x>

SUPPORTING INFORMATION

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

How to cite this article: Hardy, N. A., Matuch, C., Roote, Z., George, I., Muhling, B., Jacox, M. G., Hazen, E. L., Bograd, S. J., Crowder, L. B., & Green, S. J. (2024). Trait-based analyses reveal global patterns in diverse diets of albacore tuna (*Thunnus alalunga*). *Fish and Fisheries*, 25, 268–282. <https://doi.org/10.1111/faf.12807>