# **Title:** Trait-based analyses reveal global patterns in diverse albacore tuna diets

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## Abstract

Simplifying complex species interactions can facilitate tracking and predicting functional responses to ecological. This is particularly 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 and confirmed highly biodiverse diets with 308 prey species, and an additional 238 taxa at lower taxonomic resolution. We quantitatively synthesised prey diversity into 7 functional trait guilds using hierarchical divisive clustering algorithms as a function of 4 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 further 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. Although taxonomic information remains important for trophic ecology, species-based diet composition in albacore tuna was highly variable across geographies and years sampled. Trait-based models of albacore diets highlight 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. Our results indicate that trait information and trait guilds serve as useful classification frameworks for identifying functionally redundant food web linkages involving biodiverse prey, and will prove useful in tracking predators’ foraging responses to changing ecological states and resource variability.

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## 

## 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 (Hazen et al., 2013; Cheung et al., 2015; Morley et al., 2018), causing widespread ecological change and undesirable ecosystem states (Polovina et al., 2011; Molinos et al., 2016). Altered pelagic ecosystems can lead to changes in fisheries production and uncertain economic futures (Cheung et al., 2010; Blenckner et al., 2015; Free et al., 2019; Bell et al., 2021). 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 (Thackeray et al., 2010; Scheffers et al., 2016).

Accounting for trophic interactions is often the missing link to forecasting species redistributions under climate change (Lan et al., 2021; Green et al., 2022), 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 (Link, 2007; Carroll et al., 2019). These hurdles may be overcome by modelling functional ecological relationships using synthetic parameters, or traits (Zakharova et al., 2019; Green et al. 2022).

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 (McGill et al., 2006; Kiørboe et al., 2018). 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 (Pomerleau et al., 2015; Parravicini et al., 2020), 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 (McGill et al., 2006; Kiørboe et al., 2018; Green et al., 2022).

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; Young et al., 2010; Romanov et al., 2020; Portner et al., 2022). 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; Young et al., 2015; Duffy et al., 2017; Pethybridge et al., 2018; Portner et al., 2022; Valls et al., 2022; Nickels et al., 2023). 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 seek 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 aggregates historical data on albacore diets from published and grey literature dating from 1880–2020 globally. Our aims are 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.

## 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 (Supporting Information, Table S1) queried from 1900 until 2020 using diet analysis search terms and synonymous scientific names for albacore (*Thunnus alalunga*; Supporting Information, 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 (Supporting Information, 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 1880–2015 and that were digitised and transcribed (Figure 1a; Supplementary Data, Table S3). Several reports presented aggregate diet information for multi-year sampling programs (Supplementary Data, Table S3) and for analyses in these cases, we used the last year of sampling completed. Albacore were 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; Joubin & Rouie, 1918; Glaser et al., 2015; 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 500 m in depth), or purse-seining gear (for metainformation on specific depth and sampling information for each study see Supplementary Data, Table S3).

### 2.2 Prey trait information

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For each prey species and life stage (i.e., larva, juvenile, adult) identified (Supplementary Data, 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; Supplementary Data, Table S5). These trait data were extracted from a broader database of traits that inform predator-prey interactions for albacore (Gleiber et al., 2022). This database used 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 searched descriptive published literature for each species using Web of Science and Google Scholar (for detailed trait data collection methodology see Gleiber et al., 2022). 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). However, albacore do not occur beyond mesopelagic depths, 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 (Supplementary Information, Figure S1; Supplementary Data, Table S4). Albacore rarely consumed larvae, 11 species in total were reportedly consumed as larvae, however 6 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 5 of these 11 species were classified primarily consumed as larvae and with larval traits used for this analysis.

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 (Supplementary Information, Figure S1; Supplementary Data, Table S4). For 15 species (~5%),prey length information was reported but not life stage. Reported total lengths ranged from 1.5–24.5 cm, and these prey species’ life stages were therefore inferred relative to their known length at maturity (Supplementary Information, Figure S1; Supplementary Data, Table S4). There were 221 species (72%) identified in albacore diets without meta-information and assumed to be either juveniles or adults (Supplementary Information, Figure S1). Trait information was often similar between juvenile and adult life stages (Gleiber et al., 2022), thus for 127 of these species (41%), no further estimation of prey life stage was needed (Supplementary Information, 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 (Supplementary Information, Figure S1). Here, the most plausible life stage consumed was then assessed on a case-by-case basis (described and annotated in Supplementary Data, 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 Supplementary 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 out 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 Supplementary Data, Table S3). Further detail and resources used in estimating the mean and range in albacore lengths for a given study are further described in Supplementary Information, Appendix C.

Based on the results of a linear regression, there was no significant difference (p-value > 0.05) 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 (Supplementary Information, Figure S1). Overall, our synthesis uses the following prey life stages consumed by albacore: 5 larval life stages, 210 juveniles, and 93 adults (Supplementary Data, 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 (n = 69 observations) by each study (n = 26). 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 habitat use trait information (Table 1; Supplementary Data, 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; Supplementary Data, Table S4) in *vegan* (v2.5-7) (Oksanen et al., 2020) and *cluster* (v2.1.2) (Maechler et al., 2021) and visualised using and *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 (Supplementary Data, 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 Dunny 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 3 studies in this dataset (9 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 reduced dataset. Due to overdispersion in frequency of occurrence data containing large variation in species composition values, and in meeting 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 4 studies), as well as. 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 use a fourth-corner, model-based approach (Dray & Legendre, 2008; Brown et al., 2014), 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 (QxR) or the fourth corner solution to a multi-matrix problem. We built 3 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 ‘*glm1path’*, using penalised likelihood to impose a constraint on estimates of model parameters (Hastie et al., 2009; Brown et al., 2014). 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.

## Results

### 3.1 Taxonomic and trait diversity in albacore diets

This synthesis reveals the large biodiversity of prey consumed by albacore globally (Figure 1) with 308 prey species, and 238 at lower taxonomic resolution (Supplementary Data, Table S7). Prey species mainly hailed from 7 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), one hydrozoan (Figure 3a). In addition to these classes, prey identified at higher taxonomic resolution included one appendicularian, one branchiopod, and one elasmobranch (an unknown Squalidae species) (Supplementary Data, Table S7). Whilst the North Pacific, North Atlantic, and in the Mediterranean Sea received the greatest sampling effort and most of the albacore prey known to date were identified in these regions of the world (Figure 1b/c); an unknown and potentially large diversity of prey remains to be identified in the South Pacific, South Atlantic, and Indian Oceans (Figure 1b/c). Additionally, out of 308 prey species, 201 were observed in < 10% of stomach samples within any study (Supplementary Information, Figure S3).

Individual traits varied across phylogeny and recurred across unrelated prey taxa (Figure 3a). The dominant habitat use trait values in the prey assemblage were the most 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, Figures S4 & S5). 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 rarest prey guild globally was the coastal and shelf demersal taxa (4) (Figure 3b). The hierarchical divisive clustering technique for 7 optimal clusters performed well in grouping taxa that are also clustered based on their trait values in multivariate space (Supplementary Information, Figures S4 and S5).

### 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 & 5). North Atlantic diet composition from earlier 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 & 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 varied including 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-2010’s 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 (Supplementary Information, Figure S6) 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 0.1–0.2 (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.

## 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 7 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, trait-based frameworks enable functional simplification of diverse prey and functionally redundant food web linkages (Link, 2007), especially 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.

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 describe 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.

We posit that investigating trait-based diet shifts in albacore will be a powerful framework for tracking foraging responses to environmental variability. Our study shows clear differences in trait-based diet composition across the years and locations sampled. It may be that the productivity of individual species alternates and shifts across environmental gradients and inter-annual 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). Further, linkages between traits that describe prey habitat use and migratory behaviour, alongside prey taxonomy, to their contribution to predator provides an important inference for spatial and temporal variability of forage for predators and may contribute to identification of foraging hotspots in large pelagic ecosystems.

### 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 also highlights variable sampling of albacore tuna diets in space and time, with long gaps between studies ranging from a few years to over fifty years apart depending on ocean basin. 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 (Young et al., 2015; Duffy et al., 2017; Bizzarro et al., 2022; WCPFC, 2023). 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 (McGill et al., 2006; Kiørboe et al., 2018). This is a key knowledge gap in marine and freshwater ecosystems (Green et al., 2022).

## 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 generate 7 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 variability in 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.

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## Authorship Statement

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.

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## Data Accessibility

Both the data and code will be made publicly available through a CC BY 4.0 public-use licence upon acceptance of this manuscript for publication. Given the nature of the data and commercial value of the study species we cannot make data publicly available prior to acceptance for publication of this product. The database for global and historical albacore diet composition from digitised published and grey literature will be made available on the University of Alberta’s Dataverse Borealis repository. All code for analyses will be made publicly available on Github (<https://github.com/CHANGE-Lab/albacore-diet-global>).

## Tables

**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). 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.

|  |  |  |
| --- | --- | --- |
| Trait | Variable type | Definitions & relationships of traits for predator-prey interactions |
| Vertical habitat use | Categorical (demersal, epipelagic, 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, 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) | The relationship of this trait with predation is complicated due to an evolutionary arms race whereby 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. |

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

|  |  |  |  |
| --- | --- | --- | --- |
| **Diet data (L)** | **Trait variables (Q)** | **Environmental 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 |

## Figure Legends

**Figure 1.** **a)** Geographic distribution of published albacore diet papers, reports and grey literature from 1880–2020, 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.

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

**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 Supplementary Data, Table S5).

**Figure 4.** Composition of prey trait guilds within historical albacore diets (y axis; relative % frequency of occurrence [FO]) across locations and dates sampled from 1880–2015 (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.

**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.

## Supplementary Materials & Data

Supplementary Information includes literature search terms, treatment of albacore diet data, meta-information and prey trait information, as well as supplementary results illustrations. Supplementary Data contain tables that further support data treatment and decisions described in the manuscript and Supplementary Information. For ease of revisions a version of the supplementary data has been made accessible here: <https://docs.google.com/spreadsheets/d/1soUZX6tkBJ94EL4WZ_m1pixWEmqvXkgv/edit#gid=436510484>