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

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## Abstract

Simplifying complex species interactions can facilitate prediction of changes in ecosystem function and structure under climate change. This is particularly important for highly migratory pelagic predators, which exploit 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 identified to species, and 279 at lower taxonomic resolution. We quantitatively synthesised prey diversity into 7 functional trait guilds using four traits that influence predator-prey encounter rates – prey habitat association, seasonal and diel vertical migration behaviour – using hierarchical divisive clustering algorithms. We further explore 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. Species-based diet composition 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, compared to 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.

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## 

## Introduction

Pelagic ecosystems are among the last frontiers on Earth, politically and ecologically. Yet 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 species extirpations and undesirable ecosystem states (Polovina et al., 2011; Molinos et al., 2016). Altered pelagic ecosystem states can lead to changes in fisheries production and uncertain economic futures (Cheung et al., 2010; Blenckner et al., 2015; 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 in order 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 (Muhling et al., 2019). Marine species redistributions are typically predicted on the basis of 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 numerous issues including the accuracy of prey distribution information (Muhling et al. 2019), 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 to synthetic and non-taxonomic predictors for those relationships, positioning scientists to predict ecological outcomes in new contexts (McGill et al., 2006; Kiørboe et al., 2018; Green et al., 2022). 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 functional groupings of prey into ‘guilds’ are a common ecological practice of dimension or variable reduction (Pomerleau et al., 2015; Parravicini et al., 2020), based on shared traits describing similar roles for those species in ecosystem processes (Gitay & Noble, 1997) in order to model complex species distribution and interactions.

Trait-based approaches may be particularly useful for tunas – that have taxonomically broad diets (Duffy et al., 2017; Pethybridge et al., 2018) and there is little evidence for the influence of predator size on prey size selection (Romanov et al., 2020). While these foraging properties make them 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 investigate evidence for selection for certain types of forage (Glaser, 2010; Valls et al., 2022). Previous diet analyses related shifts and niche partitioning in the diets of yellowfin, bluefin, bigeye and albacore tunas across predator species, latitude, predator life stage, 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), and shifts in albacore distribution have 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 be used to explain tuna foraging ecology across space and time and 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 identifying 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 (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 data types (i.e., frequency of occurrence and other metrics).

We obtained diet data from 26 studies that were suitable for meta-analysis (Supporting Information, Table S2); this included 69 independent, aggregate (i.e. by geographic region, year, or season sampled) observations of adult and juvenile albacore diet composition, from 1880–2015 (Supplementary Data, Table S3). We digitised and transcribed data reported typically for a specific geographic location (Figure 1a), year, and season sampled. However, several reports presented information that was further aggregated for multi-year sampling programs (Table S3) and for analyses in these cases, we use 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, longlining at specified depths, or purse seining gear (Table S3).

### 2.2 Prey life stage estimation

Albacore consume post-larval and juvenile prey as well as adult life stages. Given that traits could vary between life stages for many species, we aimed to match traits to the life stage most commonly consumed by albacore predators for each prey species. Of the 308 prey recorded to species, 72 (or 23%) had associated life stage information reported within their corresponding diet study, with 42 reported as post-larvae, young-of-year, or juveniles, and 37 species consumed as adults (Supplementary Information, Figure S1). Albacore rarely consumed larvae (i.e., 11 species in total). Of these 72 species, 13 were reported at multiple life stages in albacore diets, however, one life stage was typically dominant across diet studies (i.e., with an order of magnitude greater frequency of occurrence than any other life stage). For example, of 11 species with reported consumption of the larval life stage, 6 species were typically consumed as juveniles (i.e. across multiple studies) and thus were assigned as juveniles for the purpose of this meta-analysis (Supplementary Data, Table S4; Supplementary Information, Figure S1).

When life stage 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 a given study (Figure S1; Table S4). For an additional 15 species (nearly 5% of species),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 inferred relative to their known length at maturity (Figure S1; Table S4). The remaining 221 species (72% of the species) were identified in albacore diets without metainformation and assumed to be either juveniles or adults. Trait information was often similar between juvenile and adult life stages (Gleiber et al., 2022). Thus for 127 of these taxa (41% of the species), no further estimation of prey life stage was needed.

Trait information differed by life stage for 94 prey species (31% of the species) remaining; 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 (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 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). Depending on the data reported, we used either a measured maximum albacore fork length (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). Where albacore lengths were not reported, we 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. There was no significant difference 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 (Figure S1). Further detail in estimating the mean and range in albacore lengths for a given study are further described in Supplementary Information (Supplementary Information, Appendix B). Overall, our synthesis uses the following prey life stages consumed by albacore: 5 larval life stages, 210 juveniles, and 93 adult prey (Supplementary Data, Table S5).

### 2.3 Prey trait information

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For each prey species and life stage (i.e., larva, juvenile, adult), 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 and (ii) horizontal habitat association, (iii) presence of diel vertical migration, and (iv) presence of seasonal migration and seasonal aggregation behaviour (Table 1; Table S5). These trait data were compiled for a broader database of traits that inform predator-prey interactions for albacore (Gleiber et al., 2022). We further describe how prey species’ trait values were used in Supporting Information, Appendix C.

### 2.4 Trait-based analyses

All data manipulation, statistical analysis and graphical illustrations were performed in *R* (version 4.2.1) (R Core Team, 2022).

#### Taxonomic and trait diversity in albacore diets

Species accumulation was calculated and plotted using *BiodiversityR* (version 2-14.1; Kindt & Coe, 2005) in relation to ocean basins where sampling locations occurred and the final year sampled (n = 69 observations) by each study (n = 26). Prey species’ phylogenetic information were 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 trait information displayed using *ggtree* (v3.3.1.900) (Yu et al., 2017) to visualise relationships between taxonomic and trait diversity in the data.

#### Albacore prey trait guilds

For the 292 prey species with complete trait information, key prey trait guilds were identified using a divisive hierarchical clustering algorithm (Anderberg, 1973; Legendre & Legendre, 1998) on a Gower dissimilarity matrix (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) using the *diana* algorithm in *vegan* (v2.5-7) (Oksanen et al., 2020) and *cluster* (v2.1.2) (Maechler et al., 2021) and visualised with *ggplot2* (v3.3.5) (Wickham, 2016) and *dendextend* (v1.15.2) (Galili, 2015)*.*

We used a consensus approach for validating cluster results – optimising cluster selection and partition by assessing several stability and internal validation metrics (Supplementary Data, Table S6) (Brock et al., 2008) and visualised using non-metric multidimensional scaling (nMDS) plots (Field et al., 1982) using *vegan*. 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.

#### Trait-based vs taxonomic diet variation

Historical albacore diet composition across geographies were visualised using frequency of occurrence data from 26 studies that yielded 60 observations of diet composition, because the other 3 studies in this dataset and their 9 observations included presence only data. To visualise overall 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 further statistical analysis of trait-based variance in albacore diet composition across geographies, all data from the 26 studies and 69 observations were transformed to presence/absence to meet the model data distribution requirements. Poorly sampled locations were excluded from analyses (samples from South Pacific, South Atlantic and Indian Oceans), as well as rare species that only occurred once or twice in this reduced dataset. We therefore compare the diet composition for albacore from sampling locations in the North Pacific (samples mainly come from the California Current System), North Atlantic (largely representing North Atlantic Drift), and Mediterranean Sea, providing us with 57 observations 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: an environmental variable (R matrix, here containing geographic locations sampled) and prey trait information (Q matrices), producing the trait-environment interaction (QxR) or the fourth corner solution to a multi-matrix problem. We therefore built 3 models to test the role of species identity (no traits) or two types of trait information (individual trait values Q1 and seven 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 include 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-environment 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

Our synthesis reveals the large biodiversity of prey consumed by albacore globally (Figure 1). Prey hailed from 7 classes representing 203 families; mainly of ray-finned fishes (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 appendicularian, one branchiopod, one hydrozoan, and one elasmobranch (an unknown Squalidae species) (Supplementary Information, Figure S3). Of these, 308 taxa were reported to species level, with a further 279 taxa identified at variable resolutions from genus to order. Whilst the rate of species accumulation appears to level off in well-sampled locations such as the North Pacific, North Atlantic, and in the Mediterranean Sea (Figure 1b/c), an unknown and likely just as large diversity of prey remains to be studied 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 (Figure S3). Individual traits varied across phylogeny and recurred across unrelated prey taxa (Figure 2).

### 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 (Table 1, Figure 3a). We selected 7 clusters by optimising cluster validation outputs: (1) higher average distance between species clusters (Rousseeuw, 1987); (2) lower average distance within species clusters (Handl et al., 2005); (3) high silhouette width coefficient value and Dunny Smith residuals (Dunn†, 1974; Rousseeuw, 1987); and lastly, (4) optimal evenness or balance of cluster composition indicated by the number of species in each cluster (Legendre & Legendre, 1998) (Supplementary Data, Table S6).

The most taxonomically abundant trait guild consisted of diel migrating mesopelagics (trait guild 2), distinct from the non-diel migrating mesopelagics (1) and least taxonomically abundant (Figure 3). 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). Finally, the rarest prey guild globally was the coastal and shelf demersal taxa (4). 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 (Figure 3b; Supplementary Information, 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) . The Mediterranean was characterised by a relatively high contribution of samples containing seasonal shelf taxa, with pulses of resident shelf taxa, diel migrating mesopelagics and oceanic epipelagics at different points in time (Figure 4). North Atlantic samples were also characterised by high prevalence of samples containing the seasonal shelf taxa and resident shelf taxa (Figures 4 & 5), the latter group mainly prevalent in earlier 1930’s samples alongside consistent albeit relatively low prevalence of non-diel migrating mesopelagics at that time. From 1968 however, North Atlantic samples oscillate between higher contributions of the seasonal shelf taxa, coast and shelf epipelagics and oceanic epipelagics. These guilds were also highly prevalent in North Pacific diets, and samples from this basin were also characterised by oscillations between coast and shelf epipelagics and oceanic epipelagics (Figures 4 & 5),. Oceanic epipelagics appeared to dominate South Pacific sampling in most years, with intermittent higher prevalences of seasonal shelf taxa and non-diel migrating mesopelagics. 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 in number, and diets varied including two important seasons for resident shelf taxa, one season dominated by coast and shelf epipelagics, and consistent but low prevalences of non-diel migrating mesopelagics.

Overall, non-diel migrating mesopelagics were primarily observed in diets prior to 1950’s samples from the North Atlantic and with high prevalence in select years in the mid-2010s in the Indian and South Pacific Oceans. The coast and shelf demersals were the rarest group across geographies, and observed mainly in North Pacific samples in the 1940’s and North Atlantic samples from 1957. Due to low sample sizes, data from locations in the South Pacific, South Atlantic, and Indian Oceans are illustrated (Figure 4) but were not used in further trait-based models. Taxonomic variation in regional dietary signatures (Supplementary Information, Figure S5) was significantly mediated by trait information and trait guilds, particularly for samples from the North Pacific and the Mediterranean (Figure 5).

## 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 279 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 habitat association, seasonal and diel vertical migration behaviour. 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 and rapid 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 involving highly migratory pelagic predators. A traits approach may be of particular use for retaining data on diets containing less common species in analysis such as species distribution models and network-based food web models, as these typically risk being excluded from analyses seeking to investigate predator-prey interactions due to insufficient data or insufficient weighting of these species in models. Rare prey species likely contribute to diet characterization in sharing forms of traits likely to be consumed with more common prey species. Thus, trait values or trait guilds are more tractable analytical currencies for ecologists in the context of changing species distributions and trophic interactions (Green et al., 2022). 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 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.

Traits have proven useful in describing albacore foraging dynamics in prior studies. 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; 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), 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 reanalysis of the same data found that three habitat trait guilds accounted for a large proportion of diet composition observations from the North Atlantic and Mediterranean. Mediterranean samples were especially dominated by two trait guilds overall: the 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 sampling locations from the North Atlantic and North Pacific were also more diverse than observed elsewhere, and included prevalent consumption of 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 review shows clear differences in trait-based diet composition across years and locations sampled. Investigating the extent to which the consumption of trait guilds relates to environmental drivers and climate states requires access to disaggregated diet data (i.e. prey from each individual predator) sampled consistently over time and space. It may be that individual species productivity alternate and shift 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 offshore mesopelagics and coastal to offshore epipelagics in relation to environmental shifts). The extent to which species taxonomic, phylogenetic and trait information explains variation in diet composition needs to be formally tested.

### 4.2 Synthesis limitations, knowledge accessibility and gaps to overcome

This review also highlights how variable the sampling of albacore tuna diets has been 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 aggregate 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 just as large as in the North Pacific.

Very large disaggregated datasets are needed to understand resource use in highly migratory pelagic predators at both broad and finer spatial scales. 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). 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. While disaggregated historical data cannot be expected back to the late 1800’s, we highlight the need for open science practices moving forward – publicly available raw diet data on commercially valuable pelagic predators.

Access to disaggregated diet data at high taxonomic resolution where information on predator size information and prey size (e.g. lengths and widths) are recorded will enable more accurate pairing of trait information with individual prey items (Zakharova et al., 2019). For each trait in this meta-analysis, we needed to select a single trait value per species, and also estimate the most likely life stage consumed for a large proportion of the data. We believe that traits for prey consumed are representative of the life stage-appropriate habitat use and migratory behaviour traits, but greater accuracy could be achieved and a very lengthy data curation process used to ensure current accuracy in trait data could be significantly shortened with disaggregated 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). 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. We reveal a comprehensive taxonomic and trait-based portrait of the trophic plasticity of albacore. 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. 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 to understand how stable or flexible trait-based biogeographic resource use may be for highly migratory pelagic predators, as pelagic ecosystems are altered by climate change and shift to novel states. Ultimately, further modelling applications that use trait database products in predator diet analyses frameworks will shed light on the extent to which future data collection and modelling efforts in pelagic systems will benefit from a focus on traits (rather than taxonomic identity alone) when seeking to characterise the effect of trophic interactions on predator redistribution.

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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

The database for global and historical albacore diet composition from digitised published and grey literature will be made available on Dataverse’s Borealis repository. All code for analyses will be made publicly available on Github (<https://github.com/CHANGE-Lab/albacore-diet-global>). 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.

## 

## Tables

**Table 1.** Trait variables and values that influence the prey encounter phase of the predation process (Green et al., 2019).

|  |  |  |
| --- | --- | --- |
| 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 (note that species can occur elsewhere, but this trait informs us of their main habitat use). |
| Horizontal habitat use | Categorical (coastal, continental shelf, oceanic) | Represents the typical position from the coastal to offshore waters that prey resources primarily occupy (note that species can occur elsewhere, but this trait informs us of their main habitat use). 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/S1) | Diet composition ~ traits variables + ocean basin |
| Q2 – Trait guilds (Figure 3) | 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. A total of 26 studies reported diet data for 69 individual sampling locations and 36 distinct sampling years. Of the 308 prey identified to species-level 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 2020.

**Figure 2.** Prey and trait diversity across phylogeny. Grey shading indicates no data available for a particular species and trait.

**Figure 3.** Seven optimal albacore prey trait guilds generated by divisive hierarchical clustering for 292 specieswith complete trait information for vertical and horizontal habitat use, seasonal and diel vertical migration. Displayed: a) a radial cluster dendrogram and overlaid description of the main trait values associated with each cluster (including the number of species within clusters), and b) non-metric multidimensional scaling (nMDS) plot illustrating each species as an assemblage of four trait values and coloured in relation to their classified trait guild.

**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.

**Figure 5.** Correlation coefficients for the trait-environment relationship modelled using the fourth corner solution for a) individual trait information, and b) the trait guilds model and their interaction with the explanatory variable for ocean basin sampled. Coefficients for all trait-environment 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, and the strength and direction of the relationship.

## Supplementary Materials

Supplementary Information includes literature search terms, treatment of albacore diet data, metainformation 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