



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

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Complete List of Authors:	<p>Hardy, Natasha; University of Alberta, Biological Sciences            Matuch, Cindy; University of California Santa Cruz            Roote, Zachary; University of Alberta, Biological Sciences            George, Iris; University of Alberta, Biological Sciences            Muhling, Barb; University of California Santa Cruz Institute of Marine Sciences; NOAA Fisheries Southwest Fisheries Science Center            Jacox, Michael; NOAA Fisheries Southwest Fisheries Science Center Environmental Research Division; NOAA Physical Sciences Laboratory            Hazen, Elliott; NOAA Fisheries Southwest Fisheries Science Center; NOAA Fisheries Southwest Fisheries Science Center Environmental Research Division            Bograd, Steven; University of California Santa Cruz Institute of Marine Sciences; NOAA Fisheries Southwest Fisheries Science Center Environmental Research Division            Crowder, Larry; Stanford University Hopkins Marine Station            Green, Stephanie J.; University of Alberta, Biological Sciences</p>
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Abstract:	<p>Simplifying complex species interactions can facilitate tracking and predicting functional responses to ecological stressors. This is important for highly migratory pelagic predators, exploiting diverse prey fields as they respond to dynamic environments. We reconstructed the historical resource use of albacore tuna (<i>Thunnus alalunga</i>) globally from the 1900s–2015 and confirmed highly biodiverse diets with 308 prey species, and an additional 238 taxa at coarser taxonomic resolution. We 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 explored variability in historical composition of albacore diets across geographies based on species identity, individual trait information, and functional trait guilds using a multi-matrix modelling framework. Taxonomic information remains important for trophic ecology, however species-based diet composition in albacore tuna was highly variable across geographies and years sampled, making interpretation of these patterns difficult. By simplifying species identity into habitat-based traits, we highlight changes in prey resources consumed, such as the historical</p>

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

**Authors:** Natasha A. Hardy\*<sup>1</sup>, [Cindy Matuch](#)<sup>2</sup>, [Zachary Roote](#)<sup>1</sup>, [Iris George](#)<sup>1</sup>, Barbara A. Muhling<sup>3,4</sup>, Michael G. Jacox<sup>5,6</sup>, Elliott L. Hazen<sup>4,5</sup>, Steven J. Bograd<sup>3,5</sup>, [Larry B. Crowder](#)<sup>7</sup>, Stephanie J. Green<sup>1</sup>

**Corresponding authors:** [nahardy.wildlife@gmail.com](mailto:nahardy.wildlife@gmail.com) & [stephanie.green@ualberta.ca](mailto:stephanie.green@ualberta.ca);  
Department of Biological Sciences, CW 422 Biological Sciences Building, University of  
Alberta, Edmonton, Alberta, Canada, T6G 2E9

#### **Author affiliations**

<sup>1</sup> Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada

<sup>2</sup> University of California Santa Cruz, Santa Cruz, CA, United States

<sup>3</sup> Institute of Marine Sciences, University of California Santa Cruz, Santa Cruz, CA, United States

<sup>4</sup> NOAA Southwest Fisheries Science Center, La Jolla, CA, United States

<sup>5</sup> NOAA Southwest Fisheries Science Center, Environmental Research Division, Monterey, CA, United States

<sup>6</sup> NOAA Physical Sciences Laboratory, Boulder, CO, United States

<sup>7</sup> Hopkins Marine Station of Stanford University, Pacific Grove, CA, United States

**Abstract**

Simplifying complex species interactions can facilitate tracking and predicting functional responses to ecological stressors. This is important for highly migratory pelagic predators, exploiting diverse prey fields as they respond to dynamic environments. We reconstructed the historical resource use of albacore tuna (*Thunnus alalunga*) globally from the 1900s–2015 and confirmed highly biodiverse diets with 308 prey species, and an additional 238 taxa at coarser taxonomic resolution. We 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 explored variability in historical composition of albacore diets across geographies based on species identity, individual trait information, and functional trait guilds using a multi-matrix modelling framework. Taxonomic information remains important for trophic ecology, however species-based diet composition in albacore tuna was highly variable across geographies and years sampled, making interpretation of these patterns difficult. By simplifying species identity

37 into habitat-based traits, we highlight changes in prey resources consumed, such as the historical  
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40 demersal taxa. Trait information and trait guilds serve as useful classification frameworks for  
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43    **Table of Contents**

44        1.    Introduction

45        2.    Methods

46            2.1 Historical diet data collation

47            2.2 Prey trait information

48            2.3 Prey life stage estimation

49            2.4 Trait-based analyses

50                2.4.1 Taxonomic and trait diversity in albacore diets

51                2.4.2 Albacore prey trait guilds

52                2.4.3 Trait-based vs taxonomic diet variation

53        3.    Results

54            3.1 Taxonomic and trait diversity in albacore diets

55            3.2 Albacore prey trait guilds

56            3.3 Historical trait-based albacore diet composition

57        4.    Discussion

58            4.1 Synthesis of albacore diet diversity and historical trait relationships

59            4.2 Synthesis limitations and knowledge accessibility

60        5.    Conclusions

61    Acknowledgements

62    Authorship Statement

References

Data Accessibility

Tables

Figure Legends

Supplementary Materials

## 1. Introduction

Stressors such as climate change and intensive fishing efforts (Casini et al., 2009; Poloczanska et al., 2016) are altering the distributions and composition of pelagic communities (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; Kjørboe 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; Olson et al., 2016; 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.

## 2. Methods

### 2.1 Historical diet data collation

Our synthesis required quantitative data on adult or juvenile albacore diet composition obtained from stomach content analyses that identified consumed prey to species-level. To obtain these data, we compiled published and grey literature, research theses, and historical reports for albacore diets by searching bibliographic databases (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*

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 was created by using online repositories for species-level information, primarily FishBase (Froese & Pauly, 2020), SeaLifeBase (Palomares & Pauly, 2020), and the IUCN Red List of Threatened Species (IUCN, 2020), and by searching descriptive published literature for each species using Web of Science and Google Scholar (for detailed trait data collection methodology see Gleiber et al., 2022). 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 (Goñi et al., 2011; Williams et al., 2015; Nikolic et al., 2017), 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 by each study. To report on the trait-based diversity of prey in relation to taxonomic diversity, species' phylogenetic information was extracted from the Open Tree of Life Data using the package *rotl* (version 3.0.12) (Michonneau et al., 2016) and parsed to a phylogenetic tree using *ape* (version 5.6-2) (Paradis & Schliep, 2019) and *stringr* (version 1.4.0) (Wickham, 2021) with integrated species-specific 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 *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 Dunn's Smith residuals (Dunn, 1974; Rousseeuw, 1987) representing optimal cluster compactness and separation qualities; and lastly, (4) optimal evenness or balance of cluster composition indicated by the number of species in each cluster (Legendre & Legendre, 1998). Trait values that influence a species' occupancy within a cluster were visualised using heat maps illustrating the importance of trait values to the composition of each cluster.

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287 *2.4.3 Trait-based and taxonomic diet variation*

288

289 Historical albacore diet composition across geographies was visualised using frequency of  
290 occurrence data from 23 studies that yielded 60 observations (independent years and locations  
291 sampled) of diet composition, because 3 studies in this dataset (9 observations) included  
292 presence only data and there were insufficient studies reporting numerical abundance ( $n = 13$   
293 studies, 23 observations) and mass-based ( $n = 10$  studies, 32 observations) information on prey  
294 contributions to diets. To visualise frequency-based contributions of prey trait guilds to albacore  
295 diets, we calculated a normalised index of contribution for each prey species relative to (i) the  
296 trait guild they were classified in and (ii) the sum of frequency of occurrence data within each  
297 observation per study. Of note, several species with incomplete trait information are therefore  
298 ‘not classified’ with trait guilds and are included in illustrations of diet composition.

299 For statistical modelling of trait-based variance in albacore diet composition across  
300 geographies, rare species that occurred once or twice in this dataset were removed. Due to  
301 overdispersion in frequency of occurrence data containing large variation in species composition  
302 values, and in order to meet model assumptions of normality, we used data on species  
303 presence/absence in diets, which was also the most consistently reported and translatable metric  
304 of contribution historically. Poorly sampled locations were excluded from further analyses  
305 (samples from South Pacific [ $n = 7$  observations], South Atlantic [ $n = 2$ ], and Indian [ $n = 3$ ]  
306 Oceans, altogether from 4 studies). We therefore compare the diet composition for albacore from  
307 sampling locations in the North Pacific ( $n = 27$ , samples mainly come from the California

308 Current System), North Atlantic ( $n = 21$ , largely representing North Atlantic Drift), and  
309 Mediterranean Sea ( $n = 9$ ), providing us with 57 observations from 22 studies of albacore diet  
310 composition, and including 98 species.

311 We use a fourth-corner, model-based approach (Dray & Legendre, 2008; Brown et al.,  
312 2014), which builds on the generalised linear modelling (GLM) framework (Nelder &  
313 Wedderburn, 1972) to simultaneously test how the composition of albacore diets (L matrix of  
314 species presence/absence) differed as a function of two different types of explanatory variables: a  
315 geographic variable (R matrix, here containing locations sampled) and prey trait information (Q  
316 matrices), producing the trait-geographic interaction (QxR) or the fourth corner solution to a  
317 multi-matrix problem. We built 3 models to test the role of species identity (with no traits) or two  
318 types of trait information (individual trait values Q1 and trait guilds Q2), and geographic location  
319 (R) in explaining the presence of prey types (L) across the global data set (Table 2).

320 We used a binomial distribution for presence/absence data, analysed via logistic  
321 regression (with logit link function) using the *traitglm* function in the R package *mvabund*  
322 (version 4.1.12) (Wang et al., 2021). We included a species effect in models (i.e., a different  
323 intercept term for each species), akin to fitting a random effect variable to account for differences  
324 in absolute number of species occurrences (Brown et al., 2014; Wang et al., 2021). Additionally,  
325 models were fit with a LASSO penalty, specifying the fitting method as '*glm1path*', using  
326 penalised likelihood to impose a constraint on estimates of model parameters (Hastie et al., 2009;  
327 Brown et al., 2014). This constraint shrinks coefficients to zero when not statistically significant,  
328 providing a combined approach for variable selection, p-value adjustment for multiple models,

and parameter estimation to evaluate the magnitude and significance of an explanatory variable (Hastie et al., 2009). Trait-geographic relationships for individual trait variables and constructed trait guilds were illustrated as heat maps indicating the interaction strength, and positive or negative correlation between trait information and geographies sampled. Model fit was assessed by plotting multivariate residuals against fitted values and plotting quantile-quantile (Q-Q) plots. Multivariate data were previously screened for broad trends using conditional boxplots (Zuur et al., 2010), for overdispersion and outliers by nMDS plots (Field et al., 1982) using *vegan*. All model assumptions were met.

### 3. Results

#### *3.1 Taxonomic and trait diversity in albacore diets*

This synthesis reveals the large biodiversity of prey consumed by albacore globally (Figure 1) with 308 prey species, and 238 at coarser taxonomic resolution (Supplementary Data, Table S7). Prey species mainly hailed from 7 classes representing 203 families in the total dataset including

345 prey identified at coarser taxonomic resolution than species; ray-finned fishes (Actinopterygii, n  
346 = 108 families of prey), cephalopods (n = 29), and crustaceans (Malacostraca n = 45,  
347 Hexanauplia n = 6), and also including pelagic gastropods (n = 6), salps (n = 2), and one  
348 hydrozoan (Figure 3a). In addition to these classes, prey identified at finer taxonomic resolution  
349 included one appendicularian, one branchiopod, and one elasmobranch (an unknown Squalidae  
350 species) (Supplementary Data, Table S7). Whilst the North Pacific, North Atlantic, and the  
351 Mediterranean Sea received the greatest sampling effort and most of the albacore prey known to  
352 date were identified in these regions of the world (Figure 1b/c). An unknown and potentially  
353 large diversity of prey remains to be identified in the South Pacific, South Atlantic, and Indian  
354 Oceans (as demonstrated by cumulative species richness curves, Figure 1b/c).

355 Individual traits varied across phylogeny and recurred across unrelated prey taxa (Figure  
356 3a). The dominant habitat use trait values in the prey assemblage were those characteristic of  
357 pelagic and oceanic ecosystems, including epipelagic and mesopelagic vertical habitat use,  
358 oceanic and continental shelf horizontal habitat use, seasonal migration and aggregation  
359 behaviour and diel vertical migration (Figure 3a).

360

### 3.2 *Albacore prey trait guilds*

We obtained complete trait information for 292 prey species and these were optimally classified into seven trait guilds reflecting different combinations of four traits affecting predator-prey encounter processes, vertical and horizontal habitat use, seasonal migration and diel migration traits (Table 1, Figure 3; Supporting Information, Appendix D, Figure S4). The most species rich trait guild consisted of diel migrating mesopelagics (trait guild 2), distinct from the least species rich non-diel migrating mesopelagics (1) (Figure 3b). The second and third most abundant groups included the oceanic (or ‘offshore’) epipelagics (5) and coastal and shelf epipelagics (3), followed by seasonal, continental shelf taxa (6) and resident continental shelf taxa (7) (Figure 3b). Finally, the second-rarest prey guild globally was 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, Figure S4).

### 376 3.3 Historical trait-based albacore diet composition

377

378 Almost all trait guilds were observed in albacore diets in nearly all locations sampled (Figure 4).

379 Albacore diet composition from the Mediterranean was characterised by consistent high reliance

380 on seasonal shelf taxa, with differing temporal patterns of contribution to diets of resident shelf

381 taxa, diel migrating mesopelagics and oceanic epipelagics at different points in time (Figure 4).

382 Throughout the historical period assessed, North Atlantic samples were characterised by

383 consistent high prevalence of samples containing seasonal shelf taxa (Figures 4 & 5). North

384 Atlantic diet composition from the 1930's samples were characterised by a mix of most trait

385 guilds. From 1968 however, North Atlantic diets varied mainly in contributions of the seasonal

386 shelf taxa, coast and shelf epipelagics and oceanic epipelagics. These guilds and the diel

387 migrating mesopelagics were also common in North Pacific diets, with greater relative

388 contribution to diets of coast and shelf epipelagics and oceanic epipelagics than in other ocean

389 basins (Figures 4 & 5). South Pacific samples were characterised by varying composition of

390 oceanic epipelagics, non-diel migrating mesopelagics, seasonal and resident continental shelf

391 species. Notably in this region, a relatively high contribution of unclassified species were

392 observed in albacore diets lacking complete trait information. Indian Ocean observations were

393 few, and diets varied including two sampling periods containing mixed composition of nearly all

394 trait guilds, while one sampling period was dominated by coast and shelf epipelagics. Overall,

395 non-diel migrating mesopelagics were primarily observed in diets prior to 1950's samples from

396 the North Atlantic and in select years in the mid-2010's in the Indian Ocean and South Pacific.

397 The coast and shelf demersals were the rarest group across geographies, observed primarily in

398 North Pacific samples from 1946 and North Atlantic samples from 1957.



Underlying taxonomic variation in regional dietary signatures (Supplementary Information, Figure S5) was significantly explained by both trait information and trait guilds, particularly for samples from the North Pacific and the Mediterranean, although correlation coefficients for notable relationships ranged from 0.1–0.2 (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.

## 4. Discussion

### 4.1 Synthesis of albacore diet diversity and historical trait relationships

We reconstructed historical resource use for albacore tuna (*Thunnus alalunga*) globally, highlighting biodiverse diets in this predator (n = 308 prey identified to species, plus an additional 238 prey taxa identified to genus or higher). We quantitatively synthesised this large prey diversity into 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

418 mesopelagics, oceanic epipelagics, coastal and shelf epipelagics, coastal and shelf demersal taxa,  
419 seasonal continental shelf, and resident continental shelf taxa. Importantly, this study identifies  
420 both taxonomic and trait-based variability in diets of albacore tuna globally and identifies trait-  
421 based dietary signatures in albacore beyond taxonomic variability.

422 Our results indicate that both trait information and constructed functional trait guilds  
423 serve as useful classification tools for tracking large-scale shifts in albacore diets in time and  
424 space. Importantly, trait-based frameworks categorise or condense long lists of diverse prey and  
425 functionally redundant food web linkages (Link, 2007) into simpler and tractable groups based  
426 on ecological function, and rendering that diversity more interpretable, especially salient for  
427 highly migratory pelagic predators. Here, we display the results of two models: 1) built using  
428 individual trait information which provides results on significance testing of individual trait  
429 information when assessing individual trait importance is needed, and 2) built on trait guilds  
430 where the user has assessed that a functional grouping of traits is needed. While the results of  
431 both models, run simultaneously, supported each other, the individual trait information provided  
432 higher resolution information on specifically which levels of trait variables most explained  
433 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 (Pomerleau et al., 2015; Parravicini et al., 2020).

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

450 'specialised' (Consoli et al., 2008), of narrow trophic niche width (Teffer et al., 2015), and of  
451 short food chain length and low trophic adaptability (Pethybridge et al., 2018) compared to the  
452 longer food chain lengths and higher trophic complexity of Pacific tuna diets. Our re-analysis of  
453 the same data substantiates earlier observations and found that three trait guilds based on habitat-  
454 use accounted for a large proportion of diet composition observations from the North Atlantic  
455 and Mediterranean. Mediterranean samples were especially dominated by seasonal and resident  
456 continental shelf taxa. However, in the North Atlantic dominant prey trait guilds shifted over  
457 time, and the detailed taxonomic identification by Bouxin and Legendre in the 1930's revealed  
458 particularly trait-diverse diet composition. Trait guilds identified in samples from the North  
459 Atlantic and North Pacific were also more diverse than observed elsewhere, and included  
460 frequent consumption of and shifts between continental shelf, offshore to coastal, mesopelagic  
461 and epipelagic trait guilds.

462 Our study shows clear differences in trait-based diet composition across the years and  
463 locations sampled. It may be that the contribution to diets of individual species alternates and  
464 shifts across environmental gradients and inter-annual productivity cycles, whilst that of trait  
465 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.

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

483

484 *4.2 Synthesis limitations and knowledge accessibility*

485

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

496 This meta-analysis also highlights variable sampling of albacore tuna diets in space and  
497 time, with long gaps between studies ranging from a few years to over fifty years apart  
498 depending on ocean basin. Historically, the North Pacific and Atlantic basins were the most  
499 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; Kjørboe et al., 2018). This is a key knowledge gap in marine and freshwater ecosystems (Green et al., 2022).

## 5. Conclusions

Syntheses of historic trophic interactions are crucial for establishing baselines in understudied systems and understanding how they may change. By digitising and reconstructing historical data on albacore diet composition, we reveal a comprehensive taxonomic and trait-based portrait of the trophic plasticity of albacore, foundational to future analyses of variation in resource use under changing environmental and forage conditions. We condense biodiverse diet composition of albacore by generating 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 variable 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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880



## 881 **Data Accessibility**

882

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

1   **Tables**

2

3   **Table 1.** Description of the four trait variables and values that influence the prey encounter phase of the predation process extracted  
4   from the Pelagic Species Trait Database (Gleiber et al., 2022). Described here are traits that corresponded to the most consumed prey  
5   life stage, and while species can occur elsewhere, this informs us of their main habitat use trait (section 2.3). Note several  
6   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.
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1

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

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

3

4

5

1    **Figure Legends**

2

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

9

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

11

**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.

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

7  
8 **Supplementary Materials & Data**

9  
10 Supplementary Information includes literature search terms, treatment of albacore diet data, meta-information and prey trait  
11 information, as well as supplementary results illustrations. Supplementary Data contain tables that further support data treatment and  
12 decisions described in the manuscript and Supplementary Information. For ease of revisions a version of the supplementary data has

- 1 been made accessible here:
- 2 [https://docs.google.com/spreadsheets/d/1soUZX6tkBJ94EL4WZ\\_m1pixWEmqvXkgv/edit#gid=436510484](https://docs.google.com/spreadsheets/d/1soUZX6tkBJ94EL4WZ_m1pixWEmqvXkgv/edit#gid=436510484)

For Review Only

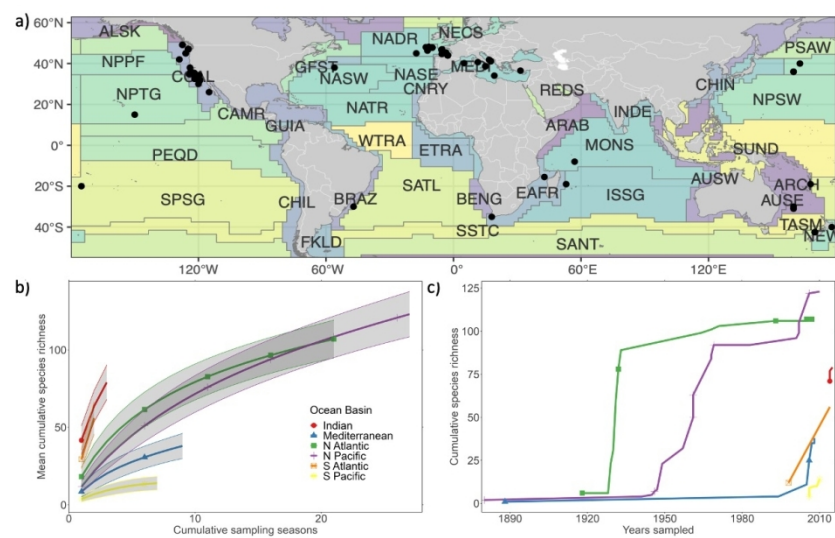


Figure 1. a) Geographic distribution of published albacore diet papers, reports and grey literature from 1880–2020, including Longhurst biogeographical province codes (Reygondeau et al., 2013) to visualise biogeographic distribution of data. A total of 26 studies reported diet data for 69 individual 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.

338x190mm (111 x 111 DPI)



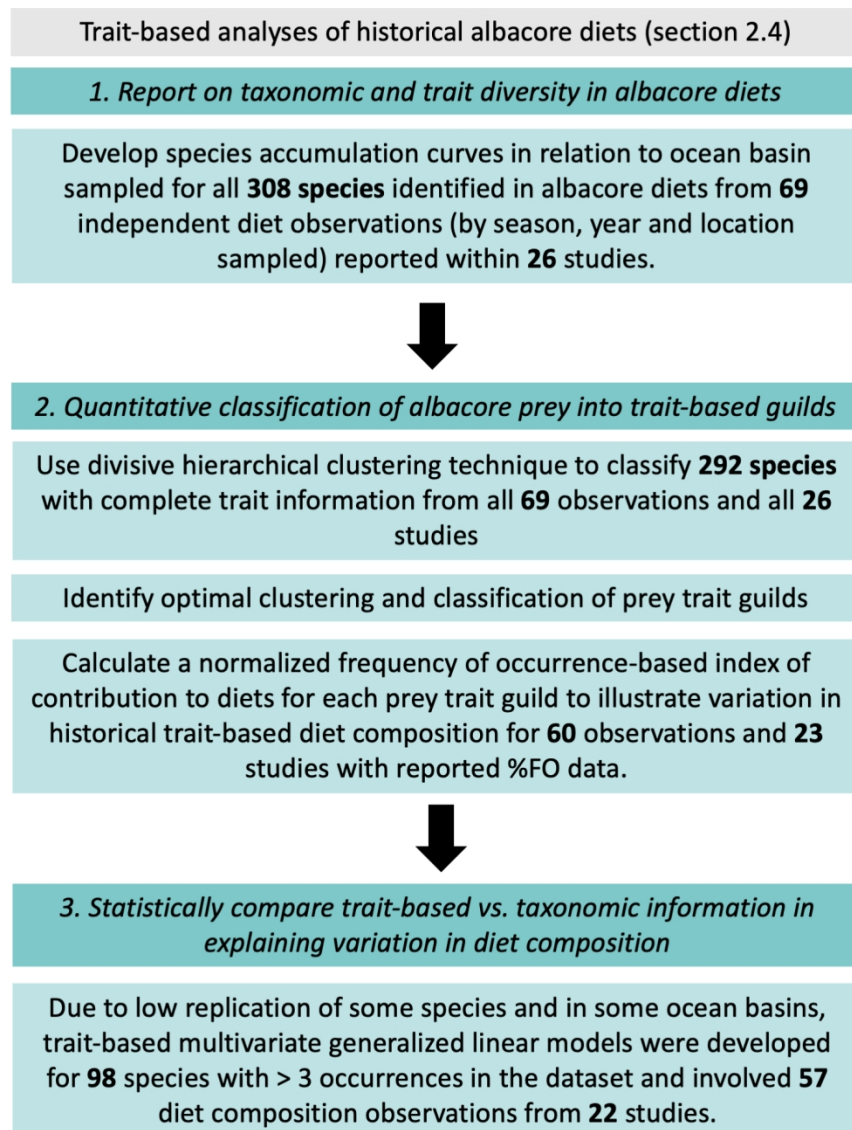


Figure 2. Flow chart of the workflow for statistical analyses of historical albacore diets.

190x260mm (197 x 197 DPI)

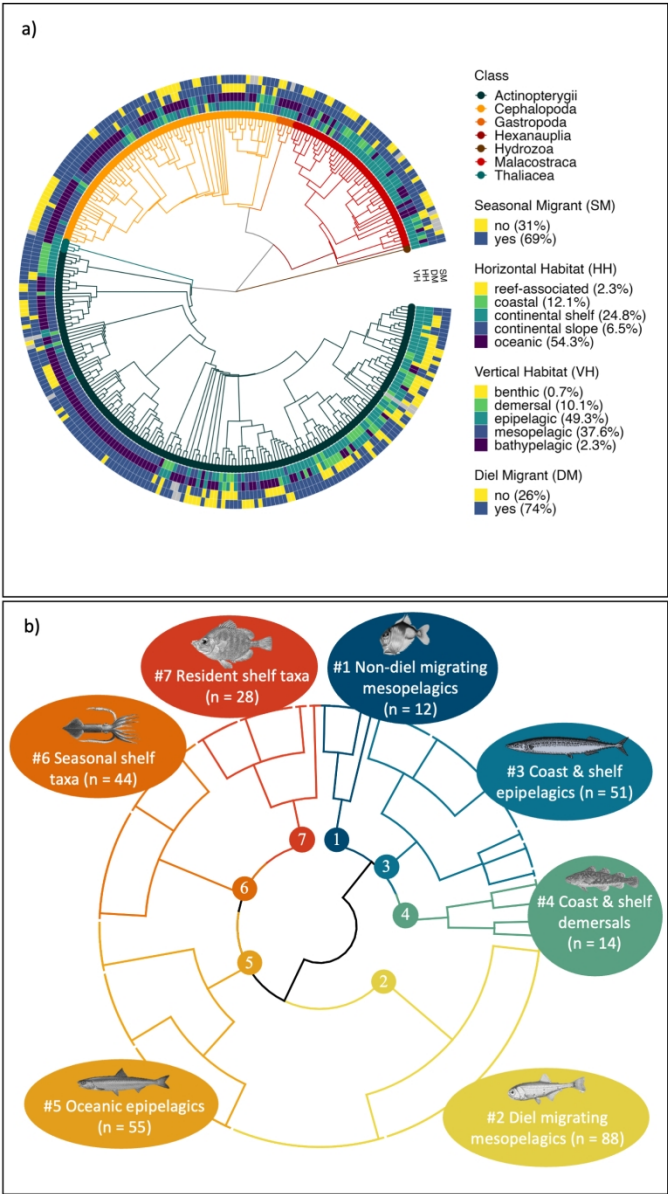
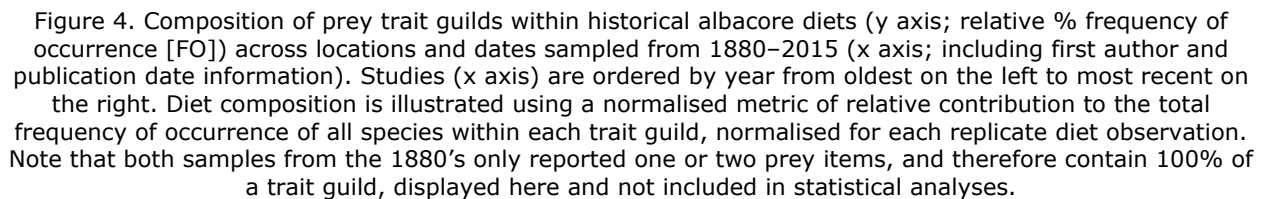


Figure 3. Diversity of a) prey traits across phylogeny for 308 species (grey shading indicates no data available for a particular species and trait); and diversity quantitatively simplified to b) radial cluster dendrogram of seven optimal albacore prey trait guilds generated by divisive hierarchical 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).

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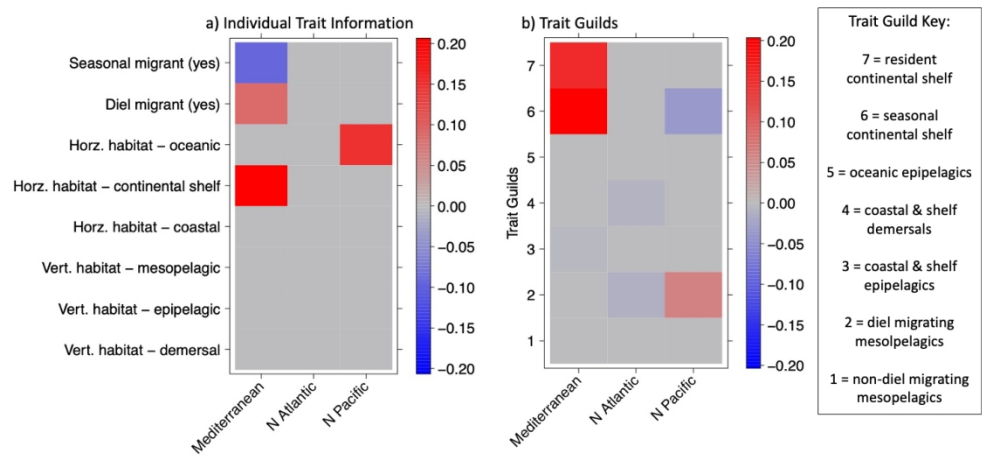


Figure 5. Correlation coefficients for the trait-geographic relationship modelled using the fourth corner solution for a) individual trait information (Horz = horizontal habitat use, in relation to the coast; Vert = vertical habitat use, in relation to water column position), and b) the trait guilds 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.

338x190mm (111 x 111 DPI)

## Supplemental Information

### Appendix A – Literature Search

**Table S1.** Literature search terms used to identify published papers and historical reports of albacore tuna diets queried from 1900 until 2020 using the Web of Science (Clarivate Analytics, 2020), Aquatic Sciences and Fisheries Abstracts (ASFA, 2020) and Federal Science Library Canada (FSLN, 2020) bibliographic databases. Both the diet research terms and synonymous scientific names for albacore tuna were combined by a Boolean ‘AND’ clause. Note that additional references from the 1880's were cited within older reports were queried and included this meta-analysis.

Diet research terms	Albacore tuna synonymous scientific names
(diet* OR forag* OR prey) AND	("Thunnus alalunga" OR "Scomber alalunga" OR "Albacora alalunga" OR "Germo alalunga" OR "Germo alalunga" OR "Germo germo" OR "Germo germon" OR "Germo germon steadi" OR "Orcynus alalunga" OR "Orcynus alatunga" OR "Orcynus germo" OR "Orcynus germon" OR "Orcynus pacificus" OR "Scomber alalunga" OR "Scomber alalunga" OR "Scomber alatunga" OR "Scomber albicans" OR "Scomber germo" OR "Scomber germo" OR "Scomber germon" OR "Thunnus alalunga" OR "Thunnus alalunga" OR "Thunnus germo" OR "Thunnus pacificus" OR "Thynnus alalunga" OR "Thynnus alalunga" OR "Thynnus pacificus")

**Table S2.** Published and historical reports of albacore tuna diet that provided detailed stomach content data. Several older papers, typically prior to the 1980's, needed to be scanned and digitised to PDF format. These are available upon request and all data digitised from published papers and reports are available in our diet database. For every diet report, we recorded the date

range, months and seasons of sampling, the median geographic location of albacore tuna collections, the number of albacore tuna collected, fishing gear and time of day for collections.

CiteAuth	CiteYear	CiteSource	CiteTitle
Aloncle, H.	1973	Thesis	Rythmes alimentaires et circadiens chez le germon <i>Thunnus alalunga</i> dans le Nord-Est atlantique
Bello, G.	1999	Journal of Molluscan Studies	Cephalopods in the diet of albacore, <i>Thunnus alalunga</i> , from the Adriatic Sea
Bernard et al.	1985	CalCOFI Reports	Stomach contents of albacore, skipjack, and bonito
Clemens & Iselin	1963	FAO World Sci. Meet. Biol. Tunas and Related Species, Sec. 5, Exper. Pap., (30) : 1–13	Food of Pacific albacore in the California fishery
Consoli et al.	2008	Marine Biology	Feeding habits of the albacore tuna <i>Thunnus alalunga</i> (Perciformes, Scombridae) from central Mediterranean Sea
Dos Santos & Haimovici	2002	Bulletin of Marine Science	Cephalopods in the Trophic Relations off Southern Brazil
Glaser et al.	2015	Journal of Marine Systems	Through the stomach of a predator: Regional patterns of forage in the diet of albacore tuna in the California Current System and metrics needed for ecosystem-based management
Goni et al.	2011	Marine Biology	Variability of albacore ( <i>Thunnus alalunga</i> ) diet in the Northeast Atlantic and Mediterranean Sea
Hart, JL	1948	Pacific Biological Station	Accumulated Data on Albacore
Iversen, RTB	1962	Fishery Bulletin	Food of albacore tuna, <i>Thunnus germon</i> (Lacepède), in the central and northeastern Pacific
Jordan & Gilbert	1880	Proceedings of the National Academy of	Description of two species of scopoloid fishes, <i>Sudis ringens</i> and <i>Myctophum</i>

		Sciences	<i>crenulare</i> from Santa Barbara Channel, California.
Joubin & Rouie	1918	Bulletin de l'Institut Océanographique de Monaco	Observations sur la nourriture des thons de l'Atlantique ( <i>Germo alalunga</i> Gmelin)
Legendre & Bouxin*	1934; 1936; 1940	Blondel la Rougery	La Faune pélagique de l'Atlantique au large du Golfe de Gascogne recueillie dans des estomacs de Germons: première partie: poissons; deuxième partie: céphalopodes; troisième partie: invertébrés (céphalopodes exclus), parasites du germon.
Logan et al.‡	2013	Deep Sea Research Part II: Topical Studies in Oceanography	Contribution of Cephalopod prey to the Diet of Large Pelagic Fish Predators in Central North Atlantic Ocean
Madigan et al.	2015	Proceedings of the National Academy of Sciences	Assessing niche width of endothermic fish from genes to ecosystem
Matthews et al.	1977	NOAA Technical Report	Food of Western North Atlantic Tunas ( <i>Thunnus</i> ) and Lancetfishes ( <i>Alepisaurus</i> )
McHugh, JL	1952	Bulletin of the Scripps Institution of Oceanography	The food of albacore ( <i>Germo alalunga</i> ) off California
Ortiz de Zarate, V	1987	Instituto Español de Oceanografía	Datos sobre la alimentacion del atun blanco ( <i>Thunnus alalunga</i> ) juvenil capturado en el golfo de vizcaya
Pinkas et al.	1971	Fish Bulletin	Food habits of albacore, bluefin tuna, and bonito
Prince Albert de Monaco	1888	Comptes Rendus de l'Académie des Sciences	Sur l'alimentation des naufragés en pleine mer (On the nutrition of castaways in the open ocean)
Pusineri et al.	2005	Journal of Marine Science	Food and feeding ecology of juvenile albacore, <i>Thunnus alalunga</i> , off the Bay of Biscay: a case study
Romanov et al.	2020	Marine and Freshwater Research	Trophic ecology of albacore tuna ( <i>Thunnus alalunga</i> ) in the western

			tropical Indian Ocean and adjacent waters
Romero et al.	2012	Helgoland Marine Research	Pelagic cephalopods of the central Mediterranean Sea determined by the analysis of the stomach content of large fish predators
Salman & Karakulak	2009	Journal of Marine Biological Association of the United Kingdom	Cephalopods in the diet of albacore, <i>Thunnus alalunga</i> , from the eastern Mediterranean
Teffer et al.‡	2015	Marine Biology	Trophic niche overlap among dolphinfish and co-occurring tunas near the northern edge of their range in the western North Atlantic
Watanabe et al.	2004	Fisheries Science	Feeding habits of albacore <i>Thunnus alalunga</i> in the transition region of the central North Pacific
Williams et al.	2015	Deep Sea Research Part II: Topical Studies in Oceanography	Vertical behavior and diet of albacore tuna ( <i>Thunnus alalunga</i> ) vary with latitude in the South Pacific Ocean
Young et al.	2010	Marine Biology	Feeding ecology and niche segregation in oceanic top predators off eastern Australia
<p>*These publications were combined as they consisted of three part publication on the taxonomic composition of albacore diets</p> <p>‡These publications met nearly all criteria for review, but are not included in further analyses as prey were reported at Family, Order and Class levels.</p>			

**Table S3.** Meta-information for published papers and reports on location, year, months, seasons of sampling, fishing gear used, depth sampled and time of day, the number of non-empty stomachs (stomachs\_used); measured or estimated mean albacore length (pred\_flmean) and variation about the mean when measured (pred\_flmean\_se); albacore minimum (pred\_flmin) and maximum (pred\_flmax) measured or estimated fork lengths; reported or estimated life stage (pred\_life), and descriptiona of our estimation (pred\_flest) for albacore life history stage (pred\_life\_est), age (pred\_age\_est) and lengths (pred\_flmean\_est) based on basin-scale fisheries



catch data and age and growth work (est\_note, est\_ref). Note that several papers and reports presented aggregate information for an entire multi-year program. Accessible here:

[https://docs.google.com/spreadsheets/d/1soUZX6tkBJ94EL4WZ\\_m1pixWEmqvXkgv/edit#gid=661663717](https://docs.google.com/spreadsheets/d/1soUZX6tkBJ94EL4WZ_m1pixWEmqvXkgv/edit#gid=661663717)

**Table S4.** Reported information for prey species and all reported life stages

(pre\_age\_reported\_1\_), lengths (maxL) and type of length measurement taken (maxl\_type), as well as the associated maximum gape limit (maxGape) for the albacore sampled from the same study as the prey taxa. Appended are the estimated life stage (life\_stage) and associated notes used to select the final life stage assigned to each species for selection of appropriate trait information. \*\*\*See notes below table for definition of abbreviations. Accessible here:

[https://docs.google.com/spreadsheets/d/1soUZX6tkBJ94EL4WZ\\_m1pixWEmqvXkgv/edit#gid=1070878054](https://docs.google.com/spreadsheets/d/1soUZX6tkBJ94EL4WZ_m1pixWEmqvXkgv/edit#gid=1070878054)

## Appendix B – Trait-data collection & Analyses

Four trait variables were extracted from a global database of albacore prey traits (Gleiber et al., 2022) for taxa identified to species and for the estimated primary life stage consumed (Supplementary Data, Table S5): (i) vertical and (ii) horizontal habitat association, (iii) presence of diel vertical migration, and (iv) presence of seasonal migration. We 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 for descriptive published literature for each species using Web of Science and Google Scholar. Of the 308 species identified in albacore diets, we obtained complete trait information for 292 species for the life stage consumed, for the four habitat use traits used in this meta-analysis (Supplementary Data, Table S5).

Vertical and horizontal habitat use traits were directly extracted from online repositories and corroborated alongside species distribution maps, reported depth range and typical depth strata inhabited (Gleiber et al., 2022). Where published literature expanded on or differed from a general value reported by species information repositories, we used the published literature and data. For example, if a species is listed as ‘bathypelagic’ in FishBase, but we do not have access to the original data and published papers report their distribution as typically ‘mesopelagic’, we selected their vertical habitat use trait to be ‘mesopelagic’ for the purposes of this analysis. Trait values for the presence and nature of diel vertical migration or seasonal migration behaviour were collected by keyword searching for each of these terms and for the prey species scientific name on Google Scholar (2020), Web of Science (Clarivate Analytics, 2020), Aquatic Sciences and Fisheries Abstracts (ASFA, 2020) and Federal Science Library Canada (FSLN, 2020).

bibliographic databases. This task was performed and repeated by up to 6 individual data collectors and values were cross-checked between data collectors, multiple published papers, and datasets.

Of note, we further edited vertical habitat use information for two species, *Janicella spinicauda* (Oplophoridae) and *Lampanyctus crocodilus* (Myctophidae), which were classified primarily as ‘bathypelagic’ (> 1300 m depth) and appear as such in the database but are also known to occur in the mesopelagic zone listed as secondary habitat in our database. The mesopelagic zone is where these prey were most likely encountered by albacore tuna that are not known to occur in or be able to dive to the bathypelagic depths. Thus for analyses, we relabelled those two species as ‘mesopelagic’ in order to retain them rather than exclude them from analyses.

**Table S5.** For the 308 prey identified to species, and for the primary consumed life stage assessed and assigned in section 2.3 of the methods of this paper, here we include taxonomic information (class, order, family, species), estimated prey life stages (life\_stage) and associated notes (life\_note). Values for four trait variables that influence the prey encounter (vertical and horizontal habitat use, diel vertical and seasonal migration; respectively labelled: vert\_habitat, horz\_habitat, diel\_migrant\_cat and season\_migrant\_cat) phase of the predation process were downloaded for each species from the publicly available Pelagic Species Trait Database (Gleiber et al., 2022)\*. For the 292 species with complete trait information, we used the four traits (vert\_habitat, horz\_habitat, diel\_migrant\_cat, season\_cat) for building prey functional groups (prey.trait.guild) described in section 2.4 (Table S6). Additional information is included for the maximum frequency of occurrence (maxFO), maximum percent numerical abundance (maxN)

and percent mass consumed (maxM) observed across all studies. For multiple species reported as presence absence, these values are '0'. Accessible here:

[https://docs.google.com/spreadsheets/d/1soUZX6tkBJ94EL4WZ\\_m1pixWEmqvXkgv/edit#gid=1573200869](https://docs.google.com/spreadsheets/d/1soUZX6tkBJ94EL4WZ_m1pixWEmqvXkgv/edit#gid=1573200869)

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## Appendix C – Estimation of albacore prey size/age consumed

Of the 308 identified prey recorded to species, 72 (or 23% of species) were reported with associated life stage information reported within their corresponding diet study. Of these, 42 reported as post-larvae, young-of-year, or juveniles, and 37 species consumed as adults, 13 of which overlapped (Supplementary Information, Figure S1; Supplementary Data, Table S4).

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 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 a given study (Supplementary Information, Figure S1; Supplementary Data, 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 (Supplementary Information, Figure S1; Supplementary Data, Table S4). The remaining 221 species (72% of the species) were 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% of the species), no further estimation of prey life stage was needed (Supplementary Information, Figure S1).

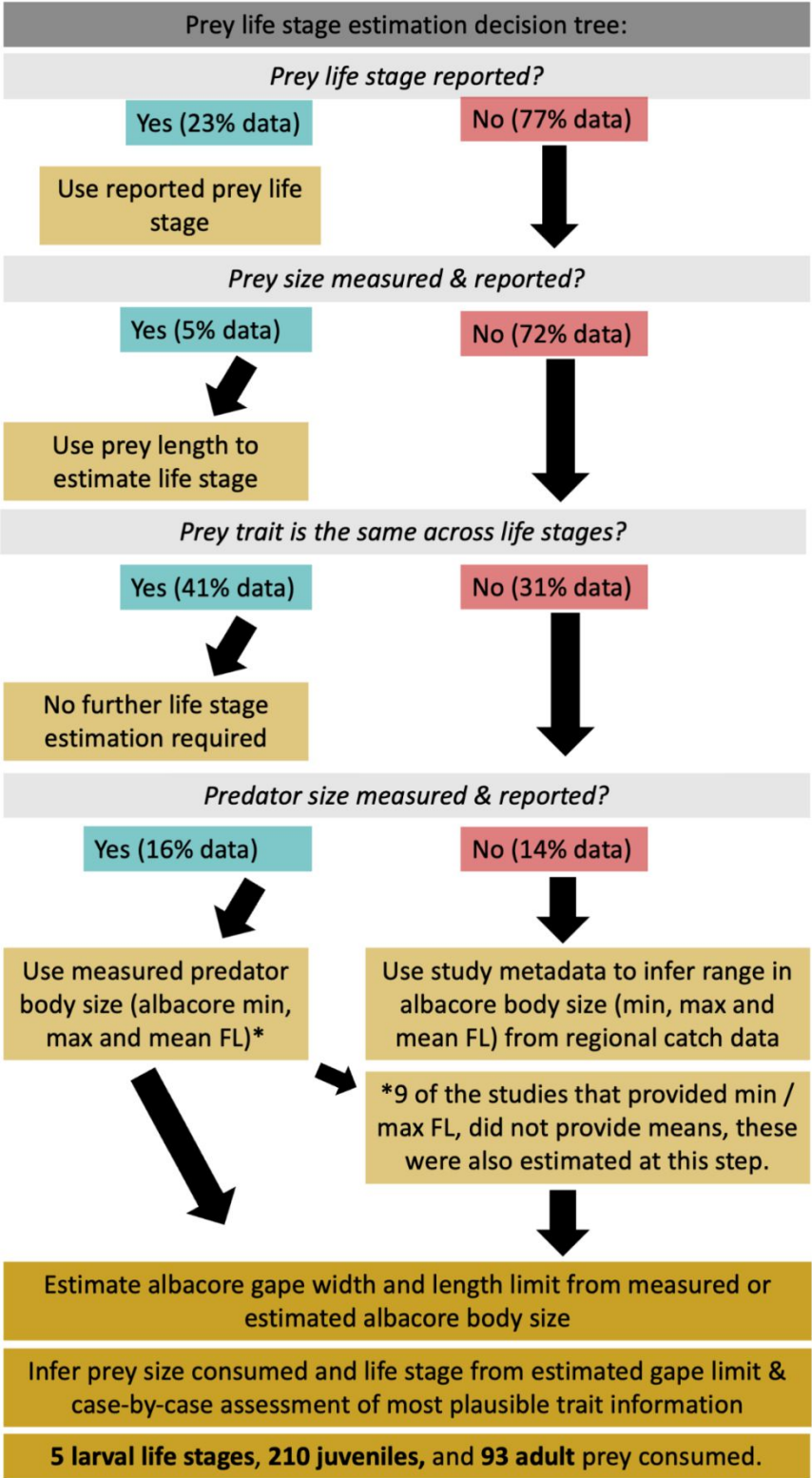
For 94 prey species, we lacked meta-information to assist in their direct life stage estimation and selection of appropriate trait information for juvenile and adult life stages. We corroborated decisions on selection of appropriate trait information among these species using albacore gape length limits calculated from maximum measured or estimated albacore fork lengths and using the equation developed by Ménard et al. (2006) for yellowfin tuna ( $L_m = 0.0823 \text{ FL} + 1.758$ ) to estimate gape limits ranging from 6.4–11.5 cm across studies and locations sampled. Here we described how data on measured albacore length information were handled and how we estimated fork length information if this was also not measured or reported (Figure S1).

Out of 26 research papers, 16 measured albacore fork length (FL) range, minima, and maxima (Figure S2). Of these, seven also reported the mean FL and five an estimated age range or life stage for albacore sampled (e.g., adult, juvenile) (Supplementary Data, Table S3). We also estimated mean FL for the 9 studies that reported FL range but not means (Figure S2), and all FL data for the remaining 10 studies that lacked size or life history information using metadata collected on fishing gear used and matched to gear-specific length data from relevant regional fisheries management organisations.

Of the 10 studies that lacked size or life history information for albacore, four reported the method of sampling (i.e., troll, trawl, longline). For these four studies and to complete the missing mean fork length (FL) for 7 studies noted above, 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. This was done by matching the range and mean FL

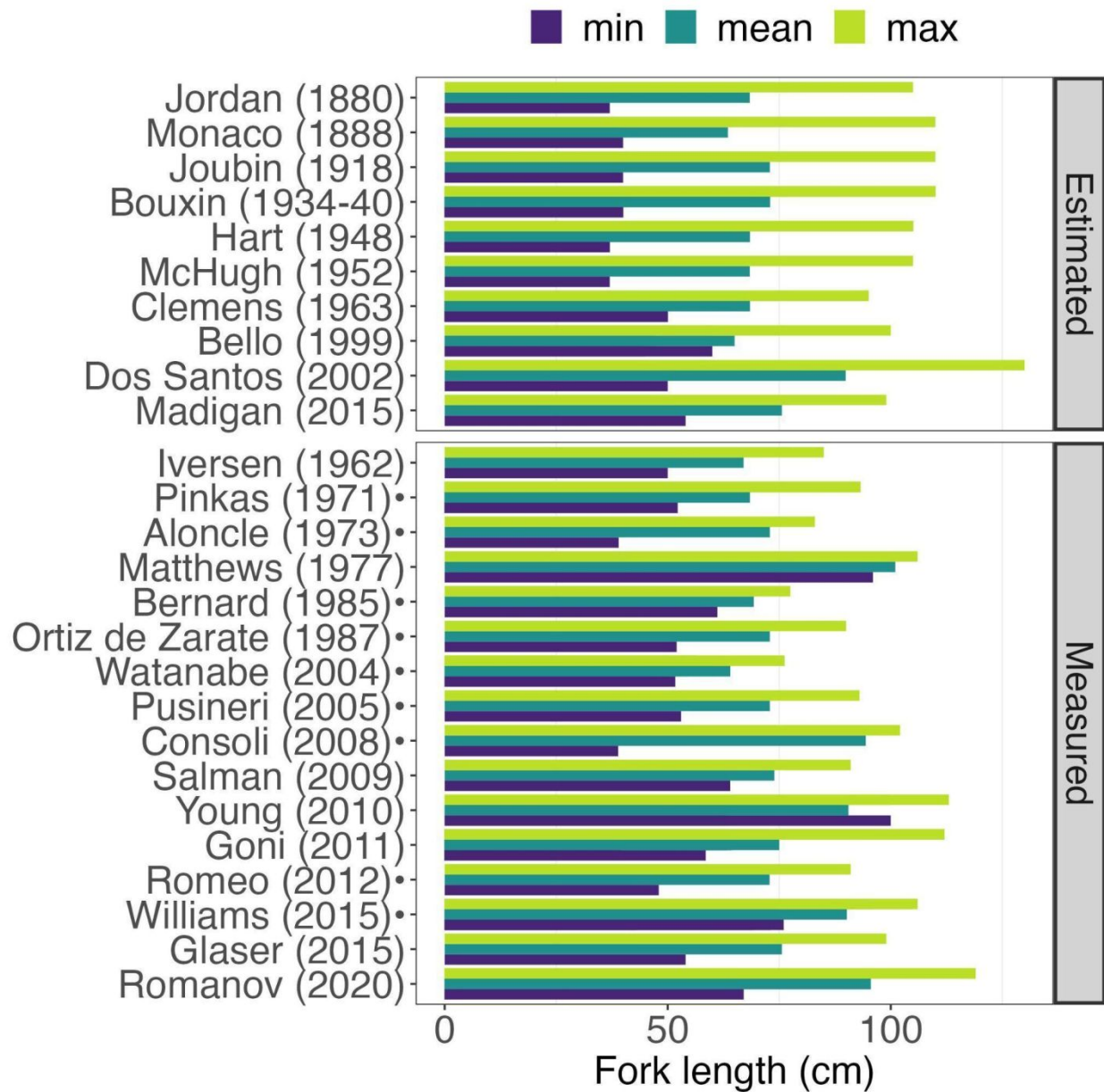
for albacore caught given year fished and specified gear type to the year sampled and gear type reported within these 10 studies. We then estimated the likely life stage(s) sampled using region-specific age and growth curves, and reported sizes at maturity (described in detail for each study in Supplementary Data, Table S3).

Finally, six historical studies lacked any information about sampled albacore length or age, did not provide catch method and/or were outside any record-keeping timeframes for fisheries catch data. Here, we estimated the likely life stage(s) for albacore based on studies that sampled the same geographic area (Supplementary Data, Table S3). We confirmed our life-stage estimations using known albacore ontogenetic and migratory behaviours in the large marine ecosystems sampled (Nikolic et al., 2017). Based on the results of a linear regression fit to both measured and reported FLs, there was no significant difference ( $p\text{-value} > 0.05$ ) between the variances of measured or estimated mean, minimum and maximum FL (Figure S2). Overall, we estimate that sampled albacore ranged from 37–119 cm FL with mean estimates of 47–101 cm FL (Supplementary Information, Figure S2).



**Figure S1.** Decision tree for prey species life stage estimation process described in section 2.3.





**Figure S2.** Albacore tuna fork length minima (min), mean and maxima (max) obtained from measured and reported data from 16 publications and estimated for another 10 publications. Of the 16 publications reporting length information, 9 publications (annotated with •) did not include a mean. This value was estimated in the protocol described in the methods of this manuscript. Mean, minimum and maximum FLs were not significantly different based on linear regression analysis (p-value >0.05).

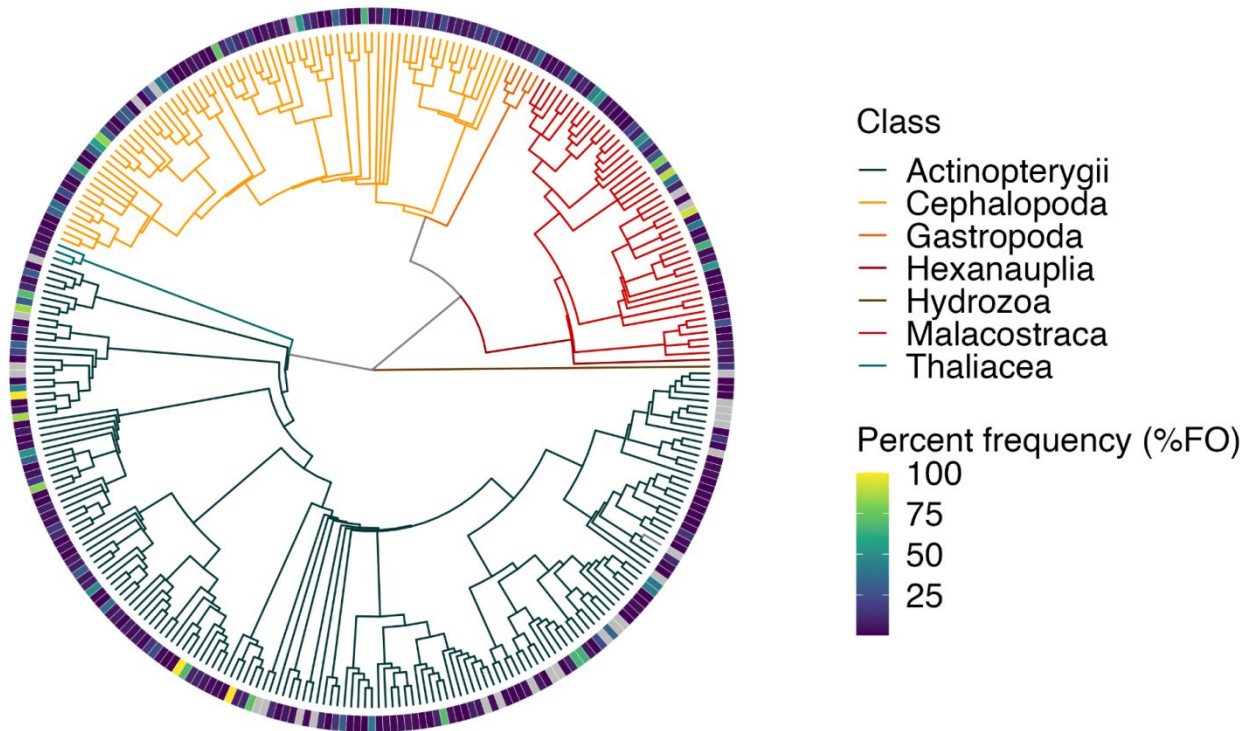
**Appendix D – Supplemental Results**

All prey taxa identified are provided in Table S7.

**Table S7.** Extended list of taxonomic identifications for prey from albacore stomach contents

from published and grey literature from the 1880's to 2020. This table includes all taxonomic identifications made, and includes the authors' level of certainty for inclusion in analyses ('IncludeSP' column), as well as prey taxonomy (class, order, family, species), taxonomic assignment (prey\_tax), taxonomic level of identification used for filtering data for analyses (tax\_level), common names and reference databases checked for trait and taxonomic information, as well as reported or estimated prey life stages and associated notes on old species names reported. Accessible here:

[https://docs.google.com/spreadsheets/d/1soUZX6tkBJ94EL4WZ\\_m1pixWEmqvXkgv/edit#gid=176756372](https://docs.google.com/spreadsheets/d/1soUZX6tkBJ94EL4WZ_m1pixWEmqvXkgv/edit#gid=176756372)

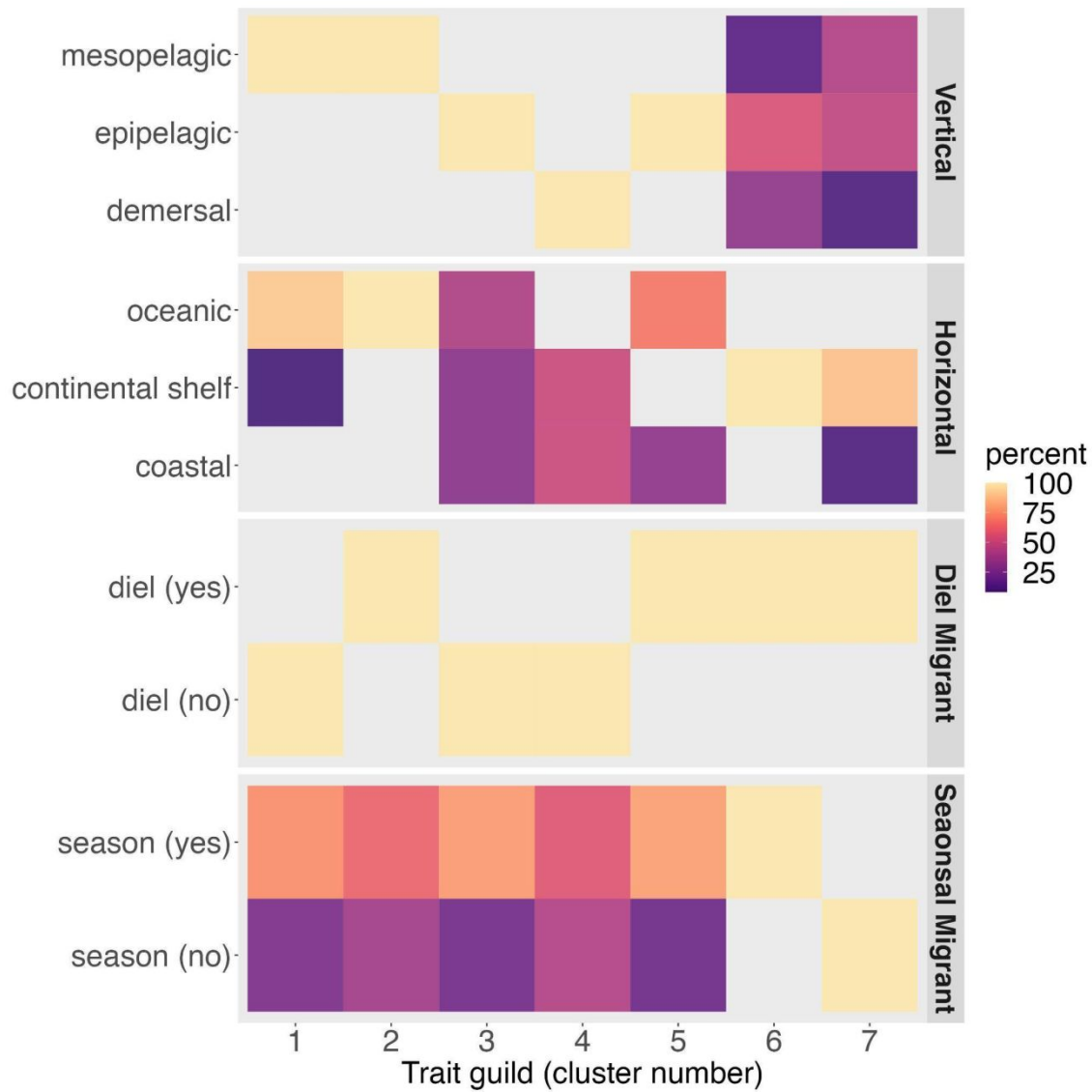


**Figure S3.** The maximum percent frequency of occurrence observed across phylogeny. Grey shading indicates no quantitative diet data were available for a particular species and trait. This illustrated that out of 308 prey species, 201 were observed in < 10% of stomach samples within any study.

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) (Figure S4; Supplementary Data, Table S6).

**Table S6.** Clustering algorithm statistical output table. 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). Accessible here:

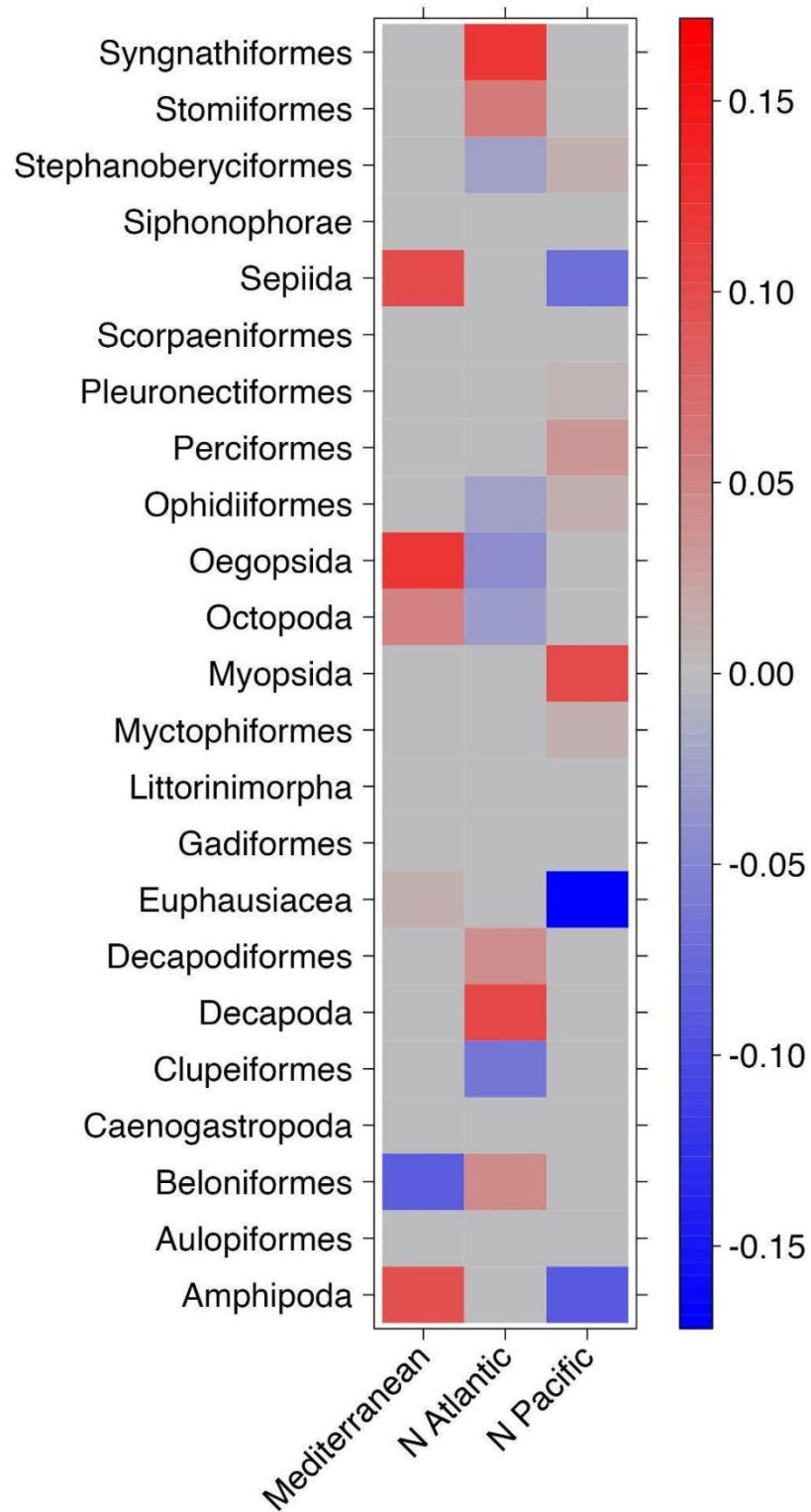
[https://docs.google.com/spreadsheets/d/1soUZX6tkBJ94EL4WZ\\_m1pixWEmqvXkgv/edit#gid=1573200869](https://docs.google.com/spreadsheets/d/1soUZX6tkBJ94EL4WZ_m1pixWEmqvXkgv/edit#gid=1573200869)



**Figure S4.** Trait heat map illustrating the distribution of trait values within each trait guild

(cluster), as a proportion of species within each trait guild associated with each trait value, using hierarchical divisive clustering algorithms ( $k = 7$ ), for vertical habitat ('Vertical'), horizontal habitat use ('Horizontal'), diel vertical migration ('Diel Migrant') and seasonal habitat use ('Seasonal Migrant').

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**Figure S5.** Correlation coefficients for the fourth corner solution and significant relationships between taxonomic variability (Order) and ocean basins sampled. Here we aggregate 98 species by their phylogenetic Order to illustrate the results of taxonomic variability. 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.



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