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

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Abstract:	Simplifying complex species interactions can facilitate tracking and predicting functional responses to ecological. This is particularly important for highly migratory pelagic predators, exploiting diverse prey fields as they respond to dynamic environments. We reconstructed the historical resource use of albacore tuna (Thunnus alalunga) globally and confirmed highly biodiverse diets with 308 prey species, and an additional 238 taxa at lower taxonomic resolution. We quantitatively synthesised prey diversity into 7 functional trait guilds using hierarchical divisive clustering algorithms as a function of 4 traits that describe habitat use and influence predator-prey encounter rates – prey habitat association vertically in the water column, horizontally along the coastal to pelagic gradient, seasonal and diel vertical migratory behaviour. We further explored variability in historical composition of albacore diets across geographies based on species identity, individual trait information, and functional trait guilds using a multi-matrix modelling framework. Although taxonomic information remains important for trophic ecology, species-based diet composition in albacore tuna was highly variable across geographies and years sampled. Trait-based models of albacore diets highlight the historical importance of near-surface epipelagic prey resources from coastal to oceanic habitats, and

seasonally migrating continental shelf prey, with less frequent pulses of deeper water and demersal taxa. Our results indicate that trait information and trait guilds serve as useful classification frameworks for identifying functionally redundant food web linkages involving biodiverse prey, and will prove useful in tracking predators' foraging responses to changing ecological states and resource variability.

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2

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21 **Abstract**

22

23 Simplifying complex species interactions can facilitate tracking and predicting functional

24 responses to ecological. This is particularly important for highly migratory pelagic predators,

25 exploiting diverse prey fields as they respond to dynamic environments. We reconstructed the

26 historical resource use of albacore tuna (*Thunnus alalunga*) globally and confirmed highly

27 biodiverse diets with 308 prey species, and an additional 238 taxa at lower taxonomic resolution.

28 We quantitatively synthesised prey diversity into 7 functional trait guilds using hierarchical

29 divisive clustering algorithms as a function of 4 traits that describe habitat use and influence

30 predator-prey encounter rates – prey habitat association vertically in the water column,

31 horizontally along the coastal to pelagic gradient, seasonal and diel vertical migratory behaviour.

32 We further explored variability in historical composition of albacore diets across geographies

33 based on species identity, individual trait information, and functional trait guilds using a multi-

34 matrix modelling framework. Although taxonomic information remains important for trophic

35 ecology, species-based diet composition in albacore tuna was highly variable across geographies

36 and years sampled. Trait-based models of albacore diets highlight the historical importance of

37   near-surface epipelagic prey resources from coastal to oceanic habitats, and seasonally migrating

38   continental shelf prey, with less frequent pulses of deeper water and demersal taxa. Our results

39   indicate that trait information and trait guilds serve as useful classification frameworks for

40   identifying functionally redundant food web linkages involving biodiverse prey, and will prove

41   useful in tracking predators' foraging responses to changing ecological states and resource

42   variability.

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72

73   1. **Introduction**

74

75   Stressors such as climate change and intensive fishing efforts (Casini et al., 2009; Poloczanska et

76   al., 2016) are altering the distributions and composition of pelagic communities (Hazen et al.,

77   2013; Cheung et al., 2015; Morley et al., 2018), causing widespread ecological change and

78   undesirable ecosystem states (Polovina et al., 2011; Molinos et al., 2016). Altered pelagic

79   ecosystems can lead to changes in fisheries production and uncertain economic futures (Cheung

80   et al., 2010; Blenckner et al., 2015; Free et al., 2019; Bell et al., 2021). Within pelagic systems,

81   highly migratory predators such as tunas and billfishes contribute to valuable and extensive

82   international fisheries (Sala et al., 2018). These species evolved to migrate across ocean basin

83   scales to exploit seasonal food resources for growth and warmer waters for reproduction

84   (Mariani et al., 2016). However, anomalies and long-term changes in climate are producing

85   mismatches among predator migration and the productivity of forage resources, with

86   implications for fisheries productivity (Thackeray et al., 2010; Scheffers et al., 2016).

87   Accounting for trophic interactions is often the missing link to forecasting species

88   redistributions under climate change (Lan et al., 2021; Green et al., 2022), especially for highly

89   migratory marine species (Lehodey et al., 2010; Muhling et al., 2019). Marine species

90   redistributions are typically predicted based on habitat use and changing physical oceanographic

91   properties (Morley et al., 2018). Despite empirical relationships between the biomass of prey

92   species and their prevalence in predator diets, efforts to model predator distributions in relation

93   to the distribution of key prey are often plagued by the accuracy of prey distribution information

94   (Muhling et al. 2019) and the number and functional redundancy of interacting species (Link,

95   2007; Carroll et al., 2019). These hurdles may be overcome by modelling functional ecological

96   relationships using synthetic parameters, or traits (Zakharova et al., 2019; Green et al. 2022).

97   Trait-based approaches to modelling predator-prey interactions aim to simplify

98   taxonomically complex interactions among hundreds of species by using functional ecological

99   and non-taxonomic predictors for those relationships (McGill et al., 2006; Kiørboe et al., 2018).

100   For example, the strength of predator-prey interactions can be modelled as a function of single or

101   multiple individual prey trait variables influencing the predation process (Arrizabalaga-Escudero

102   et al., 2019; Green et al., 2022). Additionally, grouping prey into 'guilds' is a common

103   ecological practice of dimension or variable reduction (Pomerleau et al., 2015; Parravicini et al.,

104   2020), based on shared traits describing similar trophic or other functional roles for those species

105   (Gitay & Noble, 1997) in order to model complex species distribution and interactions. Notably,

106   this practice is instrumental in designing diet matrices for ecosystem mass balance models or

107   food web modelling (Hui, 2012). Functional and non-taxonomic predictors for species

108   interactions position scientists to predict ecological outcomes in new contexts (McGill et al.,

109   2006; Kiørboe et al., 2018; Green et al., 2022).

110   Functional trait-based approaches may be particularly useful for tunas because they

111   have taxonomically broad diets (Duffy et al., 2017; Pethybridge et al., 2018) and continue to

112   consume very small prey with increasing predator body size (Ménard et al., 2006; Young et al.,

7

113   2010; Romanov et al., 2020; Portner et al., 2022). While these foraging properties make tunas

114   salient indicator species to track changing prey communities and predator-prey interactions

115   under climate change, they also make them excellent candidates for trait-based modelling to

116   synthesise complex interactions with numerous prey species and to investigate evidence for

117   selection for certain types of forage (Glaser, 2010; Valls et al., 2022). Previous diet analyses of

118   yellowfin, bluefin, bigeye and albacore tunas revealed dietary shifts and niche partitioning

119   across predator species and life stage, latitude and environmental drivers (Allain et al., 2012;

120   Young et al., 2015; Duffy et al., 2017; Pethybridge et al., 2018; Portner et al., 2022; Valls et al.,

121   2022; Nickels et al., 2023). Additionally, shifts in albacore distribution have previously been

122   linked to prey availability (Pearcy, 1973). Many of these studies hypothesise about the role of

123   traits in driving observed patterns and shifts. However, the extent to which trait information

124   could explicitly explain tuna foraging ecology across space and time, and to predict their

125   resource use under changing environmental states remains poorly understood.

126   Using albacore (*Thunnus alalunga*) as a case study, we seek to move beyond descriptive

127   diet analyses to identify non-taxonomic predictors for trophic relationships in highly migratory

128   pelagic predators and commercially valuable species. Our synthesis aggregates historical data on

129   albacore diets from published and grey literature dating from 1880–2020 globally. Our aims are

8

130   threefold, to: (1) reconstruct historical resource use for albacore across geographies from

131   published, aggregate, mean diet composition data; (2) use functional traits to distil diverse

132   predator-prey interactions into key trait-based guilds; and (3) explore species-based and trait-

133   based variability in the historical composition of albacore diets across the geographies sampled.

134

135   2. **Methods**

136

137   *2.1 Historical diet data collation*

138

139   Our synthesis required quantitative data on adult or juvenile albacore diet composition obtained

140   from stomach content analyses that identified consumed prey to species-level. To obtain these

141   data, we compiled published and grey literature, research theses, and historical reports for

142   albacore diets by searching bibliographic databases (Supporting Information, Table S1) queried

143   from 1900 until 2020 using diet analysis search terms and synonymous scientific names for

144   albacore (*Thunnus alalunga*; Supporting Information, Table S1). We also investigated diet

145   reports cited within articles, which expanded our range to include several reports from the 1880s.

146   Studies typically reported a mix of diet metrics (i.e., frequency of occurrence, numerical

147   abundance and/or other metrics). However, except for frequency of occurrence data, few studies

148   consistently reported on other metrics.

149   We obtained diet data from 26 studies that were suitable for meta-analysis (Supporting

150   Information, Table S2); this included 69 independent observations (i.e., by specific geographic

151   location, region, year, and/or season sampled) of adult and juvenile albacore diet composition

152   from 1880–2015 and that were digitised and transcribed (Figure 1a; Supplementary Data, Table

153   S3). Several reports presented aggregate diet information for multi-year sampling programs

154   (Supplementary Data, Table S3) and for analyses in these cases, we used the last year of

155   sampling completed. Albacore were typically collected either via scientific sampling programs

156   (i.e., National Oceanic and Atmospheric Administration [NOAA], Centre National de la

157   Recherche Scientifique [CNRS]), or in collaboration with commercial fishing operations (Bello,

158   1999; Joubin & Rouie, 1918; Glaser et al., 2015; Romanov et al., 2020), and using surface troll,

159   pole-and-line, longline gear fished at specified depths (ranging from set at the surface down to

160   over 500 m in depth), or purse-seining gear (for metainformation on specific depth and sampling

161   information for each study see Supplementary Data, Table S3).

162

163   *2.2 Prey trait information*

164

165   For each prey species and life stage (i.e., larva, juvenile, adult) identified (Supplementary Data,

166   Table S4), we collected information for four habitat use traits known to affect the likelihood of

167   pelagic predators encountering and consuming prey (Green et al., 2019). These were: (i) vertical

168   habitat use defined as position in the water column, and (ii) horizontal habitat association with

169   respect to distance from the coast through to oceanic ecosystems, (iii) presence of diel vertical

170   migration, and (iv) presence of seasonal migration and/or seasonal aggregation behaviour (Table

171   1; Supplementary Data, Table S5). These trait data were extracted from a broader database of

10

172   traits that inform predator-prey interactions for albacore (Gleiber et al., 2022). This database

173   used online repositories for species-level information, primarily FishBase (Froese & Pauly,

174   2020), SeaLifeBase (Palomares & Pauly, 2020), and the IUCN Red List of Threatened Species

175   (IUCN, 2020), and searched descriptive published literature for each species using Web of

176   Science and Google Scholar (for detailed trait data collection methodology see Gleiber et al.,

177   2022). We further describe how prey species' trait values were used and in some instances

178   modified for analyses in Supporting Information, Appendix B. For example two species

179   primarily occur at bathypelagic depths and are classified as such in the pelagic species trait

180   database (Gleiber et al. 2022). However, albacore do not occur beyond mesopelagic depths,

181   where these species are also secondarily known to occur, they were thus reclassified as

182   mesopelagic for the purposes of inclusion in analyses for this study. Similarly, for analyses and

183   due to low representation of certain trait-values, reef-associated and coastal prey species were

184   combined into the 'coastal' category, and continental shelf and continental slope species were

185   combined into 'continental shelf' (Table 1).

186

187   *2.3 Prey life stage estimation*

188

189   Juvenile and adult albacore generally consume post-larval and juvenile prey life stages, as well

190   as adults of some species (Allain et al. 2012; Muhling et al. 2019; Romanov et al. 2020). Given

191   that traits could vary between life stages for many species and the requirement for our analyses

192   to select one trait value per trait per species, we needed to select traits for the life stage most

11

193   consumed by albacore predators for each prey species. Of the 308 identified prey species, 72

194   (23% of species) were reported with associated life stage information (Supplementary

195   Information, Figure S1; Supplementary Data, Table S4). Albacore rarely consumed larvae, 11

196   species in total were reportedly consumed as larvae, however 6 of these were consumed with <

197   1% frequency of occurrence and % numerical abundance, and were much more commonly

198   consumed as post-larvae or juveniles, thus only 5 of these 11 species were classified primarily

199   consumed as larvae and with larval traits used for this analysis.

200   When specific information was not provided, it was necessary to estimate prey life stage

201   from available information on the size and age class of either the predator or prey in each study

202   (Supplementary Information, Figure S1; Supplementary Data, Table S4). For 15 species (~5%),

203   prey length information was reported but not life stage. Reported total lengths ranged from 1.5–

204   24.5 cm, and these prey species' life stages were therefore inferred relative to their known length

205   at maturity (Supplementary Information, Figure S1; Supplementary Data, Table S4). There were

206   221 species (72%) identified in albacore diets without meta-information and assumed to be either

207   juveniles or adults (Supplementary Information, Figure S1). Trait information was often similar

208   between juvenile and adult life stages (Gleiber et al., 2022), thus for 127 of these species

209   (41%), no further estimation of prey life stage was needed (Supplementary Information, Figure

210   S1).

211   Trait information differed by at least one trait value and by life stage for remaining 94

212   prey species (31%); for example, these could include a benthic adult with a pelagic juvenile life

213   stage (Supplementary Information, Figure S1). Here, the most plausible life stage consumed was

214   then assessed on a case-by-case basis (described and annotated in Supplementary Data, Table

215   S4). As albacore are epipelagic predators, the pelagic stage of these prey was most likely

216   consumed, and albacore are more likely to consume smaller juvenile prey, for example

217   epipelagic juvenile hake (less than 10 cm and up to 20 cm length) than benthopelagic adult hake

218   (~40–90 cm) (Bailey et al., 1982).

219   We corroborated these decisions based on calculated maxillary length (or 'gape limit')

220   for the fork lengths (FL) of albacore sampled to determine whether adult prey could feasibly

221   have been consumed from a published relationship between length and gape for closely-related

222   yellowfin tuna (Ménard et al., 2006; described in Supplementary Information, Appendix C).

223   Depending on the data reported, we used either a measured maximum albacore FL) (51 species

224   [16%]), or an estimated maximum FL for the population of albacore sampled for each study that

225   did not measure or report albacore lengths sampled (43 species [14%]), as inputs to the equation

226   (Figure S1) (Ménard et al., 2006). Albacore lengths were reported for 16 out of 26 studies, and

227   for 10 studies where albacore lengths were not reported, we coarsely matched gear-specific

228   length data (range and mean FL) from relevant regional fisheries management organisations

229   (ICCAT, 2020; ISC, 2006) to albacore diet studies by year and gear type used. We then

230   estimated the likely life stage(s) sampled using region-specific age and growth curves, and sizes

231   at maturity (described in detail for each study in Supplementary Data, Table S3). Further detail

232   and resources used in estimating the mean and range in albacore lengths for a given study are

233   further described in Supplementary Information, Appendix C.

234   Based on the results of a linear regression, there was no significant difference (p-value >

235   0.05) between the variances of mean, minimum and maximum FL for studies where these

13

236   parameters were measured or where these parameters were estimated in this study (Figure S2).

237   This process of estimating albacore length information resulted in estimated gape limits of 6.4–

238   11.5 cm across studies and locations sampled, and affected only 14% of decisions on prey life

239   stage and selection of appropriate trait information, while providing useful meta-information for

240   future studies aiming to investigate patterns in albacore diets (Supplementary Information,

241   Figure S1). Overall, our synthesis uses the following prey life stages consumed by albacore: 5

242   larval life stages, 210 juveniles, and 93 adults (Supplementary Data, Table S5).

243

244   *2.4 Trait-based analyses*

245

246   The analytical workflow developed for this study is illustrated in Figure 2. All data

247   manipulation, statistical analyses and graphical illustrations were performed in *R* (version 4.2.1)

248   (R Core Team, 2022) and statistical routines and software packages used are described in

249   reproducible detail herein. All graphical illustrations were produced in ggplot2 (v3.3.5)

250   (Wickham, 2016).

251

252 *2.4.1 Taxonomic and trait diversity in albacore diets*

253

254 To report on the historical taxonomic diversity of prey in albacore diets, species accumulation

255 was calculated and plotted using *BiodiversityR* (version 2-14.1; Kindt & Coe, 2005) where the

256 cumulative total number of species identified in albacore diets was calculated in relation to ocean

257 basins and the year(s) sampled (n = 69 observations) by each study (n = 26). To report on the

258 trait-based diversity of prey in relation to taxonomic diversity, species' phylogenetic information

259 was extracted from the Open Tree of Life Data using the package *rotl* (version 3.0.12)

260 (Michonneau et al., 2016) and parsed to a phylogenetic tree using *ape* (version 5.6-2) (Paradis &

261 Schliep, 2019) and *stringr* (version 1.4.0) (Wickham, 2021) with integrated species-specific

262 habitat use trait information (Table 1; Supplementary Data, Table S5) displayed using *ggtree*

263 (v3.3.1.900) (Yu et al., 2017) to simultaneously visualise relationships across taxonomic and trait

264 diversity.

265

266 *2.4.2 Albacore prey trait guilds*

267

15

268   To simplify this large prey diversity, we aimed to quantitatively classify prey species into trait-

269   based guilds (Figure 2). For the 292 prey species with complete trait information, key trait guilds

270   were identified using a divisive hierarchical clustering algorithm (Anderberg, 1973; Legendre &

271   Legendre, 1998). This was built on a Gower dissimilarity matrix for mixed variable types (here

272   binomial and categorical) (Gower, 1971) to identify relational structure among albacore prey in

273   relation to ecological trait data for the four habitat use variables: two binomial variables

274   (seasonal and diel vertical migration) and two multi-level categorical variables (vertical and

275   horizontal habitat use) (Table 1; Supplementary Data, Table S4) in *vegan* (v2.5-7) (Oksanen et

276   al., 2020) and *cluster* (v2.1.2) (Maechler et al., 2021) and visualised using and *dendextend*

277   (v1.15.2) (Galili, 2015).

278   We used a consensus approach for validating cluster results and for optimising cluster

279   selection and partition by assessing several stability and internal validation metrics

280   (Supplementary Data, Table S6) (Brock et al., 2008). Specifically, we assessed: (1) inter-cluster

281   variation – maximum separation of species between clusters – indicated by higher average

282   distance between species clusters (Rousseeuw, 1987); (2) intra-cluster variance or minimum

283   separation of species within clusters indicated by lower average distance within species clusters

16

284   (Handl et al., 2005); (3) high silhouette width coefficient value and Dunny Smith residuals

285   (Dunn, 1974; Rousseeuw, 1987) representing optimal cluster compactness and separation

286   qualities; and lastly, (4) optimal evenness or balance of cluster composition indicated by the

287   number of species in each cluster (Legendre & Legendre, 1998). Trait values that influence a

288   species' occupancy within a cluster were visualised using heat maps illustrating the importance

289   of trait values to the composition of each cluster.

290

291   *2.4.3 Trait-based and taxonomic diet variation*

292

293   Historical albacore diet composition across geographies was visualised using frequency of

294   occurrence data from 23 studies that yielded 60 observations (independent years and locations

295   sampled) of diet composition, because 3 studies in this dataset (9 observations) included

296   presence only data and there were insufficient studies reporting numerical abundance (n = 13

297   studies, 23 observations) and mass-based (n = 10 studies, 32 observations) information on prey

298   contributions to diets. To visualise frequency-based contributions of prey trait guilds to albacore

299   diets, we calculated a normalised index of contribution for each prey species relative to (i) the

300   trait guild they were classified in and (ii) the sum of frequency of occurrence data within each

301   observation per study. Of note, several species with incomplete trait information are therefore

302   'not classified' with trait guilds and are included in illustrations of diet composition.

303   For statistical modelling of trait-based variance in albacore diet composition across

304   geographies, rare species that occurred once or twice in this reduced dataset. Due to

305   overdispersion in frequency of occurrence data containing large variation in species composition

306   values, and in meeting model assumptions of normality, we used data on species

307   presence/absence in diets, which was also the most consistently reported and translatable metric

308   of contribution historically. Poorly sampled locations were excluded from further analyses

309   (samples from South Pacific [n = 7 observations], South Atlantic [n = 2], and Indian [n = 3]

310   Oceans, altogether from 4 studies), as well as. We therefore compare the diet composition for

311   albacore from sampling locations in the North Pacific (n = 27, samples mainly come from the

312   California Current System), North Atlantic (n = 21, largely representing North Atlantic Drift),

313   and Mediterranean Sea (n = 9), providing us with 57 observations from 22 studies of albacore

314   diet composition, and including 98 species.

315   We use a fourth-corner, model-based approach (Dray & Legendre, 2008; Brown et al.,

316   2014), which builds on the generalised linear modelling (GLM) framework (Nelder &

317   Wedderburn, 1972) to simultaneously test how the composition of albacore diets (L matrix of

318   species presence/absence) differed as a function of two different types of explanatory variables: a

319   geographic variable (R matrix, here containing locations sampled) and prey trait information (Q

320   matrices), producing the trait-geographic interaction (QxR) or the fourth corner solution to a

321   multi-matrix problem. We built 3 models to test the role of species identity (with no traits) or two

322   types of trait information (individual trait values Q1 and trait guilds Q2), and geographic location

323   (R) in explaining the presence of prey types (L) across the global data set (Table 2).

324   We used a binomial distribution for presence/absence data, analysed via logistic

325   regression (with logit link function) using the *traitglm* function in the R package *mvabund*

326   (version 4.1.12) (Wang et al., 2021). We included a species effect in models (i.e., a different

327   intercept term for each species), akin to fitting a random effect variable to account for differences

328   in absolute number of species occurrences (Brown et al., 2014; Wang et al., 2021). Additionally,

329   models were fit with a LASSO penalty, specifying the fitting method as '*glm1path*', using

330   penalised likelihood to impose a constraint on estimates of model parameters (Hastie et al., 2009;

331   Brown et al., 2014). This constraint shrinks coefficients to zero when not statistically significant,

332   providing a combined approach for variable selection, p-value adjustment for multiple models,

333   and parameter estimation to evaluate the magnitude and significance of an explanatory variable

334   (Hastie et al., 2009). Trait-geographic relationships for individual trait variables and constructed

335   trait guilds were illustrated as heat maps indicating the interaction strength, and positive or

336   negative correlation between trait information and geographies sampled. Model fit was assessed

337   by plotting multivariate residuals against fitted values and plotting quantile-quantile (Q-Q) plots.

338   Multivariate data were previously screened for broad trends using conditional boxplots (Zuur et

339   al., 2010), for overdispersion and outliers by nMDS plots (Field et al., 1982) using *vegan*. All

340   model assumptions were met.

341

342   ### 3. Results

343

344   *3.1 Taxonomic and trait diversity in albacore diets*

345

346   This synthesis reveals the large biodiversity of prey consumed by albacore globally (Figure 1)

347   with 308 prey species, and 238 at lower taxonomic resolution (Supplementary Data, Table S7).

348   Prey species mainly hailed from 7 classes representing 203 families in the total dataset including

349   prey identified at coarser taxonomic resolution than species; ray-finned fishes (Actinopterygii, n

350   = 108 families of prey), cephalopods (n = 29), and crustaceans (Malacostraca n = 45,

351   Hexanauplia n = 6), and also including pelagic gastropods (n = 6), salps (n = 2), one hydrozoan

352   (Figure 3a). In addition to these classes, prey identified at higher taxonomic resolution included

353   one appendicularian, one branchiopod, and one elasmobranch (an unknown Squalidae species)

354   (Supplementary Data, Table S7). Whilst the North Pacific, North Atlantic, and in the

355   Mediterranean Sea received the greatest sampling effort and most of the albacore prey known to

356   date were identified in these regions of the world (Figure 1b/c); an unknown and potentially

357   large diversity of prey remains to be identified in the South Pacific, South Atlantic, and Indian

20

358   Oceans (Figure 1b/c). Additionally, out of 308 prey species, 201 were observed in < 10% of

359   stomach samples within any study (Supplementary Information, Figure S3).

360   Individual traits varied across phylogeny and recurred across unrelated prey taxa (Figure

361   3a). The dominant habitat use trait values in the prey assemblage were the most characteristic of

362   pelagic and oceanic ecosystems, including epipelagic and mesopelagic vertical habitat use,

363   oceanic and continental shelf horizontal habitat use, seasonal migration and aggregation

364   behaviour and diel vertical migration (Figure 3a).

365

366   *3.2 Albacore prey trait guilds*

367

368   We obtained complete trait information for 292 prey species and these were optimally classified

369   into seven trait guilds reflecting different combinations of four traits affecting predator-prey

370   encounter processes, vertical and horizontal habitat use, seasonal migration and diel migration

371   traits (Table 1, Figure 3; Supporting Information, Appendix D, Figures S4 & S5). The most

372   species rich trait guild consisted of diel migrating mesopelagics (trait guild 2), distinct from the

373   least species rich non-diel migrating mesopelagics (1) (Figure 3b). The second and third most

374　　abundant groups included the oceanic (or 'offshore') epipelagics (5) and coastal and shelf

375　　epipelagics (3), followed by seasonal, continental shelf taxa (6) and resident continental shelf

376　　taxa (7) (Figure 3b). Finally, the rarest prey guild globally was the coastal and shelf demersal

377　　taxa (4) (Figure 3b). The hierarchical divisive clustering technique for 7 optimal clusters

378　　performed well in grouping taxa that are also clustered based on their trait values in multivariate

379　　space (Supplementary Information, Figures S4 and S5).

380

381　　*3.3 Historical trait-based albacore diet composition*

382

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

404   Underlying taxonomic variation in regional dietary signatures (Supplementary

405 Information, Figure S6) was significantly explained by both trait information and trait guilds,

406 particularly for samples from the North Pacific and the Mediterranean, although correlation

407 coefficients for notable relationships ranged from 0.1–0.2 (Figure 5). The model built on

408 individual trait information provides results on significance testing of each individual trait, while

409 the model built on trait guilds assumes all traits used to build those guilds are of interest. It is

410 useful to observe that the results of both models are congruent, and thus both approaches are

411 likely interchangeable in this context.

412

413   4. Discussion

414

415   *4.1 Synthesis of albacore diet diversity and historical trait relationships*

416

417   We reconstructed historical resource use for albacore tuna (*Thunnus alalunga*) globally,

418   highlighting biodiverse diets in this predator (n = 308 prey identified to species, plus an

419   additional 238 prey taxa identified to genus or higher). We quantitatively synthesised this large

420   prey diversity into 7 functional trait guilds using four sets of traits influencing predator-prey

421   encounter rates: prey vertical and horizontal habitat association, seasonal and diel vertical

422   migration behaviour. Trait guilds included: diel migrating mesopelagics, non-diel migrating

423   mesopelagics, oceanic epipelagics, coastal and shelf epipelagics, coastal and shelf demersal taxa,

424   seasonal continental shelf, and resident continental shelf taxa. Importantly, this study identifies

425   both taxonomic and trait-based variability in diets of albacore tuna globally and identifies trait-

426   based dietary signatures in albacore beyond taxonomic variability.

427   Our results indicate that both trait information and constructed functional trait guilds

428   serve as useful classification tools for tracking large-scale shifts in albacore diets in time and

429   space. Importantly, trait-based frameworks enable functional simplification of diverse prey and

430   functionally redundant food web linkages (Link, 2007), especially for   highly migratory

431   pelagic predators. Here, we display the results of two models: 1) built using individual trait

432   information which provides results on significance testing of individual trait information when

433   assessing individual trait importance is needed, and 2) built on trait guilds where the user has

434   assessed that a functional grouping of traits is needed. While the results of both models, run

435   simultaneously, supported each other, the individual trait information provided higher resolution

436   information on specifically which levels of trait variables most explained variance in diet

437   composition and for each ocean basin assessed in this meta-analysis. It is encouraging that the

438   model built on trait guilds produced similar results, the foundation of which were individual

439   traits, because this lends support to projects that have needed to simplify diversity in diet

440   analyses through quantitatively or qualitatively clustering prey species into guilds.

441   Traits have proven useful in describing albacore foraging dynamics in prior studies of

442   tuna diets (Young et al., 2010). In the South Pacific, previous studies describe albacore diets as

443   largely consisting of mesopelagic and epipelagic prey, and to a lesser extent include surface

444   migrating bathypelagic and coastal reef-associated taxa (Allain, 2005; Allain et al., 2012; Olson

445   et al., 2016; Young et al., 2010). Albacore diets in the Indian Ocean have previously been

446   characterised by a reliance on mixed epipelagic to mesopelagic resident prey stocks (Romanov et

447   al., 2020). Our reanalysis of these data within the global synthesis corroborated and extended

448   these previous descriptive observations.

449   Trait information was rarely used in an explanatory capacity in the North Pacific, North

450   Atlantic and Mediterranean. Most studies from the North Atlantic and Mediterranean, home to

451   some of the earliest and most detailed investigations of albacore diets (especially from the

452   1930's; Bouxin & Legendre, 1936; Legendre, 1934, 1940), categorised the diets of albacore as

453   'specialised' (Consoli et al., 2008), of narrow trophic niche width (Teffer et al., 2015), and of

454   short food chain length and low trophic adaptability (Pethybridge et al., 2018) compared to the

455   longer food chain lengths and higher trophic complexity of Pacific tuna diets. Our re-analysis of

456   the same data substantiates earlier observations and found that three trait guilds based on habitat-

457   use accounted for a large proportion of diet composition observations from the North Atlantic

458   and Mediterranean. Mediterranean samples were especially dominated by seasonal and resident

459   continental shelf taxa. However, in the North Atlantic dominant prey trait guilds shifted over

460   time, and the detailed taxonomic identification by Bouxin and Legendre in the 1930's revealed

461   particularly trait-diverse diet composition. Trait guilds identified in samples from the North

462   Atlantic and North Pacific were also more diverse than observed elsewhere, and included

463   frequent consumption of and shifts between continental shelf, offshore to coastal, mesopelagic

464   and epipelagic trait guilds.

465   We posit that investigating trait-based diet shifts in albacore will be a powerful

466   framework for tracking foraging responses to environmental variability. Our study shows clear

467   differences in trait-based diet composition across the years and locations sampled. It may be that

468   the productivity of individual species alternates and shifts across environmental gradients and

469   inter-annual cycles, whilst that of trait guilds may be more stable and offer predictive insights

470   (e.g., the productivity of mesopelagics and coastal to shelf epipelagics in relation to

471   environmental shifts). Further, linkages between traits that describe prey habitat use and

472   migratory behaviour, alongside prey taxonomy, to their contribution to predator provides an

473   important inference for spatial and temporal variability of forage for predators and may

474   contribute to identification of foraging hotspots in large pelagic ecosystems.

475

476

477   *4.2 Synthesis limitations and knowledge accessibility*

478

479   Investigating the extent to which varying consumption of trait guilds relates to environmental

480   drivers and climate states will require further access to disaggregated diet data (i.e. prey from

481   each individual predator) sampled consistently over time and space. Additionally a limitation of

482   this study and recommendation of future work is to formally test the extent to which species

483   taxonomic, phylogenetic and trait information explains variation in diet composition. In applying

484   traits to analysing ecological interactions, it will be important to quantify the extent to which

485   traits recur across unrelated taxa (i.e. phylogenetically conserved or not) (Ives & Helmus, 2011).

486   Trait and phylogenetic information are likely not completely redundant and ideally should both

487   be accounted for in modelling frameworks (Ovaskainen et al., 2017), as both provide different

488   and useful information in characterising trophic interactions between albacore and their prey.

489   This meta-analysis also highlights variable sampling of albacore tuna diets in space and

490   time, with long gaps between studies ranging from a few years to over fifty years apart

491   depending on ocean basin. Historically, the North Pacific and Atlantic basins were the most

492   studied and taxonomically diverse regions for albacore diet composition, with over 100 species

493   of prey identified in each region, particularly in the productive upwelling system of the Northeast

494   Pacific where most samples were taken in this basin (from 1942 to 2010). In contrast,

495   Pethybridge et al. (2018) found decreased dietary diversity in the productive upwelling regions

496   of the Southeast Pacific (from 2000 to 2015) and for which diet data for albacore were not

497 available for this meta-analysis. Additionally, sampled locations tended to be aggregated within

498 biogeographic provinces of an ocean basin, such as the California Current System for the North

499 Pacific and North Atlantic Drift for the North Atlantic. In most studies examined in this meta-

500 analysis, samples were concentrated in either frontal, upwelling or offshore gyre zones, thus

501 likely more indicative of regional-scale rather than basin-scale processes. We note that published

502 or open-access historical data were sparse for the South Pacific, South Atlantic and Indian

503 Oceans, where we expect the taxonomic and trait biodiversity of prey consumed could be larger

504 than currently identified.

505   Large, disaggregated datasets are needed to further resolve resource use in highly

506 migratory pelagic predators at both broad and finer spatial scales, including information on

507 predator and prey sizes (e.g. lengths and widths). This information is critical to understanding

508 ontogenic shifts in predator diets, as well as changes in forage and fisheries species productivity

509 under changing climate states. An additional data need is that of consistent reporting of more

510 informative metrics than frequency of occurrence, such as contribution to diets based on

511 numerical abundance and biomass of prey consumed (Nickels et al., 2023). Indeed, several

512 project-based, global-scale databases exist for the trophic ecology and resource use of albacore,

29

513   yellowfin, bluefin and bigeye tunas (Young et al., 2015; Duffy et al., 2017; Bizzarro et al., 2022;

514   WCPFC, 2023). The maintenance, expansion and collaborative accessibility of these datasets

515   will enable the production of powerful and predictive models for tuna resource use under climate

516   change. Critically, Young et al. (2015) note both a lack of long-term monitoring and inadequate

517   sampling in some regions, and to that we add that the availability of such data after collection is

518   also a significant hurdle. Tewksbury et al. (2014) and Young et al. (2015) also highlight the

519   ongoing need for international cooperation and collaboration on data.

520   Further, the need for sound design, maintenance and accessibility of large databases is

521   echoed for species' trait information. Many such efforts are publicly available for some

522   taxonomic groups and classes (Froese & Pauly, 2020; Palomares & Pauly, 2020). However,

523   researchers often expend significant effort and personnel towards further processing data from

524   these databases to fill knowledge gaps (Kim et al., 2018), as well as testing and creating

525   synthetic classifications from species-level data. Knowledge on the underlying distribution of

526   traits across environmental gradients is critical to their use as synthetic predictors in changing

527   ecosystems (McGill et al., 2006), and thus trait-based functional groupings of species present us

528   with powerful tools to examine linkages between species, functional responses, and

529   environmental change (McGill et al., 2006; Kiørboe et al., 2018). This is a key knowledge gap in

530   marine and freshwater ecosystems (Green et al., 2022).

531

532   5. Conclusions

533

534   Syntheses of historic trophic interactions are crucial for establishing baselines in understudied

535   systems and understanding how they may change. By digitising and reconstructing historical

536   data on albacore diet composition, we reveal a comprehensive taxonomic and trait-based portrait

537   of the trophic plasticity of albacore, foundational to future analyses of variation in resource use

538   under changing environmental and forage conditions. We generate 7 functional trait-based guilds

539   of prey consumed, applicable beyond this work to classifying prey in albacore and other tunas.

540   We highlight the utility of both functional trait guilds and prey trait information for synthesising

541   variation in predator diets, which here significantly advanced our understanding of globally

542   diverse and temporally variability in albacore diets. Trait-based models revealed broad

543   biogeographic signatures in albacore diets and corroborated known ecological differences

544   between sampled geographies, warranting further development of trait-based analyses and

545   investigation into the stability or flexibility of trait-based biogeographic resource use in highly

31

546   migratory pelagic predators. Ultimately, further modelling applications that use trait information

547   in predator diet analysis frameworks are needed for tracking forage species dynamics and

548   predators' foraging responses to changing ecological states and resource variability.

549

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551

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565

566   **Authorship Statement**

567

568   NH led the design, data collection, analysis and writing. LC, SG and BM contributed to the

569   framework and design of the meta-analysis. NH, SG, CM, IG and ZR co-developed data

570   collection protocols. NH, CM, IG and ZR co-developed methods for data re-analysis and

571   graphics. LC, SG, EH, SB and MJ acquired funding for and supervised this project, providing

572   direct intellectual support and contributions from the conceptualization through to publication of

573   the research. All authors contributed text and substantial revision to the final manuscript.

574

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863

864   **Data Accessibility**

865

866   Both the data and code will be made publicly available through a CC BY 4.0 public-use licence

867   upon acceptance of this manuscript for publication. Given the nature of the data and commercial

868   value of the study species we cannot make data publicly available prior to acceptance for

869   publication of this product. The database for global and historical albacore diet composition from

870   digitised published and grey literature will be made available on the University of Alberta's

871   Dataverse Borealis repository. All code for analyses will be made publicly available on Github

872   (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.

47

		Represents whether prey species are seasonally abundant in the system, either in the form of seasonal spawning aggregations or seasonal migrations within
Seasonal migration	Binary (yes/no)	the system, or local resident prey present at similar abundances year-round.

1

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

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

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

1   **Figure 3.** Diversity of **a)** prey traits across phylogeny for 308 species (grey shading indicates no data available for a particular species

2   and trait); and diversity quantitatively simplified to **b)** radial cluster dendrogram of seven optimal albacore prey trait guilds generated

3   by divisive hierarchical clustering for 292 species associated with complete trait information, overlaid description of the main trait

4   values associated with each cluster (including the number of species within clusters). Traits included: vertical and horizontal habitat

5   use, seasonal and diel vertical migration (available with trait guild information for each species in Supplementary Data, Table S5).

6

7   **Figure 4.** Composition of prey trait guilds within historical albacore diets (y axis; relative % frequency of occurrence [FO]) across

8   locations and dates sampled from 1880–2015 (x axis; including first author and publication date information). Studies (x axis) are

9   ordered by year from oldest on the left to most recent on the right. Diet composition is illustrated using a normalised metric of relative

10   contribution to the total frequency of occurrence of all species within each trait guild, normalised for each replicate diet observation.

11   Note that both samples from the 1880's only reported one or two prey items, and therefore contain 100% of a trait guild, displayed

12   here and not included in statistical analyses.

13

50

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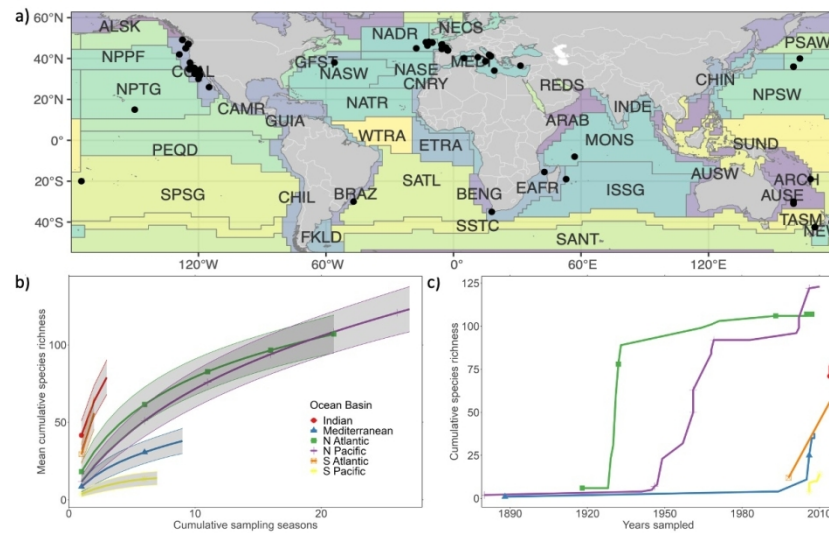
Figure 1. a) Geographic distribution of published albacore diet papers, reports and grey literature from 1880–2020, including Longhurst biogeographical province codes (Reygondeau et al., 2013) to visualise biogeographic distribution of data. A total of 26 studies reported diet data for 69 individual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

Trait-based analyses of historical albacore diets (section 2.4)

1. Report on taxonomic and trait diversity in albacore diets

Develop species accumulation curves in relation to ocean basin sampled for all **308 species** identified in albacore diets from **69** independent diet observations (by season, year and location sampled) reported within **26** studies.

2. Quantitative classification of albacore prey into trait-based guilds

Use divisive hierarchical clustering technique to classify **292 species** with complete trait information from all **69** observations and all **26** studies

Identify optimal clustering and classification of prey trait guilds

Calculate a normalized frequency of occurrence-based index of contribution to diets for each prey trait guild to illustrate variation in historical trait-based diet composition for **60** observations and **23** studies with reported %FO data.

3. Statistically compare trait-based vs. taxonomic information in explaining variation in diet composition

Due to low replication of some species and in some ocean basins, trait-based multivariate generalized linear models were developed for **98** species with > 3 occurrences in the dataset and involved **57** diet composition observations from **22** studies.

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

190x260mm (197 x 197 DPI)
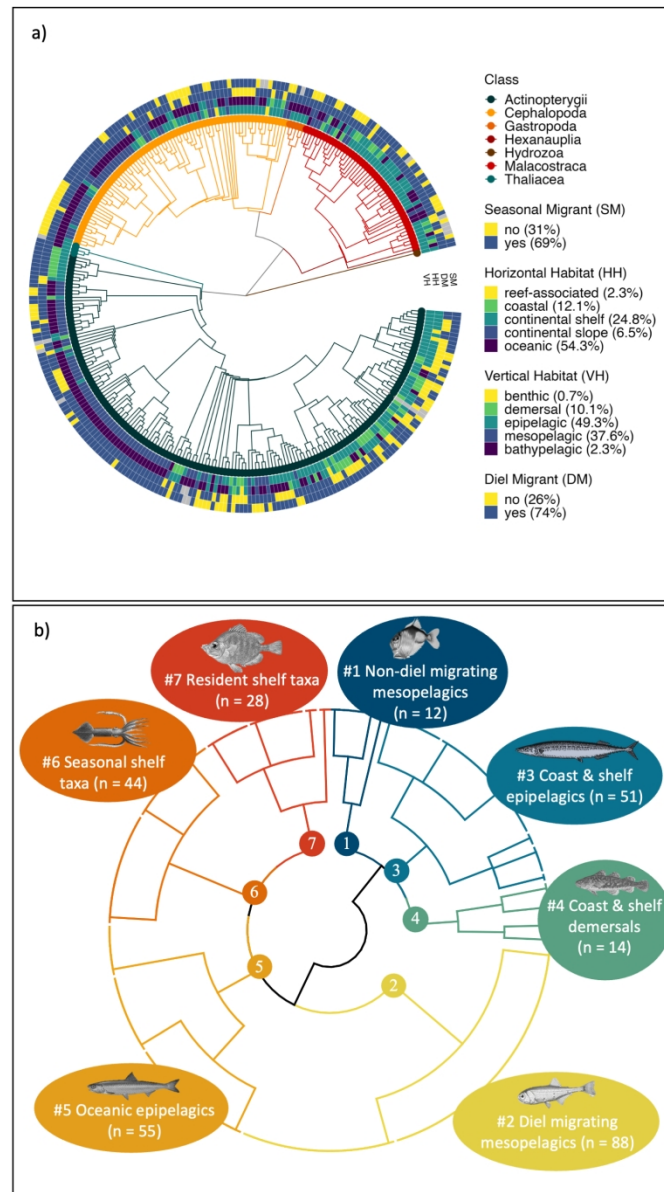
Figure 3. Diversity of a) prey traits across phylogeny for 308 species (grey shading indicates no data available for a particular species and trait); and diversity quantitatively simplified to b) radial cluster dendrogram of seven optimal albacore prey trait guilds generated by divisive hierarchical 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).

190x339mm (197 x 197 DPI)

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.

1799x1640mm (72 x 72 DPI)
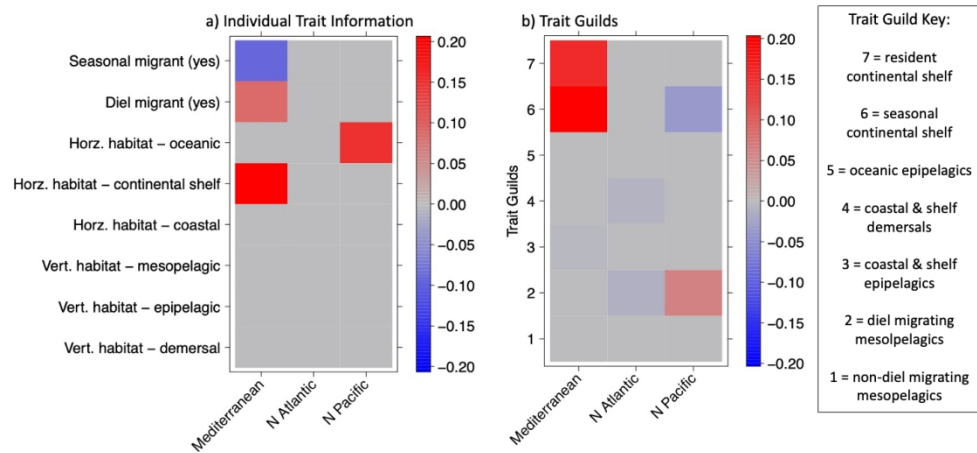
Figure 5. Correlation coefficients for the trait-geographic relationship modelled using the fourth corner solution for a) individual trait information (Horz = horizontal habitat use, in relation to the coast; Vert = vertical habitat use, in relation to water column position), and b) the trait guilds 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 alalonga" OR "Germo alalonga" OR "Germo alalunga" OR "Germo germo" OR "Germo germon" OR "Germo germon steadi" OR "Orcynus alalonga" 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 alalonga" OR "Thunnus alalunga" OR "Thunnus germo" OR "Thunnus pacificus" OR "Thynnus alalonga" 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 *Thunnus alalunga* dans le Nord-Est atlantique
Bello, G.	1999	Journal of Molluscan Studies	Cephalopods in the diet of albacore, *Thunnus alalunga*, 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 *Thunnus alalunga* (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 (*Thunnus alalunga*) 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, *Thunnus germo* (Lacepède), in the central and northeastern Pacific
Jordan & Gilbert	1880	Proceedings of the National Academy of	Description of two species of scopeloid fishes, *Sudis ringens* and *Myctophum*

		Sciences	*crenulare* from Santa Barbara Channel, California.
Joubin & Rouie	1918	Bulletin de l'Institut Océanographique de Monaco	Observations sur la nourriture des thons de l'Atlantique (*Germo alalonga* 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 (*Thunnus*) and Lancetfishes (*Alepisaurus*)
McHugh, JL	1952	Bulletin of the Scripps Institution of Oceanography	The food of albacore (*Germo alalunga*) off California
Ortiz de Zarate, V	1987	Instituto Español de Oceanografía	Datos sobre la alimentacion del atun blanco (*Thunnus alalunga*) 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, *Thunnus alalunga*, off the Bay of Biscay: a case study
Romanov et al.	2020	Marine and Freshwater Research	Trophic ecology of albacore tuna (*Thunnus alalunga*) 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, *Thunnus alalunga*, 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 *Thunnus alalunga* 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 (*Thunnus alaguna*) 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
*These publications were combined as they consisted of three part publication on the taxonomic composition of albacore diets ‡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.			

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

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

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 (Oplophoroidae) 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

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 metainformation 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 ($Lm = 0.0823\ FL + 1.758$) 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-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).
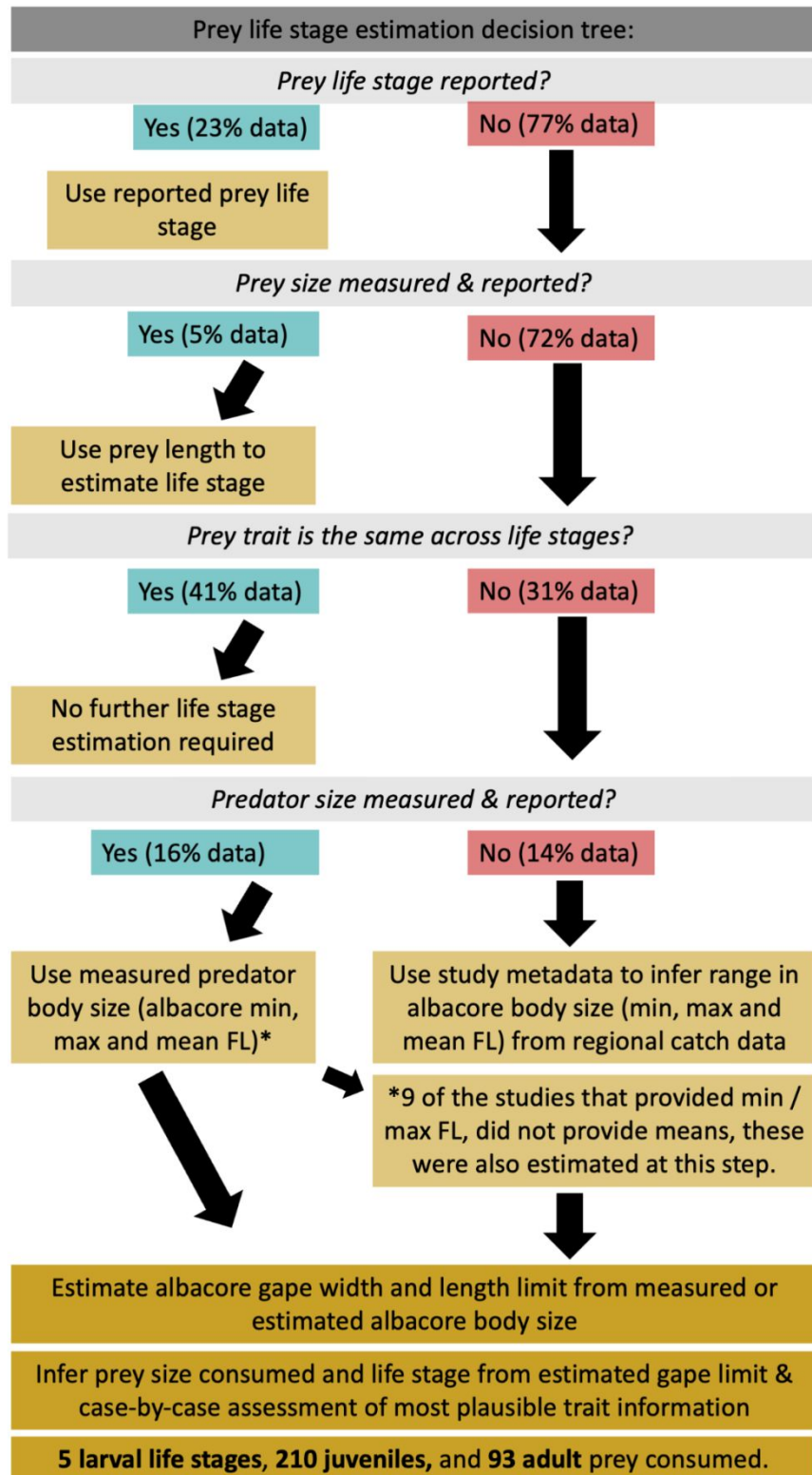
Figure S1. Decision tree for prey species life stage estimation process described in section 2.3.
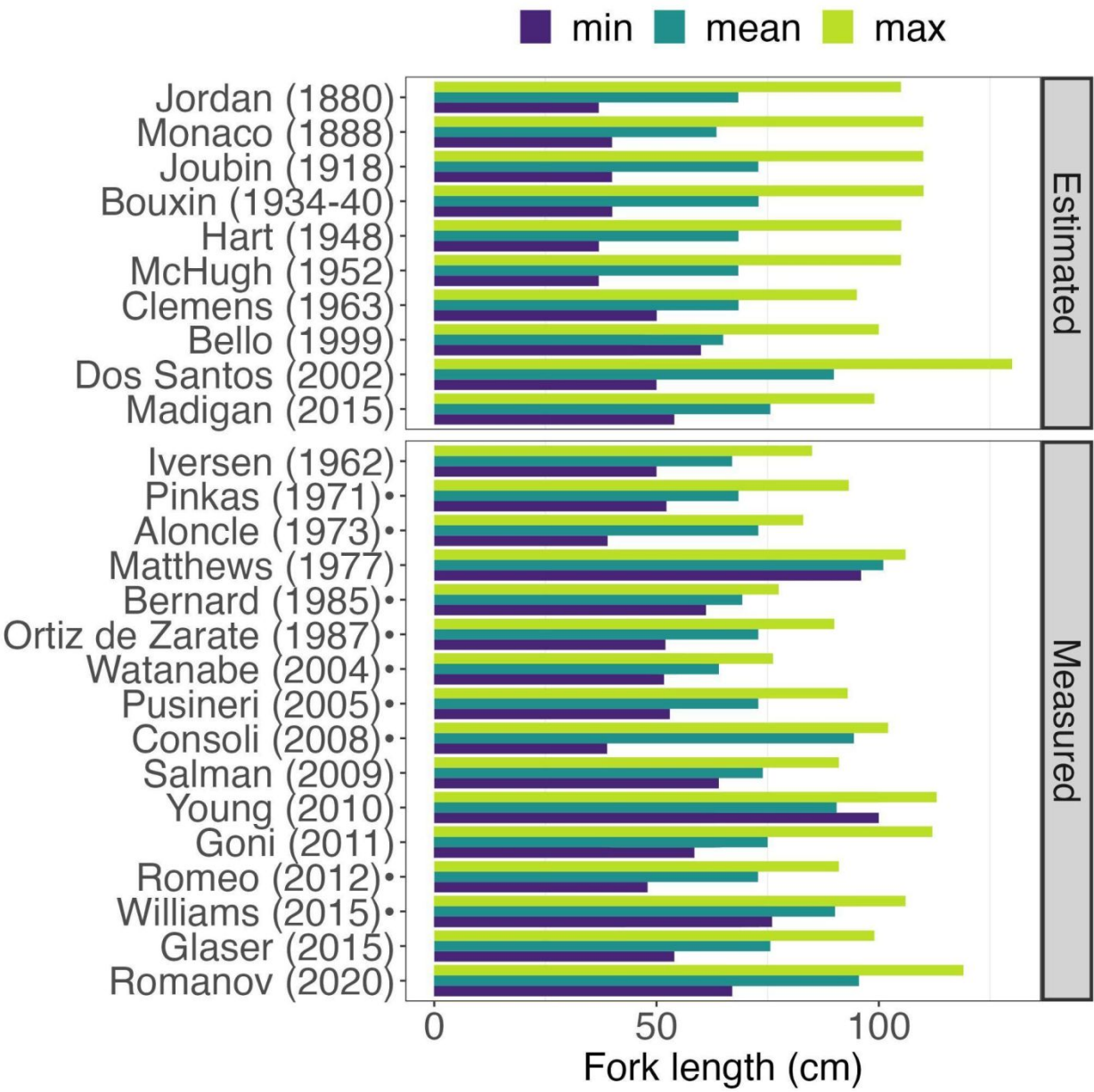
Figure S2. Albacore tuna fork length minima (min), mean and maxima (max) obtained from measured and reported data from 16 publications and estimated for another 10 publications. Of the 16 publications reporting length information, 9 publications (annotated with •) did not include a mean. This value was 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=
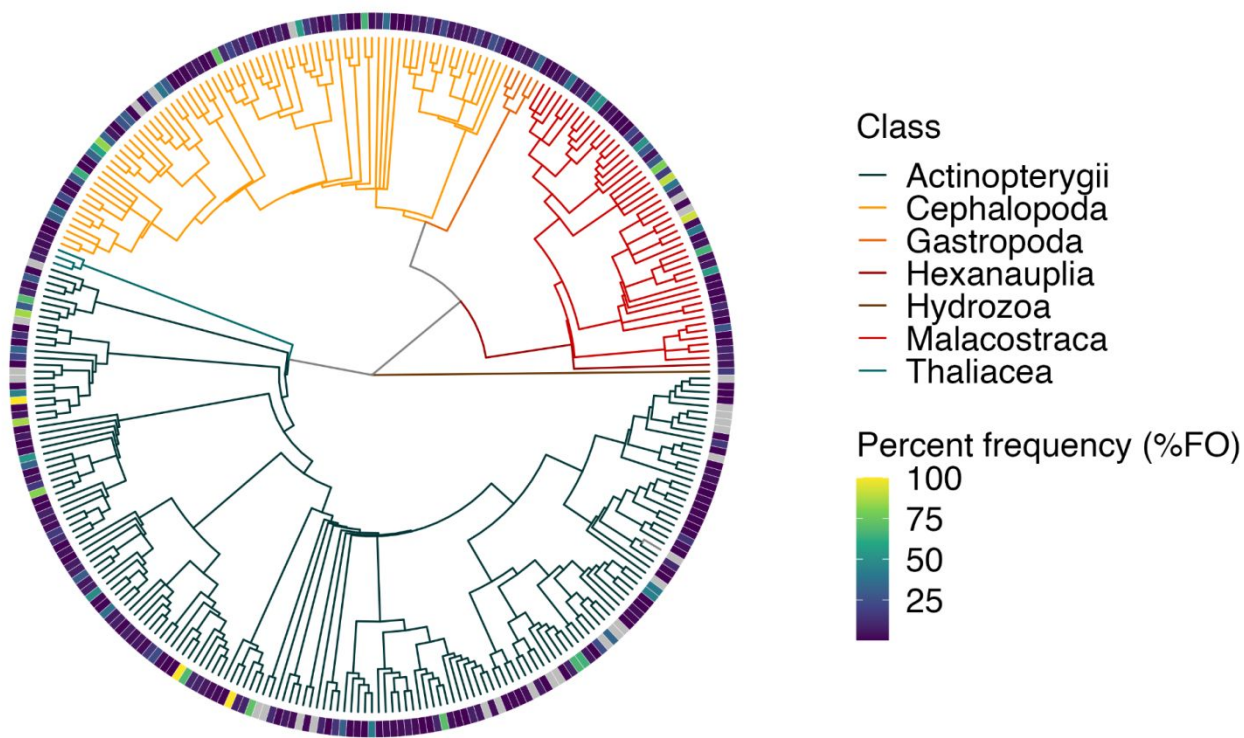
176756372

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.

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=
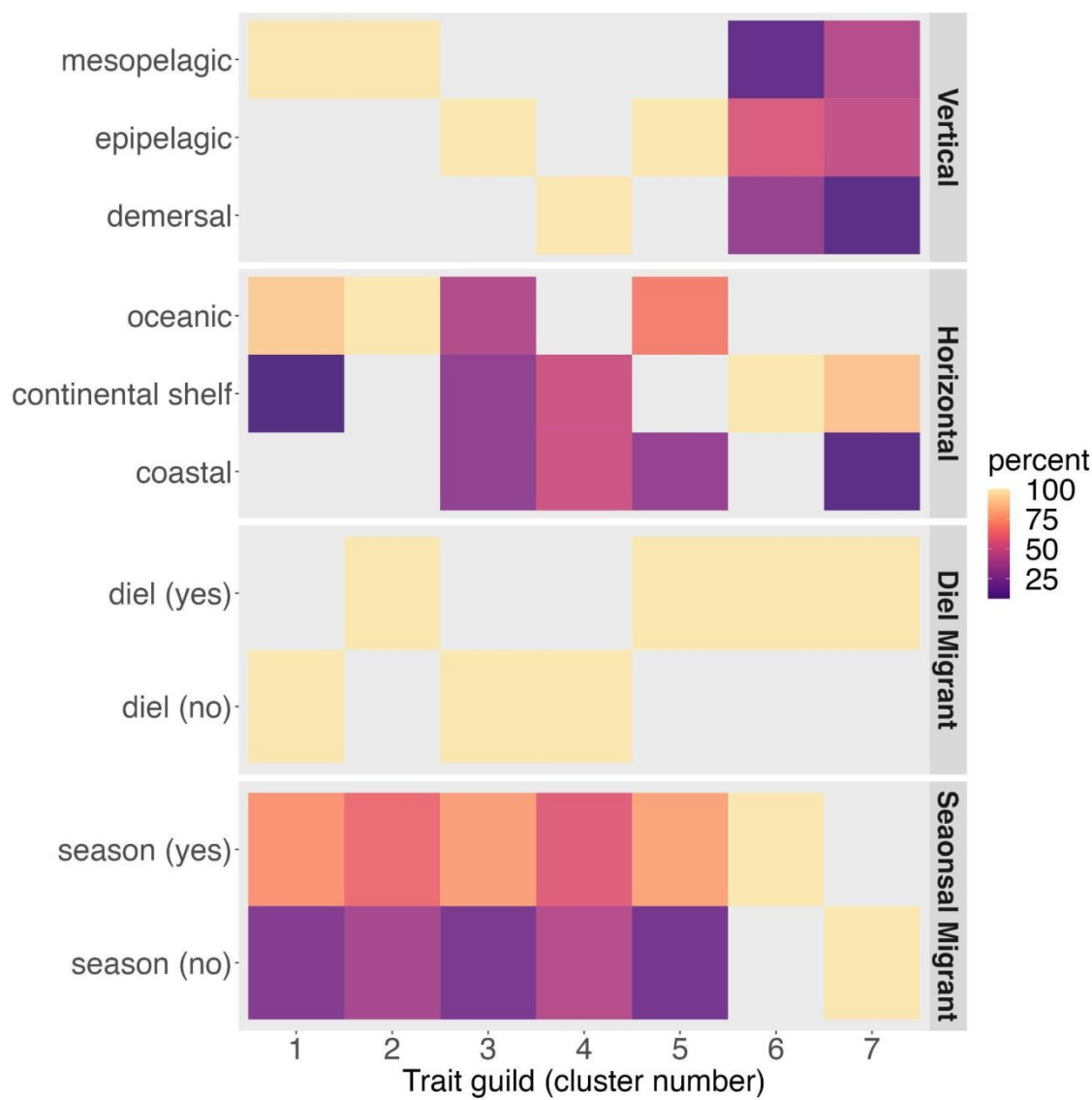
1573200869

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
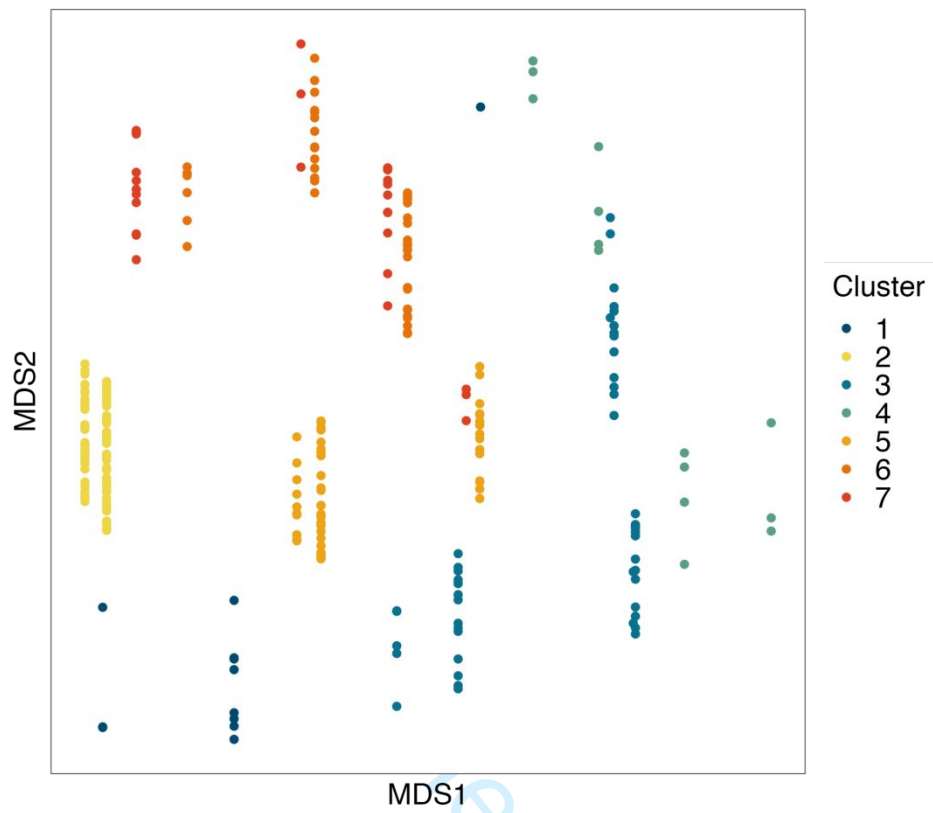
('Seasonal Migrant').

Figure S5. Non-metric multidimensional scaling (nMDS) plot illustrating each species as an

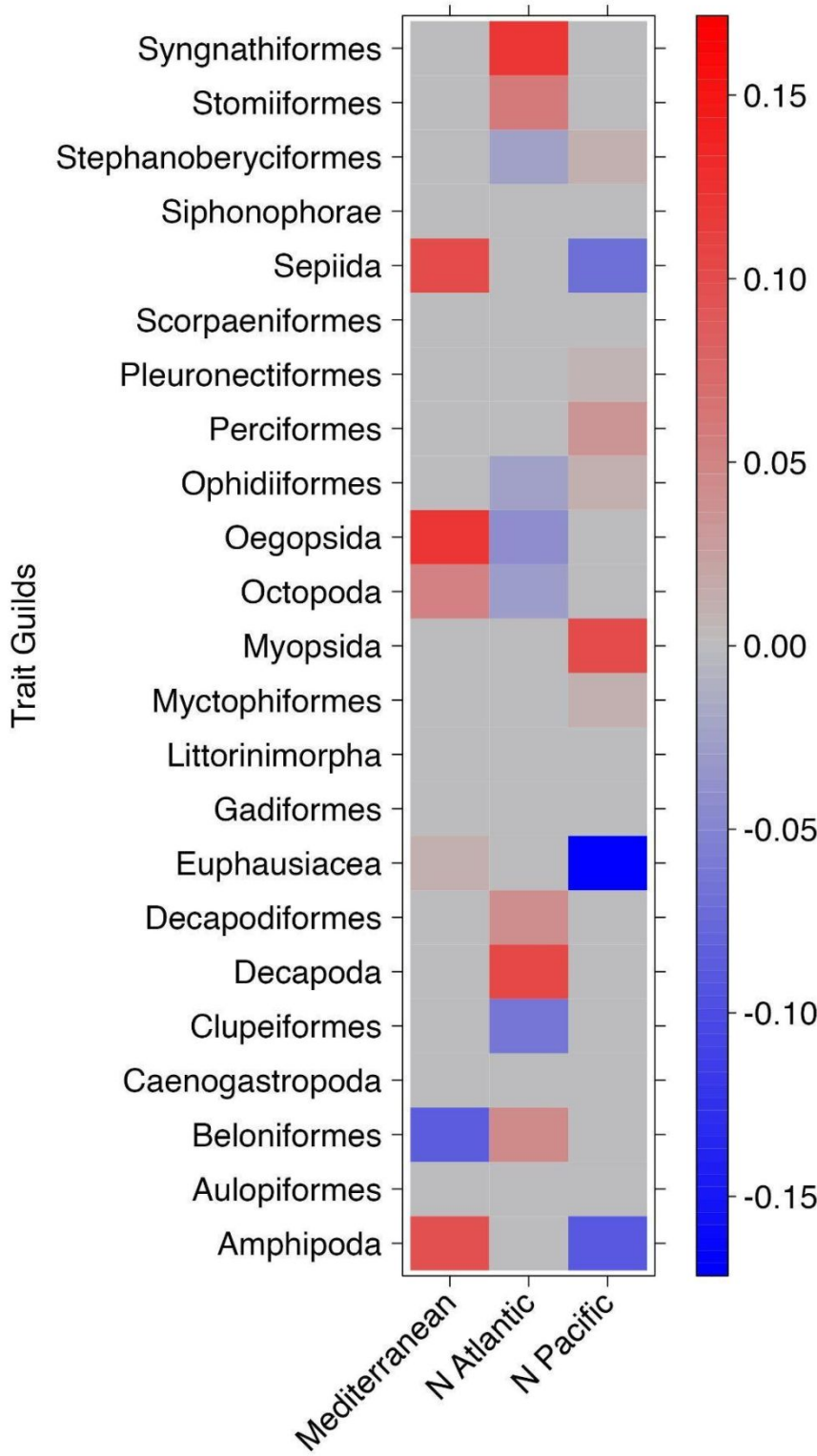assemblage of four trait values and coloured in relation to their classified trait guild.

Figure S6. Correlation coefficients for the fourth corner solution and significant relationships between taxonomic variability 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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