

Trait-based indicators of resource selection by albacore tuna in the California Current Large Marine Ecosystem

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ABSTRACT

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As global climate change reorganizes marine ecosystems, understanding how predators will respond to variable prey resources is critical to forecasting future community dynamics. Prey traits that affect the foraging process and recur across unrelated taxa offer a means to better anticipate predator resource use by simplifying complex foraging dynamics. Here we compare taxonomic and trait-based indicators of resource use and selection for albacore tuna (*Thunnus alalunga*), a commercially valuable pelagic predator undergoing climate-driven range shifts. We synthesized datasets from 2005 to 2019 to evaluate diets of albacore tuna in relation to prey availability estimates from shipboard surveys in the California Current Large Marine Ecosystem. Analyses with these data reveal that albacore and trawl surveys sample different aspects of the pelagic system, with albacore consuming a subset of taxa identified within trawls. Albacore consistently selected coastal prey that are schooling, undefended, silvery and countershaded, and have high energy density — suggesting that ecological mechanisms driving albacore foraging outcomes may be conserved across time and space. Ecological traits mediating predator-prey interactions consistently distinguished albacore diets from assemblages sampled by trawls across years and regions. We demonstrate that a traits-based approach simplifies taxonomically diverse predator-prey interactions and may be a valuable tool to facilitate predictions of prey resource use in changing environments.

1. Introduction

Prey availability strongly influences predator habitat selection, energetics, and ultimately population dynamics (Carroll et al., 2017;

Petchey, 2000). However, open ocean (pelagic) predators have broad geographic ranges and exploit diverse prey communities across space and time (Nickels et al., 2023; Portner et al., 2017). Both diet complexity and sampling limitations complicate the search for strong trends in prey

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use and are barriers to creating prey-resource selection functions (i.e., evaluating consumption relative to resource availability; [Hunsicker et al., 2011](#)). As a result, distribution models for pelagic predators typically focus exclusively on environmental conditions ([Wisz et al., 2013](#)), incorporate only a few common prey items, or have limited explanatory power ([Torres et al., 2008](#)).

Traits-based approaches are emerging as a tool for anticipating how abiotic and biotic interactions will affect both the distribution and abundance of organisms in changing environments ([Barnett et al., 2019](#)). These approaches are rooted in optimal foraging, including the marginal value theorem, which provides a framework for predicting predator foraging decisions based on the relative profitability of prey ([Charnov, 1976](#)). Hypotheses about feeding interactions are formulated around the morphological, behavioral, nutritional, and life history characteristics of prey that are predicted to impact the foraging process (i.e., encounter, pursuit, attack, capture, consumption). The initial analysis requires estimates of predator diet composition, environmental prey availability, and trait information for the potential prey species involved ([Railsback and Harvey, 2013](#)). Identifying traits that are selectively consumed by a focal predator facilitates forecasting of predator-prey interaction strengths in novel and data-limited contexts ([Iannone et al., 2016](#); [Linardich et al., 2021](#)). This approach has proven useful in simplifying complex foraging dynamics for pelagic predators that encounter diverse prey across their ranges ([Hardy et al., 2023](#)) and ultimately can facilitate predictions of prey resource use in environments that are being reassembled by climate change.

Here, we use a highly migratory marine predator that supports commercial fisheries globally ([Nikolic et al., 2017](#)), the albacore tuna (*Thunnus alalunga*, hereafter “albacore”), as a test case for quantifying trait-based prey selection in pelagic ecosystems. Juvenile North Pacific albacore (~2–6 years old) migrate to productive foraging grounds in the California Current Large Marine Ecosystem (CCLME) each summer until they mature and migrate to spawning grounds in the Central Tropical Pacific ([Childers et al., 2011](#)). Intensifying ocean climate change in the CCLME, including the prevalence and intensity of marine heat waves, is expected to alter the location and extent of suitable habitat for albacore as well as hundreds of other taxa in the next century, although at different rates and directions ([Hazen et al., 2013](#); [Liu et al., 2023](#); [Morley et al., 2018](#)). Northward shifts in the location of fisheries landings for the species historically ([Clark et al., 1975](#)), and especially over the past two decades, suggest that changes in the distribution of albacore in the CCLME may already be occurring ([Frawley et al., 2021](#); [Phillips et al., 2014](#)).

Historical albacore distribution and abundance have been linked to dynamic environmental conditions in the CCLME ([Phillips et al., 2014](#)), and are thought to be influenced by trophic interactions ([Pearcy, 1973](#)). On a population level, albacore diets are taxonomically rich (hundreds of prey species) and variable across time and space ([Hardy et al., 2023](#); [Nickels et al., 2023](#); [Nikolic et al., 2017](#)). In the CCLME, information on the distribution of common prey species has not been incorporated into habitat suitability models for albacore (e.g., [Muhling et al., 2019](#)), owing to a lack of data and the sheer number and functional redundancy of interacting species ([Carroll et al., 2017](#); [Link, 2007](#)). Identifying traits

that recur across diverse taxa within the system, and evaluating the extent to which they are indicative of albacore prey selection, could facilitate better predictions of this predator’s distribution and productivity as pelagic communities are reassembled by climate change.

Decades of coastal ocean monitoring by the US National Oceanic and Atmospheric Administration (NOAA) in the CCLME provide an unparalleled opportunity to explore relationships between pelagic predator diets (here, albacore) and the relative composition of pelagic species that might be available to them as prey. Long-term monitoring programs include extensive, annual trawl surveys to sample small-bodied pelagic organisms (i.e., micronekton, body size of 2–20 cm; henceforth referred to as ‘forage’), and annual stomach-content analysis of albacore. These data inform a range of ecological and resource management objectives, including quantifying historical variation in community composition between warm and cool oceanographic states ([Santora et al., 2017](#)), the impacts of marine heat waves on diversity and productivity ([Brodeur et al., 2019](#)), and the development of ecosystem indicators ([Harvey et al., 2020](#); [Hunsicker et al., 2022](#)). Trawl survey data are also valuable for understanding spatio-temporal patterns in the availability of prey to important coastal predators such as Chinook salmon, Pacific hake, and sea lions ([Friedman et al., 2018](#); [Thompson et al., 2019](#); [Wells et al., 2012, 2023](#)). Given that trawls sample depths (~30 m; [Sakuma et al., 2016](#)) within the foraging depth of juvenile albacore in the CCLME (upper 100 m; [Childers et al., 2011](#)) and systematically sample many of the same prey at size ranges consumed by albacore ([Glaser et al., 2015](#); [Nickels et al., 2023](#)), they can provide insights about forage availability in relation to our understanding of resource use by albacore.

This study aims to identify taxonomic and trait-based indicators of diet selection in albacore tuna, by comparing diet composition to long-term systematic surveys of pelagic forage assemblages in a 2005–2019 time series across the CCLME. We investigate patterns of: 1) composition of albacore diets compared to trawl assemblages through multivariate ordination and model-based analyses, and 2) electivity, an index of prey selectivity calculated by comparing prey use by albacore in the scope of the available prey community, estimated by trawls. We conduct our comparative analyses from both a taxonomic and traits-based lens, using 13 traits that we predict influence phases of the predation process (i.e., encounter, pursuit, capture, consumption; [Green et al., 2019](#)) to characterize the potential prey species found in the CCLME. Ultimately, our goal is to identify preferred prey traits to enhance our understanding of relationships between albacore diets in the context of available prey to facilitate predictions of prey resource use in changing environments.

2. Methods

We compared the composition of prey recorded in juvenile albacore diets with the availability of pelagic forage species, including taxa consumed by albacore, as represented by trawl surveys in the CCLME in 2005–19. Albacore stomachs were collected June–November (n = 1206 with prey), and trawls sampled in May–September (May–June since 2013) to a depth of 30–45 m (n = 2528; see [Supplemental Methods](#); [Table 1](#), [Fig. 1](#), [Fig. S1](#)). Each diet and trawl sample was assigned to one of three regions within the CCLME which represent distinct physical

Table 1

Datasets used in analyses of albacore tuna diet selection in the CCLME. n = count of stomachs or trawls from the dataset, years = years of summer sampling included. SWFSC = NOAA Southwest Fisheries Science Center, NWFSC = NOAA Northwest Fisheries Science Center.

Type	Datasets & affiliations	n	Years	References
Diet	Albacore tuna stomach contents, SWFSC Fisheries Resources Division	750	2007 – 2019	Nickels et al. (2023)
	Albacore tuna stomach contents, Scripps Institution of Oceanography	371	2005 – 2006	Glaser (2010)
	Albacore tuna stomach contents, Stanford University	85	2008 – 2010	Madigan et al. (2015)
Trawl	Rockfish Recruitment and Ecosystem Assessment Survey, SWFSC Fisheries Ecology Division	1684	2005 – 2018	Sakuma et al. (2016) , Santora et al. (2021)
	Stock Assessment Improvement Program, NWFSC Fisheries Ecology Division	499	2005 – 2011	Phillips et al. (2009)
	Coastwide Cooperative Pre-Recruit Survey, NWFSC Fisheries Ecology Division	345	2011 – 2019	Brodeur et al. (2019)
Trait	Pelagic Species Trait Database, University of Alberta			Gleiber et al. (2022) , Gleiber et al. (2024)

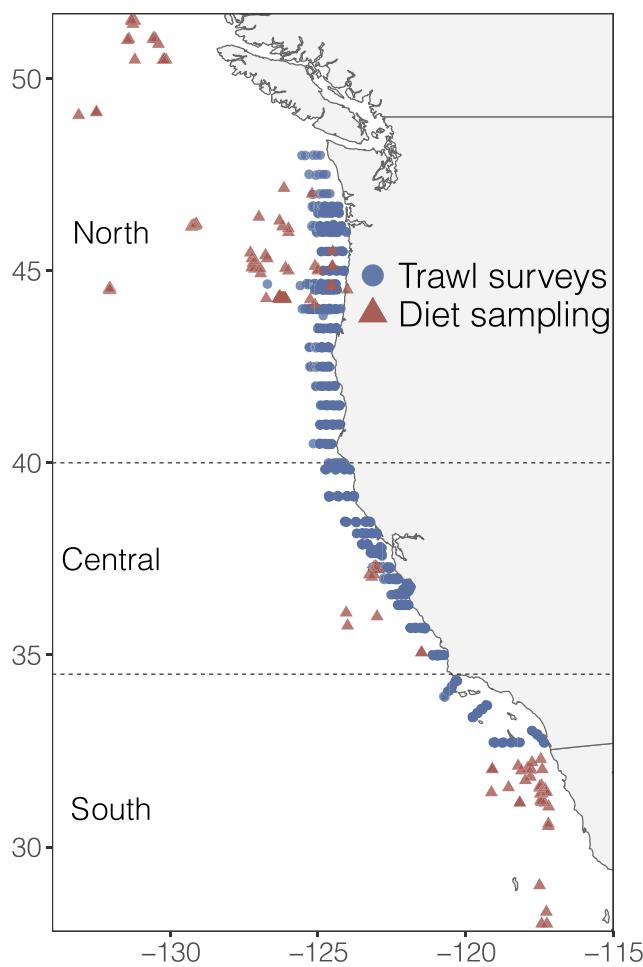


Fig. 1. Sampling effort from albacore tuna diet studies and systematic trawl surveys in the California Current Large Marine Ecosystem (CCLME). Precise location information for diet data from Nickels et al. (2023) is unavailable due to confidentiality of commercial fishing locations, thus sampling presence is represented by the centroids of sample locations within each region as reported in that study. Figure S1 details year and survey-specific sampling locations.

oceanographic conditions: North ($>40.5^{\circ}\text{N}$), Central ($34.5\text{--}40.5^{\circ}\text{N}$), and South ($<34.5^{\circ}\text{N}$; see descriptions in Nickels et al., 2023; Sakuma et al., 2016; Fig. 1). Comparative analyses of trawl and stomach samples in this study were conducted regionally by year as only 28% of stomachs had concurrent trawls in the same month and year.

2.1. Data standardization

We conducted data standardization steps to ensure that information included from diet sampling and trawl surveys could be compared with one another to assess taxonomic- and trait-based patterns of albacore prey selection. First, we used the World Register of Marine Species (www.marinespecies.org) to standardize taxonomic information between all datasets (Step 1, Fig. 2). When required, we grouped species, genera, or families at higher levels of taxonomic identification to allow consistent comparisons between studies (Table S1). We also excluded unidentified prey items in gut contents (13%) from analyses (Step 2, Fig. 2), which included removing 71 stomachs that only contained unidentified prey items.

Next, we calculated the relative abundance of all taxa within albacore diets and trawls. To do this, counts of each taxa were transformed into proportional abundances per stomach or trawl. Proportional abundance (p) is calculated by dividing the number of observations of a

taxa in an individual stomach or trawl by the total number of organisms across all taxa in that same stomach or trawl. Using p as an abundance metric enables comparison of relative abundance across various datasets and reduces the influence of taxa with high overall abundance but low frequency.

Only taxa that contributed $>1\%$ mean proportional abundance (%N) of the diet or trawls across all years in any region were included in analyses ($n = 26$ taxa; Table S2; Step 3, Fig. 2). Taxa contributing $<1\%$ N ($n = 132$) were combined into higher-level taxonomic groups if possible (e.g., Myctophidae, Paralichthyidae); otherwise they were broadly aggregated into “other” groups. Aggregating the data in this way overcomes difficulties of zero inflated data, enables easier interpretation of results, and is consistent with recent CCLME tuna diet studies (Nickels et al., 2023; Portner et al., 2022). These combined groups only contributed a total of 4% and 6%N of the diet and trawl data, respectively, while often encompassing many taxa. Using only these taxa and combined groups, we recalculated %N for diet and trawls within each region (North, Central, and South CCLME) for all years combined, and each individual region/year combination (Fig. 3; Table S3). To assess the compatibility of trawls for sampling prey within the size spectra consumed by albacore in the CCLME, we compared the sizes of prey in the diets to those collected by trawls (see *Supplemental Methods*; Step 4, Fig. 2).

2.2. Trait data collection

Trait data were extracted from the Pelagic Species Trait Database, an open-source database of traits that inform pelagic predator-prey interactions (<https://doi.org/10.5683/SP3/0YFJED>; Gleiber et al., 2022, 2024). For each of the taxonomic groups, we included primary habitat association, behavioral, morphological, and nutritional quality traits hypothesized to affect how an albacore encounters, captures, and consumes prey (Green et al., 2019; Hardy et al., 2023; Table 2). While the influence of prey body size on predator diet selection is well known (Brown et al., 2004; Green et al., 2022), prey length data from trawls and diets were only available for a subset of taxa and individuals, prohibiting us from including body size as a trait in analyses.

We used traits associated with the taxon-specific life stage(s) of prey likely consumed by albacore (adult, juvenile; Hardy et al., 2023; Nickels et al., 2023; Table 3). In instances where data were not available for a life stage-specific trait, the alternate life stage or similar species trait information was used as a proxy (Table S5). For taxa aggregated to genus, family, or order, we assigned traits based on the species that predominantly comprise these taxonomic groups in the diet (Table S5). When trait data were aggregated across multiple species and/or life stages, numeric traits were summarized as the mean, while categorical and binary traits were described by the predominant category among the species considered for the aggregated taxon (Table S5).

2.3. Multivariate analyses

2.3.1. Taxonomically-based

We visualized differences in the taxonomic communities consumed by albacore relative to those sampled by pelagic trawl surveys using non-metric multidimensional scaling (nMDS). In each region, we performed nMDS on an unconstrained Bray-Curtis dissimilarity matrix from the proportional abundance (p) of taxa in individual stomachs and trawls. The ordination was fit with three dimensions and 1000 iterations performed in *vegan* in R (version 2.6-4; Oksanen et al., 2013). One taxon (pipefishes) and 14 rows of data were removed from analyses, as they consisted of multivariate outliers and contributed to overdispersion of the data (McCune and Grace, 2002). These included two individual trawls and 12 stomachs that consisted nearly exclusively of a single taxa. The resulting nMDS included 31 taxa from 689 diets and 950 trawls (Step 5, Fig. 2).

To examine variance among diet and trawl species composition, we fit multivariate generalized linear models (mvGLMs) to the relationships

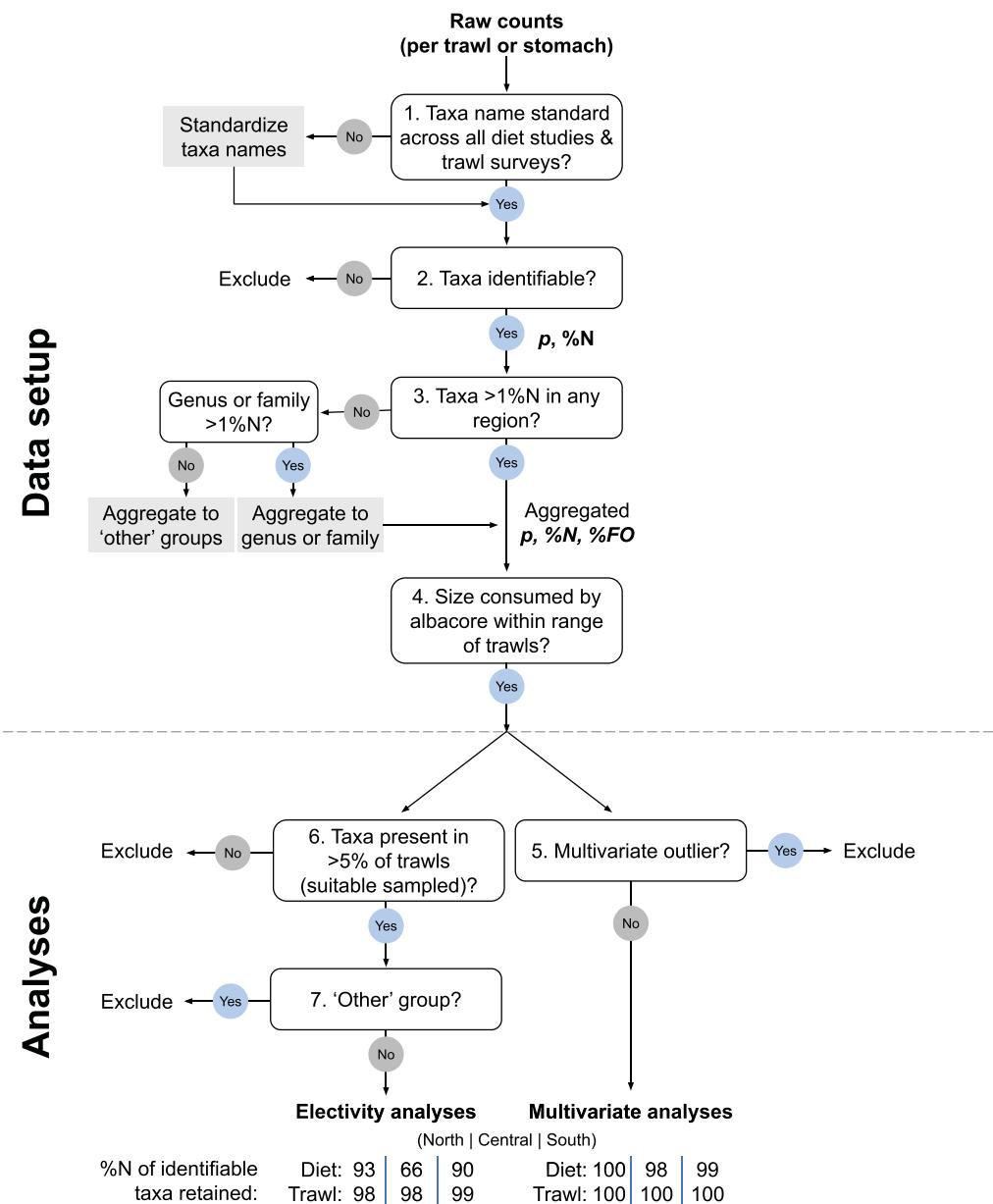


Fig. 2. Schematic illustrating the data filtration and manipulation framework for preparing information from diet studies and scientific trawl surveys sampling pelagic communities for electivity and multivariate analysis that assess resource selection by albacore tuna in the CCLME.

between the response variables (taxon proportional abundances, p) and the explanatory variables: *resource sampler* (diet vs. trawl), *region* (North, Central, South CCLME) and *year* (2005–2019). The mvGLM was fitted with a binomial distribution (with logit link) for proportional data, performed in the *mvabund* package in R (version 4.2.1; Wang et al., 2012). Model assumptions of heterogeneity of variance and normality were respectively checked by plotting residuals versus fitted values, and by quantile-quantile plots. Model fit was interpreted by analysis of deviance, tested using log-likelihood ratios, and p-values calculated from 999 resampling iterations via PIT-trap resampling (Bates et al., 2015; Wang et al., 2012). To then identify which species expressed significant effects between resource samplers, regions, and years, post-hoc univariate tests were performed on models built for each region due to three-way interactions, with adjusted p-values fitted to each species in *mvabund*, adjusted for multiple testing of variables, and calculated using a stepdown resampling algorithm (Westfall and Young, 1993). Influential species response variables were classified as

characterizing diet samples, trawl samples, or their overlap, based on consensus of multiple outputs: (i) correlation coefficients with composition in albacore diets, (ii) univariate adjusted p-values for species, and (iii) test statistic rank describing species' contribution to explaining variance.

2.3.2. Trait-based

To understand trait-based relationships between pelagic assemblages sampled by albacore and trawl surveys, we investigated the variance in community composition among three matrices: 1) proportional abundance (p) of taxa (L), 2) spatiotemporal variables describing sampling method (diet, trawl), region, and year sampled (R), and 3) trait information for 13 habitat use, morphological, and nutritional composition traits (Q; Table 2). We combined two multi-matrix modeling techniques known as 'RLQ' and 'fourth corner modeling' (Brown et al., 2014; Dray and Legendre, 2008; Legendre et al., 1997). The RLQ routine, performed with the *ade4* package in R (version 1.7–19; Dray et al., 2014),

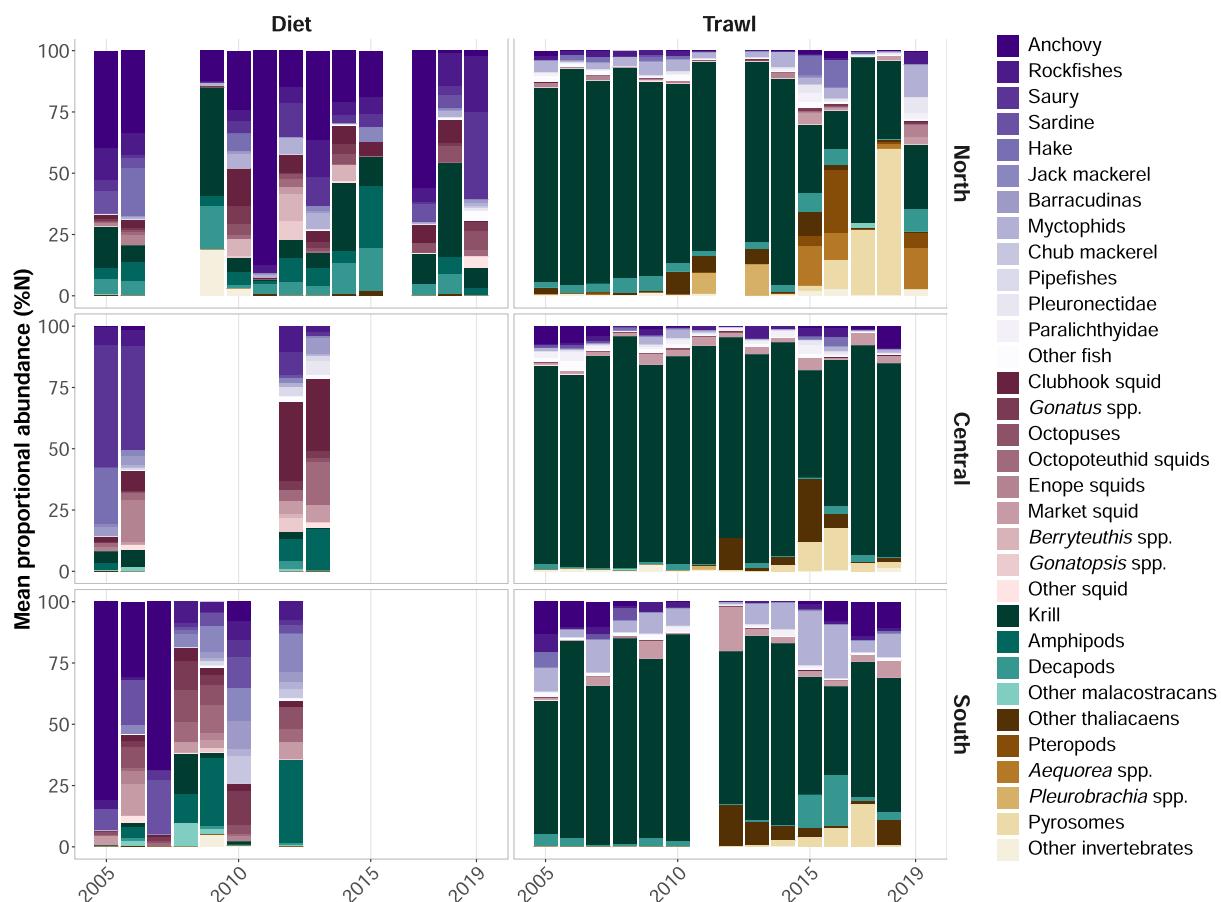


Fig. 3. Taxonomic composition of albacore tuna diets and trawl surveys, calculated as mean proportional (%N) abundance of each taxa within samples across years and regions of the CCLME. Absence of bars indicate years by region in which data were not collected or were unavailable for a given year and region. See Table S3 for sample sizes.

investigates and summarizes the joint structure among the matrices, provides ordination scores for species, samples, traits, and spatiotemporal variables along orthogonal axes, and yields a graphical summary of the main structures. We apply a correspondence analysis to the taxon matrix (L), and Hill-Smith analysis for mixed categorical and continuous variables in both the covariate matrix (R) and trait matrix (Q; Hill and Smith, 1976).

We then used a trait-based multivariate generalized linear modeling (traitGLM) framework to identify significant relationships between traits and spatiotemporal predictors. We fit traitGLMs using a binomial distribution (with logit link function) for a matrix of species proportional abundance (L) within diets and trawl samples, including spatiotemporal covariates (R), using the *traitglm()* function in *mvabund* (Brown et al., 2014; Dray and Legendre, 2008; Wang et al., 2012). We built three trait-based models which used subsets of the traits matrix, relating to at least one of three different predation processes: 1) encounter (habitat use, behavior), 2) attack and capture (morphology), and 3) consumption rates (nutritional composition). We included a species effect in the models, akin to fitting a random effects variable to account for differences in absolute number of species occurrences. Models were fit with a LASSO penalty, specifying the fitting method as ‘*glm1path*’, using penalized likelihood to impose a constraint on estimates of model parameters (Brown et al., 2014; Hastie et al., 2009). This constraint shrinks coefficients to zero when not statistically significant, providing a combined approach for model selection, p-value adjustment for multiple models, and parameter estimation to evaluate both the magnitude and significance of an explanatory variable (Hastie et al., 2009). Correlation coefficients for significant interactions between spatiotemporal variables (i.e., resource sampler, region, and year) and traits were plotted as

a heatmap. Model fit was assessed by plotting multivariate residuals against fitted values and quantile-quantile plots to ensure that model assumptions of normality of data distribution and homogeneity of variance were respected. Multivariate data were previously screened for broad trends using conditional boxplots (Zuur et al., 2010), and for overdispersion and outliers by nMDS plots using *vegan*.

2.4. Prey electivity index analyses

We estimated albacore prey electivity from both taxonomic- and trait-based perspectives. Electivity relates the proportional contribution of each prey type within the predator's diet to proportional abundances across all prey types sampled from the environment (trawl surveys). Generally, electivity is inferred to be associated with prey selection within the ambient forage assemblage, and at least in part driven by ecological mechanisms of foraging across all stages of the predation process (Charnov, 1976). Thus, predators are interpreted to selectively consume a given prey that occurs at higher relative abundances in the diet than in the environment. Prey that occur at lower relative abundances than in the diet could reflect avoidance or that they simply have lower encounter rates. To reduce the extent to which patterns of electivity reflect trawl sampling limitations (i.e. mesh/gape size, speed, and depth), we first identified prey taxa from albacore stomachs that were likely to be suitably sampled (i.e., captured in trawls) given the design of the trawls, and those with low catchability in trawl gear for exclusion from further analyses. Specifically, we used frequency of occurrence (% FO; proportion of stomachs or trawls with the taxa present) to describe taxa as common (>5%FO) or rare (<5%FO), and reasoned that common prey in the diet would be suitably sampled if also common in trawls in

Table 2

Prey traits predicted to influence encounter, attack, capture, and consumption of prey by gape-limited fish predators (Green et al., 2019). We used these traits to examine resource use and electivity by albacore tuna from a traits-based perspective. Traits descriptions are reproduced from the Pelagic Species Trait Database (Gleiber et al., 2022, 2024).

Trait category	Trait	Data type: Trait forms	Description	Predicted predation process phase/mechanism
Habitat	Vertical habitat	Categorical: epipelagic, mesopelagic, demersal	Water column position primarily occupied (species can occur elsewhere, but trait informs primary habitat).	Encounter due to habitat overlap
	Horizontal habitat	Categorical: coastal, continental shelf, oceanic	Position from the coastal to offshore waters primarily occupied. Coastal = coastal and reef associated; continental shelf = shelf and slope; oceanic = offshore.	
Behavior	Diel migration	Binary: yes, no	Presence of diel/diurnal vertical migration behavior	Attack, Capture
	Seasonal migration	Binary: yes, no	Presence of seasonal migration behavior	
Morphological	Gregariousness	Categorical: solitary, shoaling, schooling	Primary aggregation type. solitary: n = 1; shoaling: n = 2–100, schooling: n = >100.	Attack
	Length:height ratio	Continuous	Body shape ratio, total length:body height. Mean value from all database observations for that species and stage.	
Nutritional quality	Physical defenses	Binary: yes, no	Presence of an exoskeleton or defensive spines	Attack
	Transparency	Binary: yes, no	Presence of transparency	
	Silvering	Binary: yes, no	Presence of silvered coloration	
	Countershading	Binary: yes, no	Presence of countershaded coloration	
Lipid	Lipid	Continuous	Lipid content, % of wet weight. Mean value from all literature observations for that species.	Consumption, predation outcome
	Protein	Continuous	Protein content, % of wet weight. Mean value from all literature observations for that species.	
	Energy density	Continuous	Energy density, kJ/g wet weight. Mean value from all literature observations for that species.	

any region, but unsuitably sampled if they were rare in trawls in all regions. Only two prey that were common in diets were assessed as unsuitably sampled by trawls (Table S2, Fig. S2): the highly neustonic saury, and mesopelagic octopoteuthid squid. These taxa were thus excluded from prey electivity analyses (Step 6, Fig. 2). We used Vanderploeg and Scavia's relativized electivity (E^* ; Vanderploeg and Scavia, 1979), calculated as:

$$W_i = (r_i/p_i)/(\sum r_i/p_i)$$

$$E^*_i = [W_i - (1/n)]/[W_i + (1/n)]$$

where r_i and p_i are the proportional abundances (%N; Fig. 3) of prey taxa (or trait) type i in the diet and trawls, respectively, and n is the number of prey taxa (or trait) types. This index ranges from +1 to -1 and is neutral when $E^* = 0$, indicating the predator consumes the prey types proportionally to the available prey community (trawls). E^* is recommended for assessing electivity in the natural environment, compared to other indices, since it is stable with relative changes in prey abundances (Lechowicz, 1982). Instances where a prey type is not present in the diet ($r_i = 0$) or not present in the trawls ($p_i = 0$) are indicated separately in the results and excluded from comparative analyses. Electivity analyses are region-specific and only shown for the North and South CCLME, where sufficient years with concurrent diet and trawl sampling were available for comparison ($n = 11$ years North, 4–Central, 8–South; Fig. S1).

2.4.1. Taxonomically-based prey electivity

For taxa-based prey electivity, E^* was calculated using mean %N in the diet and trawls for each combination of region and year using taxa aggregated into groups representing >1%N of the diets or trawls, to reduce the error associated with calculating electivity indices for rare prey. E^* calculations were region-specific, only including taxa present in the diet in that specific region to better meet the assumption that all predators in the analysis had equal access to the same potential food types considered (Lechowicz, 1982). This resulted in $n = 20$ taxa (North) and 22 (South) in our electivity analyses, and excludes unsuitably-sampled taxa (above), as well as the four combined 'other' prey groups

(Steps 6–7, Fig. 2), since the key taxa represented in these groups may be different between diet and trawls, regions or years.

2.4.2. Trait-based prey electivity

For trait-based prey electivity, E^* was calculated using %N summed for each trait form in the diet and trawls for each combination of region and year. %N was calculated for categorical and binary traits by summing annual mean %N across taxa associated with each trait form within a trait (Tables 2, 3). Continuous trait values were binned into two responses (i.e., low, high) based on the median value, and %N was summed across taxa in these two trait forms. Trait-based E^* was calculated separately for each trait; thus we note that electivity can only be quantitatively compared across trait forms within each trait, since traits are not mutually exclusive. The sample size used in electivity calculations is trait-specific ($n = 2–3$) and the same in each region, as all trait forms are present in diets and trawls in each region.

To qualitatively assess differences in the relative importance of prey taxa or trait forms we compare the rank order of mean %N_{diet}, %N_{trawl}, and E^* across the time series in each region. We additionally examine overall inter-annual variability in albacore prey electivity from a taxon-versus traits-based approach by comparing the distribution of E^* annual variance across taxa and traits.

3. Results

Juvenile albacore tuna consumed a large subset of taxa found in trawls (90 % overlap; $n_{\text{diet}} = 29$ taxa vs $n_{\text{trawl}} = 32$ taxa), but in different proportional abundances (Fig. 3, Table S2). All albacore prey taxa were consumed across a similar size range as sampled by the trawls (see **Supplemental Results**; Fig. S3). The three gelatinous taxa in trawls were completely absent in diets (Table S2). We found that albacore consumed prey representing all forms of the 13 trait types we examined (Table 2).

3.1. Multivariate analyses

Albacore diet taxonomic composition overlapped with trawls, yet diets occupied a broader part of the multivariate ordination space

Table 3

Trait data for taxonomic groups included in electivity and multivariate analysis. Traits were assigned based on the lifestage in diets (J = juvenile, A = adult). For binary variables: 1 = presence of trait, 0 = absence of trait. For some taxa, values were aggregated among multiple species, or proxies from similar species (see Table S5). Trait data were extracted from the Pelagic Species Trait Database (Gleiber et al., 2022, 2024).

Species/Taxa Name	Common Name	Taxa level	Diet stage	Habitat		Behavior			Morphology				Nutritional Quality			
				Vertical	Horizontal	Gregariousness	Diel migration	Seasonal migration	Length: Height	Physical defenses	Transparent	Silvering	Counter-shading	Lipid (%)	Protein (%)	Energy Density (kJ/g)
<i>Abraaliopsis</i> spp.	Enope squids	genus	J	epipelagic	oceanic	schooling	1	0	5.31	0	1	0	0	3.49	17.40	4.40
<i>Aequorea</i> spp.	Water jellyfish	genus	A	epipelagic	oceanic	solitary	0	1	1.73	0	1	0	0	0.60	0.18	0.06
<i>Amphipoda</i>	Amphipods	order	A	epipelagic	oceanic	schooling	1	1	5.67	1	0	0	0	1.40	7.39	2.36
<i>Berryteuthis</i> spp.	Armhook squids	genus	J	mesopelagic	oceanic	schooling	1	1	5.68	0	0	0	0	1.35	10.60	4.94
<i>Cololabis saira</i>	Pacific Saury	species	J	epipelagic	oceanic	schooling	0	1	8.57	0	0	1	1	8.53	19.78	6.30
<i>Decapoda</i>	Decapods	order	J, A	epipelagic	continental shelf	schooling	1	1	7.14	1	0	0	0	1.88	15.02	4.97
<i>Doryteuthis opalescens</i>	Market squid	species	J	epipelagic	continental shelf	schooling	1	1	3.63	0	0	0	0	1.00	16.50	3.69
<i>Engraulis mordax</i>	Northern Anchovy	species	J	epipelagic	coastal	schooling	1	1	7.72	0	0	1	1	6.98	15.38	6.76
<i>Euphausiidae</i>	Euphausiids/krill	family	J, A	epipelagic	oceanic	schooling	1	1	9.34	1	0	0	0	2.17	12.31	3.73
<i>Gonatopsis</i> spp.	Armhook squids	genus	J	mesopelagic	oceanic	schooling	1	0	5.73	0	0	0	0	2.40	10.53	4.16
<i>Gonatus</i> spp.	Armhook squids	genus	J	mesopelagic	oceanic	schooling	1	1	3.36	0	0	0	0	16.00	10.54	6.29
<i>Merluccius productus</i>	Pacific hake	species	J	demersal	continental shelf	schooling	1	1	6.18	0	0	1	1	1.86	14.62	4.07
<i>Myctophidae</i>	Lanternfishes	family	A	mesopelagic	oceanic	schooling	1	1	5.52	0	0	1	1	10.98	11.55	7.52
<i>Octopoda</i>	Octopuses	order	J	epipelagic	oceanic	shoaling	1	1	3.36	0	1	0	0	2.17	10.60	3.07
<i>Octopoteuthis</i> spp.	Octopoteuthid squids	genus	J	mesopelagic	oceanic	shoaling	1	0	3.76	0	1	0	0	3.13	17.40	3.44
<i>Onychoteuthis borealijaponica</i>	Boreal clubhook squid	species	J	mesopelagic	oceanic	schooling	1	1	5.51	0	0	0	0	3.80	12.80	5.48
<i>Paralepididae</i>	Barracudinas	family	J, A	mesopelagic	oceanic	schooling	1	1	12.98	0	1	1	0	6.19	15.80	4.30
<i>Paralichthyidae</i> spp.	Flounders (left-eyed)	family	J	demersal	coastal	shoaling	1	1	3.81	0	0	0	0	7.93	16.85	3.81
<i>Pleurobrachia</i> spp.	Comb jellyfish	genus	A	epipelagic	oceanic	schooling	1	0	6.23	0	1	0	0	0.07	0.12	0.02
<i>Pleuronectidae</i>	Flounders (right-eyed)	family	J	demersal	continental shelf	shoaling	0	1	3.63	0	0	0	0	1.22	15.29	4.25
<i>Pteropoda</i>	Pteropods	order	A	epipelagic	oceanic	solitary	1	0	1.27	1	1	0	0	1.59	1.98	2.61
<i>Pyrosoma atlanticum</i>	Pyrosome	species	A	epipelagic	oceanic	schooling	1	0	3.36	0	1	0	0	0.25	0.67	0.36
<i>Sardinops sagax</i>	Pacific Sardine	species	J	epipelagic	coastal	schooling	1	1	8.94	0	0	1	1	8.18	17.74	7.25
<i>Scomber japonicus</i>	Chub mackerel	species	J	epipelagic	continental shelf	schooling	1	1	5.73	1	0	1	1	7.93	19.81	6.77
<i>Sebastes</i> spp.	Rockfishes	genus	J	epipelagic	continental shelf	schooling	0	1	4.18	1	0	0	1	1.52	14.84	4.90
<i>Syngnathidae</i>	Pipefishes	family	J	demersal	reef-associated	solitary	0	1	33.03	0	0	0	0	1.90	14.70	4.70
<i>Thaliacea</i>	Other thalacians	class	A	epipelagic	oceanic	schooling	1	0	3.05	0	1	0	0	0.23	0.19	0.36
<i>Trachurus symmetricus</i>	Jack mackerel	species	J	epipelagic	coastal	schooling	1	1	4.39	1	0	1	1	6.40	3.71	6.40

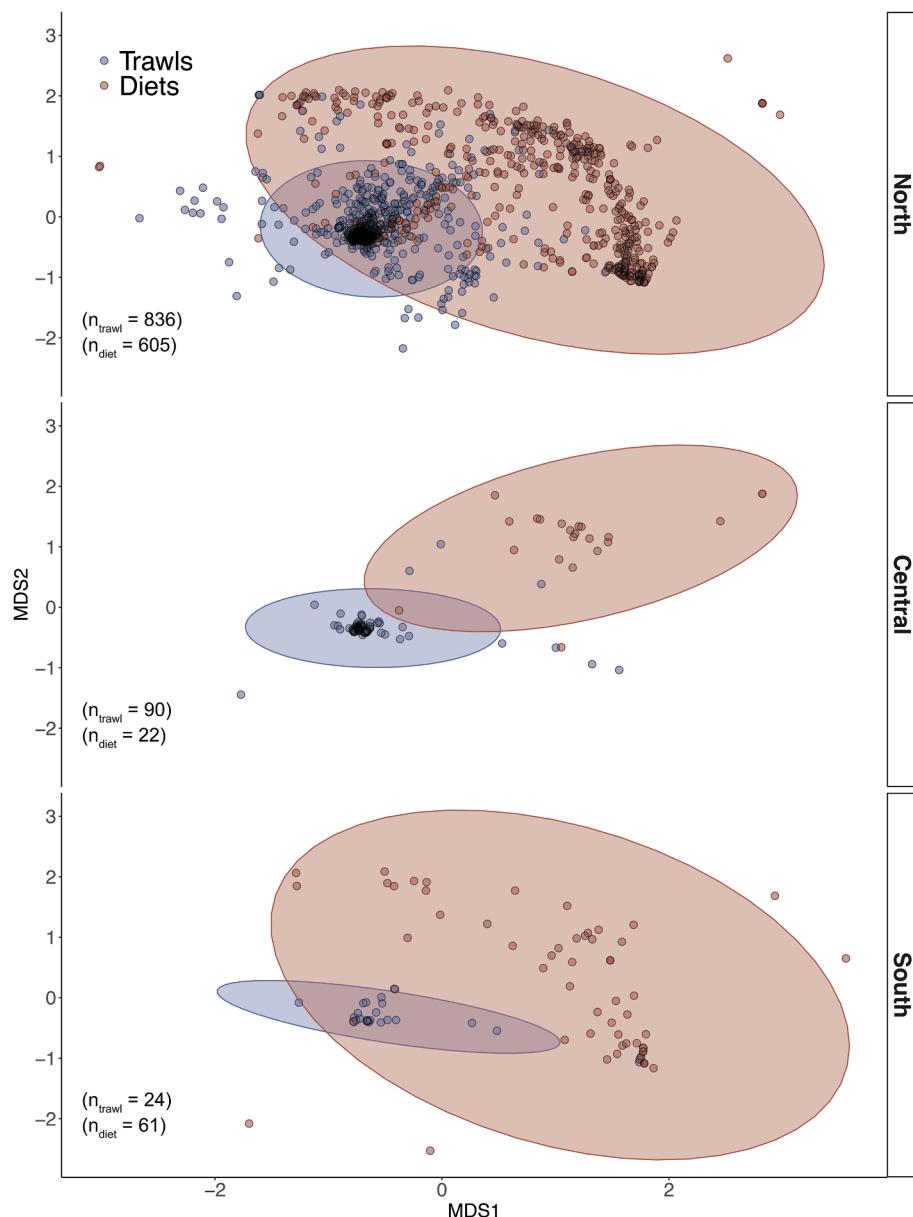


Fig. 4. Non-metric multidimensional scaling (nMDS) illustrating differences in multivariate space in the taxonomic composition of albacore diets and pelagic trawl surveys in each region of the CCLME. nMDS conducted on proportional abundances (p) of taxa in diets and trawls. Points represent composition of individual stomachs or trawls, with sample sizes (n) included for each region. Stress = 0.12, three-dimensional solution.

(Fig. 4). This pattern was consistent across regions, and represents high variability in the composition among stomachs while trawls are more similar as they are dominated by krill. All fitted variables significantly contributed to explaining variance in forage community composition: *resource sampler* explained the most variance (diet vs. trawl), followed by *region* (pairwise comparisons indicate all regions differed), and *year* (Table S6). Species that consistently characterized the trawl assemblage (i.e., strong negative correlation with diet, significant p-value) include: euphausiids, left-eyed flounders, pyrosomes, other thaliaceans, water and comb jellyfishes (see Table 3 for scientific names). Species that characterized the diet assemblage (i.e., strong positive correlation with diet, significant p-value) include: saury, chub and jack mackerels, clubhook and octopoteuthid squids, anchovy, sardine, octopuses, and amphipods (Table S7a-c). Species that overlapped between trawl and diet communities (i.e., neutral or weak correlation with either assemblage, insignificant p-value) include: rockfishes, market squid, lanternfishes, barracudinas, decapods, armhook (*Gonatus*, *Gonatopsis*) and

enope squids (Table S7a-c).

Habitat use, morphological, and nutritional traits explained significant variance in forage communities consumed by albacore relative to their sampling by trawl surveys. Diets were characterized by greater relative abundances of coastal, mesopelagic, schooling, undefended, silvered, and countershaded taxa, with higher energy density and protein content (Figs. 5, S4), while trawl survey samples were characterized by greater prevalence of oceanic, diel and seasonal migrants that were physically defended (i.e. exoskeleton). North CCLME albacore diet samples were characterized by taxa inhabiting primarily coastal horizontal habitats or mesopelagic vertical habitats (Figs. 5, S4). Central CCLME diet samples included greater prevalence of oceanic and transparent taxa, which otherwise characterized trawl samples. South CCLME diet samples included greater prevalence of coastal, mesopelagic, silvered, and higher lipid content prey.

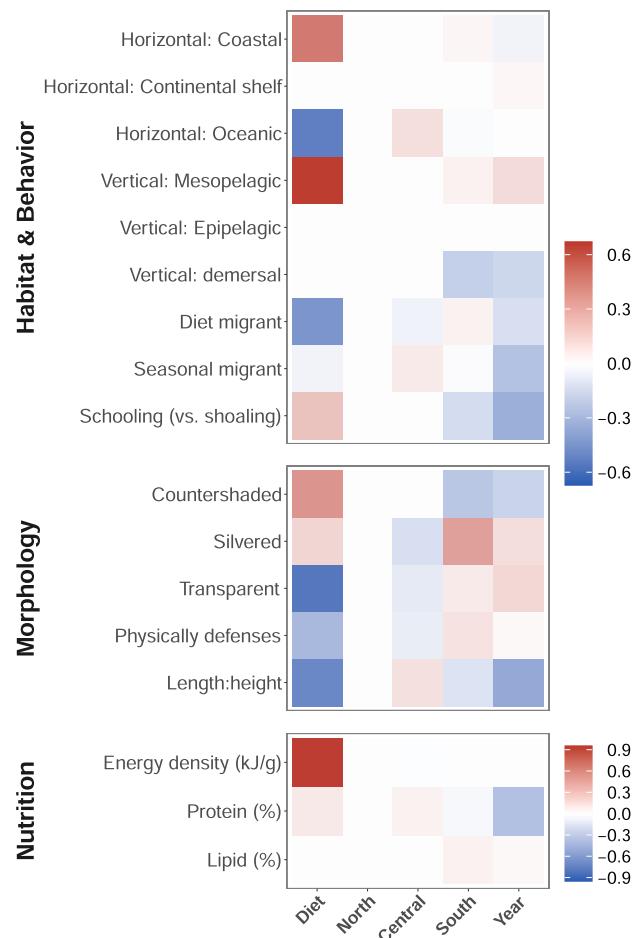


Fig. 5. Correlation coefficients for statistically significant relationships between trait values and explanatory variables (resource sampler [diet vs. trawl], region, year) for all regions of the CCLME. Brighter squares show stronger associations than paler ones, traits positively associated with diet are in red, and negatively associated with diet are in blue (e.g. characteristic of trawls). Since >50 % of observations are from the North CCLME, “Diet” is representative of the correlations in the North CCLME, and the respective region columns explain the differences from the pattern in the North. “Year” represents increasing (red) or decreasing (blue) associations between traits and diets over time.

3.2. Prey electivity

Prey electivity highlights taxa consumed at higher or lower proportions compared to the relative trawl community, while some taxa were characterized by more interannual variability (Figs. 6, 7). In the Northern CCLME, where concurrent diet and trawl sampling enabled comparative analysis for 11 years across the time series, some of the most abundant prey based solely on diet data (%N; i.e., euphausiids, hake, decapods, lanternfishes) had low E^* index values across years, indicating lower consumption relative to sampling by trawls (Fig. 6). We saw the highest apparent electivity ($E^* = 0.4\text{--}0.9$) for clubhook squid and sardine, consistent across most years they were consumed by albacore. The clubhook squid ranged from 1 to 15%N of the diet, but in trawls at proportions 2–4 orders of magnitude lower (Table S2). Anchovy, octopuses, amphipods, barracudinas, and *Gonatus* squids had variable electivity across the time series.

In the Southern CCLME, albacore had consistently high positive electivity values across years for octopuses, *Gonatus* squids, jack mackerel, and barracudinas ($E^* = 0.2\text{--}0.9$), taxa fairly abundant in diets (Fig. 7). Similar to the North, consistent negative electivity indices were seen for taxa numerically abundant in trawls, although in contrast, these taxa comprised a low proportion of albacore diets in the South. Anchovy

and sardine, the two most abundant taxa in the diets, were consumed proportionally to abundances in trawls, with some annual variability.

Trait-based electivity analyses show strikingly consistent patterns of regional and annual E^* values, highlighting key traits of prey consumed by albacore relative to availability as surveyed by trawls (Fig. 8). In both regions, albacore had strong positive electivity across years for prey that have high energy density and high protein, and are countershaded, silvered, non-physically defended, non-diel migrants, and associated with coastal habitats. Less informative traits, with overall neutral but highly variable E^* values, included: body shape (length:height) and lipid content (North), seasonal migration and vertical habitat (South). However, these traits were regionally informative, with albacore having consistently positive electivity in the North for prey that migrate seasonally and inhabit mesopelagic vertical habitats, and in the South for prey with low lipid content and smaller length:height ratio.

Finally, overall inter-annual variance in albacore prey electivity indices was lower when using trait information compared to using taxonomic identity in both regions (Fig. 9). In the Southern CCLME, variance in taxon-identity based electivity indices was multi-modal with a higher amplitude than trait-based values (Fig. 9), due to fewer species sampled during a shorter time series in this region (Fig. 7).

4. Discussion

Our analyses revealed strong inter-annual and regional variability in the taxonomic composition of albacore diets and trawl surveys in the CCLME, making it difficult to identify consistent species-based indicators of albacore diet selection. However, we found that a trait-based approach simplified the spatiotemporal complexities in feeding habits of a predator with a variable diet within a dynamic system. In particular, several ecological traits hypothesized to mediate predator-prey interactions consistently characterized albacore diets relative to trawl-sampled assemblages. As a result, we identified trait-based drivers of prey electivity in the system that persisted across regions and years. These same traits — namely, coastal habitat use, shoaling and schooling behavior, countershading and silverying coloration, lack of physical defenses, and high energy density and protein content — were indicative of albacore prey selection from both our multivariate modeling and electivity analyses (Fig. 10). Our prey electivity analysis further reinforces the utility of traits as a biological lens through which predators view and make decisions about their environment. That albacore consumed diverse taxa with consistent traits within the ambient forage assemblage (i.e. microneuston) suggests the ecological mechanisms of albacore foraging processes may be conserved across time and space.

4.1. Trawl suitability as samplers of albacore prey

Prior to exploring selective resource use by albacore tuna, we developed a decision framework that assessed the suitability of data from pelagic trawl surveys as a proxy for the biological community sampled by our focal predator based on relative prevalence and size of taxa between the diets and surveys. 93% of prey taxa met our criteria for suitability: being present in >5% of trawls, when also present in >5% of stomachs. Only two albacore prey show large differences in prevalence between diets and trawls, saury and octopoteuthid squids. Both species were present in up to 50% of the stomachs in each region, yet only <0.2% and <4% of the trawls in each region, and were strongly indicative of diet assemblages in multivariate analyses. Our observations are in line with knowledge about the behavior and habitat use of these taxa, highlighting potentially low catchability by trawl gear. Saury are likely to be poorly sampled by the trawl due to predominantly surface-oriented behavior, with their distribution historically documented in the CCLME by surface trawl surveys (Brodeur et al., 2005). In contrast, octopoteuthid squids are deep-sea species that are non-migratory, and rarely found in the epipelagic zone (Goetsch et al., 2018).

The trawls used are designed to target juvenile pelagic stages of

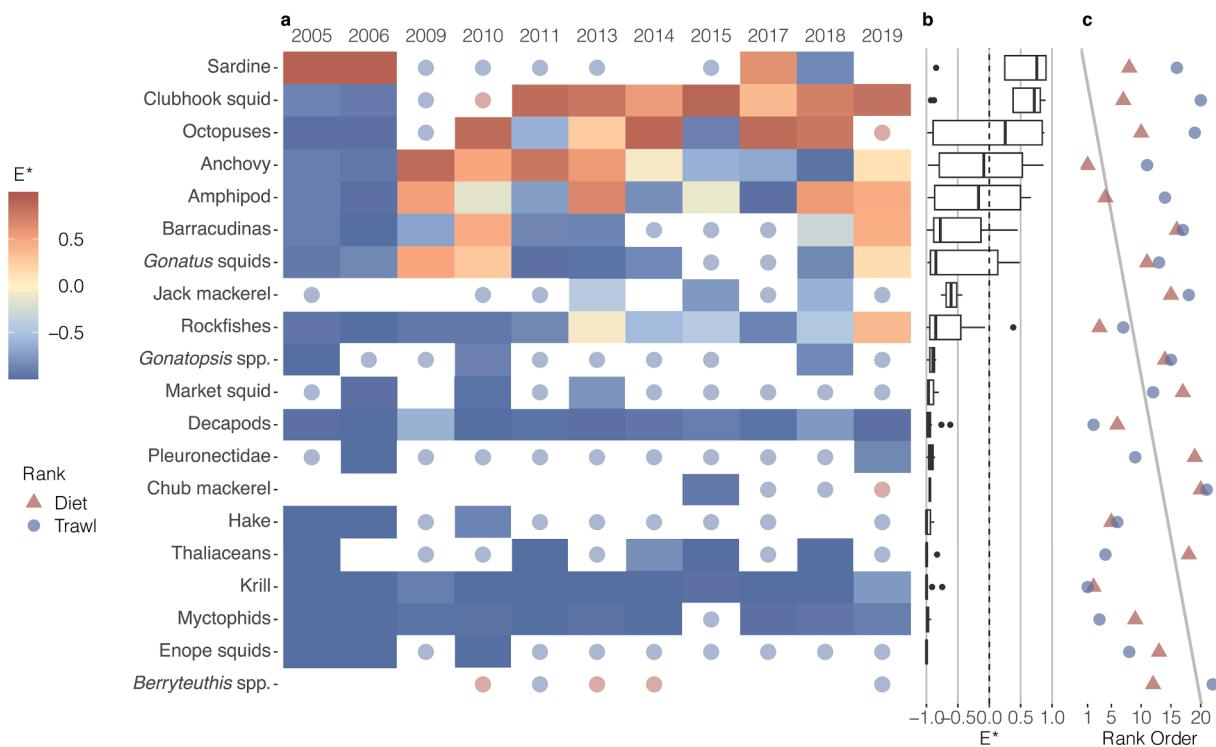


Fig. 6. Taxa-based prey electivity for albacore tuna in the Northern CCLME. a) Heatmap with annual values of Vanderploeg & Scavia's relativized electivity index (E^*) for albacore tuna prey relative to trawl surveys as a measure of environmental availability. E^* ranges from +1 to -1, and indicates the predator consumes the prey type at relatively higher (positive value, warmer colors) or lower (negative value, cooler colors) proportions compared to trawls. $E^* = 0$ when the predator consumes the prey type proportionally to trawls. Circles indicate years when a taxa was either present in only the diet (red) or only the trawls (blue), and thus values of E^* are undefined; blank squares denote years when prey were absent in both the diet and trawls. Taxa are listed in descending order based on mean E^* . We include all years with concurrent diet and trawl sampling, and all taxa present in the diet in this region ($n = 20$). b) Boxplots showing interannual variability of E^* for prey taxa. c) Comparison of prey rank order of importance based on mean electivity (E^* ; grey diagonal line), diets (% N_{diet} ; red triangles), or trawls (% N_{trawl} ; blue circles).

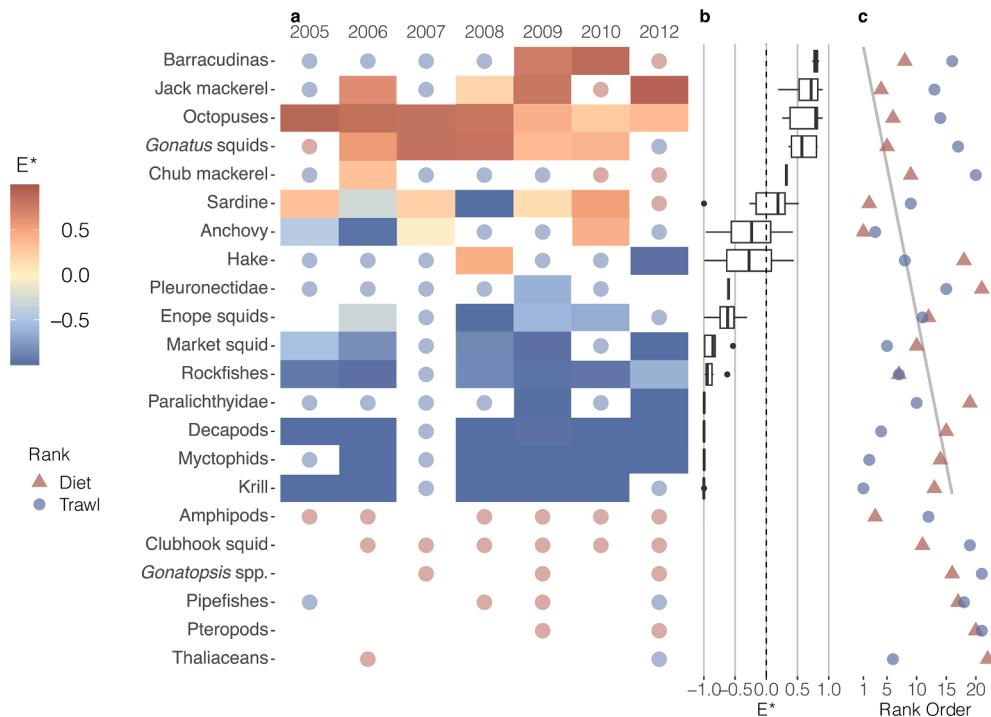


Fig. 7. Taxa-based prey electivity for albacore tuna in the Southern CCLME. See Fig. 6 caption for interpretation.

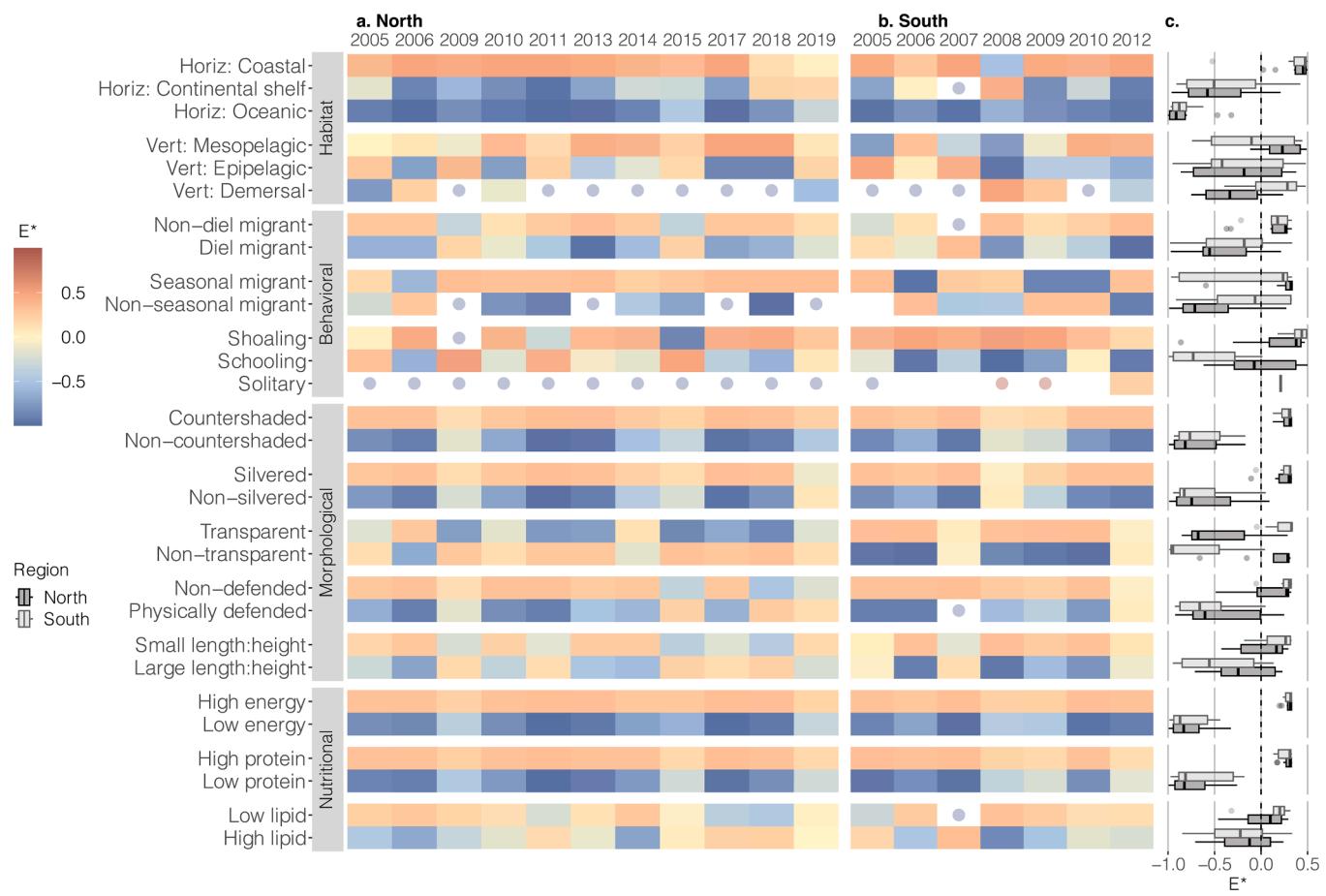


Fig. 8. Trait-based prey electivity for albacore tuna in the a) North and b) South CCLME. Heatmap shows annual values of Vanderploeg & Scavia's relativized electivity index (E^*) for the traits of prey consumed by albacore tuna relative to trawl surveys as a measure of environmental availability. Trait categories (e.g., habitat) and trait forms (e.g., 'coastal') are included with each trait (e.g., 'horiz'). Since only trait forms within the same trait are mutually exclusive, the magnitude of electivity can be compared within a trait, but not between. See Fig. 6 caption for interpretation. Trait forms are listed in descending order within each trait. c) Boxplots showing interannual variability of E^* for prey trait forms in each region.

groundfishes for stock assessments (Field et al., 2021), using a low tow speed, fine mesh size, and sampling at night. While they are not focused on larger, faster swimming taxa or life stages that may exhibit net avoidance (Santora et al., 2021b), trawls appear to sample a broad range of albacore prey, and may be useful for estimating abundances of prey for other pelagic predators. Even with more conservative criteria for inclusion (e.g., 10% FO), only one additional prey taxa would be considered 'under-sampled': the chub mackerel, which albacore only consume at juvenile stages. Future taxa-based work should consider the extent to which albacore diets may better indicate the variability in the availability of these taxa than trawl surveys (Santora et al., 2021a; Wells et al., 2023), given evidence that survey data substantially underestimate their abundances.

All prey taxa for which we had individual size information ($n_{\text{taxa}} = 17$, 60% of taxa; Fig. S3) were consumed within the size ranges sampled by trawls, predominantly juveniles for fishes and squids, providing further evidence that the trawls can be a suitable metric of albacore prey availability. While a handful of taxa are predominantly sampled by trawls at larger adult sizes compared to the smaller juvenile sizes consumed by albacore (e.g. jack and chub mackerels), we cannot distinguish if this reflects trawl suitability or albacore feeding preferences. We hope this decision tree for suitability is a framework others can use when curating diet and survey data for comparison beyond albacore and the CCLME.

4.2. Taxonomic indicators of albacore prey selection

Though albacore consumed a subset of species identified within the trawl surveys, our multivariate analysis revealed that taxonomic composition was much more variable among albacore stomachs than among trawl surveys in the CCLME. We also found that prey electivity by albacore was highly variable across years and between regions for the majority of taxa we sampled, with no taxa showing consistent positive electivity by albacore across the system over time. In some instances, albacore displayed the strongest positive electivity (i.e. high proportion in the diet relative to surveys) for taxa that were *not* numerically dominant in the diet, suggesting prior diet analyses that relied on estimates of abundance alone failed to capture the importance of these taxa. When present in diets, clubhook squid and sardine also had high positive electivity values in the North, and armhook squids, barracudinas, jack and chub mackerel in the South. In contrast, many taxa that are highly abundant in the diet had inter-annually variable or consistently negative electivity. Anchovy, which are the top diet item in both regions, had some of the most variable electivity patterns, alternating from high to low across years, suggesting they are a highly utilized prey that fluctuate with environmental conditions (Litz et al., 2008), and the landscape of other prey types available.

Finally, we identified consistent negative electivity in both regions for euphausiids, lanternfishes, and decapods: taxa numerically dominant in trawls and comprising a lower proportion of albacore diets. This pattern is consistent with optimal foraging expectations that small-

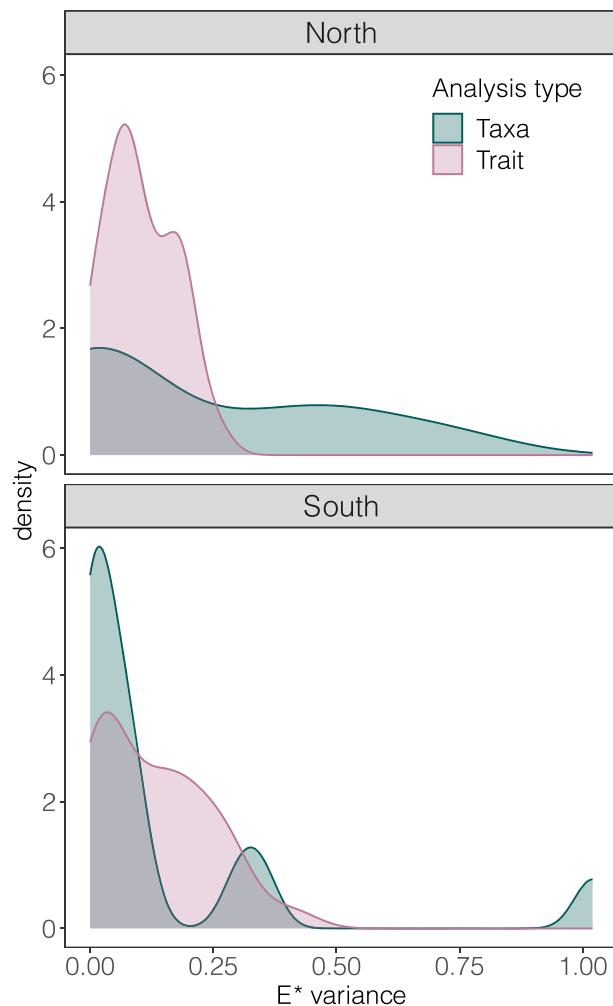


Fig. 9. Distribution of interannual variance in Vanderploeg & Scavia's relativized electivity index (E^*) values when computed using a taxa, or trait-based approach. E^* values include all years and taxa or traits with concurrent presence in diet and trawls ($n_{\text{taxa}} = \text{North}: 127, \text{South}: 65$; $n_{\text{trait}} = \text{North}: 528, \text{South}: 335$).

bodied prey with low energetic value per individual are less profitable (Charnov, 1976). Additionally, prior work on albacore prey energetics suggest the relative importance of high energy prey, compared to crustaceans that contribute to low energy intake by albacore even when consumed in high numbers (Glaser, 2010; Pinkas et al., 1971). Moving beyond diet assessment alone to examine electivity patterns can aid in identifying species indicative of selective foraging when exploring shifts in predator-prey relationships for further examination. For example, boreal clubhook squid, a cooler-water species (Muhling et al., 2019) were strongly selected for in the North, and could be an important prey to consider while the albacore distribution is in that region (Frawley et al., 2021).

4.3. Trait-based indicators of albacore prey selection

In contrast to the taxonomic approach, our multivariate and electivity analyses identify trait values that characterized albacore resource selection across regions and years, suggesting that albacore prey-trait preferences in the CCLME are consistent across time and space. The trait-based indicators of albacore diet selection identified here — schooling/shoaling behavior, coastal habitat use, the presence of countershading and silvering, lack of physical defenses, and high energy

density and protein content — illustrate the ecological processes mediating their foraging, and corroborate the hypothesized traits governing prey selection (Glaser, 2010; Nickels et al., 2023). Albacore primarily consumed and appear selective for shoaling or schooling taxa, relative to solitary, which we hypothesize reflects enhanced encounter rates with prey consistent with optimal foraging expectations (Charnov, 1976), as well as prior diet studies on tuna in this region (Glaser, 2010; Madigan et al., 2015; Nickels et al., 2023; Portner et al., 2022). Energy density is indicative of nutritional quality, which is a key mechanism driving prey selection (Emlen, 1966), and can be more important than prey abundance for top predators (cetaceans; Spitz et al., 2012). Physical defenses impact a predator's ability to capture and consume prey (Price et al., 2015), therefore it is not surprising that albacore select against prey with these traits. Countershading and silvering are common traits for species (including albacore) that occupy a pelagic niche in the water column, providing camouflage to evade predators (McFarland and Munz, 1975). However, these traits likely represent a coevolutionary arms race between predator and prey, with the tuna predator ultimately having enhanced swimming and visual capacity, such as detecting polarized light reflected off of the prey (Kamermans and Hawryshyn, 2011; Løkkeborg et al., 2014).

Prey primarily inhabiting coastal habitats were both common in the diets and highly selected, a pattern driven by consumption of anchovies and sardines. In contrast, oceanic and demersal taxa showed evidence of strong negative selection by albacore, with demersal taxa (e.g. flatfishes) rarely consumed, yet abundant in trawls. A recent analysis of global albacore diets from the 1940's–2010 also identified coastal habitats as the most common trait groups over time in the North Pacific, and demersal the rarest (Hardy et al., 2023). Our trait-based electivity analyses highlight potential mechanisms for prey selection by highly-mobile gape limited pelagic predators, and are consistent with other diet work on tunas showing utilization of high-energy, near-surface, schooling coastal prey (e.g. anchovies, sardines, saury) when present in the system (Glaser, 2010; Madigan et al., 2015; Nickels et al., 2023; Portner et al., 2022). If sampling bias (i.e. high catchability by trawls compared with capture by albacore) were driving trait electivity, we would expect traits such as slender body shape to have consistent high electivity — a pattern not borne out by our analyses, further suggesting ecological mechanisms of prey capture by albacore are at play.

4.4. Implications for anticipating foraging decisions in a changing ocean

Consistent trait selection within variable prey fields may result in the ability to successfully meet energy demands in dynamic pelagic regions. Feeding patterns of albacore and bluefin tuna in the CCLME have been varyingly described as opportunistic (Nickels et al., 2023; Nikolic et al., 2017; Portner et al., 2022), specialized on e.g., sardine or anchovy (Madigan et al., 2015; Williams et al., 2015), or generalist (Bernard et al., 1985; Pinkas et al., 1971). Our findings contextualize this taxonomic opportunism as resulting from specialization on traits. Both albacore and bluefin tuna show multiple feeding modes through time, linked to oceanographic conditions (Nickels et al., 2023; Portner et al., 2022). However, these distinct foraging strategies may confer surprisingly similar energetic intakes (Glaser, 2010; Portner et al., 2022). Ultimately, these flexible strategies may allow albacore to maintain their high metabolic rates across variable feeding conditions and migration patterns (Muhling et al., 2022), and has been documented in other pelagic predators (Smout et al., 2013). This enhanced understanding of albacore feeding ecology will allow us to more accurately model niche width, which can have implications for outcomes of competition with other predators (Brodeur, 1991; Pinkas et al., 1971; Wells et al., 2023) and prey shifts with climate change (Bellwood et al., 2003).

Examining predator-prey interactions through a trait-based lens aggregates diverse taxonomic prey information, allowing us to move beyond single-species trophic relationships. For example, anchovy and sardine share all traits included in this study, and play similar roles as

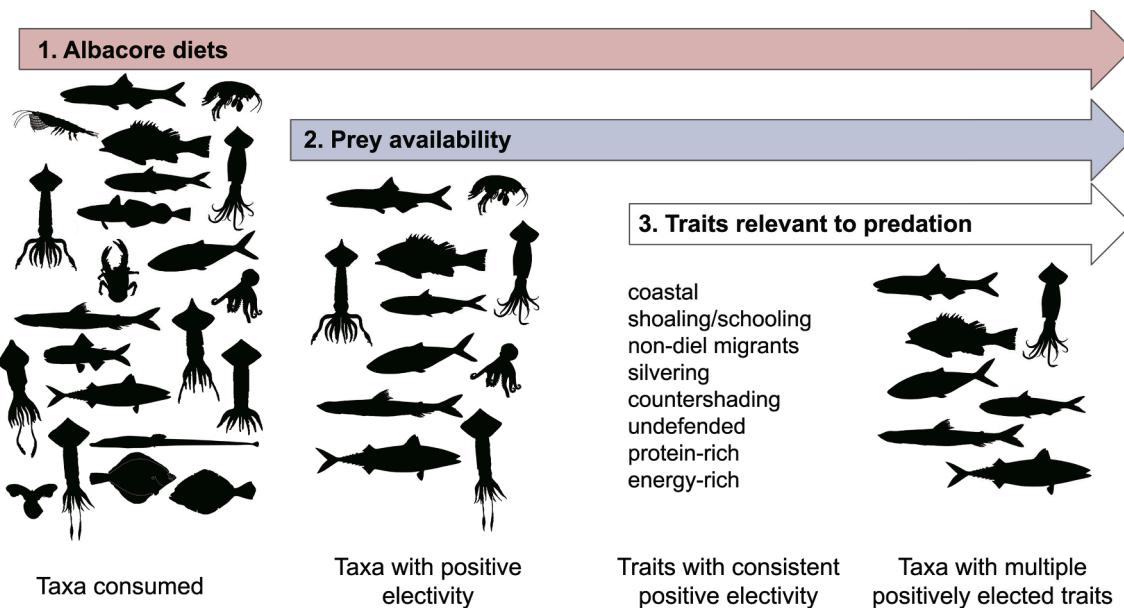


Fig. 10. The effect of data inputs on taxonomic- and trait-based indicators of resource selection by juvenile albacore tuna in the CCLME. Each arrow indicates a type of data incorporated in our analyses. As more data sources are incorporated (moving left to right), indicators of prey selection are refined, enabling us to identify a few key prey types with highly selected traits (far right) from amongst the albacore's broad diet (far left). Silhouettes describe the identity of prey 1) in the diets, 2) positively elected by albacore in any region, and 3) with >3 positively elected traits.

prey for albacore and other top predators in the CCLME (Szoboszlai et al., 2015). Thus high historical variability in the abundances of these individual prey species (McClatchie et al., 2017) may not be reflected as variability in the abundance of highly elected prey, when this functional redundancy is considered. The regional variation in albacore diet and trawl assemblages also reveals examples of prey with similar traits, but different taxonomic identity consumed in the North compared to South. Mesopelagic squids with similar traits were important in albacore diets with high positive electivity in both regions; in the North they were predominantly clubhook (*O. borealijaponica*), and armhook (*Gonatus*) in the Central and South. In the CCLME, ecological traits have been hypothesized to explain broad synchrony in forage community shifts across regions linked to environmental forcing, with co-varying taxa representing similar niches (Thompson et al., 2019).

By characterizing prey consumption and available preyscapes in terms of traits linked to selective foraging processes, we can begin to empirically test the direct mechanisms of shifts in diets over time from a predator's perspective. Changing environmental conditions (e.g., upwelling, phenology, productivity, temperature, hypoxia) are likely driving differences in forage community composition, and thus the availability of prey for albacore (Nickels et al., 2023). However, changing environmental conditions may also influence the relative profitability of different prey types to albacore, affecting foraging decisions and thus patterns of prey selectivity. Potential temporal shifts are highlighted in our multivariate modeling on assemblages, where some traits showed increasing (i.e., mesopelagic habitat) or decreasing (i.e., length:height ratio) correlations with albacore diets across years. Further work needs to link trait-based variability in diet composition to environmental gradients of change, as prey species shift in abundance due to climate and fisheries-induced pressures (Essington et al., 2018).

4.5. Opportunities for future monitoring

Trawl surveys are a key source of information on the structure and status of diverse pelagic micronekton communities in the CCMLE (Broddeur et al., 2019; Phillips et al., 2009; Sakuma et al., 2016; Santora et al., 2021b) and other ocean basins globally. However, spatiotemporal overlap between predator diet sampling and prey abundances from

surveys are often imperfect, as was the case in this study. Diet data would also be enhanced by finer-scale spatiotemporal information associated with collections (Muhling et al., 2019, 2022). Further, analyses of albacore diets in the CCLME are unbalanced spatially, with the best interannual coverage in the North, coincident with centers of albacore distribution and fishing activity in recent years (Frawley et al., 2021). The Central region was undersampled, and our results showed the strongest differences in species-based and trait-based albacore diet composition in relation to trawls in this region. This may be because the central CCLME has high biodiversity turnover and interannual variability due to its position between relatively warm and cool regions (Santora et al., 2017). Bolstering stomach sampling in this region would enable us to examine the effect of the significant environmental gradient present in the region on selectivity patterns.

Trawl surveys sample earlier in the year (late-spring/early-summer) than when albacore are foraging in the CCLME (July–September; Muhling et al., 2022; Phillips et al., 2014), thus we take a 'state of the system' approach with analyses at an annual scale. This assumes that the abundances of prey in the surveys earlier in the year are indicative of later abundances. Considering the complex life history dynamics and regional seasonality of prey species, this assumption may not hold for all prey. For example, young-of-the-year sardine and anchovy are important for albacore diets, but are only present seasonally. Advancing our understanding of predator-prey relationships for albacore and other pelagic predators would be enhanced by information about prey assemblages later in the summer. There are also species-specific lags in relationships between ocean conditions, prey, and predators. Nickels et al. (2023) showed that albacore diets in summer are associated with environmental conditions over the first six months of the year. In addition, Daly et al. (2017, 2013) showed that winter environmental preconditioning and the biomass of winter-spawned larval fish that are consumed as juvenile-stage prey by salmon (*Oncorhynchus* spp.) smolts in the marine environment are predictors of future adult salmon returns 1–2 years later. Ultimately, variability in survey timing and life history stages collected across years and between regions can make it difficult to directly compare communities, and requires innovative approaches (Thompson et al., 2019). Given that many pelagic species' prey exhibit the same trait forms across life stages and sizes, using trait-based

analysis to characterize trawl-sampled organisms could allow for more confident comparisons between samples.

5. Conclusions

Given the speed and magnitude of climate impacts on ocean assemblages, there is an urgent need for biologically meaningful indices that can be used to anticipate how top predators will respond to changing resource availability. Our analyses reveal consistent prey trait preferences across diverse taxonomic feeding patterns for albacore tuna in the CCLME, suggesting traits mediating the predation process are consistent across a variable prey field. Given that albacore share foraging behaviors and key prey species with >50 other predators in the CCLME and globally (Ainley et al., 2015; Szoboszlai et al., 2015), traits are likely to provide useful insights into foraging dynamics in a range of other systems and cases. Crucially, our study highlights the benefits of standardizing and combining data from broad survey tools such as trawls and diet studies, along with trait information, to gain generalizable insights that can be used to anticipate how predators will respond to changing foraging conditions in the future.

CRediT authorship contribution statement

Miram R. Gleiber: Writing – review & editing, Writing – original draft, Visualization, Supervision, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Natasha A. Hardy:** Writing – original draft, Visualization, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Caitlin J. Morganson:** Visualization, Investigation, Formal analysis, Data curation. **Catherine F. Nickels:** Writing – review & editing, Writing – original draft, Resources, Conceptualization. **Barbara A. Muhling:** Writing – review & editing, Writing – original draft, Resources, Methodology, Conceptualization. **Elan J. Portner:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Conceptualization. **Brian K. Wells:** Writing – original draft, Resources. **Richard D. Brodeur:** Writing – review & editing, Writing – original draft, Resources, Methodology. **Toby D. Auth:** Writing – original draft, Resources. **Jarrod A. Santora:** Writing – original draft, Resources. **Sarah M. Glaser:** Writing – original draft, Resources. **Daniel J. Madigan:** Writing – original draft, Resources. **Elliott L. Hazen:** Writing – original draft, Methodology, Conceptualization. **Larry B. Crowder:** Writing – original draft, Supervision, Methodology, Investigation, Funding acquisition, Conceptualization. **Stephanie J. Green:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Stephanie Green, Miram Gleiber, Natasha Hardy, Caitlin Morganson reports financial support was provided by Lenfest Ocean Program of the Pew Charitable Trust. Stephanie Green reports financial support was provided by Alfred P Sloan Foundation. Stephanie Green reports financial support was provided by Natural Sciences and Engineering Research Council of Canada. Natasha Hardy reports financial support was provided by Marine Environmental Observation Prediction and Response Network.

Data availability

The code written to produce analyses and illustrations for this manuscript are publicly available through a CC BY 4.0 public-use licence with attribution to authors at this link: <https://github.com/CHANGE-Lab/albacore-cclme-diet-forage>.

The NOAA SWFSC albacore diet data is available in Nickels et al. (2023). The NOAA Rockfish Recruitment and Ecosystem Assessment Survey (RREAS) data was downloaded from the NOAA Environmental Research Division Data Acquisition Portal (ERDDAP): https://coastwatch.pfeg.noaa.gov/erddap/tabledap/FED_Rockfish_Catch.html. Other datasets in this study are available in the GitHub (albacore-cclme-diet-forage), or upon request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2023.111473>.

References

Ainley, D.G., Adams, P.B., Jahncke, J., 2015. California Current system—Predators and the prey scape. *J. Mar. Syst.* 146, 1–2. <https://doi.org/10.1016/j.jmarsys.2014.10.011>.

Barnett, L.A.K., Jacobsen, N.S., Thorson, J.T., Cope, J.M., 2019. Realizing the potential of trait-based approaches to advance fisheries science. *Fish Fish.* 20, 1034–1050. <https://doi.org/10.1111/faf.12395>.

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* 67, 1–48. <https://doi.org/10.48550/arXiv.1406.5823>.

Bellwood, D.R., Hoey, A.S., Choat, J.H., 2003. Limited functional redundancy in high diversity systems: resilience and ecosystem function on coral reefs. *Ecol. Lett.* 6, 281–285. <https://doi.org/10.1046/j.1461-0248.2003.00432.x>.

Bernard, H.J., Hedgepeth, J.B., Reilly, S.B., 1985. Stomach contents of albacore, skipjack, and bonito caught off southern California during summer 1983. *CaCOFL Rep* 26, 175–183. https://www.calcofi.com/publications/calcofireports/v26/Vol_26_Bernard_et.al.pdf.

Brodeur, R.D., 1991. Ontogenetic variations in the type and size of prey consumed by juvenile coho, *Oncorhynchus kisutch*, and chinook, *O. tshawytscha*, salmon. *Environ. Biol. Fishes* 30, 303–315. <https://doi.org/10.1007/BF02028846>.

Brodeur, R.D., Fisher, J.P., Emmett, R.L., Morgan, C.A., Casillas, E., 2005. Species composition and community structure of pelagic nekton off Oregon and Washington under variable oceanographic conditions. *Mar. Ecol. Prog. Ser.* 298, 41–57. <https://doi.org/10.3384/meps298041>.

Brodeur, R.D., Auth, T.D., Phillips, A.J., 2019. Major shifts in pelagic micronekton and macrozooplankton community structure in an upwelling ecosystem related to an unprecedented marine heatwave. *Front. Mar. Sci.* 6, 212. <https://doi.org/10.3389/fmars.2019.000212>.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M., West, G.B., 2004. Toward a metabolic theory of ecology. *Ecology* 85, 1771–1789. <https://doi.org/10.1890/03-9000>.

Brown, A.M., Warton, D.I., Andrew, N.R., Binns, M., Cassis, G., Gibb, H., 2014. The fourth-corner solution—using predictive models to understand how species traits interact with the environment. *Methods Ecol. Evol.* 5, 344–352. <https://doi.org/10.1111/2041-210X.12163>.

Carroll, G., Cox, M., Harcourt, R., Pitcher, B.J., Slip, D., Jonsen, I., 2017. Hierarchical influences of prey distribution on patterns of prey capture by a marine predator. *Funct. Ecol.* 31, 1750–1760. <https://doi.org/10.1111/1365-2435.12873>.

Charnov, E.L., 1976. Optimal foraging, the marginal value theorem. *Theor. Popul. Biol.* 9, 129–136. [https://doi.org/10.1016/0040-5809\(76\)90040-X](https://doi.org/10.1016/0040-5809(76)90040-X).

Childers, J., Snyder, S., Kohin, S., 2011. Migration and behavior of juvenile North Pacific albacore (*Thunnus alalunga*). *Fish. Oceanogr.* 20, 157–173. <https://doi.org/10.1111/j.1365-2419.2011.00575.x>.

Clark, N.E., Blasing, T.J., Fritts, H.C., 1975. Influence of interannual climatic fluctuations on biological systems. *Nature* 256, 302–305. <https://doi.org/10.1038/256302a0>.

Daly, E.A., Auth, T.D., Brodeur, R.D., Peterson, W.T., 2013. Winter ichthyoplankton biomass as a predictor of early summer prey fields and survival of juvenile salmon in the northern California Current. *Mar. Ecol. Prog. Ser.* 484, 203–217. <https://doi.org/10.3354/meps10320>.

Daly, E.A., Brodeur, R.D., Auth, T.D., 2017. Anomalous ocean conditions in 2015: impacts on spring Chinook salmon and their prey field. *Mar. Ecol. Prog. Ser.* 566, 169–182. <https://doi.org/10.3354/meps12021>.

Dray, S., Choler, P., Dolédec, S., Peres-Neto, P.R., Thuiller, W., Pavoine, S., ter Braak, C.J., 2014. Combining the fourth-corner and the RLQ methods for assessing trait responses to environmental variation. *Ecology* 95, 14–21. <https://doi.org/10.1890/13-0196.1>.

Dray, S., Legendre, P., 2008. Testing the species traits–environment relationships: the fourth-corner problem revisited. *Ecology* 89, 3400–3412. <https://doi.org/10.1890/08-0349.1>.

Emlen, J.M., 1966. The role of time and energy in food preference. *Am. Nat.* 100, 611–617. <https://doi.org/10.1086/282455>.

Essington, T.E., Sanchirico, J.N., Baskett, M.L., 2018. Economic value of ecological information in ecosystem-based natural resource management depends on exploitation history. *Proc. Natl. Acad. Sci.* 115, 1658–1663. <https://doi.org/10.1073/pnas.1716858115>.

Field, J.C., Miller, R.R., Santora, J.A., Tolimieri, N., Haltuch, M.A., Brodeur, R.D., Auth, T.D., Dick, E.J., Monk, M.H., Sakuma, K.M., 2021. Spatiotemporal patterns of variability in the abundance and distribution of winter-spawned pelagic juvenile rockfish in the California Current. *PLoS One* 16, e0251638. <https://doi.org/10.1371/journal.pone.0251638>.

Rawley, T.H., Muhling, B.A., Brodie, S., Fisher, M.C., Tommasi, D., Le Fol, G., Hazen, E.L., Stohs, S.S., Finkbeiner, E.M., Jacox, M.G., 2021. Changes to the structure and function of an albacore fishery reveal shifting social-ecological realities for Pacific Northwest fisherman. *Fish. Fish.* 22, 280–297. <https://doi.org/10.1111/faf.12519>.

Friedman, W.R., Santora, J.A., Schroeder, I.D., Huff, D.D., Brodeur, R.D., Field, J.C., Wells, B.K., 2018. Environmental and geographic relationships among salmon forage assemblages along the continental shelf of the California Current. *Mar. Ecol. Prog. Ser.* 596, 181–198. <https://doi.org/10.3354/meps12598>.

Glaser, S.M., 2010. Interdecadal variability in predator-prey interactions of juvenile North Pacific albacore in the California Current System. *Mar. Ecol. Prog. Ser.* 414, 209–221. <https://doi.org/10.3354/meps08723>.

Glaser, S.M., Waechter, K.E., Bransome, N.C., 2015. Through the stomach of a predator: regional patterns of forage in the diet of albacore tuna in the California Current System and metrics needed for ecosystem-based management. *J. Mar. Syst.* 146, 38–49. <https://doi.org/10.1016/j.jmarsys.2014.07.019>.

Gleiber, M.R., Hardy, N.A., Roote, Z., Krug-Macleod, A.M., Morganson, C.J., Tandy, Z., George, I., Matuch, C., Brookson, C.B., Daly, E.A., Portner, E.J., Choy, C.A., Crowder, L.B., Green, S.J., 2024. The pelagic species trait database: an open data resource to support trait-based ocean research. *Sci. Data.* <https://doi.org/10.1038/s41597-023-02689-9>.

Gleiber, M.R., Hardy, N.A., Roote, Z., Krug-Macleod, A.M., Morganson, C.J., Tandy, Z., George, I., Matuch, C., Brookson, C.B., Daly, E.A., Portner, E.J., Choy, C.A., Crowder, L.B., Green, S.J., 2022. Pelagic Species Trait Database. *Borealis.* <https://doi.org/10.5683/SP3/0YFJED>.

Goetsch, C., Connors, M.G., Budge, S.M., Mitani, Y., Walker, W.A., Bromaghin, J.F., Simmons, S.E., Reichmuth, C., Costa, D.P., 2018. Energy-rich mesopelagic fishes revealed as a critical prey resource for a deep-diving predator using quantitative fatty acid signature analysis. *Front. Mar. Sci.* 5, 430. <https://doi.org/10.3389/fmars.2018.00430>.

Green, S.J., Dilley, E.R., Benkwitt, C.E., Davis, A.C.D., Ingeman, K.E., Kindinger, T.L., Tuttle, L.J., Hixon, M.A., 2019. Trait-mediated foraging drives patterns of selective predation by native and invasive coral-reef fishes. *Ecosphere* 10, 1–15. <https://doi.org/10.1002/ecs2.2752>.

Green, S.J., Brookson, C.B., Hardy, N.A., Crowder, L.B., 2022. Trait-based approaches to global change ecology: moving from description to prediction. *Proc. R. Soc. B.* 289, 20220071. <https://doi.org/10.1098/rspb.2022.0071>.

Hardy, N.A., Matuch, C., Roote, Z., George, I., Muhling, B.A., Jacox, M.G., Hazen, E.L., Bograd, S.J., Crowder, L.B., Green, S.J., 2023. Trait-based analyses reveal global patterns in diverse diets of albacore tuna (*Thunnus alalunga*). *Fish. Fish.* 1–15 <https://doi.org/10.1111/faf.12807>.

Harvey, C.J., Fisher, J.L., Samhouri, J.F., Williams, G.D., Francis, T.B., Jacobson, K.C., deReynier, Y.L., Hunsicker, M.E., Garfield, N., 2020. The importance of long-term ecological time series for integrated ecosystem assessment and ecosystem-based management. *Prog. Oceanogr.* 188, 102418 <https://doi.org/10.1016/j.pocean.2020.102418>.

Hastie, T., Tibshirani, R., Friedman, J.H., Friedman, J.H., 2009. The elements of statistical learning: data mining, inference, and prediction. Springer. <https://doi.org/10.1007/978-0-387-21606-5>.

Hazen, E.L., Jorgensen, S., Rykaczewski, R.R., Bograd, S.J., Foley, D.G., Jonsen, I.D., Shaffer, S.A., Dunne, J.P., Costa, D.P., Crowder, L.B., Block, B.A., 2013. Predicted habitat shifts of Pacific top predators in a changing climate. *Nat. Clim. Change* 3, 234–238. <https://doi.org/10.1038/nclimate1686>.

Hill, M.O., Smith, A.J.E., 1976. Principal component analysis of taxonomic data with multi-state discrete characters. *Taxon* 249–255. <https://doi.org/10.2307/1219449>.

Hunsicker, M.E., Ciannelli, L., Bailey, K.M., Buckel, J.A., Wilson White, J., Link, J.S., Essington, T.E., Gaichas, S., Anderson, T.W., Brodeur, R.D., Chan, K.-S., Chen, K., Englund, G., Frank, K.T., Freitas, V., Hixon, M.A., Hurst, T., Johnson, D.W., Kitchell, J.F., Reese, D., Rose, G.A., Sjodin, H., Sydeman, W.J., van der Veer, H.W., Vollset, K., Zador, S., 2011. Functional responses and scaling in predator-prey interactions of marine fishes: contemporary issues and emerging concepts. *Ecol. Lett.* 14, 1288–1299. <https://doi.org/10.1111/j.1461-0248.2011.01696.x>.

Hunsicker, M.E., Ward, E.J., Litzow, M.A., Anderson, S.C., Harvey, C.J., Field, J.C., Jacox, M.G., Melin, S., Thompson, A.R., Warzybok, P., 2022. Tracking and forecasting community responses to climate perturbations in the California Current Ecosystem. *PLOS Clim* 1, e0000014. <https://doi.org/10.1371/journal.pclm.0000014>.

Iannone, B.V., Potter, K.M., Guo, Q., Liebhold, A.M., Pijanowski, B.C., Oswalt, C.M., Fei, S., 2016. Biological invasion hotspots: a trait-based perspective reveals new sub-continental patterns. *Ecography* 39, 961–969. <https://doi.org/10.1111/ecog.01973>.

Kamermans, M., Hawryshyn, C., 2011. Teleost polarization vision: how it might work and what it might be good for. *Philos. Trans. r. Soc. B Biol. Sci.* 366, 742–756. <https://doi.org/10.1098/rstb.2010.0211>.

Lechowicz, M.J., 1982. The sampling characteristics of electivity indices. *Oecologia* 52, 22–30. <https://doi.org/10.1007/BF00349007>.

Legendre, P., Galzin, R., Harmelin-Vivien, M.L., 1997. Relating behavior to habitat: solutions to the fourth corner problem. *Ecology* 78, 547–562. [https://doi.org/10.1890/0012-9658\(1997\)078\[0547:RBTHST\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1997)078[0547:RBTHST]2.0.CO;2).

Linardich, C., Brookson, C.B., Green, S.J., 2021. Trait-based vulnerability reveals hotspots of potential impact for a global marine invader. *Glob. Change Biol.* 27, 4322–4338. <https://doi.org/10.1111/gcb.15732>.

Link, J.S., 2007. Underappreciated species in ecology: “ugly fish” in the northwest Atlantic Ocean. *Ecol. Appl.* 17, 2037–2060. <https://doi.org/10.1890/06-1154.1>.

Litz, M.N.C., Heppell, S.S., Emmett, R.L., Brodeur, R.D., 2008. Ecology and distribution of the northern subpopulation of northern anchovy (*Engraulis mordax*) off the US west coast. *Calif. Coop. Ocean. Fish. Investig. Rep.* 49, 167–182.

Liu, O.R., Ward, E.J., Anderson, S.C., Andrews, K.S., Barnett, L.A.K., Brodie, S., Carroll, G., Fiechter, J., Haltuch, M.A., Harvey, C.J., Hazen, E.L., Hernvann, P.-Y., Jacox, M., Kaplan, I.C., Matson, S., Norman, K., Pozo Buil, M., Selden, R.L., Shelton, A., Samhouri, J.F., 2023. Species redistribution creates unequal outcomes for multispecies fisheries under projected climate change. *Sci. Adv.* 9, eadg5468. <https://doi.org/10.1126/sciadv.adg5468>.

Løkkeborg, S., Siikavuopio, S.I., Humborstad, O.-B., Utne-Palm, A.C., Ferter, K., 2014. Towards more efficient longline fisheries: fish feeding behaviour, bait characteristics and development of alternative baits. *Rev. Fish Biol. Fish.* 24, 985–1003. <https://doi.org/10.1007/s11160-014-9360-z>.

Madigan, D.J., Carlisle, A.B., Gardner, L.D., Jayasundara, N., Micheli, F., Schaefer, K.M., Fuller, D.W., Block, B.A., 2015. Assessing niche width of endothermic fish from genes to ecosystem. *Proc. Natl. Acad. Sci.* 112, 8350–8355. <https://doi.org/10.1073/pnas.1505024112>.

McClatchie, S., Hendy, I.L., Thompson, A.R., Watson, W., 2017. Collapse and recovery of forage fish populations prior to commercial exploitation. *Geophys. Res. Lett.* 44, 1877–1885. <https://doi.org/10.1002/2016GL071751>.

McCune, B., Grace, J.B., 2002. Analysis of ecological communities. Gleneden Beach, Oregon.

McFarland, W.N., Munz, F.W., 1975. Part III: The evolution of photopic visual pigments in fishes. *Vision Res* 15, 1071–1080. [https://doi.org/10.1016/0042-6989\(75\)90003-6](https://doi.org/10.1016/0042-6989(75)90003-6).

Morley, J.W., Selden, R.L., Latour, R.J., Frölicher, T.L., Seagraves, R.J., Pinsky, M.L., 2018. Projecting shifts in thermal habitat for 686 species on the North American continental shelf. *PLOS ONE* 13, e0196127. <https://doi.org/10.1371/journal.pone.0196127>.

Muhling, B.A., Brodie, S., Snodgrass, O., Tommasi, D., Jacox, M., 2019. Dynamic habitat use of albacore and their primary prey species in the California Current System. *CalCOFI Rep* 60, 1–15. https://calcofi.com/publications/calcofireports/v60/Vol6_0-Muhling.pdf.

Muhling, B.A., Brodie, S., Snodgrass, O., Tommasi, D., Jacox, M., 2019. Dynamic habitat use of albacore and their primary prey species in the California Current System. *CalCOFI Rep* 60, 1–15. https://calcofi.com/publications/calcofireports/v60/Vol6_0-Muhling.pdf.

Nickels, C.F., Portner, E.J., Snodgrass, O.E., Muhling, B.A., Dewar, H., Park, J.-Y., Stock, C.A., Block, B.A., 2022. Risk and reward in foraging migrations of North Pacific albacore determined from estimates of energy intake and movement costs. *Front. Mar. Sci.* 9, 730428 <https://doi.org/10.3389/fmars.2022.730428>.

Nikolic, N., Morandeu, G., Hoarau, L., West, W., Arrizabalaga, H., Hoyle, S., Nicol, S.J., Bourjea, J., Puech, A., Farley, J.H., Williams, A.J., Fonteneau, A., 2017. Review of albacore tuna, *Thunnus alalunga*, biology, fisheries and management. *Rev. Fish Biol. Fish.* 27, 775–810. <https://doi.org/10.1007/s11160-016-9453-y>.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O’hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., 2013. Package ‘vegan’. Community Ecol. Package Version 2, 1–295. <https://github.com/vegadevs/vegan>.

Pearcy, W.G., 1973. *Albacore oceanography off Oregon – 1970*. Fish. Bull. 71, 489.

Petchey, O.L., 2000. Prey diversity, prey composition, and predator population dynamics in experimental microcosms. *J. Anim. Ecol.* 69, 874–882. <https://doi.org/10.1046/j.1365-2656.2000.00446.x>.

Phillips, J.A., Brodeur, R.D., Sunstov, A.V., 2009. Micronekton community structure in the epipelagic zone of the northern California Current upwelling system. *Prog. Oceanogr.* 80, 74–92. <https://doi.org/10.1016/j.pocean.2008.12.001>.

Phillips, A.J., Ciannelli, L., Brodeur, R.D., Pearcy, W.G., Childers, J., 2014. Spatio-temporal associations of albacore CPUEs in the Northeastern Pacific with regional SST and climate environmental variables. *ICES J. Mar. Sci.* 71, 1717–1727. <https://doi.org/10.1093/icesjms/fst238>.

Pinkas, L., Olliphant, M.S., Iverson, I.L.K., 1971. Food habits of albacore, bluefin tuna, and bonito in California waters. *Calif. Fish Game Bull.* 152. <https://escholarship.org/uc/item/7i5868rd>.

Portner, E.J., Polovina, J.J., Choy, C.A., 2017. Patterns in micronekton diversity across the North Pacific Subtropical Gyre observed from the diet of longnose lancetfish

(Alepisaurus ferox). Deep Sea Res. Part Oceanogr. Res. Pap. 125, 40–51. <https://doi.org/10.1016/j.dsr.2017.04.013>.

Portner, E.J., Snodgrass, O., Dewar, H., 2022. Pacific bluefin tuna, *Thunnus orientalis*, exhibits a flexible feeding ecology in the Southern California Bight. PLOS ONE 17, e0272048. <https://doi.org/10.1371/journal.pone.0272048>.

Price, S.A., Friedman, S.T., Wainwright, P.C., 2015. How predation shaped fish: the impact of fin spines on body form evolution across teleosts. Proc. r. Soc. B Biol. Sci. 282, 20151428. <https://doi.org/10.1098/rspb.2015.1428>.

Railsback, S.F., Harvey, B.C., 2013. Trait-mediated trophic interactions: is foraging theory keeping up? Trends Ecol. Evol. 28, 119–125. <https://doi.org/10.1016/j.tree.2012.08.023>.

Sakuma, K.M., Field, J.C., Mantua, N.J., Ralston, S., Way, M., Cruz, S., Marinovic, B.B., Carrion, C.N., 2016. Anomalous epipelagic microneuston assemblage patterns in the neritic water of the California Current spring 2015 during a period of extreme ocean conditions. CalCOFI Rep 57, 163–183. <https://swfsc-publications.fisheries.noaa.gov/publications/CR/2016/2016Sakuma2.pdf>.

Santora, J.A., Hazen, E.L., Schroeder, I.D., Bograd, S.J., Sakuma, K.M., Field, J.C., 2017. Impacts of ocean climate variability on biodiversity of pelagic forage species in an upwelling ecosystem. Mar. Ecol. Prog. Ser. 580, 205–220. <https://doi.org/10.3354/meps12278>.

Santora, J.A., Rogers, T.L., Cimino, M.A., Sakuma, K.M., Hanson, K.D., Dick, E.J., Jahncke, J., Warzybok, P., Field, J.C., 2021a. Diverse integrated ecosystem approach overcomes pandemic-related fisheries monitoring challenges. Nat. Commun. 12, 1–10. <https://doi.org/10.1038/s41467-021-26484-5>.

Santora, J.A., Schroeder, I.D., Bograd, S.J., Chavez, F.P., Cimino, M.A., Fiechter, J., Hazen, E.L., Kavanaugh, M.T., Messié, M., Miller, R.R., Sakuma, K.M., Sydeman, W.J., Wells, B.K., Field, J.C., 2021b. Pelagic biodiversity, ecosystem function, and services: an integrated observing and modeling approach. Oceanography 34, 16–37. <https://doi.org/10.5670/oceanog.2021.212>.

Smout, S., Rindorf, A., Wanless, S., Daunt, F., Harris, M.P., Matthiopoulos, J., 2013. Seabirds maintain offspring provisioning rate despite fluctuations in prey abundance: a multi-species functional response for guillemots in the North Sea. J. Appl. Ecol. 50, 1071–1079. <https://doi.org/10.1111/1365-2664.12095>.

Spitz, J., Trites, A.W., Bequet, V., Brind'Amour, A., Cherel, Y., Galois, R., Ridoux, V., 2012. Cost of living dictates what whales, dolphins and porpoises eat: the importance of prey quality on predator foraging strategies. PloS One 7, e50096. <https://doi.org/10.1371/journal.pone.0050096>.

Szoboszlai, A.I., Thayer, J.A., Wood, S.A., Sydeman, W.J., Koehn, L.E., 2015. Forage species in predator diets: synthesis of data from the California Current. Ecol. Inform. 29, 45–56. <https://doi.org/10.1016/j.ecoinf.2015.07.003>.

Thompson, A.R., Harvey, C.J., Sydeman, W.J., Barceló, C., Bograd, S.J., Brodeur, R.D., Fiechter, J., Field, J.C., Garfield, N., Good, T.P., Hazen, E.L., Hunsicker, M.E., Jacobson, K., Jacox, M.G., Leising, A., Lindsay, J., Melin, S.R., Santora, J.A., Schroeder, I.D., Thayer, J.A., Wells, B.K., Williams, G.D., 2019. Indicators of pelagic forage community shifts in the California Current Large Marine Ecosystem, 1998–2016. Ecol. Indic. 105, 215–228. <https://doi.org/10.1016/j.ecolind.2019.05.057>.

Torres, L.G., Read, A.J., Halpin, P., 2008. Fine-scale habitat modeling of a top marine predator: Do prey data improve predictive capacity. Ecol. Appl. 18, 1702–1717. <https://doi.org/10.1890/07-1455.1>.

Vanderploeg, H.A., Scavia, D., 1979. Calculation and use of selectivity coefficients of feeding: zooplankton grazing. Ecol. Model. 7, 135–149. [https://doi.org/10.1016/0304-3800\(79\)90004-8](https://doi.org/10.1016/0304-3800(79)90004-8).

Wang, Y.I., Naumann, U., Wright, S.T., Warton, D.I., 2012. mvabund—an R package for model-based analysis of multivariate abundance data. Methods Ecol. Evol. 3, 471–474. <https://doi.org/10.1111/j.2041-210X.2012.00190.x>.

Wells, B., Santora, J., Field, J., MacFarlane, R., Marinovic, B., Sydeman, W., 2012. Population dynamics of Chinook salmon *Oncorhynchus tshawytscha* relative to prey availability in the central California coastal region. Mar. Ecol. Prog. Ser. 457, 125–137. <https://doi.org/10.3354/meps09727>.

Wells, B.K., Santora, J.A., Bizzarro, J., Billings, A., Brodeur, R.D., Daly, E.A., Field, J.C., Richerson, K.E., Thorson, J.T., 2023. Trophoscapes of predatory fish reveal biogeographic structuring of spatial dietary overlap and informs fisheries bycatch patterns. Mar. Ecol. Prog. Ser. <https://doi.org/10.3354/meps14319>.

Westfall, P.H., Young, S.S., 1993. Resampling-based multiple testing: Examples and methods for p-value adjustment. John Wiley & Sons.

Williams, A.J., Allain, V., Nicol, S.J., Evans, K.J., Hoyle, S.D., Dupoux, C., Vourey, E., Dubosc, J., 2015. Vertical behavior and diet of albacore tuna (*Thunnus alalunga*) vary with latitude in the South Pacific Ocean. Deep Sea Res. Part II, Impacts of Climate on Marine Top Predators 113, 154–169. <https://doi.org/10.1016/j.dsr2.2014.03.010>.

Wisz, M.S., Pottier, J., Kissling, W.D., Pellissier, L., Lenoir, J., Damgaard, C.F., Dornmann, C.F., Forchhammer, M.C., Grytnes, J., Guisan, A., Heikkilä, R.K., Høye, T.T., Kühn, I., Luoto, M., Maiorano, L., Nilsson, M., Normand, S., Öckinger, E., Schmidt, N.M., Ternansen, M., Timmermann, A., Wardle, D.A., Aastrup, P., Svenning, J., 2013. The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. Biol. Rev. 88, 15–30. <https://doi.org/10.1111/j.1469-185X.2012.00235.x>.

Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems. Methods Ecol. Evol. 1, 3–14. <https://doi.org/10.1111/j.2041-210X.2009.00001.x>.