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Juvenile Albacore tuna (*Thunnus alalunga*) foraging ecology varies with environmental conditions in the California Current Large Marine Ecosystem

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Abstract

Juvenile North Pacific Albacore tuna (*Thunnus alalunga*) support commercial and recreational fisheries in the California Current Large Marine Ecosystem (CCLME), where they forage during summer and fall. The distributions of the commercial and recreational fisheries and estimates of forage availability have varied substantially over the past century. Time-series quantifying Albacore diet can help link forage composition to variability in Albacore abundance and distribution and, consequently, their availability to fishers. Previous diet studies in the CCLME are of relatively short duration, and long-term variability in Albacore diet remains poorly understood. We describe the diets of juvenile Albacore from three regions in the CCLME from 2007 to 2019 and use classification and regression tree analysis to explore environmental drivers of variability. Important prey include Northern Anchovy (*Engraulis mordax*), rockfishes (*Sebastes* spp.), Boreal Clubhook Squid (*Onychoteuthis borealijaponica*), euphausiids (Order: Euphausiidae), and amphipods (Order: Amphipoda), each contributing >5% mean proportional abundance. Most prey items were short lived species or young-of-the-year smaller than 10 cm. Diet variability was related to environmental conditions over the first 6 months of the year (PDO, sea surface temperature, and NPGO) and conditions concurrent with Albacore capture (region and surface nitrate flux). We describe foraging flexibility over regional and annual scales associated with these environmental influences. Continuous, long-term studies offer the opportunity to identify flexibility in Albacore foraging behavior and begin to make a predictive link between environmental conditions early in the year and Albacore foraging during summer and fall.

KEYWORDS
classification and regression tree, diet, environmental drivers, fisheries interactions, foraging strategy, prey, stomach contents

1 | INTRODUCTION

The California Current Large Marine Ecosystem (CCLME) is supported by a productive eastern boundary current and is a key foraging ground for diverse migratory predators including juvenile North Pacific Albacore tuna (*Thunnus alalunga*, hereafter Albacore) (Block et al., 2011; Childers et al., 2011). Albacore recruit to the CCLME starting around 2 years of age and return to forage each summer until they move to

spawning grounds in the Central Tropical Pacific at approximately 5 years of age (Childers et al., 2011; Wells et al., 2013). They typically arrive in the CCLME in June or July, spend summer and early-mid fall near the North American coast, and depart in October or November (Childers et al., 2011; Muhling et al., 2022). While resident in the CCLME, Albacore support the largest commercial fishery for a highly migratory species off the US West Coast and are highly sought after by recreational fishers. Inflation adjusted (2020) annual ex-vessel revenue of the West Coast Albacore surface hook-and-line fishery varied from $4 million to $51 million (mean $29 million) between 1990 and 2019, with 179–1192 vessels participating each year (mean 663) (PFMC, 2022). Landings have declined steadily from a recent peak of 16,606 mt in 2012 to <8000 mt since 2016 (PFMC, 2022).

While there has been considerable variability in overall landings and value, the relative value of the juvenile Albacore fishery has increased since the 1980s. The percentage of active vessels fishing for Albacore has grown, and it was the third most valuable fishery off of Oregon and Washington during 2010–2018 (Frawley et al., 2021). The higher percentage of active vessels directed toward Albacore was due to increased economic value as well as their greater accessibility in coastal waters (Frawley et al., 2021). Shifts in the availability and distribution of Albacore in the CCLME have been documented for more than 100 years and result in economic impacts on fishers (Childers et al., 2011; Clemens & Craig, 1965). In some instances, these shifts in availability have been linked to Albacore diet (Pearcy, 1973). Therefore, understanding diet variability will provide insight into the mechanisms that influence Albacore abundance, distribution, and associated availability to fishers in the CCLME (Muhling et al., 2019).

Albacore diet studies in the CCLME have been performed sporadically since the 1940s (Bernard et al., 1985; Glaser, 2010; Glaser et al., 2015; Hart et al., 1948; Iversen, 1962; McHugh, 1952; Pinkas et al., 1971). Prey generally include fishes, cephalopods, and crustaceans, but most studies only include 2–4 years of data, and diet composition differs markedly among studies. Northern Anchovy (*Engraulis mordax*, hereafter Anchovy) and Pacific Saury (*Cololabis saira*, hereafter Saury) are often important prey but are sometimes completely absent, while crustaceans were only important in one region of one study (Glaser, 2010). Long gaps between studies (i.e., 4–36 years) make it impossible to determine how quickly diets change and whether they represent broader food-web responses to environmental variability. The CCLME is a dynamic ecosystem that has experienced substantial, environmentally driven changes in forage availability over the past few decades (Frawley et al., 2021; Mantua & Hare, 2002; Muhling et al., 2019; Sydeman et al., 2020). How this variability impacts the diets of Albacore is yet to be determined.

Albacore diet is likely influenced by changes in the distribution, abundance, or quality of their prey in response to environmental forcing (Golet et al., 2007, 2015; Polovina, 1996). The CCLME is characterized by wind-driven upwelling, which causes variability in both the amount and distribution of primary and secondary productivity. This changing food availability for early life stages drives variability in prey populations: For example, upwelling intensity has been shown to impact the recruitment and subsequent availability of juvenile rockfishes (*Sebastes* spp.), which are important prey for seabirds (Ainley et al., 1993) and Albacore. Additionally, prey species such as Anchovy, Pacific Sardine (*Sardinops sagax*, hereafter Sardine), juvenile North Pacific Hake (*Merluccius productus*), and Boreal Clubhook Squid (*Onychoteuthis borealijaponica*) have contrasting ecological requirements and are thus distributed in areas with different surface chlorophyll-a (Chl-a) and sea surface temperature (SST) ranges (Muhling et al., 2019). As these prey species occupy distinct horizontal and vertical habitats, linking environmental conditions to shifts in prey will likely improve our understanding of Albacore distribution and availability to west coast surface fishing fleets.

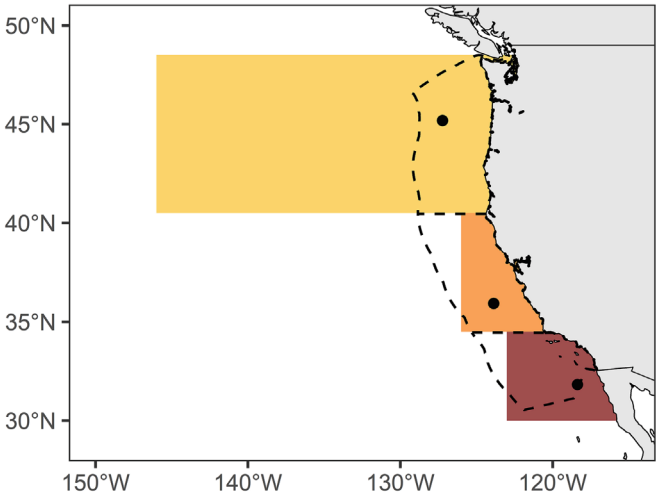

FIGURE 1 Map of sampling regions for Albacore off the US West Coast from 2007 to 2019. Northern region in yellow, Central region in orange, Southern region in red. Black points indicate the centroid of sample locations within each region. Dashed line indicates EEZ boundary.

In addition to understanding vulnerability to fishing gear, quantifying trophic links is a cornerstone of ecosystem-based fisheries management (EBFM). In EBFM frameworks, management options are informed by linkages among species, the environment, and socioeconomic factors (Link, 2017; Link & Browman, 2014; Pikitch et al., 2004). Predator–prey relationships can necessitate management tradeoffs when both species are fishery targets. Albacore are known to consume a range of coastal pelagic species (CPS) that are fished in the CCLME including Anchovy, Sardine, and Market Squid (*Doryteuthis opalescens*) (PFMC, 2020a), as well as groundfish including rockfishes (PFMC, 2020b). Thus, an improved quantitative understanding of food-web connections and how they are impacted by shifting environmental conditions can inform management strategies for several economically and ecologically important species.

Here, we present a time-series of juvenile Albacore diet in the CCLME from 2007 to 2019 and use classification and regression tree (CART) analysis to provide insight into the environmental mechanisms underlying the observed shifts in diet. The objectives of this study were to (1) characterize the spatiotemporal trends of variability in juvenile Albacore diet, (2) identify potential environmental drivers of

diet variability, and (3) discuss the interactions between juvenile Albacore diet, commercially important forage, prey habitat, and the associated links to fishery availability.

2 | METHODS

2.1 | Stomach collection

Albacore stomachs were collected through partnerships with recreational and commercial fishers from June to November 2007–2019. Commercial fishers used troll and pole-and-line gear and recreational anglers fished with hook and line using Anchovy or Sardine as live bait. Albacore were landed in three regions of the CCLME (Figure 1): (1) Northern California, Oregon, and Washington ("Northern," north of Cape Mendocino at 40.45°N); (2) Central California ("Central," between 34.45°N and 40.45°N); and (3) Southern California ("Southern," south of Point Conception at 34.45°N). Stomachs were either frozen before transport to the lab or delivered fresh and frozen on arrival for later processing. Individual fork length (from the tip of the snout to the outside edge of the fork in the caudal fin, FL), operculum length (from the tip of the lower jaw to the end of the operculum, OL), latitude and longitude of capture, and date of collection were recorded when possible. Available metadata for some individuals were limited to the landing region and year. FL were estimated from OL when only the latter was reported using an empirically derived relationship when both were measured for the same fish ($FL = 3.658 * OL - 5.455$, $R^2 = 0.98$) (Heberer & Snodgrass, 2021). Albacore FL (17% missing) were compared among the three regions using a Kruskal–Wallis test with a pairwise Wilcoxon post hoc test (Hollander & Wolfe, 1973).

2.2 | Gut content identification

Stomachs were thawed in the lab, and the contents were rinsed over 0.5-mm brass mesh sieves. Rinsed contents were stored in 70% ethanol until they were sorted and identified using a dissecting microscope. Fishes were identified by vertebrae (Clothier, 1950), otoliths (Harvey et al., 2000; Lowry, 2011), rockfish preopercula, and whole bodies. Cephalopods were identified by beak morphology (Clarke, 1986; Pinkas et al., 1971; Wolff, 1984). Crustaceans were identified by carapace, eye, or claw morphology (Isaacs et al., 1969). Prey items were counted as the total number of singular structures (e.g., vertebral column), the larger number of non-equivalent paired structures (e.g., otoliths, beaks), or half the number of undifferentiated paired structures (e.g., eyes, claws).

Prey size was measured to the nearest 0.1 mm. Up to five individuals were measured for each prey species in each stomach. Lengths are only reported for species represented by at least 10 measurements over the study period. Standard length (SL) was measured directly for whole fish and fish vertebral column lengths were converted to SL following Glaser et al. (2015). Life stage (i.e., young-of-the-year [YOY], juvenile, adult) was estimated using published age at size relationships (Table S1). Squid beak lower rostral length and octopus beak upper hood length were measured and converted into mantle lengths (ML) following published regressions, and approximate age at size was estimated for Boreal Clubhook Squid (Table S1). The regressions resulted in implausible lengths for some specimens of two species: estimated ML less than the reported hatching size of Boreal Clubhook Squid relative *Onychoteuthis horstkottei* ($n = 35$, 0.19 cm [Martínez-Soler et al., 2021]) and greater than the reported maximum size of Market Squid ($n = 2$, 30 cm [Recksiek & Frey, 1978]) were corrected to the respective minimum or maximum reported values. Crustacean lengths were measured as SL but not estimated from parts (Isaacs et al., 1969). SL were compared between the Northern and Southern regions (where data were available) for both Anchovy and Hyperiid Amphipods (suborder: Hyperiidea) with a Wilcoxon rank sum test.

Fresh Anchovy and Sardine were recorded but discarded to eliminate bias resulting from the use of live bait or chumming. Fresh chum was much larger than more digested natural prey of the same species (>10 cm vs. < 10 cm) (Glaser, 2010) and thus easy to identify. Calanoid copepods (order: Calanoida) were considered prey of prey and excluded from analysis (Pinkas et al., 1971). Small nematodes (phylum: Nematoda) and cyclopoid copepods (order: Cyclopoida) were classified as parasites rather than prey and also excluded from analysis.

Prey abundances are first presented as absolute abundance (n), that is, the total number encountered across all stomachs. The total percent abundance ($\%n_{total}$) was then calculated as n for each prey taxa divided by the sum of n for all prey. In order to normalize consumption per predator and reduce the influence of prey with high counts but low frequency of occurrence, prey counts were converted into mean proportional abundance within each stomach ($\%n_{mean} \pm SD$). This was calculated as the number of a particular prey item within a stomach divided by the total number of prey in that stomach, averaged over all stomachs. The percent frequency of occurrence ($\%FO$) of each prey was calculated as the number of stomachs in which that prey occurred divided by the total number of stomachs.

Only prey that contributed more than 1% n_{mean} were included in analysis. Prey taxa contributing less than 1% n_{mean} were combined into higher order taxonomic groups (e.g., members of family: Myctophidae were grouped together; Table S2) unless there were no closely related higher orders, in which case they were broadly categorized as "other fishes," "other squid," or "other invertebrates." Unidentifiable prey items were grouped by broad taxonomic category as "unknown fishes" or "unknown squid," separately from "other." All identifiable crustaceans were part of class: Malacostraca, so unidentifiable crustacean parts were classified as "unknown Malacostraca."

Sample availability varied between years and regions. A minimum of 30 stomachs containing prey was established as a target for each year/region characterized. If less than 30 were available, all stomachs were analyzed. More than 30 were processed when allowed by time and sample availability. Sample coverage and prey diversity within

each year and region were assessed through species accumulation curves constructed using the *iNEXT* package (Chao et al., 2014; Hsieh et al., 2016) in R (R Core Team, 2020) using Shannon diversity based on presence/absence (Shannon, 1948).

2.3 | Environmental variables

SST, Chl-*a* (as a proxy for standing phytoplankton biomass), the Biologically Effective Upwelling Transport Index (BEUTI) (Jacox et al., 2018), the Pacific Decadal Oscillation (PDO) (Mantua & Hare, 2002), and the North Pacific Gyre Oscillation (NPGO) (Di Lorenzo et al., 2008) were used to quantify environmental conditions across the study area. We considered the influence of both past and present environmental conditions on Albacore diets. Because most prey items were YOY fishes, larval squid, or short-lived crustaceans, past conditions were represented as an average of values over the first 6 months of the year and region of capture. Conditions during the first 6 months of the year were expected to impact growth and recruitment of prey given that YOY prey consumed in the summer and fall would have been spawned in the winter and spring. Conditions at the time of capture influence the availability of those individuals to Albacore predation. Average conditions during the first 6 months of the year were included in the analyses for all Albacore sampled. Present conditions were only included if both month and precise location were available (27% missing).

Monthly SST and Chl-*a* were accessed using the *rerddapXtracto* package (Mendelssohn, 2020) from the Environmental Research Division's Data Access Program (ERDDAP, datasets Multi-scale Ultra-high Resolution (MUR) SST Analysis fv04.1, Global, 0.01°, 2002–present, Monthly (JPL MUR MEaSUREs Project, 2015) and Chlorophyll-*a*, Aqua MODIS, NPP, L3SMI, Global, 4 km, Science Quality, 2003–present (Monthly Composite) (Hu et al., 2012)) in R. Conditions during the first 6 months of the year were averaged over the Exclusive Economic Zone (EEZ) aligning latitudinally with the region where the predator was collected. EEZ Shapefiles (Flanders Marine Institute, 2016) were imported following Palacios (2016). The EEZ was used as a standard boundary containing most reported catch locations (Northern 88%, Central 100%, Southern 73%) to approximate conditions influencing recruitment and development. Present conditions were average values within 0.25° latitude and longitude blocks containing the Albacore catch location.

BEUTI represents the vertical nitrate flux into the surface mixed layer and is estimated from vertical transport and the nitrate concentration at the base of the mixed layer (Jacox et al., 2018). BEUTI values were obtained from the NOAA Environmental Research Division Website in 1° latitude bins (https://oceanview.pfeg.noaa.gov/products/upwelling/dnld). Conditions during the first 6 months of the year were averaged across latitude within each landing region. The closest whole number latitude to the location of capture represented present conditions.

The PDO and NPGO were accessed using the *rsoi* package (Albers, 2020) in R. Because climate indices reflect broad trends in the state of the system, PDO and NPGO were only included as averages over the first 6 months of the year.

2.4 | CART analysis and foraging behavior

To examine the effects of SST, Chl-*a*, BEUTI, PDO, NPGO, capture region, and predator FL on juvenile Albacore diet, we performed CART analysis using the *diet* package (Kuhnert & Duffy, 2013) in R. Capture date was not included so that splits would be driven by mechanisms that may vary or recur over time. CART analysis is insensitive to unbalanced sampling and missing values of explanatory variables. "Other" and "unidentified" prey groups were not included in the CART analysis so that similarity was not inflated by these heterogeneous groups, resulting in the exclusion of stomachs where they were the only prey. Trees were built using 10-fold cross-validation and pruned using the 1-SE rule (Breiman et al., 1984; Kuhnert et al., 2012). The importance of each environmental variable was determined relative to the best predictor of diet composition across the tree as described in Kuhnert et al. (2012). Diet compositions are reported as the mean cross-validated proportions at each terminal node, and diversity is reported as the Gini index (Breiman et al., 1984). Spatial bootstrap aggregation ($n = 500$) was performed in the *diet* package on the final tree. Potential pseudo-replication of samples was investigated by constructing an experimental variogram of the bootstrap prediction residuals.

Sample coverage and species diversity in each terminal node of the pruned tree was quantified using the *iNEXT* package (Chao et al., 2014; Hsieh et al., 2016) in R using the Shannon diversity index. The Gini index used in CART partitioning takes richness and evenness among taxa into account, while the Shannon index was calculated based only on the presence/absence of prey taxa and will not be discussed beyond its use in describing sample coverage. Similarity among CART nodes was quantified using pairwise PERMANOVA in Primer v7 using type III sum of squares (Anderson et al., 2008; Clarke et al., 2014; Clarke & Gorley, 2015). PERMANOVA was chosen over other common multivariate methods for comparison among groups due to its robustness to unequal sample sizes and heterogeneity.

Juvenile Albacore feeding strategy was assessed using the Costello (1990) method as modified by Amundsen et al. (1996). Prey specific proportion (*%PS*, analogous to prey specific abundance) was calculated as the mean percent abundance by number of a prey taxa only in stomachs containing that taxa. Costello plots were created for each node by plotting the *%PS* on the y-axis and *%FO* on the x-axis. Prey taxa toward the top of the vertical axis indicate specialized feeding, either by individuals or the whole population, while prey taxa nearer the bottom were consumed in a more generalized manner. Prey taxa in the upper right dominated the diet of the population, while those in the bottom left were consumed rarely. The upper left to lower right diagonal indicates diet similarity among individuals: Prey taxa in the upper left were very important to a few individuals, while those in the lower right contributed a small percentage to the diet of most of the population.

TABLE 1 Summary of specimens by region and year, including the number of stomachs dissected ($n_{stomachs}$), the number of stomachs containing prey ($n_{stomachs\ with\ prey}$), and the fork length (FL) range and mean.

Region	Year	$n_{stomachs}$	$n_{stomachs\ with\ prey}$	FL range (cm)	FL mean ± SD (cm)
Northern					
	2009	14	13	58–90	71.4 (±12)
	2010	121	85	54–83	65 (±5)
	2011	50	44	51–85	65 (±8)
	2012	50	36	54–80	65 (±7)
	2013	65	52	56–90	69 (±9)
	2014	38	37	51–88	66 (±12)
	2015	30	30	50–58	54 (±3)
	2017	24	20	53–84	68 (±8)
	2018	49	48	56–94	66 (±8)
	2019	18	18	59–80	70 (±7)
Central					
	2012	28	27	54–87	70 (±14)
	2013	27	27	55–83	63 (±8)
Southern					
	2007	120	107	77–96	86.7 (±3)
	2008	32	28	53–82	65.3 (±10)
	2009	68	47	68–90	77.1 (±5)
	2010	118	85	59–87	77 (±6)
	2012	61	46	79–98	85 (±5)
Total		913	750	50–98	72 (±11)

3 | RESULTS

3.1 | Albacore sampled

Stomach contents were examined from 913 juvenile Albacore collected from 2007 to 2019, of which 750 contained prey (Northern: 383, Central: 50, Southern: 317; Figure 1 and Table 1). Most prey items were highly digested and were identified from hard part remains. Overall, Albacore FL ranged from 50 to 98 cm, with a mean of 72 (±11) cm. There were significant differences in Albacore mean FL between regions (Kruskal–Wallis test, $P < 0.001$) driven by a larger mean FL in the Southern region (80 ± 7 cm) when compared to the Northern (66 ± 8 cm, Wilcoxon, $P < 0.001$) and Central (66 ± 12 cm, Wilcoxon, $P < 0.001$) regions, which were not different from one another (Wilcoxon, $P > 0.05$).

3.2 | Diet description

Across all stomachs, 30,164 individual prey specimens were identified and classified into 71 taxa, including 37 identifiable to the species level (Table S2). These taxa were combined into 24 prey categories, eight of which included only one species. Twenty-three categories contributed at least 1% mean proportional abundance; only "other invertebrates" contributed less (Table 2). While there was considerable variability across years and regions (Figure 2), Anchovy was the most abundant prey overall when averaged across years (22 ± 38% n_{mean}, 32% *FO*), followed by euphausiids (7 ± 21% n_{mean}, 14% *FO*), rockfishes (5 ± 15% n_{mean}, 24% *FO*), Boreal Clubhook Squid (5 ± 14% n_{mean}, 24% *FO*), and amphipods (5 ± 15% n_{mean}, 14% *FO*). Rarefaction and extrapolation curves indicated that, at the taxonomic resolution of the analyses, the mean sample coverage for each year by region was 98% (range 92–100%; Figure S2) and, on average, less than 2% of expected prey diversity was missed.

Fish prey was found in 89% of non-empty stomachs (*%FO* = 89) and had the highest mean proportional abundance ($\%n_{mean}$ = 56 ± 40). The SL of consumed fishes ranged from 0.73 to 27 cm, with a mean of 6.19 (±3.70) cm (Figure 3 and Table S2). Notable species exceeding 10 cm length were Saury, Slender Barracudina (*Lestidiops ringens*), and Pacific Chub Mackerel (*Scomber japonicus*). The smallest fishes were *Sebastes* spp., with a mean of 2.20 (±1.16) cm SL. Anchovy in the Southern region were significantly larger (7.87 ± 0.99 cm, Wilcoxon, $P < 0.001$) than Anchovy in the Northern region (3.88 ± 0.96 cm). Based on available age-at-size estimates, Anchovy, rockfishes, Sardine, Pacific Jack Mackerel (*Trachurus symmetricus*), and Pacific Chub Mackerel consumed by Albacore were primarily YOY.

Cephalopods were found in 53% of all stomachs and had lower mean proportional abundance than fishes or crustaceans ($\%n_{mean}$ = 21 ± 30). Cephalopods were more important in the Central region ($\%n_{mean}$ = 55 ± 32) compared to the Northern (19 ± 30%) and Southern (17 ± 26%) regions. The unknown squid category contained numerous larval squid with beaks too small for accurate identification (smaller than 0.5 mm lower rostral length). The mantle lengths of consumed squids ranged from 0.19 to 36 cm, with a mean of 3.94 (±4.05) cm. The largest squid identified were Market Squid with a mean

TABLE 2 Summary of prey found in Albacore stomachs 2007–2019 by absolute abundance (total count over all stomachs, *n*), total proportional abundance (*n* for each species divided by the sum *n* of all species from all stomachs, $\%n_{total}$), mean proportional abundance (mean over all stomachs of the *n* for each species divided by the sum of *n* for all species within each individual stomach, $\%n_{mean}$), and frequency of occurrence (number of stomachs within which each prey species occurred divided by the total number of stomachs, *%FO*).

CART group	Common name	*n*	$\%n_{total}$	$\%n_{mean(\pm SD)}$	*%FO*
Fishes					
Engraulis mordax	Northern Anchovy	6492	21.5	21.9 (±37.5)	32.1
Sebastes sp.	Rockfishes	1517	5.0	5.2 (±14.6)	23.7
Cololabis saira	Pacific Saury	551	1.8	4.7 (±15.8)	16.9
Sardinops sagax	Pacific Sardine	639	2.1	4.6 (±16.3)	12.4
Lestidiops ringens	Slender Barracudina	221	0.7	2.3 (±12.3)	9.1
Trachurus symmetricus	Pacific Jack Mackerel	677	2.2	2.1 (±9.1)	10.3
Myctophidae		274	0.9	1.8 (±9.0)	10.7
Scomber japonicus	Pacific Chub Mackerel	217	0.7	1.8 (±10.6)	5.3
Other fish*		560	1.9	1.5 (±8.3)	8.9
Unknown fish*		976	3.2	10.5 (±24.0)	33.7
Cephalopods					
Onychoteuthis borealijaponica	Boreal Clubhook Squid	1026	3.4	5.2 (±14.4)	24.0
Octopoteuthis sp.		562	1.9	2.2 (±8.5)	13.6
Gonatus sp.		330	1.1	1.7 (±8.5)	11.2
Berryteuthis sp.		310	1.0	1.5 (±10.0)	3.6
Doryteuthis opalescens	Market Squid	579	1.9	1.0 (±6.4)	4.8
Octopoda		643	2.1	2.3 (±8.5)	16.3
Other squid*		134	0.4	1.0 (±7.4)	6.9
Unknown squid*		1286	4.3	6.1 (±15.8)	24.1
Crustaceans/other invertebrates					
Euphausiidae		8805	29.2	6.7 (±21.4)	14.0
Amphipoda		1788	5.9	5.1 (±14.9)	18.9
Decapoda		563	1.9	2.8 (±12.1)	11.9
Phronima sp.		355	1.2	2.1 (±8.2)	13.1
Unknown malacostraca*		1613	5.4	5.3 (±17.1)	18.5
Other invertebrates*		46	0.2	0.7 (±6.2)	2.9
Total		30,164			

Note: * indicates groups that were not included in CART analysis.

mantle length of 9.10 (±4.27) cm, and the smallest were *Octopoteuthis* sp. with a mean mantle length of 1.42 (±1.53) cm. Based on age-at-size, Boreal Clubhook Squid were an average of less than 2 months old with a maximum of approximately 8 months.

Crustaceans were the most abundant prey, accounting for 44% of all identified prey ($\%n_{total}$), but had a lower mean proportional abundance than fish prey ($\%n_{mean} = 22 \pm 32$) due to the lower frequency of occurrence of crustaceans (*%FO* = 51). Euphausiids were most important in the Northern region ($\%n_{mean}$ Northern = 12 ± 28 vs. Central = 1 ± 8 and Southern = 1 ± 10), while amphipods were more important in the Central and Southern regions ($\%n_{mean}$ Northern = 2 ± 9 vs. Central = 7 ± 13 and Southern = 9 ± 20). Euphausiids were identified to species when possible but were usually too damaged or represented only by loose eyes. Identifiable species were *Euphausia pacifica*, *Thysanoessa spinifera*, and *Nematoscelis difficilis*. Consumed crustaceans varied from 0.23 to 2.44 cm SL, with a mean of 1.63 (±0.60) cm SL. The largest crustacean measured was *E. pacifica*, with a mean SL of 2.03 (±0.26) cm. Hyperiid Amphipods, which were also mature adults, were measured from both Northern and Southern regions. Northern region Hyperiids presented a mean SL of 0.91(±0.25) cm, while Southern region Hyperiids were larger, with a mean SL of 1.95(±0.22) cm (Wilcoxon, $P < 0.001$).

3.3 | CART analysis and foraging behavior

CART analysis was performed on 686 stomachs, excluding 64 stomachs that contained only "other" or "unknown" prey, resulting in a tree with five splits (six terminal nodes) and a cross-validated error rate of 0.24 (SE = 0.024; Figure 4). All stomachs from the same year/

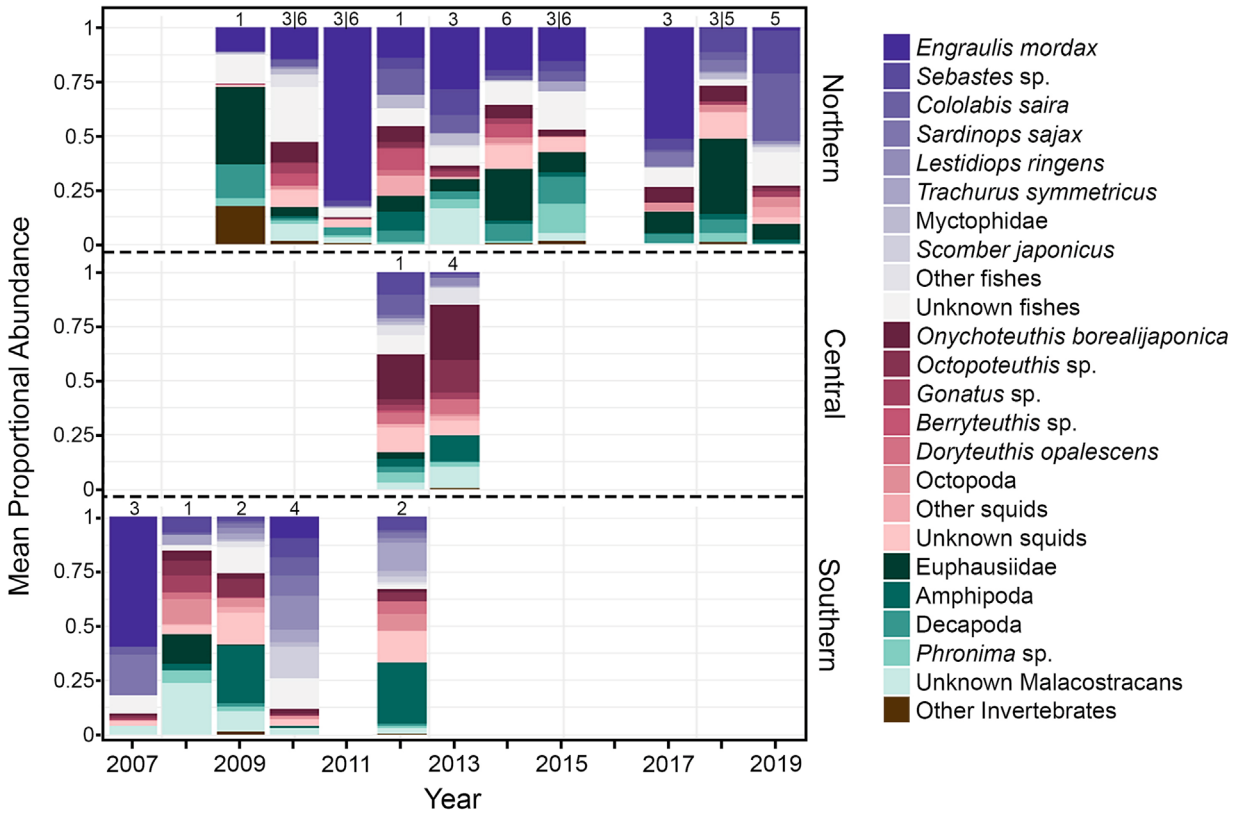

FIGURE 2 Mean proportional abundance by year and region. Fish prey are in purples, cephalopods are in reddish-browns, and crustaceans are in greens. Numbers above bars indicate CART nodes.

region clustered into the same terminal node with the exception of overlap between node 3 with nodes 5 or 6. Each terminal node was significantly different (PERMANOVA, $P < 0.001$, *pseudo-t* = 2.11–11.04; Table 3). The variables that best explained diet variability in our dataset were PDO_{6mo} (Rank = 1), BEUTI (Rank = 0.93), SST_{6mo} (Rank = 0. 44), SST (Rank = 0.27), $NPGO_{6mo}$ (Rank = 0.25), Region (Rank = 0.23), CHL_{6mo} (Rank = 0.15), and $BEUTI_{6mo}$ (Rank = 0.11). Albacore FL and CHL did not contribute to tree partitioning (Rank = 0). The full range of environmental covariates observed in each terminal node is given in Figure S1. Spatially bootstrapped predictions ($n = 500$) for mean proportional diet composition for each node are given in Figure S3. An experimental variogram of the spatial bootstrap prediction results demonstrated a minimal effect of distance on variance (Figure S4), suggesting minimal pseudo-replication of samples. Rarefaction and extrapolation curves showed that the sample coverage for all nodes reached 99% (Figure S5), indicating that sample size was adequate to capture nearly all the expected diversity within each node at the level of aggregation used.

The deepest split separated out Albacore collected at low PDO_{6mo}. Within the low PDO_{6mo} branch, diets were separated into low/moderate and high SST_{6mo} nodes. Node 1, after low/moderate SST_{6mo}, contained Albacore from all three regions and reflected the most diverse diets ($D = 0.85$; Table 3). Euphausiids were the most important prey ($\%n_{mean} = 15 \pm 32$) by a narrow margin above Boreal Clubhook Squid ($\%n_{mean} = 15 \pm 29$). After high SST_{6mo}, node 2 only included stomachs from the Southern region and was the only node to contain no Anchovy; amphipods were the predominant prey ($\%n_{mean} = 37 \pm 33$). In the high PDO_{6mo} branch, Albacore collected when BEUTI was low in node 3 had the least diverse diets ($D = 0.38$). Containing stomachs from the Northern and Southern Regions, node 3 was dominated by Anchovy ($\%n_{mean} = 62 \pm 42$). At moderate/high BEUTI, stomachs from the Central and Southern regions were separated into node 4. The most important prey was Slender Barracudina ($\%n_{mean} = 16 \pm 32$), and diet diversity was high ($D = 0.84$). In the Northern Region, Albacore collected after low $NPGO_{6mo}$ in node 5 consumed predominantly euphausiids ($\%n_{mean} = 33 \pm 40$), while Albacore collected after moderate/high $NPGO_{6mo}$ in node 6 consumed Anchovy as their most important prey ($\%n_{mean} = 25 \pm 40$).

Diet similarity was generally greatest within nodes, although there was some overlap with the between node values (Table 4). The most similar nodes were 3 and 6, which contained high proportions of Anchovy compared to the other nodes. Nodes 1 and 5 were the second most similar, both containing relatively high proportions of euphausiids and low proportions of Anchovy. These two node pairs had higher similarity than the within node values for the more diverse nodes 6, 4, and 1. The least similar nodes were 2 and 3, with node 2 containing a high proportion of amphipods and node 3 dominated by Anchovy.

Foraging behaviors at both individual and population levels varied under the different environmental conditions (Figure 5). When PDO_{6mo} and SST_{6mo} were low in node 1, diets were diverse with some individual specialization on euphausiids (*%PS* = 67, *%FO* = 23) and Anchovy (*%PS* = 61, *%FO* = 12). At low PDO_{6mo} and high SST_{6mo}

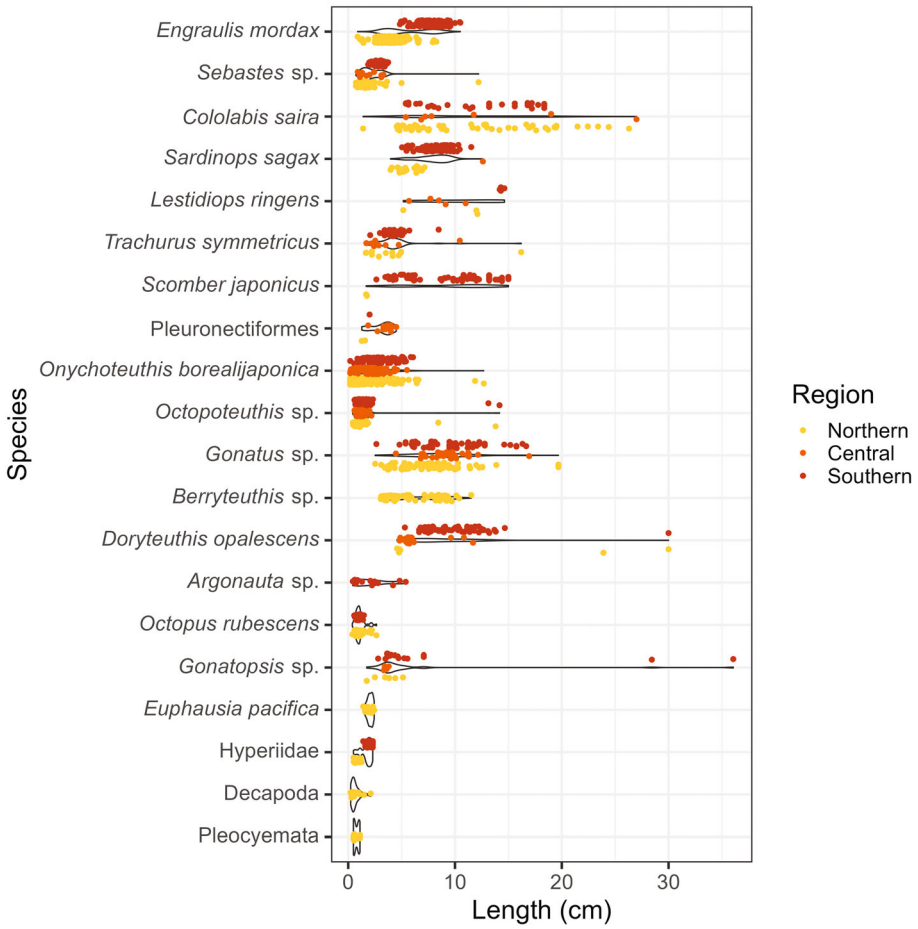

FIGURE 3 Prey standard lengths where more than 10 individuals were measured over the whole study.

in the Southern region in node 2, population-level specialization on amphipods (*%PS* = 53, *%FO* = 70) was observed. At moderate/high PDO_{6mo} and low BEUTI in node 3, feeding showed strong population specialization on Anchovy (*%PS* = 78, *%FO* = 80). In the moderate/high BEUTI branch, Albacore in the Central and Southern regions in node 4 demonstrated generalist feeding behavior similar to node 1, with Anchovy (*%PS* = 70, *%FO* = 12), Myctophids (*%PS* = 63, *%FO* = 4), and Pacific Chub Mackerel (*%PS* = 58, *%FO* = 23) the targets of a small proportion of individual specialists. In the Northern region at low $NPGO_{6mo}$ in node 5, Albacore demonstrated population-level specialization on euphausiids (*%PS* = 63, *%FO* = 53), while some individuals specialized on Sardine (*%PS* = 54, *%FO* = 8) and more than half the population consumed rockfishes (*%PS* = 22, *%FO* = 62). Generalist feeding behavior was observed at moderate/high $NPGO_{6mo}$ in node 6, with some individuals specializing on Anchovy (*%PS* = 63, *%FO* = 53), Berryteuthis Squids (*%PS* = 63, *%FO* = 53), or euphausiids (*%PS* = 63, *%FO* = 53).

4 | DISCUSSION

The CCLME is a productive and dynamic system where oceanographic conditions and the availability of forage species can be highly variable (Crone et al., 2019; Glaser, 2010; Keister et al., 2011; MacCall et al., 2016; Mantua & Hare, 2002; Sydeman et al., 2020). This is the first long-term study that describes how juvenile Albacore diets and foraging behavior shift with environmental conditions in the CCLME. We demonstrate that Albacore are opportunistic predators that exhibit variable foraging behaviors at both the individual and population level. Population-level specialization was observed on Anchovy, euphausiids, or amphipods and diets reflected a more generalist mode under differing environmental conditions. Diet variability across CART nodes indicates that regional and environmental differences impact prey composition over relatively short temporal and spatial scales. Diets differed between adjacent regions in the same year and changed significantly between successive years. We observed diverse diets that indicate Albacore successfully find food under a range of conditions across habitats. This study reveals a level of diversity in diet and foraging behavior not previously documented in the CCLME.

4.1 | Spatiotemporal trends in Albacore diet composition

The present study corroborates the findings of historical studies in the CCLME (Bernard et al., 1985; Glaser, 2010; Hart et al., 1948; Iversen, 1962; McHugh, 1952; Pearcy, 1973; Pinkas et al., 1971) that, although crustaceans and cephalopods are also important, fishes are the dominant prey of Albacore overall. The fishes consumed are diverse and utilize a range of habitats throughout the water column

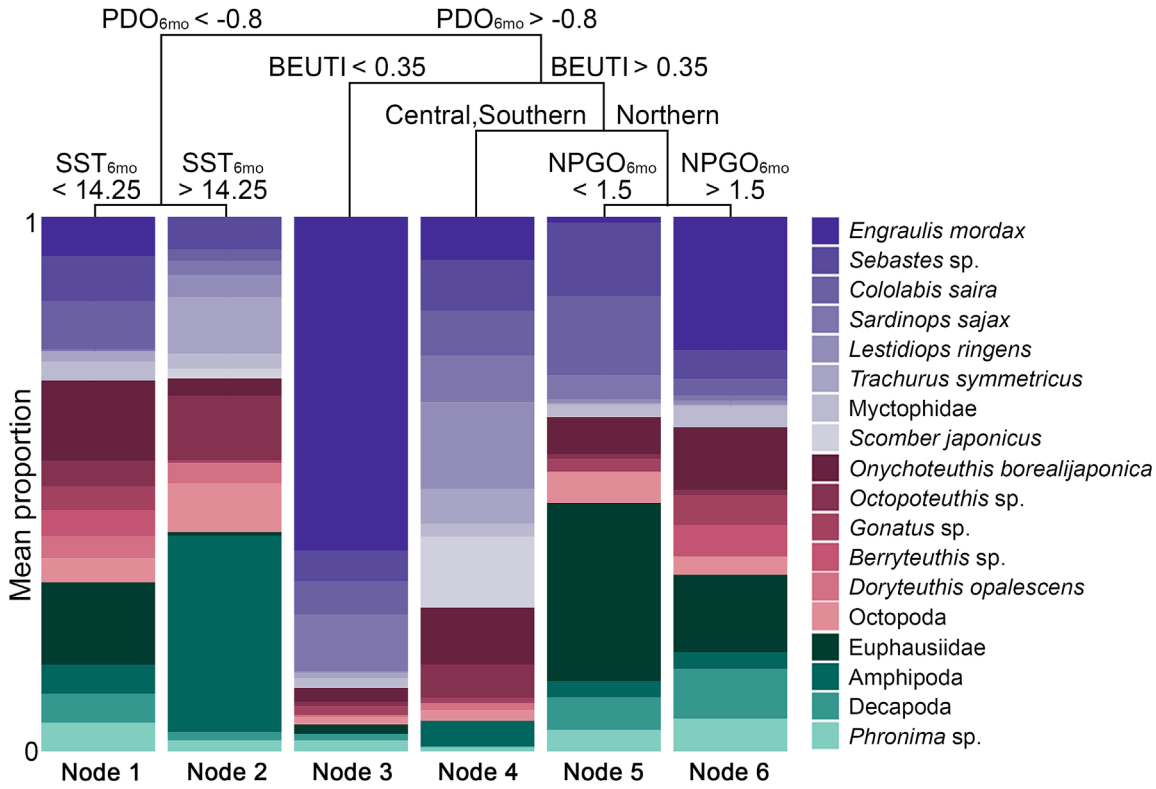

FIGURE 4 Output of CART analysis showing the most parsimonious tree (CP = 0.001, cross-validated error rate = 0.24, SE = 0.02) with the mean cross-validated proportional prey composition for each terminal node. Branch lengths are not proportional to the variance explained by each split. Values of split variables are rounded to two decimal places. Fish prey are in purples, cephalopods are in reddish-browns, and crustaceans are in greens. BEUTI in mmol m^{-1} s^{-1}, SST_{6mo} in °C.

TABLE 3 Summary of the terminal nodes identified by CART analyses: the values of $BEUTI_{6mo}$ and SST_{6mo}, the prey item making the largest contribution, regions included, sample size (*n*), and Gini index of diversity (*D*).

Node	$xPDO_{6mo}$	SST_{6mo} °C	BEUTI mmol m^{-1} s^{-1}	$NPGO_{6mo}$	General diet description	Regions	*n*	*D*
1	−1.23 to −0.95	**10.2 to 14.0**	0.01 to 9.78	0.56 to 1.38	Euphausiids 15%	N, C, S	91	0.85
2	−1.23 to −0.95	**14.5 to 14.7**	0.10 to 0.71	0.56 to 1.38	Amphipods 37%	S	89	0.63
3	−0.65 to 1.82	10.4 o 14.5	**−0.29 to 0.26**	−1.95 to 1.64	Anchovy 62%	N, S	203	0.38
4	−0.34 to 0.55	12.5 to 14.9	0.73 to 5.33	0.86 to 1.64	Barracudina 16%	**C, S**	104	0.84
5	0.2 to 0.78	11.4	0.44 to 9.10	**−1.96 to −1.95**	Euphausiids 33%	N	60	0.67
6	−0.65 to 1.82	10.4 to 12.5	0.55 to 15.6	**−1.10 to 1.64**	Anchovy 25%	N	139	0.75

Note: Bold text indicates the environmental variable associated with the split directly preceding each terminal node.

although Anchovy and Saury most frequently recur. Across studies, the relative importance of these two species has shifted over time and by region. In both the Northern and Southern regions, we observed a continuation of the trends of decreasing Saury and increasing Anchovy importance documented between the 1940s and the 2000s (Glaser, 2010; McHugh, 1952; Pearcy, 1973; Pinkas et al., 1971). In the Central region, Anchovy were more important in the late 1940s and 1983 (Bernard et al., 1985; Glaser, 2010; McHugh, 1952), while Saury dominated in the 1950s, 1960s and early 2000s (Glaser, 2010; Iversen, 1962; Pinkas et al., 1971). In the present study, Anchovy were absent from the Central region where few Saury were found. Anchovy was present in Albacore diets in the Southern region 2010 even though the spawning biomass (estimated from egg and larval abundance) of the central Anchovy subpopulation was very low that year (MacCall et al., 2016). This result demonstrates that trophic flows can be maintained even when prey are relatively rare and that surveys and fisheries landings may not reflect available forage. However, there is currently no stock assessment or fishery of the northern subpopulation that overlaps the Northern region of the present study, which would allow us to more directly compare Anchovy availability and consumption in the Northern region (Kuriyama et al., 2022). When characterizing diets, a regional approach is needed, and caution must be used when inferring forage from fisheries or survey data.

Unique to the Central region was the increased importance of cephalopods. In the late 1960s, the relative caloric importance of cephalopods reached 63% (Glaser, 2010; Pinkas et al., 1971). In this study, the $\%n_{mean}$ of cephalopods in the Central Region was 50 ± 35% (2012) and 60 ± 29% (2013) in comparison to an average of 19 ± 30% and 17 ± 26% in the Northern and Southern regions, respectively. Even when Anchovy or Saury were the dominant prey (Bernard et al., 1985; Glaser, 2011; Iversen, 1962; McHugh, 1952), cephalopod importance was still highest in the Central region. While the relatively high importance of cephalopods in the Central region was apparent in multiple studies, additional years of data are needed to determine if the lower reliance on fishes persists and the associated environmental forcing mechanisms.

In addition to fishes and cephalopods, there were some years and regions in the present study where crustaceans were the dominant component of the diets. Euphausiids were dominant in the Northern region in 3 years and amphipods in the Southern region in 2 years. Crustaceans can occur in high numbers in stomachs but have relatively small size, low biomass, and low energy density, which can cause them to contribute relatively low energy intake (Glaser, 2010) even when numerically dominant (Pinkas et al., 1971). While crustaceans were observed in other studies of juvenile Albacore, assessment of their importance is sensitive to differences in method.

While this 12-year study revealed the influence of environmental conditions on diets, shifts associated with recent temperature anomalies were not apparent. In the Northern region, where data were available, we did not see distinct diet signatures reflecting the 2014–2016 (Bond et al., 2015) or 2019–2020 marine heat waves (Weber et al., 2021), or the El Niño event of 2015–2016 (Jacox et al., 2016), which were split into three nodes along with other years in the CART. It is possible that Albacore respond to warming events by altering their distributions to follow preferred prey, rather than by prey switching. With the exception of the PDO and NPGO climatic indices, environmental conditions showed more spatial than temporal variation (Figure S1), with the greatest differences apparent between regions rather than across time. Temporal trends may become more apparent in longer time series within each region.

TABLE 4 Below diagonal, average pairwise Morisita–Horn similarity (1 = completely similar, 0 = completely dissimilar) for individuals between nodes. Along diagonal bold, average within node Morisita–Horn similarity. Above diagonal, pairwise pseudo *t*-statistics between nodes from the PERMANOVA (all $P \leq 0.001$).

Node	1	2	3	4	5	6
1	**0.13**	4.89	7.46	3.05	2.14	2.11
2	0.10	**0.36**	11.04	4.91	5.93	6.41
3	0.09	0.03	**0.49**	7.67	8.10	6.11
4	0.09	0.12	0.11	**0.15**	4.02	4.02
5	0.17	0.09	0.07	0.08	**0.27**	3.24
6	0.13	0.05	0.21	0.07	0.14	**0.16**

4.2 | Relationship with environmental predictors

CART analysis revealed that environmental variables from the first 6 months of the year and conditions at the time of capture both

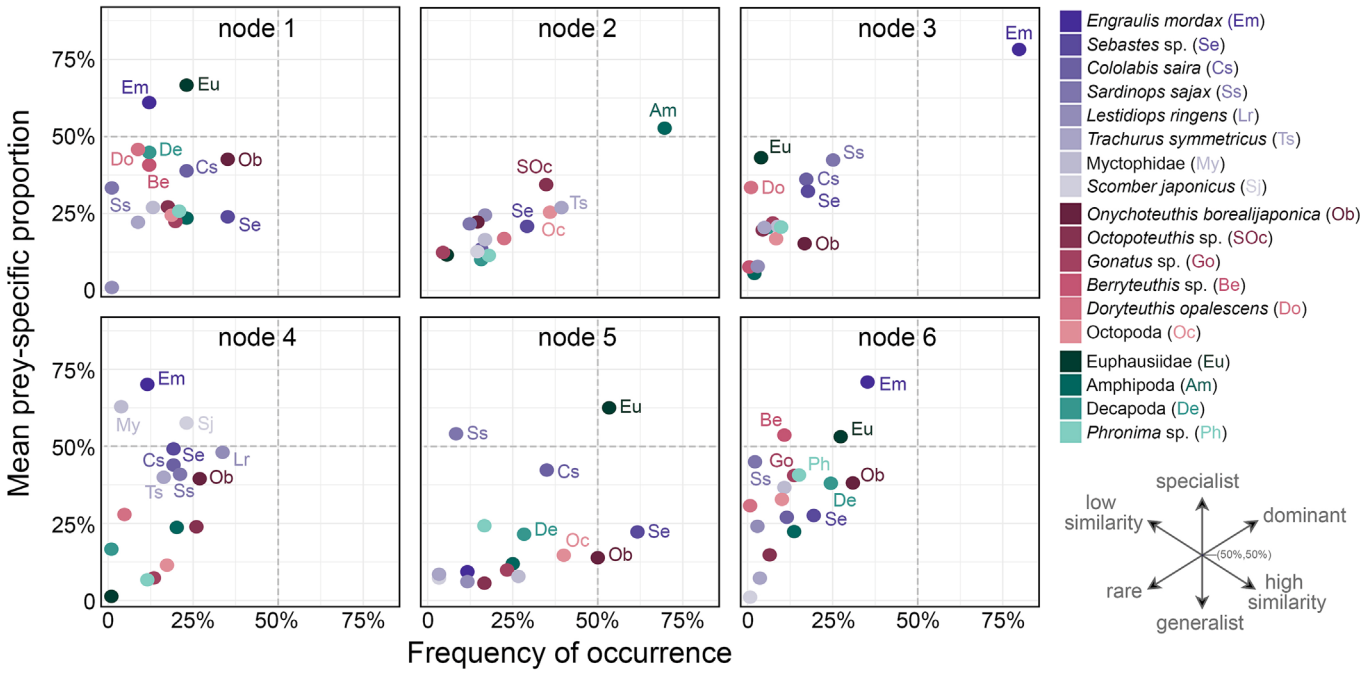

FIGURE 5 Costello diagrams of Albacore diet by node. For ease of reading, only species exceeding 33% on either axis are labelled in each plot. Key modified from Amundsen et al. (1996).

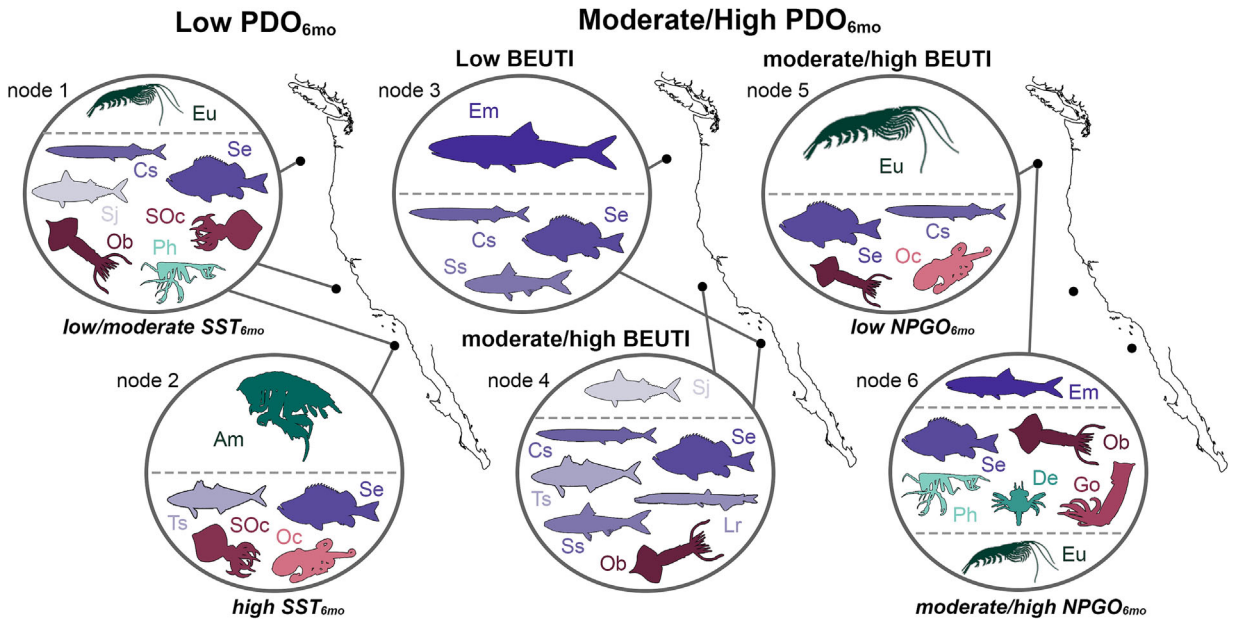

FIGURE 6 Conceptual diagram of juvenile Albacore diet under varying environmental conditions. Silhouettes and abbreviations describe the identity of prey. Labels are the same as in Figure 5. Fish prey are in purples, cephalopods are in reddish-browns, and crustaceans are in greens. Dashed lines separate potential species composition of individual stomachs.

contributed to explaining Albacore diets. Time lags of several months between primary production and responses from higher trophic levels are a common feature of marine food chains. For example, Ainley et al. (1993) found that the proportion of juvenile rockfish in the diets of Common Murres (*Uria aalge*) in June–July increased when upwelling was mild or pulsed the previous January–February. Conditions over the first 6 months of the year would have influenced the growth, development, and recruitment of YOY fishes and juvenile squids fed upon by Albacore. The link to consumed adult crustaceans, which are difficult to age but typically live around 1–2 years, is less direct. Conditions at the time of Albacore capture likely influence prey distribution and availability to predators by defining the overlap of suitable habitat (Muhling et al., 2019).

Both PDO_{6mo} and $NPGO_{6mo}$, which are indicators of basin-scale forcing, contributed to tree partitioning. In the CCLME, wintertime preconditioning links large-scale atmospheric forcing to ecosystem productivity later in the year (Schroeder et al., 2013). Low PDO is associated with cool SST anomalies in the CCLME (Mantua & Hare, 2002). NPGO is related to fluctuations in wind-driven upwelling and horizontal advection (Di Lorenzo et al., 2008), and low NPGO is associated with lower salinity, Chl-*a*, and nitrate levels. Low PDO_{6mo} and $NPGO_{6mo}$ were both associated with Albacore diets containing more crustacean prey in all three regions (see schematic in Figure 6). NPGO is more closely linked to conditions in the Southern and Central regions of this study (Di Lorenzo et al., 2008). Thus, it will be interesting to see if the high proportional abundance of euphausiids in the Northern region persists as the time series continues and NPGO values increase from the extreme low values observed in 2018 and 2019. While both PDO and NPGO were useful on the timescale of this study, continuation of the time series is needed to determine if their predictive power changes over time due to the changing correlations between the indices and the underlying patterns of variability they describe (Litzow et al., 2020).

SST can affect the distribution and vital rates of prey and indicates the presence of different water masses (Keister et al., 2011). SST_{6mo} was the most important predictor at low PDO_{6mo}. At high SST_{6mo} in the Southern region (node 2), amphipods were the most important prey. Albacore reliance on amphipods is likely linked to a reduced availability of preferred prey. Diets were more generalized at cooler SST_{6mo} in all three regions (node 1), but contained more euphausiids, which have a higher energy density than amphipods (Davis et al., 1998). The reduced importance of squid at higher SST_{6mo} (node 2) may be linked to higher growth rates (Bigelow, 1994; Forsythe, 2004) that could allow squid to outgrow the small, immature size ranges targeted by Albacore.

Low values of BEUTI, the index of upwelling-driven nitrate flux, were associated with consumption of Anchovy with the highest degree of specialization observed. Adult Anchovy are typically associated with strong upwelling conditions that support larger zooplankton prey (van der Lingen et al., 2006). The smaller YOY Anchovy consumed by Albacore have smaller gill-raker gaps than fully grown adults (King & Macleod, 1976), which may have allowed them to utilize the smaller zooplankton that predominate during weaker upwelling. Note, however, that Anchovy were still important under some moderate/high BEUTI conditions. The relationships with environmental forcing mechanisms are complex and require further study.

4.3 | Important prey characteristics and relationships to foraging behavior

Albacore prey exhibit a diverse range of behaviors, life history traits, and habitat preferences that can influence Albacore foraging success and energetics. Across studies, CPS are reported to be the preferred prey. CPS form schools in epipelagic surface waters, at times in multi-species schools (Crone et al., 2019; Glaser et al., 2015; Kaltenberg & Benoit-Bird, 2009; Macewicz & Abramenkoff, 1993; Robinson et al., 1995). Similarly, *E. pacifica*, the most frequently identified species of euphausiid, has been documented to form dense daytime surface swarms (Endo, 1984). Schooling prey may be easier to detect (Ioannou & Krause, 2008). Note that all taxa that had a %PS > 50 (Anchovy, euphausiids, amphipods, Pacific Chub Mackerel, Myctophids, Sardine, and Berryteuthis squids) and known to school or swarm (Crone et al., 2019; Endo, 1984; Glaser et al., 2015; Goetsch et al., 2018; Kaltenberg & Benoit-Bird, 2009). Amphipods that occur across the water column are dispersed in lower density swarms than euphausiids, reducing the number potentially consumed at once (consistent with the generally lower %PS of amphipods; Figure 5). The fishes, squids, and crustaceans typically associated with the mesopelagic zone (Catul et al., 2011; Davison et al., 2015; Roper & Young, 1975; Stevenson et al., 2009; Watanabe et al., 2006; Yamada et al., 2004) observed in this and other studies require deeper dives to access. For juvenile Albacore, which spend most of the night and some of the day in the mixed layer (Childers et al., 2011; Snyder et al., 2017), increased dive depth may increase the energetic costs of foraging by requiring Albacore to cover a greater vertical distance (Aoki et al., 2017; Muhling et al., 2022) and possibly increasing thermoregulatory burdens in colder water (Blank et al., 2007), although heating costs may be reduced by taking advantage of thermal fronts (Snyder et al., 2017). Based on their size, most rockfishes identified in Albacore stomachs would have been encountered in epipelagic or midwater zones (Moser & Boehlert, 1991; PFMC, 2020b) before settling into benthic habitats, although the few larger individuals may indicate near-bottom feeding. Similar to previous studies, results indicate that Albacore forage across the water column, likely targeting deeper waters and diverse prey when CPS are not available.

Albacore primarily prey on smaller YOY or juvenile fishes and squids both regionally (Bernard et al., 1985; Glaser, 2010; Hart et al., 1948; Iversen, 1962; McHugh, 1952; Pinkas et al., 1971) and globally (Glaser, 2010; Goñi et al., 2011; Romanov et al., 2020; Watanabe et al., 2004). Albacore can consume larger fishes, for example, the adult-sized Anchovy and Sardine used as bait and the 27 cm Saury in the present study, as well as a large Longnose Lancetfish (*Alepisaurus ferox*) measuring 44 cm consumed in the Indian Ocean by a 100-cm (FL) Albacore (Romanov et al., 2020). Thus, while capable of eating larger fishes, Albacore tend not to.

There are a number of implications to targeting small YOY fishes and squids. Juvenile schooling fishes are likely easier to catch in higher numbers than their faster adult stages. Lower swimming speeds may also make juveniles more likely to be concentrated in frontal regions targeted by Albacore (Snyder et al., 2017). The age of prey consumed also impacts trophic level. Unfortunately, detailed diet compositions are lacking for larval and juvenile stages (Robert et al., 2014). From an ecosystem management perspective, removal of pre-recruits by Albacore could impact recruitment biomass the following year but would have a smaller impact on the total population size than if Albacore foraged directly on adults (Glaser, 2011).

The energy gained from feeding depends on the energy density of the prey. Anchovy and Saury are both high energy density schooling fishes, which increases their value as prey (Glaser, 2010). The energy density of squids is generally lower than fishes (Glaser, 2010), and they may require more energy to digest (Whitlock et al., 2013). Consequently, sustained reliance on squids rather than fishes would result in either increased consumption rates or reduced energy available for functions such as growth. The size and energy density of crustaceans is also low, and consequently, their overall contribution to caloric requirements will be lower than indicated by prey number (Glaser, 2010).

Overall, there is limited overlap between species that are important in the diets of Albacore and those that are the targets of high-value fisheries in the CCLME. The fishery for the most important Albacore prey, Anchovy, is relatively low in value with a mean revenue of $1.3 million from 2009 to 2018 (PFMC, 2020a). For comparison, Market Squid support the highest value fishery for CPS, with a mean annual value of $63 million from 2009 to 2018 but only represent 1% of Albacore diet. If this pattern persists, the direct impact to Albacore of prey removals by fisheries will likely be limited.

4.4 | Availability to fishers

Albacore forage on species inhabiting epipelagic to mesopelagic depths and potentially on some prey near the seafloor (see the above discussion of rockfish size). The depths at which Albacore and other highly migratory species forage will impact their vulnerability to different types of fishing gear. When foraging on CPS, Albacore are expected to be in near-surface waters and accessible to surface gear, such as the troll and pole-and-line gears used by the west coast Albacore fleet. In contrast, while targeting species like mesopelagic squids and Myctophids, they spend limited time in surface waters between dives (Childers et al., 2011; Snyder et al., 2017) and are less vulnerable to surface gear. For example, in 1970, the surface fleet off Oregon had high catch rates when Albacore were feeding on Saury, but only deeper gear was successful when they switched to Ragfish (*Icosteus aenigmaticus*) and rockfish (Pearcy, 1973). Recreational fishers targeting Bluefin Tuna (*T. orientalis*) in the Southern CCLME also reported an increase in catchability during 2008–2016 as Bluefin switched from mesopelagic species to targeting CPS in surface waters (Portner et al., 2022).

Understanding of the forcing mechanisms related to shifts in forage composition and associated habitat can thus provide fishers and resource managers with insight into the vulnerability of target species to surface gear. Based on the CART analyses, PDO_{6mo}, SST_{6mo}, and $NPGO_{6mo}$ could potentially be used to predict shifts in Albacore availability to fishers. The finding that these conditions occur early in the

year provides the fishers an opportunity to plan ahead. Based on our findings, Albacore may be more likely to forage in surface waters and be more vulnerable to surface gear in years with moderate/high PDO_{6mo} and/or $NPGO_{6mo}$. However, given the high variability in diets observed in this study, additional work is required to determine the consistency of this pattern.

Shifts between regions also affect the availability of Albacore to fishers. In the 1970s, the commercial fishing fleet was based primarily out of Southern California, and prior to 2012, Albacore were a popular target of recreational fishers in this region (Frawley et al., 2021). We did not observe a clear dietary shift that would explain the disappearance of Albacore from the Southern region although fishes became less dominant in the diet than reported in previous studies. Species distribution models predict less suitable Albacore habitat in the CCLME in 2012 and 2015 than in 2004 and less reliably suitable habitat off of California and Baja California than in the Northern region (Muhling et al., 2019). Distributional shifts in Albacore have been observed previously, with periods of 25–30 years centered offshore of California followed by 15–20 years offshore of Oregon, Washington, and British Columbia potentially related to changing oceanographic conditions (Clark et al., 1975; Clemens & Craig, 1965). Based on historic trends, it is possible that Albacore will reestablish a more southerly distribution in the future.

4.5 | Caveats and limitations

While this study provides the longest time series for juvenile Albacore diets in the CCLME, there are several limitations to consider. Albacore were collected opportunistically, limiting sampling in some years. The method of grouping or omitting rare prey reduces taxonomic resolution but is a common practice to increase statistical power (Duffy et al., 2017; Glaser, 2010; Glaser et al., 2015), and grouping or omitting prey that contribute less than 1% of the total prey is recommended when using CART analysis to increase tree stability (Kuhnert et al., 2012). Taxonomic resolution is already limited by the inability to identify some prey to the species level. In addition, our samples were collected primarily from the Northern region. Thus, while we know there are significant regional differences, our findings are dominated by Northern samples. These factors will likely result in an incomplete description of the full diet complexity.

Due to the lack of fresh prey, it was not possible to directly measure weights. When comparing the results here to previous research, our use of $\%n_{mean}$ instead of a metric that includes weight (measured or reconstituted) or energetic contribution will likely overemphasize euphausiids and amphipods that are abundant but small. The use of a mean proportion averaged across stomachs may mitigate this difference, because, for example, euphausiids occur in high numbers in a moderate percentage of stomachs. Given that almost no Albacore in this study had fresh prey, access to a larger sample size would not likely improve efforts. In addition, prey number was directly measured and reflects encounter rates providing insight into foraging ecology. Estimating proportion by weight or energetic value would provide additional insight into predator removals and the relative energetic contributions of different prey types and is the subject of further study. Conversions into reconstituted weight require careful application of length, weight, and energetic equations from the literature, which are not currently available for all of the species and life history stages represented in Albacore diets. In addition, we only have length measurements from a subset of species and years, and some important prey species (e.g., sardine [Enciso-Enciso et al., 2022]) can show high variability in length–weight relationships.

5 | CONCLUSIONS

The relatively long time series we present provided the opportunity to characterize the diets of juvenile Albacore tuna in the CCLME and investigate variability across time, space, and environmental conditions. Similar to previous research, our results show that YOY schooling fishes are a dominant prey with Anchovy being the most important over the course of this study. From the perspective of EBFM, our results provide quantitative links between Albacore and their prey and reveal limited overlap between Albacore diets and species that support high-value fisheries. We demonstrate a higher flexibility both in forage type and foraging behavior of Albacore over relatively short temporal and spatial scales than previously reported. While diets were not examined relative to indices of abundance for forage species, this variability in diet is likely linked to prey availability, with energy-dense schooling fishes their preferred prey. The link between diet and prey availability is consistent with the finding that conditions associated with CPS recruitment are important in predicting diet. The fact that conditions early in the year were associated with shifts between crustacean and fish dominated diets suggests the potential for forecasting forage, the composition and abundance of which in turn will influence availability of Albacore to fishers.

AUTHOR CONTRIBUTIONS

Concept and design: Catherine F. Nickels, Owyn Snodgrass, Heidi Dewar, Barbara Muhling. *Data acquisition*: Catherine F. Nickels, Owyn Snodgrass. *Data analysis and interpretation*: Catherine F. Nickels, Elan J. Portner, Heidi Dewar. All authors contributed to the manuscript and approved the final version.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study contain confidential information provided by commercial fishery partners. The non-confidential portions are provided in the supplementary material of this article.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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