Characterizing the diet of Atlantic bluefin tuna Thunnus thynnus across its spatial range: a metadata analysis spanning over three decades

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ABSTRACT: Atlantic bluefin tuna *Thunnus thynnus* (ABFT) are highly migratory predators that feed across diverse foraging habitats throughout their range. ABFT diet has been characterized regionally, but a broader analysis is needed to help inform ecosystem-based management of these economically and ecologically important predators, given their environmental and spatial plasticity. We conducted a metadata analysis using assembled diet data from 1985–2020 (n = 4997 total stomachs; 4046 non-empty stomachs) for ABFT (6–328 cm straight fork length, SFL) from 9 Longhurst Provinces (LPs). ABFT trophic ecology was characterized by exploring relationships between (1) diet composition (using classification trees), (2) total stomach content weight (using generalized additive models), and (3) predator–prey size (using ordinary least squares and quantile regression) and spatial, temporal, biological, and environmental variables. Diet composition primarily differed by sampling year, LP, and ABFT SFL. Diet over the Northwest Atlantic shelf was distinct due to the prevalence of Clupeidae. Temporal splits in this region were based on consumption of Ammodytidae and Ommastrephidae in the earliest and latest years of our data set, respectively. Diet composition for the other LPs primarily differed based on SFL, with smaller ABFT (<79 cm) mainly consuming engraulids and larger ABFT (>79 cm) consuming ommastrephids and paralepidids. Total stomach content weight and prey length increased asymptotically with ABFT SFL and varied in relation to environmental, sampling, and spatial variables. Quantifying diet composition by space and ontogeny is useful for developing improved food web models to better understand ecosystem effects of fisheries. Our metadata analysis also highlights future research priorities.

KEY WORDS: Diet · Food web · Classification and regression tree · Foraging · Scombridae

1. INTRODUCTION

Atlantic bluefin tuna *Thunnus thynnus* (ABFT) are highly migratory predators with foraging habitats throughout the North Atlantic Ocean, Gulf of Mexico, and Mediterranean Sea (Mather et al. 1995, Fromentin & Powers 2005, Olson et al. 2016). ABFT undergo trans-Atlantic migrations as early as their first few years of life (Mather et al. 1995, Rooker et al. 2007). Adults seasonally make north–south migrations between productive high-latitude foraging habitats and temperate spawning grounds and can make vertical descents to

depths over 1000 m in open-ocean habitats (Block et al. 2001, Teo et al. 2007, Walli et al. 2009). Thus, individuals can exploit shelf to open-ocean and epi- to mesopelagic foraging habitats at an ocean-basin scale during their lifetimes. Similar to other temperate tunas, ABFT are energy speculators (Brill 1996) that invest energy to undertake extensive migrations in pursuit of patches of dense aggregations of prey resources separated by large areas of less productive foraging habitats. In some cases, ABFT forage in upwelling areas that provide access to mesopelagic food resources at shallower depths, thus reducing the energy needed to carry out large vertical movements to encounter prey (Battaglia et al. 2013, 2022). Foraging hotspots have been identified as shelf waters in the Mid-Atlantic Bight, Northwest and Northeast Atlantic, as well as open-ocean waters of the western and eastern central Atlantic Ocean and Mediterranean Sea (Chase 2002, Sinopoli et al. 2004, Walli et al. 2009, Butler et al. 2010, Logan et al. 2011, de la Serna et al. 2012, Pleizier et al. 2012, Battaglia et al. 2013, Olafsdottir et al. 2016). Visceral cavity endothermy in ABFT facilitates rapid digestion of prey in these hotspots (Carey et al. 1984, Walli 2007). Behavioral and physiological specializations that increase locomotory performance (Gleiss et al. 2019, Harding et al. 2021) further enhance foraging capacity.

Smaller ABFT have been reported to forage mainly on crustaceans and small schooling fishes in shelf waters of both the eastern and western Atlantic (Logan et al. 2011), while larger ABFT target lipid-rich schooling fishes in these shelf waters as well as cephalopods and mesopelagic fishes in open-ocean habitats (Chase 2002, Butler et al. 2010, Olafsdottir et al. 2016). ABFT tend to feed on an increasingly broad spectrum of prey sizes through ontogeny, including smaller lower trophic level fishes and invertebrates and larger predatory fishes (Logan et al. 2015). For any given region, ABFT diet tends to be dominated by a few species (e.g. Ortiz de Zárate & Cort 1986, Eggleston & Bochenek 1990, Chase 2002, Varela et al. 2022). Many of these important prey species have been documented in ABFT diet both historically and in recent decades. Sand lance *Ammodytes* spp., Atlantic herring *Clupea harengus*, Atlantic menhaden *Brevoortia tyrannus*, and Atlantic mackerel *Scomber scombrus* are primary prey in the Northwest Atlantic (Dragovich 1970, Barr 1991, Chase 2002, Butler et al. 2010, Logan et al. 2011, 2015, Pleizier et al. 2012, Varela et al. 2020). In the Northeast Atlantic and Mediterranean Sea, anchovies *Engraulis encrasicolus*, sardines *Sardina pilchardus*, and euphausiids *Meganyctiphanes norvegica* are the documented essential prey bases (Oren et al. 1959, Ortiz de Zárate & Cort 1986, Sanz Brau 1990, Orsi Relini et al. 1995, Ciavaglia 2011, Logan et al. 2011, de la Serna et al. 2012, Varela et al. 2014) in addition to cephalopods and mesopelagic fishes (Karakulak et al. 2009, Battaglia et al. 2013, 2022). In open-ocean habitats in the central Atlantic Ocean, ommastrephid squids are primary prey (Matthews et al. 1977, Olafsdottir et al. 2016) in addition to pomfrets (Bramidae) (Matthews et al. 1977) and barracudinas (Paralepididae)

(Olafsdottir et al. 2016). In contrast, the diet of ABFT in more oligotrophic waters of the Caribbean Sea and Gulf of Mexico has consisted mainly of low-energy prey like tunicates (Pyrosomatidae, Salpidae) and small tropical and temperate fishes (e.g. flying gurnards [Dactylopteridae] and porcupinefish [Diodontidae]) (Krumholz 1959, Dragovich 1970, Butler et al. 2015).

Changes in ABFT condition and seasonal distribution on foraging grounds have been documented in recent decades (Golet et al. 2007, 2013, Erauskin-Extramiana et al. 2019). Declines in condition and shifts in distribution have been reported in shelf foraging grounds in the Northwest Atlantic (Golet et al. 2007, 2013) where Atlantic herring have historically been the primary prey base (Chase 2002, Logan et al. 2015). In the Northeast Atlantic, ABFT have recently returned to historical North Sea foraging grounds (Aarestrup et al. 2022) where garfish *Belone belone* and Atlantic mackerel are important prey (Langert 2022). A similar return may be occurring in the Black Sea (Di Natale et al. 2019) where ABFT trophic ecology has shifted historically (Andrews et al. 2023). More broadly, recent returns to historical northern foraging grounds and expansion to new northern habitats represent the spatial and temporal plasticity of foraging habitat that is likely influenced by a complex interaction between biological and environmental factors (Horton et al. 2021, Jansen et al. 2021). Temperature preferences suggest future changes in ABFT spawning and foraging regions with climate change (Erauskin-Extramiana et al. 2019, Trueman et al. 2023). Changes in the species composition (Olson et al. 2014), abundance (Polovina 1996), and size distribution (Golet et al. 2015) of available prey bases that may occur with ocean warming or other drivers have the potential to alter the location and relative energetic value of foraging habitats throughout the North Atlantic Ocean and Mediterranean Sea. These changes in foraging habitat and diet composition have potential economic and ecological ramifications. Reductions in prey quality or abundance could negatively impact ABFT energetics and reproductive potential (Chapman et al. 2011), while spatial changes in foraging habitat could impact availability to different fishing fleets targeting this highly migratory species (Muhling et al. 2017, Erauskin-Extramiana et al. 2019).

While multiple disparate studies of regional ABFT diet have been conducted to date (Olson et al. 2016), a comprehensive and synthetic evaluation across the entirety of their geographic distribution and habitats has not yet been undertaken. Understanding the importance of underlying prey bases that support this highly migratory predator throughout its range will help inform how potential changes in trophic dynamics may affect ABFT population dynamics in the face of climate change, as well as with other natural and anthropogenic changes.

To meet these challenges, our objectives were to (1) synthesize a time series (1985–2020) of available ABFT diet data sets across the measured ABFT size range (6–328 cm straight fork length, SFL) and spatial extent (9 Longhurst Provinces, LPs; Fig. 1) along with compilation of associated environmental data; (2) explore and visualize broad-scale relationships of spatial, temporal, biological, and environmental predictor variables to ABFT diet composition using classification and regression tree (CART) analysis; and (3) develop a more comprehensive understanding of ABFT trophic ecology using fine-scale analyses of total ABFT stomach content weight and relationships of predator–prey size across these same variables using generalized additive models (GAMs) and regression analyses.

2. MATERIALS AND METHODS

All data analyses were performed in R (R Core Team 2022). R code for individual analyses is available on request.

2.1. Synthesis of diet data

Nine regional ABFT stomach content data sets from the North Atlantic Ocean (n = 4997 total stomach samples; n = 4046 non-empty stomachs) were assembled into a standardized database (Table 1). Diet items were binned to the family level of classification and organized by prey wet weight (Table S1 in the Supplement at www.XXXXXXXXXXXXXXXXXXXXX), indicating the bioenergetic importance of prey (Chipps & Garvey 2007). When available, prey length data were organized into a separate database that was summarized at the species and family level (Tables S2 & S3). Data collected for each ABFT sampled (in both databases) included collection date, location, ABFT length, and gear type. All ABFT lengths were converted to SFL (±1 cm) using available conversion equations (Baglin 1980, Murray-Brown et al. 2007, Rodriguez-Marin et al. 2015). Locations (latitude and longitude coordinates) were assigned to corresponding LPs (Longhurst 1998). The mean proportion by weight (MW%) for each prey family to ABFT diet was calculated as:

$$MW_i = \frac{1}{P}\sum_{j=1}^{P}\left(\frac{\mathrm{W_{ij}}}{\sum_{\mathrm{i=1}}^{\mathrm{Q}}\mathrm{W_{ij}}}\right) \quad (1)$$

with symbols representing individual prey item (*i*), ABFT (*j*), number of non-empty ABFT stomachs (*P*), number of food types (*Q*), and weight of prey type *i* from ABFT individual *j* (W_{ij}) (Chipps & Garvey 2007).

Sample size adequacy was assessed through the generation of cumulative prey curves for each LP using the 'iNEXT' package version 3.0.1 (Hsieh et al. 2016) in R (R Core Team 2022).

Prey curves were generated based on prey identified to the family level for all LPs except the Gulf Stream (GFST) LP, which only included a single sample. For each LP, data were further sub-divided by size class based on splits identified in the CART analysis (see Section 2.2): 171 cm SFL for the Northwest Atlantic shelves (NWCS) LP and 79 cm SFL for all other LPs (Fig. 2). Estimates of the number of prey families (±95% confidence intervals) were generated up to the actual sample size for each data set and also extrapolated to at least double the sample size to further assess how diet characterization might change with increased sampling (Chao et al. 2014).

Remote sensing environmental data were extracted and co-located for ABFT samples where location and ABFT collection date aligned with available satellite data. Sea surface temperature (SST) as a daily optimum interpolation (https://coastwatch.pfeg.noaa.gov/erddap/griddap/ncdcOisst2Agg_LonPM180.html), monthly chlorophyll *a* (chl *a*; https://coastwatch.pfeg.noaa.gov/erddap/griddap/erdMH1chlamday.html), and sea surface height data (sea surface absolute dynamic topography [ADT] and sea surface height anomaly [SLA]; https://www.aviso.altimetry.fr/en/data/products/sea-surface-height-products/global.html) were downloaded for potential use in our CART and GAM analyses. Extracted values correspond to a point in the satellite latitude–longitude grid that is closest in proximity to the recorded position and date recorded for each ABFT stomach sample.

2.2. Exploration of diet composition: CART analysis

Classification trees are a useful, non-parametric visual tool for exploring broad-scale relationships of predictor variables to diet composition (e.g. Kuhnert et al. 2012, Olson et al. 2014, Duffy et al. 2017) that may be used to guide more fine-scale analyses based on variables forming important branches (Duffy et al. 2015, Fuller et al. 2021). The CART method can deal with non-linearity, missing data, and high-order interactions between response and explanatory variables (De'ath & Fabricius 2000, Zuur et al. 2007). Trees are both exploratory and predictive, can be applied to varying size data sets, and are not restricted to a minimum sample size (Kuhnert et al. 2012). As such, CART analysis is an appropriate method for exploring complex prey composition data that have potential relationships with different types of explanatory variables (Kuhnert et al. 2012). The CART approach developed by Breiman et al. (1984) and modified by Kuhnert et al. (2012) was used to accommodate proportional prey composition data. A total of 3105 individual ABFT were included in the analysis to explore the effect of ontogenetic, spatial, temporal, and environmental variables on diet composition. Generally, tunas are considered opportunistic predators, with high taxonomic diversity in their diets (i.e. stomach content analysis often results in a long list of prey taxa) with low abundances of each type of prey

(Olson et al. 2016). To focus on the most important prey taxa based on weight contributions, and because this high diversity can overcomplicate the visual nature of classification trees, rare prey (i.e. those contributing <1% weight to the overall diet weight) were excluded from the analysis. Complementary to this, unidentified prey and coarse taxonomic groupings (e.g. unidentified teleosts, crustaceans, cephalopods, and miscellaneous contents) were also omitted from the analysis. These coarse groupings are not informative for determining diet preferences, food web linkages, or pathways of energy flow in pelagic ecosystems, an essential component to understanding ecosystem structure (Olson et al. 2014). Data from LPs with low sample sizes that did not adequately reflect regional diet (Fig. 3; GFST, Atlantic Arctic [ARCT], and Caribbean [CARB]) were also excluded. Therefore, the number of stomachs included in the CART analysis (n = 3105) is less than the total number of non-empty stomachs assembled for our analyses (n = 4046). Fourteen prey families were included in the CART analysis: 1 cephalopod: Ommastrephidae (C-Omm); 3 crustaceans: Euphausiidae (Cr-Eup), Polybiidae (Cr-Pol), Sergestidae (Cr-Ser); and 10 fishes: Ammodytidae (F-Amm), Carangidae (F-Car), Clupeidae (F-Clu), Engraulidae (F-Eng), Gadidae (F-Gad), Myctophidae (F-Myc), Paralepididae (F-Par), Scombridae (F-Scom), Sparidae (F-Spa), and Stomiidae (F-Sto). These prey families represented 79% of the total stomach content weight included in the database.

The revised CART approach applied to diet data is fully described by Kuhnert et al. (2012) with additional information described in several subsequent diet studies (e.g. Olson et al. 2014, Duffy et al. 2015, 2017, Van Noord et al. 2016, Fuller et al. 2021, Portner et al. 2022, Nickels et al. 2023). Key steps to this method as applied to ABFT are briefly described here. The analysis was implemented with the 'rpart' package version 4.1-18 (Therneau et al. 2013) in R (R Core Team 2022). Predictor variables included ABFT length (SFL), LP, year, and environmental variables (SST [°C], chl *a* [mg m^{-3}], ADT [m], and SLA [m]). Gear type was included in preliminary CART analyses for this study but was not included in the final model (Fig. 2) due to its low variable importance and identical main splits to those in the final model. Data were recursively partitioned on these predictor variables to form smaller homogeneous groups of diet composition at each node of the tree using an error criterion, and the Gini index (Breiman et al. 1984, Kuhnert et al. 2012). This index represents a diversity (*D*) measure—based on the number of prey taxa and their relative contribution to the overall diet—and ranges from 0–1, where 0 indicates no diversity in the diet composition and 1 indicates a highly diverse diet. The tree was pruned using 10-fold cross-validation and the '1 SE' rule to identify a parsimonious tree within 1 SE of the tree yielding the minimum error (Breiman et al. 1984). The length of the tree branches provides a relative indication of the importance of the split, with the longest branches representing the most important splits. Variable importance rankings were also calculated as a goodness of split

from predictor variables forming primary and surrogate splits (Breiman et al. 1984) and highlighted the importance of each predictor variable included in the analysis. Bootstrapping, using 500 trees generated from bootstrap samples of the data, was implemented to account for uncertainty in bagged predictions of diet compositions for each node in the tree (Kuhnert et al. 2012).

2.3. Exploration of stomach content weight

Total stomach content weight and related measures of stomach fullness can provide indicators of food intake and foraging success (e.g. Bachiller et al. 2013, Olson et al. 2016, Smircich et al. 2017, Funk et al. 2021). Therefore, a GAM approach (using the 'mgcv' package version 1.9-1 in R, Wood 2011) was applied to a subset of non-empty stomachs due to limited availability of biological and environmental data and adequate sample sizes (n = 2540) The ARCT, CARB, and GFST LPs were excluded due to small sample sizes (Table 1) and incomplete characterization of regional ABFT diet (Fig. 3). Empty stomachs were excluded because of the prevalence of regurgitation during capture (Chase 2002), the absence of data on predictor variables for many empty stomachs, and unknown total frequencies of empty stomachs for some individual data sets. Instead, the percent of empty stomachs was calculated using LP and gear type for a subset of data sets with available empty stomach data.

A correlation matrix was generated for the suite of predictor variables to test for strong correlations. The environmental variables SLA and ADT had a high correlation (0.68), similar to the 0.70 cutoff frequently used in GAM analyses (e.g. Nichols et al. 2022). As a result, separate models were run for each of these variables, with Akaike's information criterion corrected for small sample size (AIC_c) used to determine inclusion in the final model. SLA is calculated as the difference between satellite-derived sea surface height and a mean sea surface height calculation. ADT is equivalent to SLA combined with mean dynamic topography (Zhang et al. 2020, Lacey 2023), and therefore a high degree of correlation is expected. Variables included for consideration in the GAM were year, SFL, ADT, SST, chl *a*, LP, and gear type. Gear type was included to account for the potential influence of collection method on stomach content weight (Bertrand et al. 2002). A gamma distribution with a log link was used based on visual examination of Q-Q plots and residual variation vs. fitted values. The 'select = TRUE' function in 'mgcv' was used to select parameters for inclusion in the best model. This function allows effect values to be set to zero if unrelated to the response variable and provides a means of evaluating all predictor variables considered as a single model rather than compared to a variety of iterations of variable combinations (Marra & Wood 2011). Additional candidate models excluding individual categorical variables were also run to assess variable importance with the final

311 'best' model selected based on the lowest AIC_c value. Restricted maximum likelihood
312 ('method=REML' in 'mgcv') was used to estimate model coefficients.

313 Stomach content total weight and ABFT length were further compared through quantile
314 regression using the 'quantreg' package version 5.97 (Koenker 2011) in R. Quantile
315 regressions were performed on the 1st, 50th, and 99th percentiles to test for patterns in
316 minimum, median, and maximum stomach content weights in relation to ABFT size.

317 **2.4. Exploration of predator–prey size relationships**

318 Prey size is an important factor in fish feeding (Juanes 1994). Fish may feed indiscriminately
319 on the most abundant prey in their environment or they may feed selectively on certain
320 species and sizes from among those available, depending on different factors that
321 contribute to selection (Werner & Hall 1974, Greene 1986, Sih & Moore 1990, Juanes 1994).
322 Samples from a subset of the primary data set that included prey length measurements
323 were compiled (n = 1541 ABFT stomachs, 20405 diet items) to assess factors influencing
324 ABFT–prey size relationships. Lengths were derived directly from whole prey organisms or
325 estimated using reconstruction equations from morphological measurements of body
326 parts (e.g. cephalopod beaks) found in the diets (Smale et al. 1993, Lu & Ickeringill 2002,
327 Xavier & Cherel 2009, Açik & Salman 2010, Petrić et al. 2010, Staudinger et al. 2013, Jereb
328 et al. 2015, Kousteni et al. 2018, Foskolos et al. 2020). Data were checked for consistent
329 units and outliers by plotting points and visually examining their distribution and alignment
330 with prey size ranges.

331 Predator–prey size relationships were assessed using quantile regression. This approach is
332 commonly used to characterize fish predator–prey size dynamics (Scharf et al. 2000,
333 Chipps & Garvey 2007) as quantile regression is well suited for evaluating patterns in the
334 lower and upper bounds of predator–prey scatterplots (Scharf et al. 1998) with previous
335 applications to ABFT (Logan et al. 2015, Olafsdottir et al. 2016) and other large pelagic fish
336 predators (Ménard et al. 2006, Young et al. 2010, Logan et al. 2013, Duffy et al. 2015).
337 Quantile regression is also useful for examining predator–prey length relationships as,
338 unlike ordinary least squares regression, it is not affected by violations of assumptions of
339 normality or constant variance (Croxford 2016, Huang et al. 2017). Separate analyses were
340 performed for the full prey length database (n = 20405 prey) as well as for the 3 main prey
341 groups: teleosts (n = 14357 prey), cephalopods (n = 5507 prey), and crustaceans (n = 502
342 prey). Prey were grouped more coarsely for regression and GAM analyses than for the CART
343 analysis due to limited prey length sample sizes at the family level. Separate analyses were
344 also performed for data from the NWCS LP and all remaining LPs following CART results
345 identifying this spatial split in ABFT diet (Fig. 2). For quantile regression, patterns in
346 minimum (min) and maximum (max) predator and prey lengths were compared with the 1st

and 99th quantiles for data sets with n > 1000 (i.e. all prey, teleosts, and cephalopods), while more conservative (5th and 95th) quantiles were selected for the crustacean data set due to a smaller sample size (200 ≤ n < 1000) (Scharf et al. 1998). Results were visualized as scatterplots, and summary statistics of mean, minimum, maximum, and standard deviation (SD) were generated at the level of major taxonomic group, family, and species.

Prey size dynamics were further explored using GAMs with the same environmental, spatial, and biological variables included for consideration in the stomach weight analysis and an additional categorical prey type variable. Prey type categories using GAMs consisted of teleosts, elasmobranchs, cephalopods, crustaceans, and miscellaneous prey. Broader categories were used relative to the CART analysis for prey characterization due to limited prey length sample sizes at the family level. Similar to the GAMs for prey weight, samples were excluded from LPs with limited sample size (i.e. CARB for predator–prey length data set, as GFST and ARCT LPs lacked prey length data). Stomach sample identification number was included as a random effect to account for multiple prey lengths collected from the same individual stomach samples. The 'select = TRUE' function in 'mgcv' was used to select parameters for inclusion in the best model. A gamma distribution with a log link was used for the predator–prey GAM analysis.

3. RESULTS

3.1. General diet characterization across LPs

The full data set included 148 unique prey families (Table S1) across 9 LPs sampled between 1985 and 2020 (Table 1). Most of the stomach samples were from the NWCS (37.7%), Mediterranean Sea (MEDI, 35.3%), Canary Current coast (CNRY, 13.3%), and Atlantic sub-Arctic (SARC, 10.0%) LPs (all LPs defined in Table 1). ABFT size ranged from 6 to 328 cm SFL (Table 1). Of the 148 prey families, 14 (10 teleosts, 3 crustaceans, 1 cephalopod) accounted for >1% MW of the total data set and were included in the CART analysis (Table 2). The majority (>60% MW) of ABFT diet was represented by these prey families for the ARCT, CNRY, MEDI, North Atlantic Drift (NADR), and NWCS LPs. Stomach content weight from the remaining LPs consisted of other prey families or prey not identified to the family level ('Remaining contents' in Table 2; Table S1). The Northeast Atlantic Subtropical Gyre (NASE) and SARC regions included 25 and 37% MW, respectively, of the 14 represented families, while the GFST and CARB regions had 0 and 1% MW representation, respectively (Table 2).

Nine of the 14 prey families that comprised >1 MW% of the diet for the complete data set also contributed >5% MW within at least 1 LP region, while the remaining 5 prey families had a lower overall contribution to ABFT diet (Table 2). Clupeidae was the prominent prey

family in the NWCS LP (37.3% MW) and a secondary prey (10.6% MW) in the MEDI region. Engraulidae was the dominant prey family in neighboring areas of the eastern Atlantic in the CNRY (52.5% MW), NADR (22.9% MW), and MEDI (13.6% MW) LPs. Scombridae was important in northern foraging habitats and made up the largest weight in the ARCT (40.0% MW) and NASE (13.6% MW) LPs, as well as a secondary contribution (8.1% MW) to the NWCS LP. Paralepididae was the second most important prey family in the ARCT (25.1% MW) and SARC (16.9% MW) LPs. Ammodytidae was not the dominant prey family in any LP but did rank in the top 3 families by weight contribution in the ARCT (13.1% MW), NADR (19.7% MW), and NWCS (13.3% MW) LPs. Carangidae comprised the second highest weight of prey families included in the CART analysis in the neighboring CNRY (13.2% MW) and NASE (7.0% MW) LPs. Gadidae was a secondary prey in the CNRY (6.1% MW) and NADR (8.2% MW) LPs. Ommastrephidae, the most represented invertebrate family, was the primary prey (20.1% MW) in the SARC LP and a secondary prey in the NWCS (8.1% MW) and MEDI (8.6% MW) LPs. Euphausiidae only accounted for >5% MW in the NADR LP (6.7% MW), while Polybiidae, Sergestidae, and the remaining fish families (Myctophidae, Sparidae, and Stomiidae) accounted for <5% MW of diet weight in any given LP. Of these remaining families included in the CART analysis, Myctophidae, Polybiidae, Sergestidae, and Stomiidae were most abundant in MEDI samples, reflective of the high diet diversity (Fig. 4) and large sample size (Table 1) for this region. Sparidae was most abundant in the NASE LP in addition to the MEDI LP (Table 2).

Several LPs had dominant prey families that were not prevalent in other regions (Table S1). Pyrosomatidae, the dominant prey family in the CARB region (30.7% MW) as well as the co-dominant prey families of the NASE region (Macroramphosidae, 33.6% MW; and Centriscidae, 28.9% MW) were absent from all other LPs (Table S1). Because the CART analysis used a threshold of <1% weight to the overall diet to better visualize important prey, and these prey families contributed to this low threshold when the entire diet was considered, they were not included in the CART analysis. Similarly, LPs with small sample sizes were removed from the CART analysis (i.e. ARCT, CARB, GFST).

Observed diet was similar to estimated total number of prey families for most LPs, with diet represented by data set sample sizes falling within 75% of the estimated total number of prey families based on increased sample sizes (Fig. 3; Table S4). The observed number of prey families ranged from 5 to 88, while the estimated range was 5 to 110. The ARCT and CARB LPs, which had the lowest sample sizes among all LPs (n = 10 stomachs containing prey identifiable to family level), had observed numbers of prey families that were only 56 and 38% of the estimated number of prey families for the respective LPs (Fig. 3; Table S4).

3.2. CART analysis

The 1 SE classification tree (cross-validated error rate = 0.63, SE = 0.01), identified strong spatial differences in ABFT diet composition with the initial split of the tree differentiating ABFT diets in the NWCS LP (left side of the tree, n = 1176 ABFT) from the other regions sampled (right side of the tree, n = 1929 ABFT) (Fig. 2). The NWCS LP had the lowest diet diversity due to the prevalence of Clupeidae (37.3% MW; Table 2) found in the stomach contents (Fig. 5, node 2, D = 0.485), while by contrast, prey diversity was greatest in the non-NWCS LPs (Fig. 5, node 3, D = 0.77), particularly in the NADR and MEDI LPs (Fig. 4, D > 0.7). To focus on the important tree splits and to improve visualization and readability, the predictor variables forming the main splits of the tree are labeled, while those for the lower portions of the tree with short branch lengths are omitted (Fig. 2). Details, including variable names forming each split for each node of the tree, are provided in Table S5.

ABFT within the NWCS LP also showed differences in diet composition based on sampling year, SST, and SFL, although the short branch lengths indicate limited explanatory power relative to the long branch (i.e. the most important split) observed in the initial split of the tree that provided the greatest reduction in deviance (Fig. 2; Table S5). Clupeidae, the main prey family predicted in ABFT diet prior to 2017 (node 5, 60% MW) was replaced with Ommastrephidae (node 4, 46% MW) in recent years. Ammodytidae was more prevalent in ABFT diets prior to 1996 (node 10, 52% MW), while Clupeidae was the dominant prey between 1996 and 2017 (node 11, 77% MW). During this period when Clupeidae was dominant, the tree further split on ABFT length of 171 cm SFL (Table S5, node 11) with smaller ABFT mainly consuming Ammodytidae (node 22, 57% MW) and larger ABFT consuming Clupeidae (node 23, 86% MW). Ammodytidae, in general, are smaller prey than Clupeidae and had a smaller average (13.1 cm) and maximum (23.0 cm) length than Clupeidae (25.5 cm and 34.1 cm; Table S3). Subsequent splits for the pre-1996 data occurred based on SST (nodes 10 and 21) due to the dominance of Ammodytidae (node 20, 80% MW; node 42, 62% MW) and Clupeidae (node 21, 46% MW; node 43, 87% MW) in the diets (Fig. 2; Table S5).

For the non-NWCS LP data (i.e. the right side of the tree), the most important split, as indicated by long branch length, highlighted the importance of ABFT length, with fish >79 cm SFL mainly consuming Ommastrephidae and to a lesser extent Paralepididae (node 6, 23% and 14% MW, respectively; D = 0.763) and smaller ABFT consuming Engraulidae and to a lesser extent Clupeidae (node 7, 47% and 17% MW, respectively; D = 0.504) (Figs. 5 & 6). Engraulidae, in general, had a smaller average (8.9 cm) and maximum (16.0 cm) length relative to Ommastrephidae (15.2 and 49.3 cm) and Paralepididae (27.2 and 56.5 cm) (Table S3). Remaining branches based on temporal and environmental variables had short lengths and therefore lower explanatory power (Fig. 2; Table S5). For the larger ABFT size group, the SARC LP was distinguished from remaining regions based on the prevalence of

Paralepididae in the diet composition (node 12, 49% MW) and further split based on SST due to higher proportions of Ommastrephidae (node 24, 57% MW) and Paralepididae (node 25, 56% MW). Remaining regions were subsequently split on ADT (nodes 26 and 27) and length. For the smaller ABFT sizes (<79 cm SFL), further splits were based on sampling year (pre and post 2011, nodes 14 and 15, respectively), SLA (nodes 28 and 29), and LP (nodes 58 and 59), but all had short branch lengths.

Sampling year had the highest variable importance ranking (1.0), due to its appearance as a surrogate split variable for many of the tree nodes. Surrogate splits represent alternative splits with high correlation to the primary split and are used to partition when data are missing (see Kuhnert et al. 2012). LP closely followed year in variable importance (0.9), while SFL was identified as the third most important variable (0.72) (Fig. 2). The environmental variables considered in the analysis (SST, ADT, chl *a*, and SLA) were of lower importance in explaining dietary composition (rankings ≤0.5, Fig. 2).

Since ABFT SFL was identified as an important variable and because ontogenetic shifts in diet are common, the relationship between ABFT length and prey was further investigated using partial dependence plots (Fig. 7). An increase in proportions of Ommastrephidae and decrease in proportions of Engraulidae were noted as ABFT size increased. For other prey (e.g. Clupeidae, Ammodytidae), the bootstrapped 95% confidence band around the prediction was large (Fig. 7).

3.3. Stomach weight analyses

The best model of the stomach content weight data set explained 52.6% of deviance based on 2540 stomach samples and included ABFT SFL, ADT, chl *a*, SST, LP, and gear type by GAM (Fig. 7). Year was excluded based on the 'select=TRUE' function, and the model including ADT had a lower AIC_c value than the equivalent model with SLA used as a proxy for sea level height. Stomach content weight increased linearly with ABFT length among the smallest individuals (<~50 cm SFL), but the relationship became more non-linear among larger size classes and asymptotic among fish >200 cm SFL (Fig. 8). Stomach content weight increased linearly with SST and with chl *a* concentration among lower concentrations (0–3 mg m^{-3}), but then declined and had an increasingly large confidence interval for the less common higher chl *a* concentrations. The relationship with ADT was parabolic, with highest weights observed for the most negative and most positive ADT values. Like chl *a*, the relationship was influenced by sparse data with wide confidence intervals across the most negative ADT values. Among LPs, highest values were observed in the CNRY, MEDI, NADR, and NWCS LPs after accounting for the other predictor variables. The NASE LP had the lowest stomach content weight while the SARC region had wide confidence intervals that encompassed the range of estimates for all other LPs (Fig. 8).

Stomach samples collected from harpoon and purse seine gear types had the highest stomach content weights, while longline and mid-water trawl-caught samples accounted for the lowest values (Fig. 8).

The percentage of empty stomachs varied by LP and gear type from 0 to 60% (Table S6). Among gear types, empty stomachs were most common for bait boat (19–59%) and purse seine (41–47%) samples and lowest for longline (0–15%) and harpoon (13%) samples (Table S6). Samples from rod-and-reel fisheries were more variable across regions and included low (4%; MEDI), moderate (19%; NWCS), and high (32–36%; NADR and CNRY) empty stomach representation (Table S6).

Stomach content weight had a wedge-shaped relationship with ABFT length (Fig. 9). Minimum (1st percentile), median, and maximum (99th percentile) stomach content weight all significantly increased with ABFT length (Fig. 9).

3.4. Predator–prey size analyses

The best model explained 89.6% of the deviance based on 3938 diet items and included ABFT length (cm), SST, chl *a*, gear type, and prey type by GAM (Fig. 10). Year, ADT, and SLA were excluded based on the 'select=TRUE' function. LP was removed based on AIC_c comparison. Prey length increased with ABFT length to an asymptote of approximately 200 cm SFL and remained relatively constant across larger ABFT lengths. Prey length increased linearly with SST and across the chl *a* range of 0–3 mg m^{-3}. Prey length was greatest for the elasmobranch prey group, followed by teleosts and cephalopods (Fig. 10, Table 3). Crustaceans were the smallest length group (Fig. 10, Table 3). Prey length was lowest for ABFT caught by the purse seine fishery (Fig. 10).

Prey length (all prey combined) had a wedge-shaped relationship with ABFT length (Fig. 11). Minimum (1st percentile), median, and maximum (99th percentile) prey length all significantly increased with ABFT length for the full prey data set as well as the teleost and cephalopod prey analyses. For crustaceans, median prey length significantly increased with ABFT length, but minimum and maximum prey size relationships were not significant (Fig. 11, Table 4). For the main spatial split in the CART analysis, median and maximum prey length significantly increased with ABFT length from both the NWCS LP (left side of tree) and all remaining LPs combined (right side of tree). Minimum prey length was significant for the LPs making up the right side of the tree but not for the NWCS LP (Fig. 11, Table 4). For all remaining LPs, minimum, median, and maximum prey lengths all increased significantly with ABFT length (Fig. 11, Table 4). Prey lengths ranged from <1 to >100 cm (Trichiuridae). Other large prey (>75 cm) were fishes of the families Anguillidae, Alepisauridae, Gadidae, Pomatomidae, and Squalidae. The smallest prey (<2 cm) included cephalopods of the

families Argonautidae, Histioteuthidae, and Tremoctopodidae, crustaceans of the families Cirolanidae and Sergestidae, and larval fishes (Table S3).

4. DISCUSSION

4.1. ABFT diet composition

The NWCS LP was separated from all other sampled ABFT foraging regions due to the prevalence of clupeids as the primary stomach contents throughout this region from the Mid-Atlantic Bight up through Canadian shelf waters. Clupeidae was the main prey family within this region for most of our time series (1997–2017). Complementary to our analysis, clupeids were also identified in the literature as important prey for ABFT in this region. For larger ABFT that support commercial fisheries in the western Atlantic (>185 cm curved fork length, CFL), Atlantic herring *Clupea harengus* was identified as the main clupeid prey in more northern waters off New England and Canada (Chase 2002, Pleizier et al. 2012, Logan et al. 2015, Varela et al. 2020), and ABFT distribution within this region of the NWCS has shifted in recent decades in correlation with Atlantic herring (Golet et al. 2013). Atlantic menhaden *Brevoortia tyrannus* was the equivalent clupeid prey species in winter foraging grounds off the Mid-Atlantic Bight (Butler et al. 2010). Atlantic menhaden has recently also been identified as an important prey in the Gulf of Maine coinciding with a decline in herring stocks in this region (Nadeau et al. 2025). Both species form dense schooling aggregations, have high energy density (Durbin et al. 1983, Ahrenholz 1991, Lucca & Warren 2019, Turcotte et al. 2021, Wuenschel et al. 2024) and provide similar prey bases to ABFT in these shelf foraging grounds.

Ammodytidae, represented by sand lance *Ammodytes* spp., was the dominant prey family in the NWCS prior to 1996 and among smaller ABFT. Like clupeid prey, sand lance form dense aggregations in coastal waters (Auster & Stewart 1986) and are regionally important to juvenile and adult ABFT (Eggleston & Bochenek 1990, Chase 2002, Logan et al. 2011) as high-energy prey (Wuenschel et al. 2024). Sand lance and Atlantic herring anti-cycle in abundance (Sherman et al. 1981), and this temporal pattern follows prior indices in the region (Staudinger et al. 2020). A size split at 171 cm SFL reflects the greater prevalence of sand lance in the smaller size grouping. This length split closely matches the 185 cm CFL minimum size limit for the US commercial fishery based on length conversions (Rodriguez-Marin et al. 2015). Sand lance are important prey for smaller ABFT in the NWCS region that support recreational fisheries off the Mid-Atlantic Bight (Eggleston & Bochenek 1990, Barr 1991, Logan et al. 2011) as well as New England (Logan et al. 2015).

Scombridae, primarily Atlantic mackerel *Scomber scombrus*, was also an important prey family in the NWCS LP. Atlantic mackerel has been more common in ABFT diet in the

561 northern region of the NWCS extending from New England to Canadian coastal waters
562 (Chase 2002, Pleizier et al. 2012, Varela et al. 2020, Nadeau et al. 2025). Atlantic mackerel,
563 which has a high energy density (Wuenschel et al. 2024), was identified as the primary prey
564 species for ABFT in recent years in the Gulf of St. Lawrence (Turcotte et al. 2023).

565 Concurrent with the decline in Atlantic herring spawning stock biomass (ASMFC 2022) and
566 prevalence in ABFT diet in Canadian waters (Turcotte et al. 2023), ommastrephid squids
567 replaced herring as the dominant ABFT prey off New England, as evidenced by a split at
568 year 2017. Often an important prey group for pelagic fish predators in slope and open
569 ocean habitats (Staudinger et al. 2013, Teffer et al. 2015, Olson et al. 2016, Duffy et al.
570 2017, Poland et al. 2019, Logan et al. 2021), ommastrephid squids were more abundant in
571 recent ABFT diet assessments in New England (Nadeau et al. 2025) relative to earlier
572 studies in which they had a high frequency of occurrence but lower contribution to dietary
573 weight (Chase 2002, Logan et al. 2015). While ommastrephid squid have lower individual
574 energy density than clupeid prey in the NWCS, they are still classified as moderate-quality
575 (energy density: 4–6 kJ g^{-1}) prey (Albo-Puigserver et al. 2017, Wuenschel et al. 2024). Tunas
576 can digest these lower-lipid prey more rapidly than high-quality (energy density: >6 kJ g^{-1})
577 prey like herring, mackerel, and sand lance (Olson & Boggs 1986, Wuenschel et al. 2024).
578 Thus, ABFT could potentially compensate by consuming larger quantities of squid prey
579 during their seasonal residence in productive NWCS waters.

580 Low observed diet diversity in the NWCS (Fig. 4) is consistent with the overall dominance of
581 a few species of abundant, densely aggregating prey in ABFT diet in this region (Chase
582 2002), with clupeids, ammodytids, scombrids, and ommastrephids as the main prey
583 families over the past half century. These conditions represent a 'wasp-waist' food web
584 structure in which intermediate trophic level species diversity is low relative to
585 corresponding lower and higher trophic levels (Cury et al. 2000, 2003). Similar low diet
586 diversity has been observed in other tuna species foraging in productive nearshore waters
587 in the eastern Pacific Ocean (Olson et al. 2014, Fuller et al. 2021). This food web structure
588 can create energetic hotspots of ABFT foraging where dense, high-energy prey resources
589 can be exploited efficiently by ram feeding (Higham 2011).

590 For the remaining LPs outside the NWCS region in our data set, ABFT size was an important
591 variable in forming diet composition, with ABFT smaller than approximately 79 cm SFL
592 primarily consuming engraulid prey and larger individuals consuming ommastrephid
593 squids. Engraulidae, primarily the European anchovy *Engraulis encrasicolus*, has been
594 described as an important prey species for small ABFT in the Mediterranean Sea and
595 Northeast Atlantic (Ortiz de Zárate & Cort 1986, Orsi Relini et al. 1995, Ciavaglia 2011,
596 Logan et al. 2011, Medina et al. 2015, Van Beveren et al. 2017, Varela et al. 2018, 2019). The

clupeid *Sardina pilchardus* has also been identified as an important prey for small ABFT outside of the NWCS region in this study, primarily in the Northeast Atlantic and Mediterranean Sea (de la Serna et al. 2012, Van Beveren et al. 2017, Varela et al. 2023). Like clupeids, anchovies are energy-rich schooling prey (Spitz et al. 2010). Ommastrephid squids have been reported to be particularly important to larger ABFT in open-ocean foraging habitats of the central North Atlantic (Matthews et al. 1977, Olafsdottir et al. 2016) and Mediterranean Sea (Battaglia et al. 2013, 2022) in addition to the recent documentation on the Northwest Atlantic shelf (Nadeau et al. 2025). In our data set, ommastrephids were prevalent in the SARC and MEDI LPs. Paralepidids were also important to the ABFT diet in the SARC region. Both ommastephids and paralepidids form dense aggregations in Atlantic slope waters (Gartner et al. 2008) and are moderate to high-quality prey (Glaser 2010, Spitz et al. 2010) that encompass an important forage base for these larger ABFT that inhabit the open ocean.

Overall, temporal (sampling year), spatial (LP), and ontogenetic (ABFT SFL) variables were most important in explaining differences in diet composition across the data set, with environmental variables represented by short branch lengths and therefore limited explanatory power. The importance of sampling year likely reflects the generalist foraging behavior of ABFT (Olson et al. 2016) and associated dietary shifts with temporal changes in dominant prey, similar to those observed in other studies. As described previously, the temporal splits in dominant ABFT prey in the NWCS corresponded with annual shifts in the relative abundance of these prey resources (Hendrickson & Showell 2019, Staudinger et al. 2020, Lowman et al. 2021). Similarly, a temporal split towards Engraulidae for smaller ABFT after 2011 corresponded with a recovery of the anchovy stock in the northeast Atlantic following a period of reduced spawning stock biomass (ICES 2021, Uriarte et al. 2023). ABFT fidelity to seasonal foraging grounds over multiple years has been documented (e.g. Galuardi et al. 2010, Arregui et al. 2018), providing support for repeated use of common foraging grounds and consumption of prevalent prey in these areas.

4.2. Stomach content weight

Stomach content total weight varied with ABFT size, environmental, and spatial variables. Stomach content weight is expected to increase with ABFT length due to the related increase in stomach size and capacity, but this relationship was only strong among the smaller size classes of ABFT. The relationship became asymptotic among the largest fish sampled, with essentially no relationship among ABFT >200 cm SFL. As ABFT size increased, content variability also increased, with individuals >200 cm having stomach content weights ranging from nearly empty stomachs to cases where stomachs contained >15 kg of prey. For the lower range of chl *a* values where data were more abundant, ABFT

633 stomach content weight increased, consistent with higher foraging success in more
634 productive waters. Relatedly, the parabolic relationship with ADT reflected higher content
635 weight in foraging habitats within warm and cold core eddies. ABFT catches in the longline
636 fishery were highest in anticyclonic eddies where fish and cephalopod prey tend to
637 aggregate (Hsu et al. 2015). ABFT and other pelagic predators aggregate in anticyclonic
638 eddies where mesopelagic forage are concentrated (Arostegui et al. 2022, Pagniello et al.
639 2023). ABFT in the NWCS LP had among the highest stomach content weights, indicative of
640 the importance of this area as foraging habitat for larger fish (Chase 2002, Butler et al.
641 2010, Pleizier et al. 2012, Logan et al. 2015, Varela et al. 2020, Nadeau et al. 2025). This
642 same LP was also identified in the CART analysis as a distinct foraging area (Fig. 2). The
643 CNRY and neighboring NADR LPs emerged as an important foraging habitat for smaller
644 ABFT with high stomach content weights for the smaller size class of fish most prevalent in
645 this region. The coastal waters off the Iberian Peninsula and the Bay of Biscay within the
646 CNRY LP provide extensive forage fauna for smaller ABFT (Logan et al. 2011, Varela et al.
647 2014) and are key feeding areas where juvenile ABFT recurrently visit (Arregui et al. 2018).
648 The MEDI LP was also a region of elevated stomach content weight, further supporting its
649 role as both a spawning and foraging habitat for ABFT.

650 Variation in stomach content weight among gear types indicates that this metric of feeding
651 success can be biased by the mode of capture. Higher stomach content weight among
652 ABFT captured by harpoon and purse seine fisheries may be related to the timing of
653 capture. These fish are captured while at the surface, potentially during a period following
654 intensive foraging at depth when they move to the surface layer to re-warm their entire body
655 (Lawson et al. 2010). Harpoon and purse-seine fishing gear are considered passive gears
656 from the perspective of the ABFT that are targeted (i.e. ABFT captured during non-feeding
657 periods) and differ from the active gears (e.g. bait boats, rod and reel, longline) in the
658 present analysis that largely require ABFT to be actively foraging. Tunas captured by these
659 latter gear types may have lower stomach content weights since they are actively engaged
660 in feeding during capture and so are less likely to be fully satiated (Bertrand et al. 2002).
661 Capture time-of-day data were not available for this analysis, but timing of capture may
662 have also influenced differences in stomach content weight among gear types. For
663 example, stomach fullness for ABFT captured by the rod and reel fishery in the Mid-Atlantic
664 Bight was lowest in pre-dawn hours and increased throughout the morning with peaks in
665 early afternoon (Butler et al. 2010). Similar results were observed for tropical tunas,
666 consistent with greater feeding intensity during daylight hours (Machful et al. 2024).

667 The prevalence of empty stomachs is highly variable across studies, LPs, and gear types
668 and likely influenced by the capture methods used by specific fleets. Regurgitation can
669 occur during the capture process with certain gear types (Mason 1976, Chase 2002). Purse

seine-caught ABFT had the highest proportion (78–82%) of empty stomachs among ABFT historically sampled in the western North Atlantic Ocean (Dragovich 1970, Mason 1976). Purse seine-caught fish in the western North Atlantic included in our data set also had a high percentage of empty stomachs (47%), most of which were reported to have distended stomach rugae consistent with regurgitation (Chase 2002). Mason (1976) reported direct observations of regurgitation occurring in the process of purse seine capture and concluded that it was an important source of stomach emptiness in fish sampled from this fishery. The probability that these empty stomachs were an artifact of regurgitation rather than lack of prior feeding is further supported by the fact that for remaining non-empty stomachs in our data set, purse-seine caught fish had higher stomach content weight than fish sampled from many other fisheries.

The high percentage of empty stomachs in the bait boat fishery could be influenced by the mode of capture, which involves attracting ABFT to the boat using live bait (Rodríguez-Marín et al. 2003). Stomach contents identified as bait were not considered part of the weight, and feeding on this artificial diet source prior to capture could have contributed to the higher percentage of empty stomachs from this fishery. Relatedly, rod and reel fishing methods vary within and among regions, and the higher percent of empty stomachs for rod and reel-caught fish in some LPs could be due to the prevalence of chumming with cut bait and ABFT feeding on such artificial food sources prior to capture. Empty stomachs were less common in longline caught fish in our study (0–15%), similar to the 4–16% in historical reports for the western North Atlantic (Dragovich 1970) and 16–23% reported for southern bluefin tuna *Thunnus maccoyii* caught by longline (Young et al. 2010, Itoh & Sakai 2016). For non-empty stomachs, content weight was lower for longline-caught ABFT relative to other gear types, which could be influenced by digestion occurring between when a fish is hooked and when it is later harvested and sampled (Itoh & Sakai 2016). The prevalence of empty stomachs may also be biased by individual study methods (e.g. sieve size used for content removal, preservation method, and precision of weight measurements).

4.3. Predator–prey size relationships

ABFT diet included a broader spectrum of prey sizes with ontogeny, a pattern common among fish species (Juanes 1994, 2016, Scharf et al. 2000) including tunas (Ménard et al. 2006). The morphology and mouth size of predators are determining factors in the selection of prey size and type (Keast & Webb 1966). Vulnerability of prey is strongly influenced by their size and can be expressed as the product of the probability of encounter and the susceptibility to capture, since the probability of capture of a prey decreases as its size increases, but the probability of being encountered increases (Greene 1986, Kaiser & Hughes 1993, Scharf et al. 2000). Prey length increased with ABFT length up to

approximately 200 cm SFL, with similar prey lengths among larger ABFT up to 300 cm SFL. Prey length data for ABFT >250 cm SFL were limited, and therefore additional data are needed to better understand prey size dynamics for the largest ABFT size classes. However, this pattern resembled the relationship between ABFT length and stomach content weight. This asymptote may reflect a size threshold beyond which gape size does not limit consumption of most common adult prey (Scharf et al. 2000). Among the largest prey items in our data set (>75 cm), 2 samples were from ABFT <200 cm (173 and 187 cm SFL) while the remaining prey were from ABFT >200 cm (237–283 cm SFL). The 2 large prey from ABFT <200 cm SFL were both from families with long slender body types (Trichiuridae and Anguillidae) that do not require as great a gape size for consumption as the prey from ABFT >200 cm SFL (e.g. Alepisauridae, Gadidae, Pomatomidae, Squalidae). ABFT and prey weights may be better indicators of ontogenetic limitations in maximum prey size than length comparisons, but analyses based on weights were prevented by more limited ABFT weight data and variability in prey weights with different stages of digestion. Prey width is also an important consideration (Gill 2003), but sufficient data were also unavailable for the majority of species in our analyses. While minimum prey size significantly increased with ABFT length, this relationship was largely driven by the wide size spectrum of ABFT included in our analysis (22–313 cm SFL) and the continued inclusion of small prey (<5 cm) across large ABFT body sizes (>250 cm SFL).

Prey length also varied in relation to factors other than ABFT size. The positive relationship between prey length and both SST and chl *a* is consistent with the consumption of larger prey in warm water and more productive foraging habitats. Among gear types, prey size was smallest for purse-seine caught ABFT due to the prevalence of small cephalopods in samples with available environmental data from the Mediterranean Sea. Historical diet data from purse-seine-caught ABFT from the Northwest Atlantic did not consist of smaller prey, and the observed result is likely related to the deepwater habitat (200–2300 m) within the MEDI LP from which those samples were collected (Karakulak et al. 2009) rather than the gear type used for capture. Prey length varied by prey type, with fishes (elasmobranchs and teleosts) making up the largest ABFT prey groups due to the influence of large prey families like Alepisauridae and Squalidae. Cephalopod prey items were smaller than fishes overall, although mantle length, which is the standard measurement of squid size, underestimates total prey size (Staudinger et al. 2009). Crustaceans were the smallest major prey group, due to the prevalence of small prey like Amphipoda, Euphausiidae, and swimming crabs (Polybiidae, Portunidae).

4.4. ABFT as energy speculators

ABFT, as energy speculators, have a high metabolic demand and highly migratory lifestyle that relies on encounters with and efficient processing of concentrations of energy-dense prey that are spatially and temporally patchy (Brill 1996). Our diet analysis identified key prey families in distinct geographic regions. Food webs in both western and eastern Atlantic shelf waters provided foraging hotspots dominated by a small number of prey families at any given time period. Both juveniles and adults use the NWCS as a seasonal foraging hotspot; juveniles largely remain within this region (Galuardi & Lutcavage 2012) whereas adults display complex, long-distance movements throughout the North Atlantic but display site fidelity to the NWCS across multiple years (Galuardi et al. 2010). The main fish prey families for this region identified in our analysis (e.g. Ammodytidae, Clupeidae, and Scombridae) all have high energy density (>6 kJ g^{-1}) considered representative of high-quality prey (Albo-Puigserver et al. 2017, Wuenschel et al. 2024), with Ammodytidae providing an energy-dense forage base for both juveniles and adults. A juvenile foraging hotspot in the northeast Atlantic included the Bay of Biscay and the western Mediterranean Sea, where dense aggregations of clupeid (sardine) and engraulid (anchovy) prey of moderate to high quality (Dubreuil & Petitgas 2009, Spitz et al. 2010, Albo-Puigserver et al. 2017, Gatti et al. 2018) were the main prey base. Similar to the NWCS, electronically tagged juveniles showed high site fidelity to this foraging hotspot with return visits across consecutive years (Arregui et al. 2018). Other individuals demonstrated the complexity of the energy speculator strategy through long-distance departures from this foraging hotspot to open-ocean habitats and even to the NWCS LP (Arregui et al. 2018). Open-ocean habitats also offer potential areas of concentrated mesopelagic prey, particularly in regions with anticyclonic eddy features (Arostegui et al. 2022, Pagniello et al. 2023). In our study, Ommastrephidae and Paralepididae were major prey families in open-ocean foraging habitats in the Iceland Basin (SARC LP). These families represent moderate- to high-quality prey (Glaser 2010, Spitz et al. 2010).

By contrast, ABFT seasonal aggregations in more oligotrophic, tropical waters tend towards diets of lower energy prey resources. In the western Atlantic, ABFT diet in Gulf Stream, Gulf of Mexico, and Caribbean Sea waters have included low energy prey bases such as pelagic tunicates, small *Sargassum*-associated fishes, and small pelagic crustaceans (Krumholz 1959, Dragovich 1970, Matthews et al. 1977, Butler et al. 2015). In the eastern Atlantic, ABFT seasonal diet in oligotrophic waters of the Canary Islands is mainly the snipefish *Macroramphosus* sp. (Varela et al. 2022), a low-energy fish prey (Petrovski et al. 2023). Available diet data from these regions were distinct from the remaining more northerly foraging habitats, with most contents represented by families other than the main prey families included in the CART analysis. These more tropical foraging areas appear to offer lower-quality prey but may present energetic advantages in the form of proximity to

778 spawning habitats and/or more productive summer and autumn foraging habitats.
779 Identified foraging hotspots collectively represent a patchwork of destinations for ABFT
780 energy speculators throughout the Atlantic across various depths, temperatures, and
781 oceanographic features. Beyond the available forage bases and their relative energetic
782 value, the net energetic benefits will be influenced by other factors that affect energetic
783 costs (e.g. temperature, Blank et al. 2007; vertical and horizontal movements required to
784 reach prey aggregations).

785 **4.5. Caveats and future recommendations**

786 The trophic analyses in the current study consisted of an opportunistic synthesis of
787 available diet data rather than a long-term sampling effort specifically designed to relate
788 ABFT diet to spatial, temporal, biological, and environmental data. Opportunistic sampling
789 is common in fisheries-dependent diet studies, and resulting unbalanced sampling
790 designs may contribute to an inability to detect some factors influencing ABFT diet or false
791 identification of predictor variables indicative of incomplete spatial or temporal coverage.
792 The CARB and GFST LPs, which include the primary spawning grounds for ABFT in the
793 western Atlantic (Rooker et al. 2007) and border a recently identified spawning habitat in
794 the Slope Sea (Richardson et al. 2016, Hernández et al. 2022), respectively, were
795 represented by small sample sizes of stomachs and therefore did not reflect reliable diet
796 information for these regions. Environmental data were only available for a subset of years
797 and locations, which limited the spatial and temporal scope of the trophic analyses that
798 included these remote sensing data. Given that LPs represent regions with unique
799 environmental conditions (Longhurst 1998), environmental variables included in GAM
800 analyses may have been correlated with certain LPs and influenced observed trophic
801 relationships with environmental conditions. Seasonal and spatial variability in many
802 environmental variables, both among and within LPs, further complicates efforts to link
803 diet to environmental factors. The CART analysis is best suited for characterizing general
804 patterns in ABFT trophic ecology identified by longer branches indicative of important
805 splits, while shorter branches in the tree represent greater uncertainty and reduced
806 explanation of predictor variables to diet composition. Stomach content weight can
807 provide a measure of foraging success but is sensitive to sample collection and processing
808 methods as well as to a variety of variables not considered in this study (e.g. time of
809 capture). Analyses of prey lengths observed in the stomach contents offer further insights
810 into ABFT prey preferences, but may not always reflect overall predator–prey size dynamics
811 that are also influenced by prey width and biomass.

812 As a metadata analysis consisting of several diet studies compiled from varying temporal
813 scales, many open-ocean foraging regions were not well represented in our analysis and

would benefit from future sampling for dietary and energetic analyses. For example, open-ocean waters of the Newfoundland Basin and West European Basin have recently been identified as hotspots of ABFT seasonal occupancy based on electronic tagging (Ferter et al. 2024). The Gulf Stream region was surveyed historically (Matthews et al. 1977), but modern characterizations of ABFT diet in this region are lacking. The bordering Slope Sea has recently been considered as a spawning habitat (Richardson et al. 2016); documentation of local foraging preferences would improve our understanding of ABFT ecology in this region. ABFT can spend more than 5 mo in open-ocean waters in the Gulf of Mexico (Galuardi et al. 2010), and dominant prey identified to date (Krumholz 1959, Dragovich 1970, Butler et al. 2015) are of low caloric value (Cardona et al. 2012, Diniz et al. 2013). Expanded sampling in this region (i.e. CARB LP) would help characterize the prey base supporting ABFT in this spawning habitat, although sample access is limited for this region due to the lack of a directed commercial fishery and conservation measures implemented to limit ABFT bycatch in longline fisheries (Lauretta et al. 2021). Further dietary sampling coupled with prey energy density analyses would help identify the prey bases and potential energetic value of these foraging grounds. Long-term monitoring is essential to identify temporal dietary shifts, so continued monitoring in well-established seasonal foraging hotspots like the NWCS and CNRY LPs should also continue to be prioritized. Given observed differences in foraging migrations based on sex and natal origin (Rooker et al. 2008, Nielsen et al. 2024), coupling diet characterization with classification of sex and population of origin would improve understanding of gender- and stock-specific energetics.

Stomach content analysis, the data source for all trophic analyses in this study, also has a variety of limitations including differential digestion rates among prey species (Amundsen & Sánchez-Hernández 2019) and a short timescale of dietary information estimated to be <24 h in ABFT (Butler & Mason 1978, Carey et al. 1984, Butler et al. 2010). These limitations highlight the importance of establishing long-term monitoring of diet data across a broad spatial scale to allow for detection of trophic changes due to natural or anthropogenic sources to better inform predator–prey interactions and ecosystem-based management. Interpretation of stomach content analysis can be limited by the inclusion of more highly digested prey that are not identified to the species level. Failure to identify prey to the species level could affect the detection of potential shifts among prey at the genus or species level, like the different clupeid species recently documented in the NWCS (Nadeau et al. 2025). Future pairing of stomach content data with chemical tracers like stable isotopes and DNA barcoding would provide a more robust characterization of ABFT trophic ecology, as such tracers reflect a broader timescale (Chipps & Garvey 2007, da Silveira et al. 2020) and could better resolve prey at the species level (de Sousa et al. 2019),

851 respectively. Despite these caveats, this diet data set is the largest and most spatially and
852 temporally comprehensive that has been assembled for the North Atlantic range for ABFT
853 to date and provides novel insights into patterns in their distribution and predatory
854 behavior.

855 **4.6. Conclusions**

856 ABFT trophic ecology varies spatially, temporally, and with biological and environmental
857 factors. ABFT length was consistently important for all 3 trophic analyses, while LP was
858 important in explaining ABFT diet and content biomass. The NWCS is distinct from other
859 sampled foraging areas in the Atlantic Ocean and Mediterranean Sea due to the prevalence
860 of clupeid prey during much of the time series. This region showed temporal and size-
861 based changes in dominant prey, with ammodytids being more prevalent in the earliest
862 sampling years and for smaller ABFT, and ommastrephids more prevalent in the most
863 recent sampling years. The prevalence of clupeid and other energy-dense prey in ABFT diet
864 in this region combined with high stomach content weight supports the role of this region
865 as an important foraging area for adult ABFT prior to subsequent migration and spawning in
866 western Atlantic spawning grounds in the Gulf of Mexico (Wilson et al. 2015, Logan et al.
867 2023) as well as for ABFT of eastern Atlantic origin (Kerr et al. 2020). For the remaining
868 regions, engraulids were the primary prey base for small ABFT, with larger fish transitioning
869 to ommastrephids and paralepidids, among other prey families. Prey length and stomach
870 content weight increased with ABFT length in an asymptotic manner, with a transition
871 observed around 200 cm SFL for both relationships, and with productivity (chl *a*
872 concentration) and SST.

873 Our results reveal broad patterns in ABFT trophic ecology across their migratory range that
874 further our understanding of the prey bases that fuel this long-lived and highly migratory
875 species throughout its life. This is especially important as regions within their broader
876 North Atlantic range are under increasing risk due to rapid warming associated with climate
877 change (Pershing et al. 2015). While SST was not a primary predictor variable in our CART
878 analysis, it was associated with the occurrence of several key prey species. Indirect effects
879 (e.g. changes in species interactions) from climate change have been hypothesized to have
880 a greater effect on higher trophic levels than the direct effects (Ockendon et al. 2014).
881 Results presented here can be used as inputs to bioenergetic and food web models (e.g.
882 Mariani et al. 2017) to understand ecosystem-based responses as environmental and
883 ecological conditions continue to change (Staudinger et al. 2021). Continued dietary
884 monitoring will aid in understanding how ABFT respond to future changes in environmental
885 conditions and available forage bases and expand our ecological understanding of this
886 highly migratory top predator.

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Table 1. Summary of biological, temporal, spatial, and environmental data for Atlantic bluefin tuna *Thunnus thynnus* (ABFT) stomach samples. All mean values are reported ±1 SD. ARCT: Atlantic Arctic; CARB: Caribbean; CNRY: Canary Current coast; GFST: Gulf Stream; MEDI: Mediterranean Sea; NADR: North Atlantic Drift; NASE: Northeast Atlantic Subtropical Gyre; NWCS: Northwest Atlantic shelves; SARC: Atlantic sub-Arctic. Straight fork length (SFL) is reported as mean followed by the range (minimum to maximum). Environmental variables are sea surface temperature (SST), chlorophyll *a* concentration (chl *a*), sea surface absolute dynamic topography (ADT), and sea surface height anomaly (SLA). Gear types are: bait boat (BB), hand line (HL), harpoon (HP), long line (LL), mid-water trawl (MWTD), purse seine (PS), rod and reel (RR), and troll (TR). Stomach sample sizes (N) are listed as the total number of stomachs with contents

Longhurst Province	N	SFL (cm)	Total content weight (g)	Sampling tears (range)	SST (°C)	Gear type	Chl *a* (mg m^{-3})	ADT (m)	SLA (m)
ARCT	10	218 ± 16 (198–246)	309 ± 801	2003–2014	11.7 ± 0.9	MWTD, LL	0.8 ± 0.6	–0.3 ± 0.1	0.0 ± 0.1
CARB	11	249 ± 14 (225–276)	311 ± 370	2012	26.4 ± 1.3	LL	0.1 ± 0.0	0.2 ± 0.1	–0.0 ± 0.1
CNRY	353	49 ± 23 (25–128)	46 ± 70	2000–2018	22.1 ± 2.0	BB, MWTD, RR	0.2 ± 0.0	0.2 ± 0.1	0.1 ± 0.1
GFST	1	262 (262)	18	2012	19.8	LL	0.2	–0.2	–0.0
MEDI	1685	103 ± 69 (6–294)	176 ± 647	1998–2020	21.9 ± 2.9	BB, LL, PS, RR, TR	0.2 ± 0.1	0.0 ± 0.1	0.1 ± 0.1

NADR	49	123 ± 66 (58–245)	121 ± 239	1985–2012	17.4 ± 2.8	LL, RR	0.5 ± 0.2	–0.0 ± 0.2	0.1 ± 0.1
NASE	76	238 ± 14 (197–270)	200 ± 451	2016–2018	19.4 ± 0.3	BB	0.2 ± 0.0	0.2 ± 0.0	0.0 ± 0.0
NWCS	1438	207 ± 42 (63–328)	995 ± 1414	1988–2019	18.6 ± 2.9	HL, HP, LL, PS, RR	2.8 ± 2.3	–0.0 ± 0.1	0.1 ± 0.1
SARC	423	203 ± 27 (90–275)	276 ± 458	1998–2011	11.3 ± 0.9	LL	0.9 ± 0.3	–0.2 ± 0.1	0.1 ± 0.0

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Table 2. Stomach contents as mean percent weight (MW%) by Longhurst Province (see Table 1 for full province names) of the main prey families (>1 MW% in the full data set). Each prey family is identified by broader taxonomic classification as a teleost (TEL), cephalopod (CEPH), or crustacean (CRU). MW% of all remaining contents are listed in the final row

Prey family	Group	ARCT (n = 10)	CARB (n = 11)	CNRY (n = 353)	GFST (n = 1)	MEDI (1685)	NADR (n = 49)	NASE (n = 76)	NWCS (n = 1438)	SARC (n = 423)
Ammodytidae	TEL	13.1	0.0	0.0	0.0	0.3	19.7	0.0	13.3	0.0
Carangidae	TEL	0.0	0.0	13.2	0.0	3.4	2.9	7.0	0.0	0.0
Clupeidae	TEL	0.0	1.0	1.8	0.0	10.6	0.0	0.0	37.3	0.0

Engraulidae	TEL	0.0	0.0	52.5	0.0	13.6	22.9	0.0	0.0	0.0
Euphausiidae	CRU	0.0	0.0	4.2	0.0	1.8	6.7	0.0	0.4	0.0
Gadidae	TEL	0.0	0.0	6.1	0.0	0.8	8.2	0.0	1.3	0.1
Myctophidae	TEL	0.0	0.0	0.6	0.0	3.7	0.0	0.0	0.0	0.3
Ommastrephidae	CEPH	0.0	0.0	0.8	0.0	8.6	0.0	0.0	8.1	20.1
Paralepididae	TEL	25.1	0.0	0.0	0.0	1.7	2.3	0.0	0.2	16.9
Polybiidae	CRU	0.0	0.0	0.0	0.0	3.3	0.0	0.0	0.0	0.0
Scombridae	TEL	40.0	0.0	1.7	0.0	3.7	0.0	13.6	8.1	0.0
Sergestidae	CRU	0.0	0.0	0.0	0.0	4.7	0.0	0.0	0.0	0.0
Sparidae	TEL	0.0	0.0	0.1	0.0	1.5	0.0	4.2	0.1	0.0
Stomiidae	TEL	0.0	0.0	0.0	0.0	4.0	0.0	0.0	0.0	0.0
Remaining contents		21.8	99.0	18.9	100.0	38.3	27.3	75.1	31.1	62.6

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1413 Table 3. Summary of prey sizes by major taxonomic group. N is the total number of prey items with size information; mean,
1414 minimum (Min), and maximum (Max) prey sizes measured within each group. All prey sizes are reported in centimeters (cm)

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Prey type	N	Mean ± SD	Min	Max
Fishes				

Elasmobranch	34	43.6 ± 18.2	16.0	80.0
Teleost	14357	20.0 ± 10.0	1.2	108.0
Invertebrates				
Cephalopoda	5506	12.5 ± 7.0	0.1	49.3
Crustacea	502	3.5 ± 2.7	1.1	16.2
Echinoderm	3	0.9 ± 0.4	0.5	1.2
Mollusca	2	0.6 ± 0.2	0.4	0.7

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Table 4. Line equations of Atlantic bluefin tuna *Thunnus thynnus* predator–prey body size relationships by major taxonomic groups and Longhurst Province. Quantile regression was used to estimate the lower, median, and upper bound equations of scatter data. BFTL = predator length and PL = prey length, N = number of prey lengths. The 1st and 99th quantiles were used for 1000 > n; and the 5th and 95th quantiles were used for 200 < n < 1000. *** p < 0.00001; NS indicates a non-significant p-value

Quantiles	Lower bound	Median	Upper bound
1st, 50th, 99th	BFTL = 0.01PL – 0.07***	BFTL = 0.10PL – 1.73***	BFTL = 0.16PL + 11.01***
1st, 50th, 99th	BFTL = 0.01PL + 1.06***	BFTL = 0.12PL – 1.03***	BFTL = 0.17PL + 11.05***
1st, 50th, 99th	BFTL = 0.02PL – 3.11***	BFTL = 0.06PL – 0.81***	BFTL = 0.14PL + 6.27***
5th, 50th, 95th	BFTL = 0.00PL + 1.50^{NS}	BFTL = 0.02PL + 0.81***	BFTL = 0.07PL – 0.17^{NS}

1st, 50th, 99th	BFTL = –0.003PL + 4.76^{NS}	BFTL = 0.09PL + 1.65***	BFTL = 0.19PL + 2.61***
1st, 50th, 99th	BFTL = 0.02PL – 0.73***	BFTL = 0.13PL – 6.81***	BFTL = 0.15PL + 11.74***

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Fig. 1. Capture locations of Atlantic bluefin tuna *Thunnus thynnus* from which stomach content data were derived for our database and used in diet analyses. Longhurst Provinces that contained stomach samples were: ARCT (Atlantic Arctic), CARB (Caribbean), CNRY (Canary Current coast), GFST (Gulf Stream), MEDI (Mediterranean Sea), NADR (North Atlantic Drift), NASE (Northeast Atlantic Subtropical Gyre), NWCS (Northwest Atlantic shelves), and SARC (Atlantic sub-Arctic). Data from the ARCT, CARB, and GFST were excluded from classification and regression tree (CART) and generalized additive model (GAM) analyses due to small sample sizes

Fig. 2. (a) Classification tree for Atlantic bluefin tuna *Thunnus thynnus* (ABFT) prey family-level diet composition in relation to temporal, spatial, biological, and environmental variables. Colors correspond to fish (F, green), cephalopod (C, blue), and crustacean (Cr, red) prey groups. Branch length reflects relative importance of each split. The predictor variable forming the split is shown at each branch, and the prey family with the highest mean proportion weight is shown in each colored terminal node. (b) Variable importance is displayed in descending order. Longhurst Provinces (LPs) included in the classification tree were: CNRY, MEDI, NADR, NASE, NWCS, and SARC (full province names are given in Fig. 1). Explanatory variables were Year (sampling year), LP (LP of sampling location), Length (ABFT straight fork length, SFL; cm), Sea surface temperature (SST;°C), Sea surface absolute dynamic topography (ADT; m), Chlorophyll *a* concentration (chl *a*; mg m^{-3}), and Sea surface height anomaly (SLA; m)

Fig. 3. Cumulative prey curves generated for Atlantic bluefin tuna (ABFT) for diet samples from each Longhurst Province (LP): (a) ARCT, (b) CARB, (c) CNRY, (d) MEDI, (e) NADR, (f) NASE, (g) NWCS, and (h) SARC (see Fig. 1 for full LP names). Solid lines represent the estimated number of prey families up to the total sample size per data set (solid symbol) while dashed lines reflect extrapolated estimates beyond the actual sample sizes of the diet database. Blue curves with solid triangles are for smaller ABFT (NWCS: <171 cm straight fork length, SFL; all other LPs: <79 cm SFL) while red curves with solid circles are for larger ABFT (NWCS: ≥171 cm SFL; all other LPs: ≥79 cm SFL)

Fig. 4. Gini index of diet diversity with sampling locations (black points). Diversity is scaled from 0 (low diversity) to 1 (high diversity)

Fig. 5. (a) Spatial distribution of sampling locations and (b) mean proportion weight of prey families for the primary split in the classification tree for Atlantic bluefin tuna *Thunnus thynnus* (ABFT) prey family-level diet composition. Node 2 (blue) corresponds to the NWCS Longhurst Province (LP) and node 3 (red) includes the remaining 8 LPs included in the diet data set (see Fig. 1). The Gini index of diversity (*D*) is reported for each node. Prey families are classified as fishes (F), cephalopods (C), and crustaceans (Cr)

Fig. 6. (a) Spatial distribution of sampling locations and (b) mean proportion weight of prey families for the main secondary split in the classification tree for Atlantic bluefin tuna *Thunnus thynnus* (ABFT) prey family-level diet composition. Node 6 (blue) corresponds to ABFT ≥79 cm straight fork length (SFL) and node 7 (red) includes ABFT <79 cm SFL. The Gini index of diversity (*D*) is reported for each node. Prey families are classified as fishes (F), cephalopods (C), and crustaceans (Cr)

Fig. 7. Partial dependence plots showing mean proportion weight of each prey family included in the classification tree analysis in relation to Atlantic bluefin tuna *Thunnus thynnus* (ABFT) straight fork length (SFL; cm). Prey families are identified as fishes (F), cephalopods (C), or crustaceans (Cr). Shaded areas represent the bootstrapped 95% confidence intervals around the predictions, and the tick marks on the *x*-axis are rug plots showing sampling density

Fig. 8. Partial response plots of the best model for Atlantic bluefin tuna *Thunnus thynnus* (ABFT) stomach content biomass. The best model included (a) ABFT straight fork length (SFL; cm), (b) sea surface temperature (SST;°C), (c) chlorophyll *a* concentration (chl *a*; mg m^{-3}), (d) sea surface absolute dynamic topography (ADT; m), (e) Longhurst Province (full names given in Fig. 1), and (f) gear type (BB: bait boat; HP: harpoon; LL: long line; MWTD: mid-water trawls; PS: purse seine; RR: rod and reel; TR: troll; UN: unknown). Shaded areas (a–d) and dashed lines (e,f) represent 95% confidence intervals, and the tick marks on the *x*-axis are rug plots showing sampling density

Fig. 9. Atlantic bluefin tuna *Thunnus thynnus* (ABFT) straight fork length (SFL; cm) and total stomach content biomass (g). Each point represents a single stomach sample. Solid grey lines represent the lower (1^{st}), median (50^{th}), and upper (99^{th}) bound regression lines estimated from quantile regression analyses. ***$p < 0.001$

Fig. 10. Partial response plots of the best model for Atlantic bluefin tuna *Thunnus thynnus* (ABFT) prey length. The best model included (a) ABFT straight fork length (SFL; cm), (b) sea surface temperature (SST;°C), (c) chlorophyll *a* concentration (chl *a*; mg m^{-3}), (d) gear type (abbreviations as in Fig. 8), and (e) prey type (CEPH: cephalopods; CRU: crustaceans; ELASMO: elasmobranchs; MISC: miscellaneous prey; TEL: teleosts). Shaded areas (a–c) and dashed lines (d–e) represent 95% confidence intervals, and the tick marks on the *x*-axis are rug plots showing sampling density

Fig. 11. Atlantic bluefin tuna *Thunnus thynnus* (ABFT) and prey size relationships for (a) all prey combined, (b) teleost prey measured as total or standard length (cm), (c) cephalopod prey measured as mantle length, (d) crustacean prey measured as carapace length, (e) all prey from the NWCS Longhurst Province (LP), and (f) all prey from remaining LPs outside

NWCS (see Fig. 1). Each point represents a single prey consumed by a tuna predator. Solid grey lines represent the lower (1st), median (50th), and upper (99th) bound regression lines estimated from quantile regression analyses. All line equations are listed in Table 4