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ORIGINAL ARTICLE

Exploitation shifted trophic ecology and habitat preferences of Mediterranean and Black Sea bluefin tuna over centuries

Adam J. Andrews[1,2] | **Christophe Pampoulie**[3] | **Antonio Di Natale**[4] | **Piero Addis**[5] | **Darío Bernal-Casasola**[6] | **Veronica Aniceti**[7] | **Gabriele Carenti**[8] | **Verónica Gómez-Fernández**[9] | **Valerie Chosson**[3] | **Alice Ughi**[10] | **Matt Von Tersch**[10] | **Maria Fontanals-Coll**[10] | **Elisabetta Cilli**[2] | **Vedat Onar**[11] | **Fausto Tinti**[1] | **Michelle Alexander**[10]

[1]Department of Biological, Geological and Environmental Sciences, University of Bologna, Ravenna, Italy
[2]Department of Cultural Heritage, University of Bologna, Ravenna, Italy
[3]Marine and Freshwater Research Institute, Hafnarfjörður, Iceland
[4]Aquastudio Research Institute, Messina, Italy
[5]Department of Life and Environmental Sciences, University of Cagliari, Cagliari, Italy
[6]Department of History, Geography and Philosophy, Faculty of Philosophy and Letters, University of Cádiz, Cádiz, Spain
[7]Department of Natural History – University Museum, University of Bergen, Bergen, Norway
[8]CEPAM, CNRS, Université Côte d'Azur, Nice, France
[9]Instituto Nacional de Investigaciones Científicas y Ecológicas, Salamanca, Spain
[10]BioArCh, Department of Archaeology, University of York, York, UK
[11]Osteoarchaeology Practice and Research Centre, Faculty of Veterinary Medicine, Istanbul University-Cerrahpaşa, Istanbul, Turkey

Correspondence
Adam J. Andrews and Fausto Tinti, Department of Biological, Geological and Environmental Sciences, University of Bologna, Campus of Ravenna, Ravenna, Italy.
Email: adam@palaeome.org and fausto.tinti@unibo.it

Michelle Alexander, BioArCh, Department of Archaeology, University of York, York, UK.
Email: michelle.alexander@york.ac.uk

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Abstract

During recent decades, the health of ocean ecosystems and fish populations has been threatened by overexploitation, pollution and anthropogenic-driven climate change. Due to a lack of long-term ecological data, we have a poor grasp of the true impact on the diet and habitat use of fishes. This information is vital if we are to recover depleted fish populations and predict their future dynamics. Here, we trace the long-term diet and habitat use of Atlantic bluefin tuna (BFT), *Thunnus thynnus*, a species that has had one of the longest and most intense exploitation histories, owing to its tremendous cultural and economic importance. Using carbon, nitrogen and sulphur stable isotope analyses of modern and ancient BFT including 98 archaeological and archival bones from 11 Mediterranean locations ca. 1st century to 1941 CE, we infer a shift to increased pelagic foraging around the 16th century in Mediterranean BFT. This likely reflects the early anthropogenic exploitation of inshore coastal ecosystems, as attested by historical literature sources. Further, we reveal that BFT which migrated to the Black Sea–and that disappeared during a period of intense exploitation and ecosystem changes in the 1980s–represented a unique component, isotopically distinct from BFT of NE Atlantic and Mediterranean locations. These data suggest that

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anthropogenic activities had the ability to alter the diet and habitat use of fishes in conditions prior to those of recent decades. Consequently, long-term data provide novel perspectives on when marine ecosystem modification began and the responses of marine populations, with which to guide conservation policy.

KEYWORDS
anthropogenic impacts, Black Sea, historical baselines, stable isotope analysis, *Thunnus thynnus*, trophic shifts

1 | INTRODUCTION

During the past century, a myriad of anthropogenic impacts such as fisheries exploitation, habitat modification, pollution and climate change have had measurable and increasing consequences affecting habitat suitability, prey availability, individual life histories and in turn, the productivity, fitness and distribution of marine populations (Butchart et al., 2010; Casini et al., 2009; Howarth et al., 2014; Pauly et al., 1998; Planque et al., 2010). Due to a lack of long-term data, the onset of anthropogenic impacts remains unclear for many marine ecosystems and populations, as does their response (Jackson et al., 2001; Lotze et al., 2014; Schwerdtner Máñez et al., 2014). As such, historical baselines (e.g. population function and structure over centuries) would be useful to guide management targets on how complex populations were in the past, what more-natural distributions and behaviours looked like, and which anthropogenic impacts have driven change and should consequently be minimised to promote recovery (Caswell et al., 2020; Duarte et al., 2020; Engelhard et al., 2015).

As an example, the eastern Atlantic and Mediterranean population of bluefin tuna (BFT) (*Thunnus thynnus*, Scombridae), is one of the longest and most heavily exploited (Porch et al., 2019). Consequently, BFT range contracted and its abundance was depleted by the 21st century, which included the loss of Black Sea habitats by the 1980s (MacKenzie et al., 2009; Worm & Tittensor, 2011). Since antiquity, the Black Sea has supported BFT fisheries from the Bosphorus to the Azov Sea, as attested by archaeological remains, the writings of classical authors and tuna-trap records over several centuries (Andrews, Di Natale, et al., 2022; Cort & Abaunza, 2019; Di Natale, 2015; Karakulak & Oray, 2009; Karakulak & Yıldız, 2016). However, there is no information on the foraging ecology of Black Sea BFT, and little information on their distribution or connectivity with Atlantic and Mediterranean BFT; which is vital to promote their return (Di Natale, 2015; Di Natale et al., 2019). Despite recoveries of BFT abundance during the last decade to 1970s levels (ICCAT, 2020), BFT is yet to recolonise habitats such as the Black Sea (Di Natale, 2019). Moreover, as for many consumers, questions exist around the broader impacts of ocean overexploitation over centuries. Such as, has the depletion of inshore species and forage fishes, especially in coastal areas, induced a shift in diets and distributions of BFT? (c.f., Hilborn et al., 2017; Jackson et al., 2001; Pauly et al., 1998) and, has the pollution of coastal areas shifted BFT migrations offshore (Addis et al., 2016)? Confidence in BFT sustainability is thus stymied, in part, by a limited understanding of its population structure and trophic niche(s) prior to the 1970s, which may improve recovery targets (ICCAT, 2020).

Nowadays, the eastern Atlantic and Mediterranean stock of BFT comprises individuals ≤3.3 m in length and ≤725 kg in weight (Cort et al., 2013), and spawns predominantly in the Mediterranean from age 3–4 (Mather et al., 1995; Piccinetti et al., 2013). The majority of individuals undertake diverse feeding migrations to a range of habitats throughout the Atlantic (Druon et al., 2016; Mariani et al., 2016; Wilson & Block, 2009) from as early as age one (Dickhut et al., 2009), though tagging and fishery evidence suggest that a portion is resident in the Mediterranean all-year-round (Cermeño et al., 2015; De Metrio et al., 2004; Mather et al., 1995), and might be remnants of a population that migrated to the Black Sea each spring and potentially spawned there (Di Natale, 2015; Karakulak & Oray, 2009). For this reason amongst others, it is hypothesised that BFT comprise more complexity than is currently reflected where BFT are managed as two stocks (Cort & Abaunza, 2019; Di Natale, 2019; Fromentin, 2009). These are the eastern Atlantic and Mediterranean BFT and the genetically and isotopically distinct population of BFT spawning in the Gulf of Mexico and Slope Sea. Both stocks exhibit a high degree of natal homing despite high levels of population mixing (Brophy et al., 2020; Puncher et al., 2018; Richardson et al., 2016; Rodríguez-Ezpeleta et al., 2019; Rooker et al., 2008). Juvenile and adult BFT primarily inhabit the upper 200 m of habitats (Druon et al., 2016; Walli et al., 2009; Wilson & Block, 2009), feeding on benthic-pelagic prey such as forage fishes, cephalopods and crustaceans (Karakulak et al., 2009; Logan et al., 2011), and occasionally diving offshore to feed at great depths (Battaglia et al., 2013; Olafsdottir et al., 2016; Rumolo et al., 2020; Sarà & Sarà, 2007; Wilson & Block, 2009). The greatest shift in BFT foraging strategy appears to be at age two, once the predation of zooplankton ends and the predation of fishes begins, after which, size-classes remain more isotopically similar (Rumolo et al., 2020; Sarà & Sarà, 2007).

The study of stable isotopes using archaeological and archived bone, scales or otoliths to assess long-term population dynamics in fishes is well established (Barrett et al., 2011; Das et al., 2021; Hutchinson & Trueman, 2006; Newton & Bottrell, 2007). Recent studies have revealed the extinction of a resident trophic niche in Atlantic salmon (*Salmo salar*, Salmonidae, Guiry et al., 2016), and indicated potential millennial-scale diet shifts in the highly exploited Atlantic cod (*Gadus morhua*, Gadidae, Ólafsdóttir et al., 2021) and Atlantic populations of European hake (*Merluccius merluccius*, Merlucciidae, Llorente-Rodríguez et al., 2022). Potential habitat productivity or usage shifts have also been suggested in Atlantic and Pacific fishes during the last 500 years compared with the previous centuries (Misarti et al., 2009; Ólafsdóttir et al., 2021).

A range of ecological and environmental variables will affect the carbon ($\delta^{13}C$), nitrogen ($\delta^{15}N$) and sulphur ($\delta^{34}S$) values of fish tissues. $\delta^{15}N$ values increase with each trophic level and are thus used to estimate the trophic position of an organism in a food web (Sigman et al., 2009). In contrast, $\delta^{13}C$ and $\delta^{34}S$ signatures pass between primary producers and consumers with low levels of fractionation. This lends them to being good indicators of provenance because distinct $\delta^{13}C$ and $\delta^{34}S$ values are generally maintained across trophic levels (Guiry, 2019; Thode, 1991). Typically, habitats heavily influenced by low-salinity water (e.g. Black Sea) have lower $\delta^{15}N$ and $\delta^{13}C$ values than saline habitats of the Mediterranean and especially NE Atlantic shelf seas due to increased terrestrially derived or fixed (low $\delta^{15}N$ and $\delta^{13}C$ values) nitrogen and carbon and/or lower quantities of resuspended (remineralised, high $\delta^{15}N$ and $\delta^{13}C$ values) nitrogen and carbon from sediments or the deep-ocean (Barnes et al., 2009; Fulton et al., 2012; Magozzi et al., 2017; Rafter et al., 2019). For these reasons, offshore habitats and consumers often contain lower $\delta^{13}C$ than benthic and neritic ones (Amiraux et al., 2023; DeNiro & Epstein, 1978) yet shelf $\delta^{15}N$ values are often higher due to high levels of fractionation and more complex food webs (Logan et al., 2023). It is important to note that many factors govern the complex variation in $\delta^{15}N$ and $\delta^{13}C$ between consumers, including the environmental conditions, levels of benthic-pelagic coupling and the production in each habitat foraged (Barnes et al., 2009; Jennings et al., 2008; Sigman et al., 2009). $\delta^{34}S$ is sometimes useful to disentangle these effects. For example, low $\delta^{34}S$ values often reflect increased foraging on benthic or neritic prey while higher values indicate a greater degree of energy incorporated from pelagic production (Fry & Chumchal, 2011; Szpak & Buckley, 2020). Though, highly stratified pelagic habitats such as in the Black Sea can be expected to have relatively low $\delta^{34}S$ values due to sulphate being partially derived from microbial sulphides in sub-oxic waters. Distance from shore also influences $\delta^{34}S$ values, not because of freshwater input per se—even brackish water is dominated by marine high $\delta^{34}S$ signatures (Cobain et al., 2022; Fry & Chumchal, 2011; Guiry et al., 2022)—but rather food webs associated with coastal habitats such as seagrass beds, salt marshes and mudflats where low ^{34}S is incorporated from anoxic marine sediments during production (Guiry et al., 2022; Szpak & Buckley, 2020; Thode, 1991).

Since variables governing production change over time (e.g. changing environmental conditions and sources such as pollution), there is often intra- and inter-annual variation at the base of marine food-webs, which one needs to be aware of when drawing conclusions from temporal isotopic data—especially over the long-term (Jardine et al., 2014; Solomon et al., 2008). Some degree of temporal variation can be accounted for, like the long-term decrease in oceanic ^{13}C following industrialisation (Suess Effect: Gruber et al., 1999), while tissue type can also improve temporal inferences. For instance, BFT vertebrae retain multiple years of isotopic foraging signatures across their growth axes (Andrews et al., 2023) and therefore bone isotope values dampen out intra- and inter-annual variation, providing an average across years of foraging prior to capture.

In this study, we examine a long time-series of isotopic data on Atlantic bluefin tuna, including 98 archaeological and archived bones from 11 eastern Atlantic, Mediterranean and Black Sea locations ca. 1st century to 1941 CE, and 20 modern samples. First, we analysed their $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ isotope values to characterise the foraging ecology of Black Sea BFT, whose distribution and feeding habits remain unknown. Second, to investigate how Black Sea BFT functioned and was structured in relation to the eastern Atlantic and Mediterranean BFT, since the residency and role of BFT in the Black Sea region remains unknown (Di Natale, 2015; MacKenzie & Mariani, 2012). Finally, to investigate how BFT diet and/or migrations may have changed throughout the past two millennia in relation to commercial exploitation in light of evidence of offshore movement in the past few decades following noise pollution (Addis et al., 2016) and a shift in the size-structure of marine food webs (Baum & Worm, 2009; Pauly et al., 1998). It must be noted that temporal data produced using archaeological and historical samples can be complex to interpret since they are necessarily limited in number and might be influenced by changing fishing technologies and locations foraged available.

2 | METHODS

2.1 | Sampling and collagen extraction

Ancient BFT bones (primarily vertebrae) were sampled from archaeological sites throughout the Mediterranean, each dated by context or ^{14}C (Table S1, Figure S1), to between the 1st and 18th century CE (Table 1, Figure 1: for details see Supporting Information). Care was taken to avoid sampling the same individual twice by selecting a range of specimens with different sizes or different stratigraphic units. Modern BFT bones comprise vertebrae pertaining to the 20th c. Massimo Sella Archive, University of Bologna, Ravenna Campus (Italy) and those captured in the 21st century. Archival specimens were BFT captured in central Mediterranean tuna-traps during the early-20th c. (Table 1, Figure 1), and stored dry after the removal of soft tissues by unknown means. BFT were sampled off southern Iceland in September 2014 by long-line (fishing vessel: Jóhanna Gísladóttir, Vísir hf., Iceland) and Isola Piana (Carloforte, Sardinia) in July 2020 by tuna-trap (Carloforte Tonnare PIAM srl.); these were mechanically cleaned of soft-tissues, macerated in ambient-temperature water for up to 2 months to remove remaining soft-tissues by microbial decomposition, then dried.

To enable assessment of size effects on isotope values, we estimated the straight fork length (FL) of vertebrae specimens following Andrews, Mylona, et al. (2022) using the online resource https://tunaarchaeology.org/lengthestimations. Briefly, vertebrae rank or type was identified, vertebrae length/width/height was measured to the nearest mm, and the best-fitting power regression model was applied for each specimen (Table S2), which predicts FL to ca. 90% accuracy based on modern reference skeletons. It is assumed that relationships between vertebra size and FL were consistent between modern and historical specimens. FL was measured at sea for all modern Icelandic and three modern Sardinian samples (CF_2020_617, 667 and 673: Supporting Information), to the nearest cm.

Isotope signatures from multiple years prior to catch are retained across the growth axes of BFT vertebrae (Andrews et al., 2023). Therefore, to obtain averages of foraging across seasons and avoid overrepresenting potential sporadic seasonal changes or foraging behaviours, we aimed to (1) sample the same element (vertebrae), whenever possible, and (2) represent roughly equal portions of acellular (cortical) and cellular (spongy) bone across the growth-axis, between samples. Thus, we sampled bones using a diamond band saw to cut wedges across growth axes where the amount of inner material was lesser, but roughly proportional to the amount of outer material, between samples (Figure S2). This resulted in a sample section which integrates collagen formed over the whole life of the fish. Cutting of vertebrae was prohibited for one sample group (9–13th c. Istanbul), thus we drilled into each vertebra at an inner and outer position, analysed the isotopic compositions separately and averaged values for the final analyses (Table S2).

Bone collagen was extracted following the modified Longin method (Brown et al., 1988). Briefly, cross-sections (ca. 250–1000 mg) of bone were mechanically cleaned to remove exogenous material. Modern and archaeological 1755 CE samples were defatted by sonication for 15 min in a 2:1 dichloromethane/methanol solution, repeated a minimum of three times until the solution remained clear. Residual solvents were then evaporated overnight before samples were rinsed three times with deionised water. Samples were demineralised at +4°C in 8 mL of 0.4 or 0.6 M HCl, depending upon if they were archaeological or modern samples, respectively. To remove non-collagenous proteins potentially retained in modern samples (Guiry & Szpak, 2020), we soaked demineralised modern samples in 0.25 M NaOH for 15 min. This was repeated until the solution remained clear, prior to refluxing back to 0.6 M HCl (Longin, 1971). Demineralised collagen was gelatinised at 80°C for 48 h in 0.001 M HCl. Gelatinised collagen was filtered (60–90 μm; Ezee filters, Elkay) and freeze-dried.

2.2 | Stable isotope analyses

To determine carbon and nitrogen isotopic values, collagen (0.4–0.6 mg) was analysed in duplicate using a Sercon continuous flow 20–22 IRMS interfaced with a Universal Sercon gas solid liquid elemental analyser (Sercon) at BioArCh, Department of Archaeology (York, UK). Sulphur isotope values were determined by analysing collagen (0.9–1.2 mg) in 20% duplicate using a Delta V Advantage continuous-flow IRMS coupled via a ConfloIV to an IsoLink elemental analyser (Thermo Scientific) at SUERC as described in Sayle et al. (2019). The obtained values were corrected from the isotopic ratio of the international standards, Vienna Pee Dee Belemnite (VPDB) for carbon, air (AIR) for nitrogen and Vienna Cañon-Diablo Troilite (VCDT) for sulphur, using the δ (‰) notation.

Uncertainties on the measurements were calculated by combining the standard deviation (SDs) of the sample replicates and those of International Atomic Energy Agency (IAEA) reference material according to Kragten (1994) for carbon and nitrogen, and Sayle et al. (2019) for sulphur. The international standards used as reference material in analytical runs were; caffeine (IAEA-600), ammonium sulfate (IAEA-N-2) and cane sugar (IA-Cane) for carbon and nitrogen; and silver sulfide (IAEA-S-2 and IAEA-S-3) for sulphur. International standard average values and SD across the runs were as follows: IAEA-600 ($n = 43$), $\delta^{13}C$ raw = −27.71 ± 0.09‰ ($\delta^{13}C$ true = −27.77 ± 0.04‰) and $\delta^{15}N$ raw = +0.71 ± 0.22‰ ($\delta^{15}N$ true = 1 ± 0.2‰); IAEA-N-2 ($n = 43$), $\delta^{15}N$ raw = +20.38 ± 0.38‰ ($\delta^{15}N$ true = 20.3 ± 0.2‰); and IA-CANE ($n = 54$), $\delta^{13}C$ raw = −11.68 ± 0.10‰ ($\delta^{13}C$ true = −11.64 ± 0.03‰); IAEA-S-2 ($n = 13$), $\delta^{34}S_{VCTD}$ = 22.62 ± 0.08‰ and IAEA-S-3 ($n = 13$) $\delta^{34}S_{VCTD}$ = −32.49 ± 0.08‰. The maximum uncertainty across all samples ($n = 118$) was <0.20‰ for $\delta^{13}C$ and $\delta^{15}N$, and ($n = 104$) 0.36‰ for $\delta^{34}S$.

Since BFT are highly migratory, it is challenging to predict the proportion of time foraging in each of their Atlantic and Mediterranean habitats. We therefore used a conservative approach to correct for the Suess Effect; the long-term decrease in oceanic $\delta^{13}C$ due to the uptake of anthropogenic CO_2 following industrialisation (Gruber

TABLE 1 Summary details of modern and ancient Atlantic bluefin tuna (*Thunnus thynnus*) samples collected and analysed in the current study.

Sample ID/year CE	Location	Longitude (°E)	Latitude (°N)	*n* sampled	*n* analysed for δ^{13}C and δ^{15}N	*n* analysed for δ^{34}S	Fork length min–max (mean) cm	Sample type	Skeletal elements
2020	Carloforte, Sardinia	8.31	39.18	10	10	10	111–196 (132)	Modern	Vertebrae
2014	Southwest Iceland	−21.42	62.42	10	10	9	198–238 (218)	Modern	Vertebrae
1941	Istanbul, Turkey	28.95	41.01	2	2	2	275 & 278	Archival	Vertebrae
1925	Zliten, Libya	14.66	33.25	10	10	10	158–204 (182)	Archival	Vertebrae
1911	Venice, Italy	14.59	43.93	7	6	5	88–152 (118)	Archival	Vertebrae
	Pizzo, Italy	15.34	38.97	7	7	6		Archival	Vertebrae
1755	Conil, Spain	−6.09	36.28	10	10	9	144–220 (176)	Archaeological	Vertebrae
16–18th c.	Sassari, Sardinia	8.62	40.86	10	10	9	115–231 (178)	Archaeological	Vertebrae
10–13th c.	Mazara del Vallo, Sicily	12.58	37.65	8	8	6	—	Archaeological	5 Vertebrae, 3 cranial elements
9–10th c.	Palermo, Sicily	13.37	38.11	18	16	12	101–185 (130)	Archaeological	15 Vertebrae, 3 cranial elements
9–13th c.	Istanbul, Turkey	28.95	41.01	14	13	12	165–241 (201)	Archaeological	Vertebrae
4–5th c.	Baelo Claudia, Spain	−5.77	36.09	12	6	4	109–132 (124)	Archaeological	Vertebrae
1st c.	Cadiz, Spain	−6.31	36.53	10	10	10	90–155 (130)	Archaeological	Vertebrae
Total				128	118	104			

Note: 1911 sample groups were pooled for analyses. For further details of the archived and archaeological samples see Supporting Information. Samples from archaeological groups were not analysed if collagen yields <1%. Coordinates of 1911 and 1941 archival groups are approximations. *n* = the number of individual specimens included in analyses after quality-control.

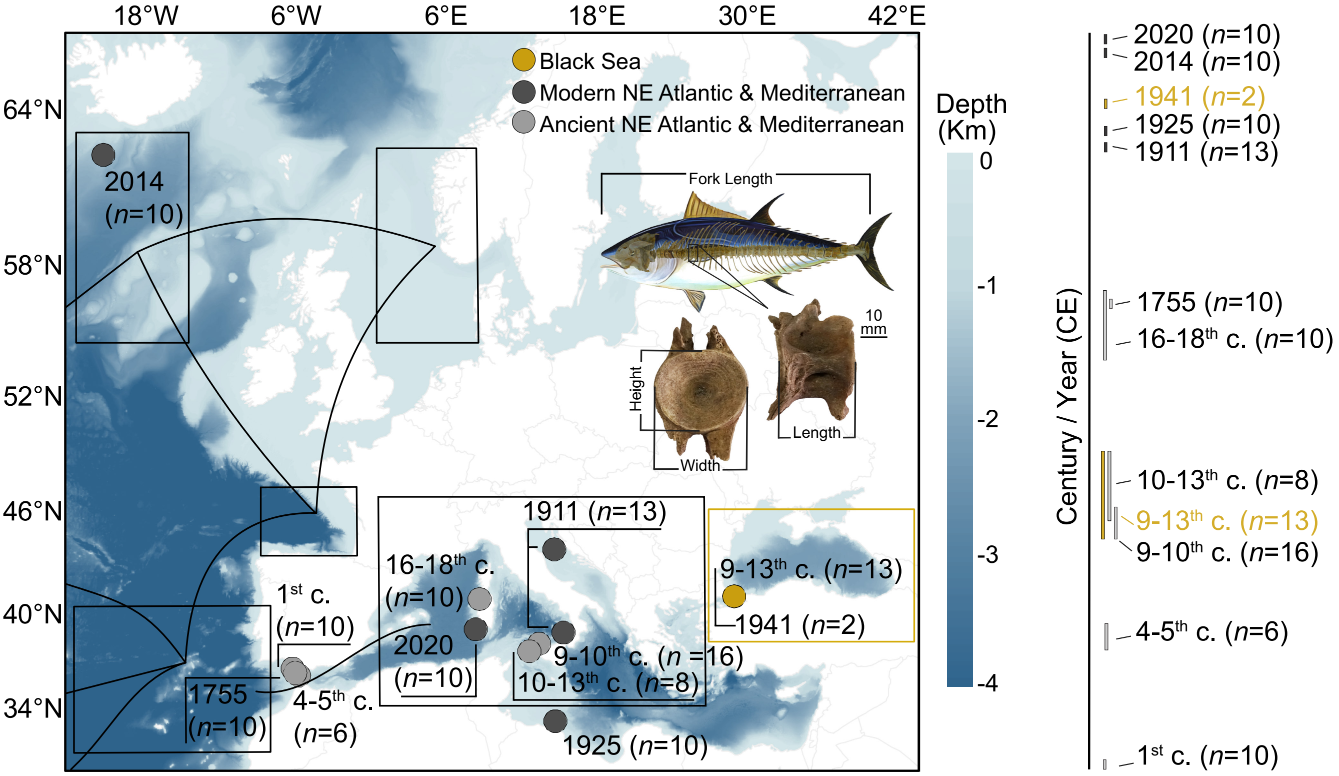

FIGURE 1 Locations and periods of capture of Atlantic bluefin tuna (BFT) samples analysed herein (coloured circles), illustrated in relation to ocean bathymetry, and major BFT habitats (black, yellow rectangles) and migration strategies (black lines) in the eastern Atlantic and Mediterranean, after Mariani et al. (2016). Samples are coloured as follows: putative Black Sea, yellow; modern NE Atlantic and Mediterranean, black; ancient (archaeological) NE Atlantic and Mediterranean, grey. n = number successfully analysed. Map created using ESRI ArcMap (v.10.6, https://arcgis.com). Illustration indicates fork length measurements used and provides an example of a vertebra related to its vertebral position and measurements (height, width and length) used to reconstruct fork length of the modern and ancient samples.

et al., 1999). Our correction assumed that the majority of foraging was conducted in the NE Atlantic Ocean, which experienced the greatest degree of anthropogenic ^{13}C change among BFT habitats (Eide et al., 2017). Therefore, applying corrections for this region would likely lead to an overcorrection but reduce the possibility of under-correction. Modern δ^{13}C values were thus corrected for the influence of the Suess Effect, using Equation (1) as per Hilton et al. (2006) and Ólafsdóttir et al. (2021):

$$\delta^{13}\text{C Suess correction factor} = \alpha \times \exp\left(\text{years from } 1850 \times b\right), \quad (1)$$

where α = the annual rate of decrease for the study water body, approximated as −0.015‰, based on previous estimates for the NE Atlantic Ocean (Quay et al., 2003), and b = the global decrease in oceanic δ^{13}C established as 0.027 by Gruber et al. (1999). Thus, we added 0.08‰, 0.11‰ and 0.18‰ to 1911, 1925 and 1941 δ^{13}C values, and 1.26‰ and 1.48‰ to 2014 and 2020 δ^{13}C values, respectively. An alternative approach assuming NE Atlantic residency (Clark et al., 2021) was not used but yielded similar estimates which did not alter the interpretation of our results.

Insufficient collagen (defined as <1% total sample weight) resulted in 10 (13%) archaeological samples being excluded from analyses (six 4–5th c., one 9–13th c., two 9–10th c., one 1911, Table S2). The quality of δ^{13}C and δ^{15}N values for the remaining 118 samples was controlled by confirming atomic C:N ratios (3.0–3.4) fell within the accepted ranges for archaeological and modern samples (Guiry & Szpak, 2020, 2021). Since variation in lipid content between samples can potentially drive differences in δ^{13}C values (Guiry & Szpak, 2020), we studied the relationship between C:N Ratios and δ^{13}C which revealed a non-significant correlation (Pearson's r = −.12, p = .23, Figure S3).

Quality control criteria for sulphur isotopes are relatively poorly defined for fishes. The quality of 104 samples analysed for δ^{34}S (which passed the assessment above) was assessed by %S values. Following Nehlich and Richards (2009) we calculated the theoretical sulphur content of BFT collagen from its Type 1A and 2A collagen amino acid sequences (NCBI BioProject: PRJNA408269) following Nehlich and Richards (2009). We estimated the theoretical sulphur content of BFT collagen at 0.47% (Table S3), therefore two 9–13th c. Istanbul samples (MRY3285 and MET12545, Table S2) were excluded from the dataset using the range (0.4%–0.8%) suggested by Nehlich and Richards (2009). However, modern BFT fell outside of the C:S (125–225) and N:S (40–80) criteria for archaeological collagen suggested by (Nehlich & Richards, 2009), and consequently, this additional criterion was not applied. To confirm that our results were robust to variable

C:S and N:S values (Table S2), we performed non-exact pairwise Wilcoxon tests in R (R Core Team, 2013) which reported that BFT δ^{34}S values do not significantly differ between samples falling inside or outside of the Nehlich and Richards (2009) C:S and N:S Ratio criteria (Wilcoxon, $p > .05$). Finally, we returned to quality checks after final data analyses and found no significant differences were found in N:S or C:S between samples from the pre- versus post 16th century (Wilcoxon, $p > .05$).

2.3 | Statistical analyses

We tested statistical pairwise differences in distribution between Black Sea, modern NE Atlantic and Mediterranean, and ancient NE Atlantic and Mediterranean isotope values, using non-exact pairwise Wilcoxon tests in R. To estimate the probability of a priori defined spatial groups being found within the same niche as each other we applied the overlap function using default settings and 10,000 iterations in the R package nicheROVER (Swanson et al., 2015). To avoid conflating temporal and spatial effects of Black Sea foraging, we used sample location to group all archaeological samples named 'Ancient NE Atlantic and Mediterranean', excluding 9–13th c. Istanbul samples, which formed their own group with 1941 Istanbul samples, named 'Black Sea'. 21st c. samples were grouped with the remaining archival samples and named 'Modern NE Atlantic and Mediterranean'. We tested the relationship between fork length (FL) and each isotope value using the *lm* linear regression function in R, for each of the three sample groups. A base10 log-linear model was applied to FL values as per Nakazawa et al. (2010) and Jennings (2005). Black Sea regressions were calculated excluding the 1941 Istanbul individuals ($n = 2$) to avoid confounding spatial and temporal patterns. We tested the statistical differences between inner and outer vertebrae isotope values for the 9–13th c. Istanbul samples using exact pairwise Wilcoxon tests.

Generalised additive models (GAMs) were used to assess linear and non-linear relationships between time (Century/Year CE) and space (Longitude E), and δ^{13}C, δ^{15}N and δ^{34}S values. Following Zuur et al. (2009), we selected a model with the lowest Akaike information criterion (AIC) using a backwards elimination of smoothed and unsmoothed factors (Table S4). Gaussian models with link functions were thus applied to a different suite of effects for each stable isotope as follows using the restricted maximum likelihood (REML) approach in the R package mgcv (Wood, 2012). The final models fitted for δ^{13}C and δ^{15}N was: $\delta X \sim s(\text{longitude}) + \text{Year:group}$, where group indicated a priori placement of samples into Black Sea or modern and ancient NE Atlantic and Mediterranean samples and only results for the latter were retained. This elimination of the Black Sea samples for temporal investigation reduced the possibility of spatial trends confounding temporal trends. The final model fitted for δ^{34}S was: $\delta^{34}S \sim s(\text{longitude, by} = \text{group}) + s(\text{Year})$, where the group indicated a placement of samples into pre-16th c. samples or post-16th c. samples, set based on visual observation of temporal changes in δ^{34}S values to assess spatial variability for both periods. Plotting factor pairs confirmed that collinearity was absent. Residuals were observed to be randomly distributed, and observations were positively correlated with predicted values in each case.

3 | RESULTS

Representing a temporal range of the last two millennia, we analysed a total of 118 BFT bone samples for δ^{13}C and δ^{15}N and 104 BFT bone samples for δ^{34}S. δ^{13}C values ranged from −15.8‰ to −11.3‰, δ^{15}N values ranged from 6.2‰ to 11.6‰ and δ^{34}S values ranged from 11.4‰ to 19.5‰ (Figure 2a,b). We observed a distinct clustering of Black Sea samples which generally had lower δ^{13}C, δ^{15}N and δ^{34}S values, than ancient or modern NE Atlantic and Mediterranean samples. The Black Sea trophic niche was statistically significantly different from Atlantic and Mediterranean sample niches across all three isotopes (Figure 2a,b, $p < .05$ to $< .001$) and had low overlap probabilities with both ancient (0%–3.5% CI) and modern (0%–12.0% CI) NE Atlantic and Mediterranean BFT niches (Figure S4).

Significant differences were also found between NE Atlantic and Mediterranean samples where modern samples generally had lower δ^{13}C ($p < .001$) and higher δ^{34}S values than ancient samples ($p < .01$, Figure 2c,e). Regressions revealed no significant relationships between δ^{13}C values and FL, though significant differences in δ^{13}C and δ^{15}N between inner and outer vertebrae pairs suggest the Black Sea niche is more different to NE Atlantic and Mediterranean niches at earlier than later life stages (Figure 2c,d). A significant positive relationship was found between δ^{15}N values and FL for modern NE Atlantic and Mediterranean samples ($p < .01$) and between δ^{34}S values and FL for ancient NE Atlantic and Mediterranean ($p < .01$) and ancient Black Sea samples ($p < .05$) whereas no significant relationship was found between δ^{15}N values and FL for ancient samples or between δ^{34}S values and FL for modern samples (Figure 2d,e).

GAMs fitted spatial and temporal models across a wide range of sample locations. Ancient and modern sample distributions overlapped considerably, where ancient samples were mostly caught around the western and central Mediterranean (around the strait of Gibraltar and Sardinia) while modern samples the central Mediterranean (around Sicily and Sardinia but including the Adriatic Sea and off Libya) except for southwest Iceland. It is important to note that splitting data for pre- and post-16th c. inferences increased sample distribution overlap temporally. For spatial (longitude) models, distributions included Black Sea (Istanbul, Turkey) sample locations. GAMs indicated δ^{13}C values were significantly influenced by longitude ($p < .001$, Table 2) whereby Atlantic locations and central Mediterranean and Black Sea locations had lower δ^{13}C values than the western Mediterranean samples (Figure 3a). There was no significant relationship between δ^{13}C or δ^{15}N values and time (year, Figure 3d,e). δ^{15}N was significantly explained by latitude

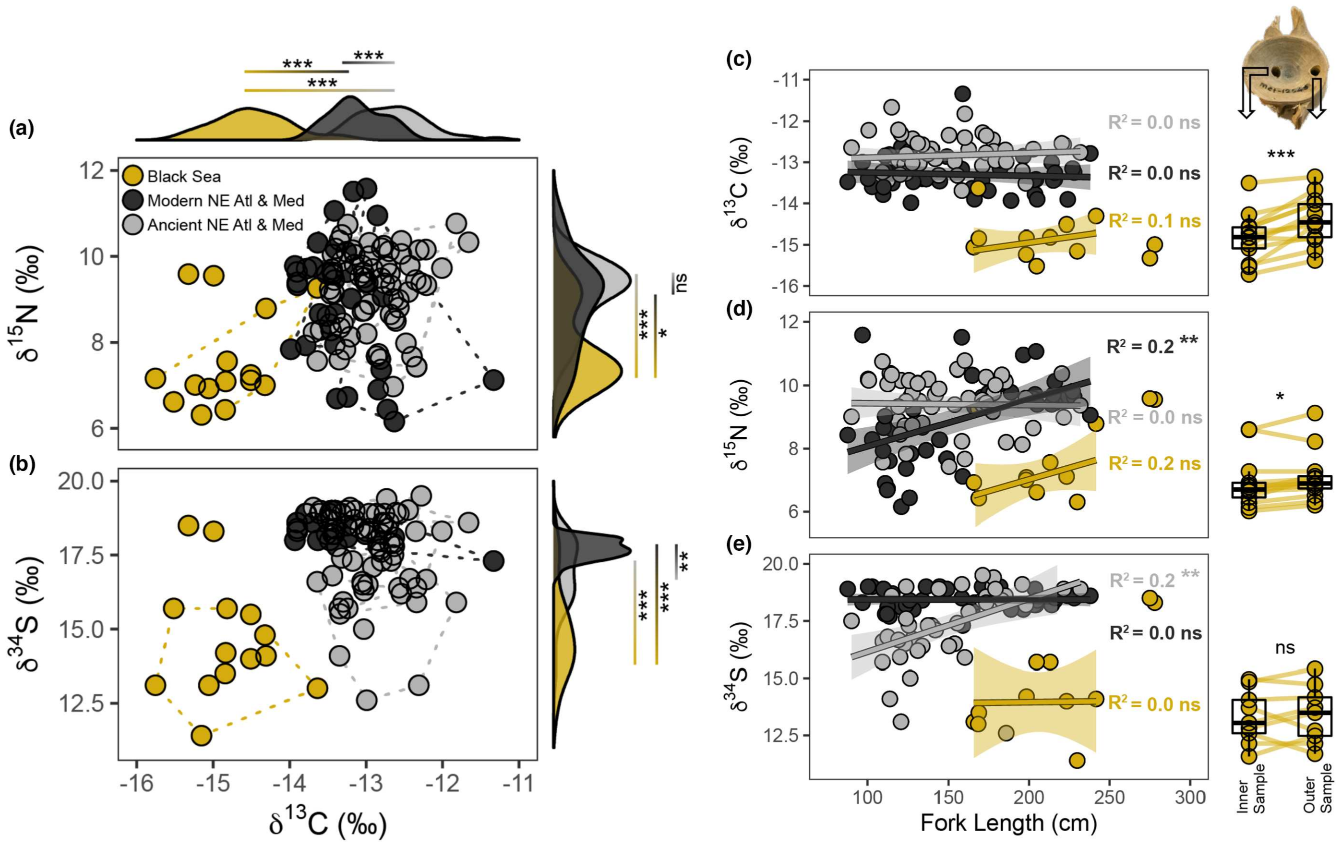

FIGURE 2 Findings of an isotopically distinct Black Sea niche of Atlantic bluefin tuna (BFT) and the relationship between foraging behaviours and body size. $\delta^{13}C$ and $\delta^{15}N$ scatterplots (a) and $\delta^{13}C$ and $\delta^{34}S$ scatterplots (b). Samples (symbols) are coloured according to their provenance as putative Black Sea (yellow), modern (black), ancient (grey) NE Atlantic and Mediterranean. Convex hull total areas (TA's) are shown for each sample group as dashed lines and density distributions are shown for each isotope with significance between groups tested by non-rank paired Wilcoxon tests. Relationships between fork length (FL) and isotope ratios (C, $\delta^{13}C$; D, $\delta^{15}N$ and E, $\delta^{34}S$) are shown using scatterplots and a lm smooth estimated using ggplot geom_smooth where shading indicates 95% CIs. Relationships were tested using linear regressions after FL was $\log_{10}$ transformed, where the regression coefficient (R^2) and significance were calculated. Black Sea regressions excluded the two 1941 Istanbul samples. Boxplots show differences in inner and outer vertebrae sample values for ancient Black Sea samples and each isotope (c–e) with yellow lines joining pairs of samples from the same specimen and significance between groups as tested by ranked paired Wilcoxon tests. Boxplots show group means, 25th and 75th percentile as outer edges and outliers illustrated outside of 95th percentiles (black whiskers). Significance is represented as 'ns' >.05, '*' <.05, '**' <.01 and '***' <.001.

($p < .001$) whereby central Mediterranean locations and Black Sea locations had lower $\delta^{15}N$ values (Figure 3b). $\delta^{34}S$ values were significantly explained by time ($p < .001$) where post-16th c. $\delta^{34}S$ values were greater (ca. 18%–19%) than pre-16th c. values (ca. 12%–18%, Figure 3f). Variation in pre-16th c. $\delta^{34}S$ values were significantly explained by longitude ($p < .001$) where a gradient existed of decreasing $\delta^{34}S$ values with eastward Mediterranean locations (Figure 3c). However, it must be noted that $\delta^{34}S$ values and longitude trends follow those of FL and thus both factors may contribute to $\delta^{34}S$ variability in ancient samples. Predictions of GAM models (Figure S5) support that spatial and temporal factors did not co-vary, and that there was no spatial relationship in $\delta^{34}S$ values across all samples.

4 | DISCUSSION

Our results identify a previously unknown increase in Mediterranean BFT $\delta^{34}S$ values around the 16th century, and that BFT which migrated to the Black Sea represented a unique component; isotopically distinct from both modern and ancient BFT of the NE Atlantic and Mediterranean. Low $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values of BFT from Istanbul dating at 9–13th c. and 1941 are indicative of sustained and consistent foraging within the Black and Marmara Sea, due to the hydrography of the region. One reasonably predicts that highly stratified, low surface salinity waters, above an anoxic layer would result in low $\delta^{15}N$ values due to primary nitrogen fixation by phytoplankton (Fulton et al., 2012), low $\delta^{13}C$ values due to low salinity (Magozzi et al., 2017) and low $\delta^{34}S$ where sulphate is derived from microbial sulphides in sub-oxic waters (Neretin et al., 2003). Observations indeed show low $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values at the ecosystem level in the Black Sea, including in BFT prey (e.g. anchovy, *Engraulis encrasicolus*, Engraulidae: ca. −20‰ $\delta^{13}C$, 6‰ $\delta^{15}N$) (Bănaru et al., 2007; Çoban-Yıldız et al., 2006; Das et al., 2004; Lenin et al., 1997; Mutlu, 2021). Contextual $\delta^{34}S$ isotope data from this region is limited, though we theorise that ancient BFT foraged on benthic-pelagic prey of Marmara, NW shelf ecosystems of the Black

TABLE 2 Generalised additive models parameter estimates for BFT δ^{13}C, δ^{15}N and δ^{34}S, and variance structure of the data for the spatiotemporal models.

	δ^{13}C			δ^{15}N			δ^{34}S		
Predictors	**Estimate**	***t/F***	***p***	**Estimate**	***t/F***	***p***	**Estimate**	***t/F***	***p***
Intercept	−13.01	−97.73	<.001	8.44	28.45	<.001	17.56	196.4	<.001
Year: Mediterranean	−1.6e-4	−1.813	.073	9.6e-5	0.482	.63	3.99	46.81	**<.001**
Longitude	3.73	6.45	**<.001**	4.20	9.80	**<.001**			
Longitude: pre 16th c.	—	—	—	—	—	—	1.00	46.26	**<.001**
Longitude: post 16th c.	—	—	—	—	—	—	1.00	0.31	.86
Residual variance	0.21			0.99			0.72		
R^2	.66			.36			.78		
Deviance explained	68.0%			39.3%			78.9%		
df	8.11			8.52			8.39		

Note: Significant predictors are shown in boldface, judged at the .05 level. *t/F* indicates *t* or *F* statistic for each test. Results for Year are shown only for Mediterranean samples. Longitude pre/post-16th c. indicates samples pre and post 16th c. were pooled to assess the effect of latitude in both periods.

Sea and the Azov Sea, because BFT δ^{34}S values were lower than the pelagic zones of these habitats (ca. 17‰, Lenin et al., 1997). This may be explained by low δ^{34}S values being linked with neritic or benthic feeding in fishes (Cobain et al., 2022; Leakey et al., 2008; Szpak & Buckley, 2020), supporting archaeological bone finds and classical authors over millennia (Andrews, Di Natale, et al., 2022; Karakulak & Oray, 2009).

4.1 | BFT had an isotopically unique Black Sea niche

Since BFT bone is likely to record multiple years of foraging behaviour (Andrews et al., 2023), the observed significantly different Black Sea isotope values and low NE Atlantic and Mediterranean overlap proportions suggest that most Black Sea BFT migrated consistently to–or were resident in–this region over multiple years for foraging while NE Atlantic and Mediterranean BFT seldomly used this region as a foraging habitat. Indeed, high-site fidelity has been reported in BFT (Block et al., 2005; Cermeño et al., 2015) but our findings would go further, supporting tagging data (De Metrio et al., 2004) to suggest that current Atlantic foraging behaviours are probably not characteristic of all BFT, even at large body size (Rouyer et al., 2022).

From the 15th c., Bosphorus trap fisheries recorded BFT migrations into the Black Sea from April, with the majority believed to return to the Marmara Sea or Aegean Sea by September, due to poor winter conditions (Cort & Abaunza, 2019; Karakulak & Oray, 2009). We consider it likely that low δ^{13}C, δ^{15}N and δ^{34}S values in BFT from Istanbul were promoted by autumn or winter foraging in the Marmara or Black Sea, as predicted by early-20th c. scientists (Devedjian, 1926; Sara, 1964)–and supporting sparse catch data (Di Natale et al., 2019)–because the Aegean Sea and the Mediterranean proper are higher ^{13}C environments (Magozzi et al., 2017; Wells et al., 2021). Nonetheless, it remains challenging to assess proportions of time spent foraging in each habitat from isotope data alone. Since May–July is the spawning period for BFT in the Mediterranean, it therefore remains unknown if BFT individuals from the Black Sea skipped spawning or represented a separate spawning population (Di Natale, 2015; MacKenzie & Mariani, 2012).

Isotopic analysis of inner and outer Black Sea vertebrae samples suggests that earlier life stages (with lower δ^{13}C and δ^{15}N values), may have been more resident in the Black or Marmara Sea while later life stages (with higher δ^{13}C and δ^{15}N values) were more Mediterranean, which is indicative of increased spawning migrations to the Mediterranean with age. Alternatively, our data may support spawning in the Black Sea where Mediterranean overwintering and/or foraging increased with age. There are uncertainties on reports of BFT eggs and larvae found in the Black Sea (Di Natale, 2015; Mather et al., 1995), although adaptation to spawn this low-salinity environment is possible for BFT (MacKenzie & Mariani, 2012) and adults have been found in the Black Sea with ripe gonads (Di Natale, 2015). Genomic analysis is required to exclude the possibility that Black Sea BFT represented a separate spawning population but since preliminary genetic results (Andrews et al., 2021) did not support this theory and juveniles have never been caught in this region (Di Natale, 2015), we find it more likely that the Black Sea migration and the Marmara Sea residency was a prey-dependent, learned behaviour, as part of a collective memory, which takes time to rebuild (De Luca et al., 2014; Petitgas et al., 2010). Regardless, the return of Black Sea BFT will depend heavily on the recovery of ecosystems and trophic cascades in the Marmara Sea, Black Sea and Azov Sea, which remain poor after overexploitation (Demirel et al., 2020; Ulman et al., 2020). Climatic cooling and the increase in alien species resulted in heavy modification during the 20th c., and induced the collapse of multiple stocks (Karakulak & Oray, 2009; Oguz & Gilbert, 2007; Shiganova et al., 2001; Zaitsev, 1992). However, there is some evidence of Black Sea BFT returning (Di Natale et al., 2019), which may indicate that ecosystem recovery has begun.

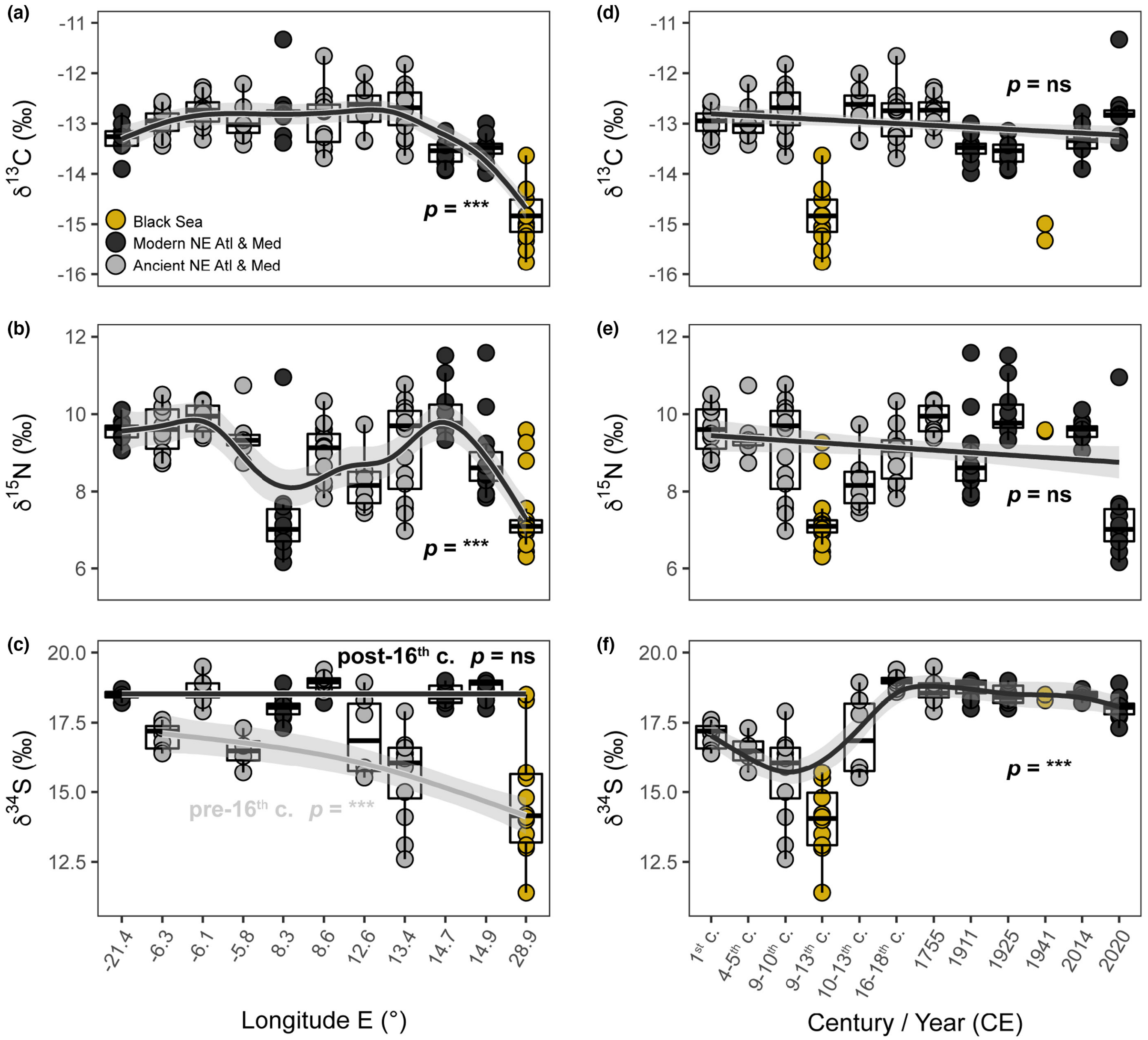

FIGURE 3 Spatial and temporal relationships with isotope values explaining variation in Atlantic bluefin tuna (BFT) foraging ecology. Relationships between isotope values and Longitude (a–c) or Century/Year CE (d–f) analysed using generalised additive models (GAM) are illustrated as smoothed (non-linear) or non-smoothed (linear) lines of fit with 95% CI shading as calculated using the geom_smooth function in ggplot2 with gam or lm specified, respectively. *p*-values are shown as estimated in GAM models where 'ns' >.05, '*' <.05, '**' <.01 and '***' <.001. Black Sea samples were excluded from century/year lines of fit. Boxplots are shown for each BFT sample group with group means, 25th and 75th percentile as outer edges and outliers illustrated outside of 95th percentiles (black whiskers). Samples (circles) are coloured according to their provenance as putative Black Sea (yellow), modern (black) and ancient (grey) NE Atlantic and Mediterranean sample groups. Plots for each stable isotope are illustrated separately: δ^{13}C (a, d), δ^{15}N (b, e) and δ^{34}S (c, f).

4.2 | Two millennia of stability in BFT trophic position

Isotope values of BFT bone across centuries broadly reflected benthic-pelagic foraging, at moderate trophic levels (δ^{15}N) which increased significantly with size, supporting several studies (Estrada et al., 2005; Karakulak et al., 2009; Logan, 2009; Logan et al., 2011; Sarà & Sarà, 2007). Spatial relationships suggested that NE Atlantic and central-eastern Mediterranean fish foraged less in shelf waters, and more offshore (depleted ^{13}C); probably due to deep-diving opportunities in these locations (Battaglia et al., 2013; Olafsdottir et al., 2016; Wilson & Block, 2009), and/or their lower δ^{13}C baselines as a result of less benthic-pelagic coupling (Magozzi et al., 2017; Pinzone et al., 2019). Spatial relationships in δ^{15}N values further suggested that some Mediterranean catches, like the 2020 sample with low δ^{15}N values, may have foraged mostly, or solely offshore (Logan et al., 2023; Rafter et al., 2019; Wells et al., 2021). Relationships between size and δ^{15}N values in modern samples also support that smaller adults akin to 2020 catches (ca. 100–200 cm FL) may remain in the Mediterranean after spawning (Addis et al., 2016; Cermeño et al., 2015).

Lack of temporal δ^{13}C and δ^{15}N trends does not suggest that exploitation and climate have not shifted BFT diet and distribution over centuries–they surely have (Faillettaz et al., 2019; Fromentin et al., 2014). However, we found no isotopic evidence for a change in BFT trophic position across millennia despite marine ecosystem changes such as 'fishing down marine food webs' and the loss of large size-classes (Baum & Worm, 2009; Pauly et al., 1998). This finding appears striking considering that prey size has been shown to be an important driver of BFT condition (Golet et al., 2015), and that other tunas have shifted in isotope composition during the past two decades in the Atlantic (Lorrain et al., 2020). However, BFT is likely to be highly generalist, as supported by relatively its low δ^{15}N values (for predatory marine fish), which may have provided resilience against changes in marine food webs. Indeed, an increase in generalist BFT foraging strategies have been hinted at recently, on the importance of gelatinous prey (Günther et al., 2021), which is likely to promote resilience to changes in prey availability or size, as has been shown for marine cetaceans over time (Samarra et al., 2022). We acknowledge, however, that the presence of spatial and size relationships added noise to our dataset, which limits temporal observations. This issue may be overcome through the application of compound specific isotope analysis (CSIA) to disentangle source versus trophic effects (e.g. Logan et al., 2023) and confirm that despite regime shifts (Beaugrand et al., 2015; Conversi et al., 2010; Drinkwater, 2006; Siano et al., 2021; Tomasovych et al., 2020), BFT have been robust to ecosystem changes.

4.3 | Early coastal degradation induced a pelagic shift in BFT

Compared with carbon and nitrogen, sulphur offered greater sensitivity to detect temporal foraging shifts, probably due to its greater variation in benthic versus pelagic prey (Fry et al., 1982). In BFT, we observed a novel post-16th c. shift in δ^{34}S, to values indicative of predominantly pelagic energy sources (ca. 18–19‰, Thode, 1991) in the absence of δ^{34}S shifts at the base of marine food webs during the past two millennia (Newton & Bottrell, 2007). Thus, we propose an increased preference for neritic or benthic opportunistic foraging until the ~16th century, which may have reduced due to the early degradation of coastal ecosystems during this period (Hoffmann, 2005; Jackson et al., 2001). Within the Mediterranean and Black Sea, we found that δ^{34}S declined with distance from the Atlantic. Yet, size-effects were also evident, perhaps reflecting that smaller BFT are more residentiary and neritic-feeding than larger individuals (Cermeño et al., 2015; Rouyer et al., 2022)—and perhaps more so historically than today. δ^{34}S values are relatively consistent among pelagic marine habitats worldwide (Thode, 1991), suggesting that our observation is indeed benthic-related. Given that δ^{34}S of benthic production (e.g. seagrass) varies spatially (Frederiksen et al., 2008), we cannot exclude that the observed δ^{34}S shift may alternatively reflect reduced foraging locally on low ^{34}S Mediterranean habitats (e.g. inshore habitats linked to seagrass production). GAM predictions nonetheless did not support a solely spatial explanation, showing a lack of a spatial relationship in δ^{34}S across all samples, while temporal patterns were indeed evident. Black Sea foraging of low δ^{34}S individuals is another unlikely explanation, given that δ^{13}C values were consistent with higher δ^{34}S Mediterranean individuals and unlike samples from Istanbul.

Whether BFT have shifted to forage on more pelagic prey or in higher ^{34}S habitats than previously, our observations are strongly supported by 16th c. transcripts documenting the overexploitation of BFT prey and disturbance of inshore habitats off Spain; specifically linking these with a lower productivity of tuna traps, which was not overcome until trap technology developed into more offshore operations (Andrews, Di Natale, et al., 2022). We theorise that post-Middle Age exploitation induced an early tipping point in BFT foraging in the Mediterranean, while a second tipping point (perhaps more difficult to cross) in trophic position appears not to have been reached following more recent intensive exploitation of marine ecosystems. Today, BFT take varying degrees of benthic prey, but pelagic prey makes up the predominant component (Karakulak et al., 2009; Logan et al., 2011, 2023; Sarà & Sarà, 2007).

The recent dominance of invertebrates in anthropised marine ecosystems (Howarth et al., 2014) seems to contradict our novel δ^{34}S conclusion since they provide inshore foraging opportunities. However, BFT may feed heavily on gelatinous prey and cephalopods (Günther et al., 2021) and are predominantly inhabiting basin regions rather than inshore waters in the Mediterranean (Cermeño et al., 2015). Moreover, a similar shift in sulphur isotopes between ancient and modern samples is apparent in the overexploited Atlantic cod (Nehlich et al., 2013), and therefore further research is required to better define the onset of coastal marine exploitation and modification of food webs for baselines of modern ecosystem status. The δ^{34}S shift appears to have occurred across BFT's eastern range, as evident in the two archived specimens collected by M. Sella from Istanbul in 1941. This implies that a return of BFT to the Black Sea will not only be dependent on the restoration of inshore areas since BFT fed more pelagically prior to its disappearance from the region.

4.4 | Consequences for management and conservation

While limited in sample size, the isotopic data presented here provide the first information on the foraging ecology of the Black Sea niche of BFT, with which to guide their return. They suggest that limiting catches throughout the eastern Mediterranean may promote divergent migration strategies, even if these may have a behavioural rather than evolutionary basis. The potential need to manage Mediterranean BFT as more than one stock has been previously hinted at, in-part due to proposed Mediterranean residency of some individuals (Cermeño et al., 2015; Cort & Abaunza, 2019;

De Metrio et al., 2004; Di Natale, 2019; Fromentin, 2009; Mather et al., 1995; Riccioni et al., 2010), and requires further genomic, CSIA and tagging studies. Our novel finding of a pre-industrial shift in BFT foraging highlights the importance of recovering neritic prey and habitats, which probably cannot be recovered to ancient levels (Atmore et al., 2021; Duarte et al., 2020), but are nonetheless likely to promote the recovery of BFT across its eastern range. Our results demonstrate the uniqueness of the isotopic niche of Black Sea BFT, which unfortunately disappeared due to overexploitation, hence reducing the diversity of BFT life histories which potentially has consequences for the ability of BFT to adapt to dynamic environments. We conclude, however, that the inability to re-establish ancient inshore habitats should not hinder the return of BFT to the Black Sea. Instead, we suggest that effort should be made to recover the heavily overexploited and degraded ecosystems of the Marmara Sea, Black Sea and Azov Sea; which could promote occurrence of BFT in the region.

AUTHOR CONTRIBUTIONS

AJA, FT and MA designed the study. AJA, PA, DB-C, VA, VO, GC, VG-F, VC and AU collected vertebrae samples for analysis. AJA, MVT, MF-C, EC and AU conducted the laboratory work. AJA analysed the data. AJA, ADN, FT, CP and MA wrote the paper. All authors reviewed the paper.

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CONFLICT OF INTEREST STATEMENT

No conflicts of interest exist.

DATA AVAILABILITY STATEMENT

All data analysed herein can be retrieved from the Table S2.

ORCID

Adam J. Andrews https://orcid.org/0000-0002-9000-6523

Fausto Tinti https://orcid.org/0000-0002-8649-5387

Michelle Alexander https://orcid.org/0000-0001-8000-3639

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