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Review Article

Exploitation history of Atlantic bluefin tuna in the eastern Atlantic and Mediterranean—insights from ancient bones

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Overexploitation has directly, negatively affected marine fish populations in the past half-century, modifying not only their abundance but their behaviour and life-history traits. The recovery and resilience of such populations is dependent upon their exploitation history, which often ex-tends back millennia. Hence, data on when exploitation intensified and how populations were composed in historical periods, have the potential to reveal long-term population dynamics and provide context on the baselines currently used in fisheries management and conservation. Here, we setup a framework for investigations on the exploitation history of Atlantic bluefin tuna (*Thunnus thynnus*; BFT) in the eastern Atlantic and Mediterranean by collating records of their zooarchaeological remains and critically reviewing these alongside the literature. Then, we outline how novel multidisciplinary applications on BFT remains may be used to document long-term population dynamics. Our review of literature provides clear evidence of BFT overexploitation during the tmid-20h century CE. Furthermore, a strong case could be made that the intensi-fication of BFT exploitation extends back further to at least the 19th century CE, if not the 13th–16th century CE, in the eastern Atlantic and Mediterranean. However, a host of archaeological evidence would suggest that BFT exploitation may have been intensive since antiquity. Alto-gether, this indicates that by the currently used management baselines of the 1970s, population abundance and complexity was already likely to have declined from historical levels, and we identify how biomolecular and morphometric analyses of BFT remains have the potential to further investigate this.

Keywords: biomolecular analyses, fish remains, historical baselines, historical marine ecology, *Thunnus thynnus*, zooarchaeology.

Introduction

Overexploitation has negatively impacted marine fish populations in various ways during the last half-century (Jackson *et al.*, 2001; Pauly *et al.*, 2002; Butchart *et al.*, 2010). While depleting the abun-dance of populations, overexploitation has been shown to im-pact population complexity through e.g. the extinction of sub-populations, the contraction of geographical ranges, the restructuring of age classes, as well as modifying a host of other life-history traits which are intertwined such as fecundity, maturation, growth, migration and spawning behaviour, and diet use (Jennings *et al.*, 1998; Rochet, 1998; Heino *et al.*, 2015; Hutchings and Kuparinen, 2021).

A prerequisite for documenting these changes is the availability of fisheries and ecological data from different time points to be compared. However, prior to 1970 and especially 1950 this data is lacking; precluding the opportunity to contexualize recent change in a historical perspective when exploitation rates were lower and when climate conditions were different (Erlandson and Rick, 2010; Lotze *et al.*, 2014). Accordingly, we have a poor understanding on the long-term drivers of population dynamics (Jackson *et al.*, 2001; Erlandson and Rick, 2010; Schwerdtner Máñez *et al.*, 2014; Rodrigues *et al.*, 2019), whether exploitation has caused plastic or evolutionary (inherited) responses (Heino *et al.*, 2015; Hutchings and Kuparinen, 2021), and thus, it is unknown how resilient populations are now, compared to their natural potential (Pauly, 1995; Pauly *et al.*, 2002; Butchart *et al.*, 2010; Erlandson and Rick, 2010; Neubauer *et al.*, 2013; Rodrigues *et al.*, 2019).

Therefore, past reference points (or historical baselines) of population abundance and complexity have the potential to improve the management and conservation of marine fish populations—especially those which have been recently overexploited, yet have a long exploitation history (Lotze *et al.*, 2014; Schwerdtner Máñez *et al.*, 2014). Indeed, population recovery is dependent upon the duration and intensity of exploitation (Neubauer *et al.*, 2013; Hutchings and Kuparinen, 2021), and the sustainability of catches is dependent upon identifying how/when anthropogenic activities and climatic events can negatively impact populations, and minisming these (Hilborn *et al.*, 2003; Berkeley *et al.*, 2004). Here, we critically review archaeological and historical information to qualitatively investigate the exploitation history of Atlantic bluefin tuna (*Thunnus thynnus*; BFT) in the eastern Atlantic and Mediterranean. Furthermore, we setup a framework to enable quantitative investigations of historical exploitation impacts by collating a database of zooarchaeological records and identifying how these as well as archived fish remains may provide novel historical baselines for population abundance and complexity.

Few species have an exploitation history as long and as intensive as BFT, which was famously overexploited since at least the 1980s (Porch *et al.*, 2019) and supported one of the first commercial fisheries (beginning ~8th century BCE; García-Vargas and Florido del Corral, 2010; Di Natale, 2014). The status of the east-ern Atlantic and Mediterranean BFT population is currently judged against management baselines from the 1970s, i.e. from when fisheries catch data was more accurately collected for this species. Yet, we hypothesize that exploitation had already impacted BFT by the 1970s according to the huge economic and cultural importance of this population historically, as documented by many reviews (e.g. MacKenzie and Myers, 2007; MacKenzie *et al.*, 2009; Fromentin, 2009; Karakulak and Oray, 2009; Di Natale, 2010, 2014; Longo and Clark, 2012; Orenc *et al.*, 2014; Cort and Abaunza, 2019; Porch *et al.*, 2019; Di Natale *et al.*, 2020).

The historical exploitation of BFT has predominantly been investigated from historical literature sources, such as the locations of tuna traps (Pagá García *et al.*, 2018), and their catches, from the 16th century CE onwards (Ravier and Fromentin, 2001, 2004; Pagá García *et al.*, 2017). However, the use of zooarchaeological remains (BFT bones and scales) has been neglected and restricted to selected periods and regions (Morales-Muñiz, 1993; Felici, 2018; García-Vargas *et al.*, 2018; Nielssen and Persson, 2020; Mylona, 2021). Despite this, fish remains can offer additional biological insights into past population abundance and complexity, not feasible with fishery catch data, especially *via* multidisciplinary applications of biomolecular and morphometric analyses (Erlandson and Rick, 2010; Orton, 2016; Morales-Muñiz *et al.*, 2018).

Biomolecular applications on fish remains can provide quantitative metrics of demographic and adaptive change over time, as already achieved using genetics/genomics for archaeological (Oosting *et al.*, 2019) but predominantly archived fish samples (Nielsen and Hansen, 2008). Isotopic and element analyses can enable the detection of changes in past environmental conditions, diet, habitat use, and growth (Orton, 2016; Matsubayashi *et al.*, 2017; Blankholm *et al.*, 2020; Guiry *et al.*, 2020). Moreover, archaeological fish bone is a particularly promising archive of information since DNA and proteins can be well preserved and remodelling rates are slow (Ferrari *et al.*, 2020). In addition, morphometric studies offer equally promising opportunities to study growth rate changes over time by studying the growth rings of vertebrae or otoliths (ear bones; Van Neer *et al.*, 1999; Bolle *et al.*, 2004; Ólafsdóttir *et al.*, 2017).

Qualitative metrics produced by traditional zooarchaeology, i.e. observations on the number and sizes of remains found in archaeological assemblages, differ significantly from those derived using biomolecular tools and morphometrics. Traditional zooarchaeological data are vital in providing an indication of when and where species were exploited, how species were distributed (Barrett *et al.*, 2004; Hoffmann, 2005), and which sizes of fish were exploited (Maschner *et al.*, 2008; Barrett, 2019). However, like historical data (e.g. tuna trap catches), raw archaeological data (e.g. the number of fish bones) require interpretation. They are by nature incomplete because of a long series of processes depending on which fish were available, could be fished, were consumed, and how remains were disposed of. In addition, their recovery depends on how well remains preserve, are retrieved and reported.

The objectives of this study were to (1) collate zooarchaeological BFT records, (2) critically assess the extent of historical exploitation based on these records and the literature, and (3) outline how BFT remains might be used to generate quantitative historical baselines for population abundance and complexity. This knowledge is of importance to glean historical insights on the long-term drivers of population dynamics and the impact of exploitation.

A background on Atlantic bluefin tuna

BFT is a highly migratory pelagic predator (up to 3.3 m in length and 725 kg in weight: Cort *et al.*, 2013), whose populations were under threat from overexploitation until very recently (Porch *et al.*, 2019). Since 1980, BFT have been managed as two stocks (Fromentin and Powers, 2005), a hypothesis supported by recent isotopic (Rooker *et al.*, 2008) and genomic (Puncher *et al.*, 2018) studies. These are a western Atlantic population that spawns predominantly in the Gulf of Mexico, and an eastern Atlantic population that spawns predominantly in the Mediterranean: off the Balearic Islands, Sicily, Malta, Libya, and in the Levantine Sea (García *et al.*, 2005; Piccinetti *et al.*, 2013). Both populations comprise of individuals that migrate into the Atlantic Ocean to feed, including as juveniles (Cort and Abaunza, 2019), exhibiting high-levels of connectivity and homing to spawning grounds between April and July to optimum spawning temperatures of ∼24°C (Rooker *et al.*, 2008). The role of additional spawning areas, i.e. the Slope Sea (West of Cape Hatteras, USA: Richardson *et al.*, 2016), the Bay of Biscay (Rodriguez *et al.*, 2021), or other Atlantic areas (Azores, Canary Islands, Ibero-Moroccan, and Gulf of Guinea, Mather *et al.*, 1995; Piccinetti *et al.*, 2013), are yet to be defined.

The current work will deal only with the proportionally (∼10 times) larger eastern Atlantic and Mediterranean stock, which in 2007 was considered depleted, consistent with a 60% decline in spawning biomass (adult fish) from 1970s levels (ICCAT, 2007), a restructuring of the population toward younger individuals (Fromentin, 2009; Siskey *et al.*, 2016), and modelling predictions of impending collapse (MacKenzie *et al.*, 2009). These losses in abundance and population complexity were driven by overfishing that occurred especially following the demand of BFT for farming (fattening in cages) from the 1990s onwards (Porch *et al.*, 2019). Thus, the 1990s and early 2000s experienced record annual catches of > 60000 t, before ICCAT (International Commission for the Conservation of Atlantic Tunas) imposed strict quotas to limit catches from 2003 (Fromentin, 2003; ICCAT, 2017). In the last decade, quotas have (along with several years of favourable oceanographic conditions for spawning) recovered recruitment and spawning biomass of the eastern Atlantic and Mediterranean stock to 1970s levels, and therefore, quotas have increased (ICCAT, 2020). However, we suggest that archaeological and historical data may reveal if population abundance and complexity had reduced by 1970, and if so, quantify by how much.

Materials and methods

Zooarchaeological records were data-mined from reports in multiple languages, including unpublished reports. We accumulated records identified only as BFT or large specimens of the genus *Thunnus* with the caveat that juvenile BFT remains are challenging to distinguish morphologically from albacore (*Thunnus alalunga*). Both species have overlapping distributions in the eastern Atlantic and Mediterranean, although albacore inhabits offshore waters (Bard, 1974) and would not be routinely caught with in-shore fishing methods used to target BFT in any period described herein. In addition, albacore reaches a maximum length of ∼1.5 m at 13 years (Bard, 1974), whereas the same size BFT is ∼6 years old (Rodríguez-Marín *et al.*, 2004). Therefore, species can, in theory, be identified by size and vertebral growth rings (Rodríguez-Marín *et al.*, 2006)—unless remains are fragmented. Molecular identification methods, i.e. Zooarchaeology by Mass Spectrometry (ZooMS) collagen protein fingerprinting (Rick *et al.*, 2019) or genetic barcoding (Puncher *et al.*, 2019) were not utilized by any of the studies included, therefore, we assume that these records are in fact BFT but urge caution in their future use and interpretations.

We mapped the location of archaeological BFT remains alongside fish processing facilities—called *cetariae* in antiquity (active from 550 years BCE to 700 years CE, from the RAMPPA Project: https://ramppa.uca.es/), and 16th–20th century CE BFT trap catch sites (from Pavesi, 1889; Devedjian, 1926; Ravier and Fromentin, 2001; Pagá García *et al.*, 2017) to provide context for zooarchaeological remains and indicate potential new sources of BFT archaeological remains yet to be explored. Our database of zooarchaeological records is unlikely to be absolute due to difficulties in accessing grey literature and because new records are in constant discovery. To tackle this, we established the accessible online portal https://tunaarchaeology.org/, allowing researchers to access records and input new records.

Scavenging and subsistence fishing (140000 years BCE–10t hcentury BCE)

Zooarchaeological evidence is paramount to understand the extent, scale, and development of fishing in prehistory, i.e. before writ-ten sources exist. The earliest evidence of BFT are vertebrae dating to the Eemian Period (∼140000 years BCE), recovered from near Svenborg, Denmark (SNM Copenhagen, Pers. Comm. K. Kjaer), and vertebrae associated with Neanderthal habitations in Gorham's Cave, Gibraltar (26000–22000 years BCE, Brown *et al.*, 2011). It is unclear if these finds represent fishing, or cases of opportunistic scavenging following episodic beaching events, perhaps caused by orca (*Orcinus orca*, Cort and Abaunza, 2019). Paintings of BFT in Genovese's Cave on the isle of Levanzo (near Sicily, Italy), dated to ∼9200 years BCE (Tusa, 1999; Spoto, 2002), are the earliest reliable sources of evidence that BFT fishing had begun in the Mediterranean, and was clearly of some cultural importance by the Mesolithic. This is supported by the recovery of BFT vertebrae from a wide spatial extent of sites dating from 10000–5800 years BCE in modern-day Spain, France, and Croatia (Supplementary Table S1), and especially in the Aegean Sea between 9000 and 3200 years BCE (Figure 1), which we consider to be the result of increased archae-ological effort throughout Greece.

Vertebrae recovered from these prehistoric cave sites are mostly few (Supplementary Table S1), yet, at Franchthi and Saliagos (Aegean Sea, Greece), the recovery of hundreds or thousands of vertebrae (Evans and Renfrew, 1968; Rose, 1994) indicate that by the Neolithic, BFT was already being caught at some scale. This may suggest that Neolithic coastal communities were expert fishers (Evans and Renfrew, 1968), but we caution that species identifications from these early excavations might not be reliable. In any case, such catches could simply reflect episodic events where, for example, prey lured BFT into shallow waters and enabled fishing. Likewise, predators such as orca could have beached or corralled BFT into shallow waters as is commonly observed around the Strait of Gibraltar (Wilson and Mittermeier, 2014; Cort and Abaunza, 2019). It is unlikely that Neolithic catches evidence fishing on scale greater than subsistence, because large BFT would be challenging to catch by hook and line or harpoon – the predominant fishing methods in this period (Mylona, 2014; Nielssen and Persson, 2020). Nets were probably not used to target BFT in prehistory due to limitations in the strength of organic yarns (Mylona, 2014), precluding the opportunity to catch BFT on its spawning migration when it does not take bait (Lozano Rey, 1952), other than by spearfishing in a few suitable locations. However, by the 12th century BCE, Mycenaean ceramics depicting early beach-seine fishing of BFT (Hadjianastiasiou, 1991; Sarà, 1998), suggest that such fishing methods had developed during the Bronze Age in the Aegean, though a lack of zooarchaeological records are available to corroborate this (Supplementary Table S1). Nonetheless, hook and line boat fishing was still carried out

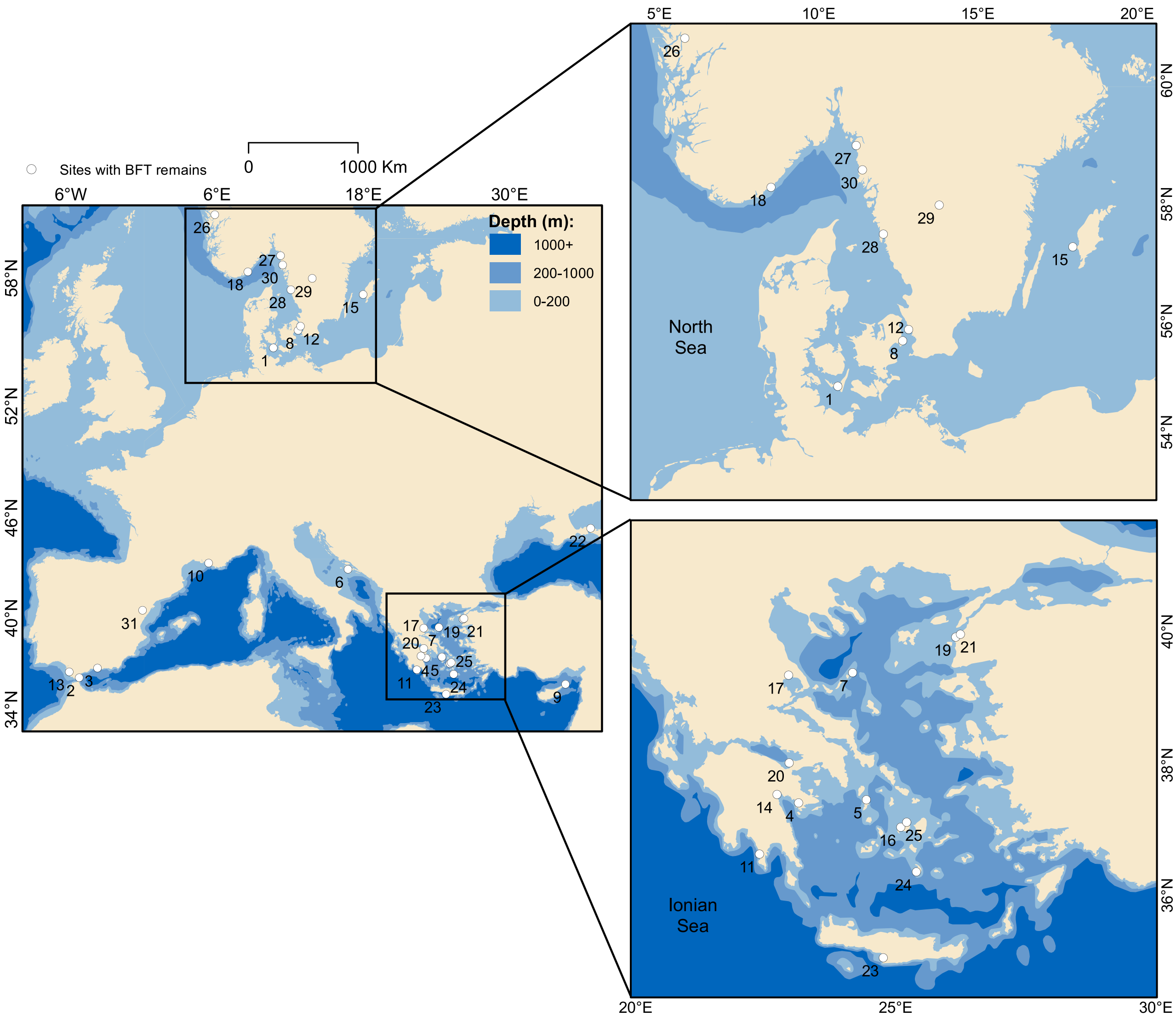

Figure 1. Map of Atlantic bluefin tuna (*T. thynnus;* BFT) archaeological remains recovered prior to the 9th century BCE. For numbering refer to Supplementary Table S1.

at least a century later as depicted on Cypriot ceramics (Iacovou, 1988).

It is evident that prehistoric BFT capture also occurred in the northeastern Atlantic, albeit probably on a smaller scale (Supplementary Table S1). Scores of archaeological excavations in Norway, Sweden, and Denmark report BFT remains dating to 6800–3500 years BCE (as reviewed in Enghoff *et al.*, 2007; Nielssen and Persson, 2020; Supplementary Table S1; Figure 1) when conditions in the northeastern Atlantic were warmer than at present and were probably favoured by BFT (Enghoff *et al.*, 2007). Early Nordic fishing appears to have targeted BFT and orca together with harpoons (Nielssen and Persson, 2020), perhaps while orca corralled BFT into shallow waters as we suspect in the Mediterranean. BFT remains have also been found far into the Baltic Sea, at Neolithic Gotland (5200–4000 years BCE; Ericson, 1989; Knape and Ericson, 1983). The Baltic Sea was more saline during this period than today (Enghoff *et al.*, 2007), but BFT would still have exhibited the same low salinity tolerance here as during their residency in the Black Sea, where they were also clearly distributed from at least 2000 years BCE (Rose, 1994; Uerpmann and van Neer, 2000; Lyashenko, 2006; Figure 1).

Commercial Phoenician-Punic, Greek, and Roman fisheries (9th century BCE–7th century CE)

During the beginning of the 1st millennium BCE, the large-scale trade of goods throughout the Mediterranean was vastly accelerated due to the Phoenician colonization of the western Mediterranean. Accordingly, it is believed that BFT fisheries were commercialized around the 8th century BCE in the western Mediterranean (Di Natale, 2012, 2014; Cort and Abaunza, 2019). The earliest attestable evidence of trade (transport) is from 7th century BCE amphorae containing BFT vertebrae and scales, which were found at an inland site in southern Spain and according to their design, originated from the Malaga region (Aguayo de Hoyos *et al.*, 1987). Remains of Punic-era salting factories at Cadiz and Sicily from the 6th century BCE (Figure 2) also testify this early trade in the Mediterranean. BFT remains have been found at major Punic sites, e.g. Lixus, Ceuta,

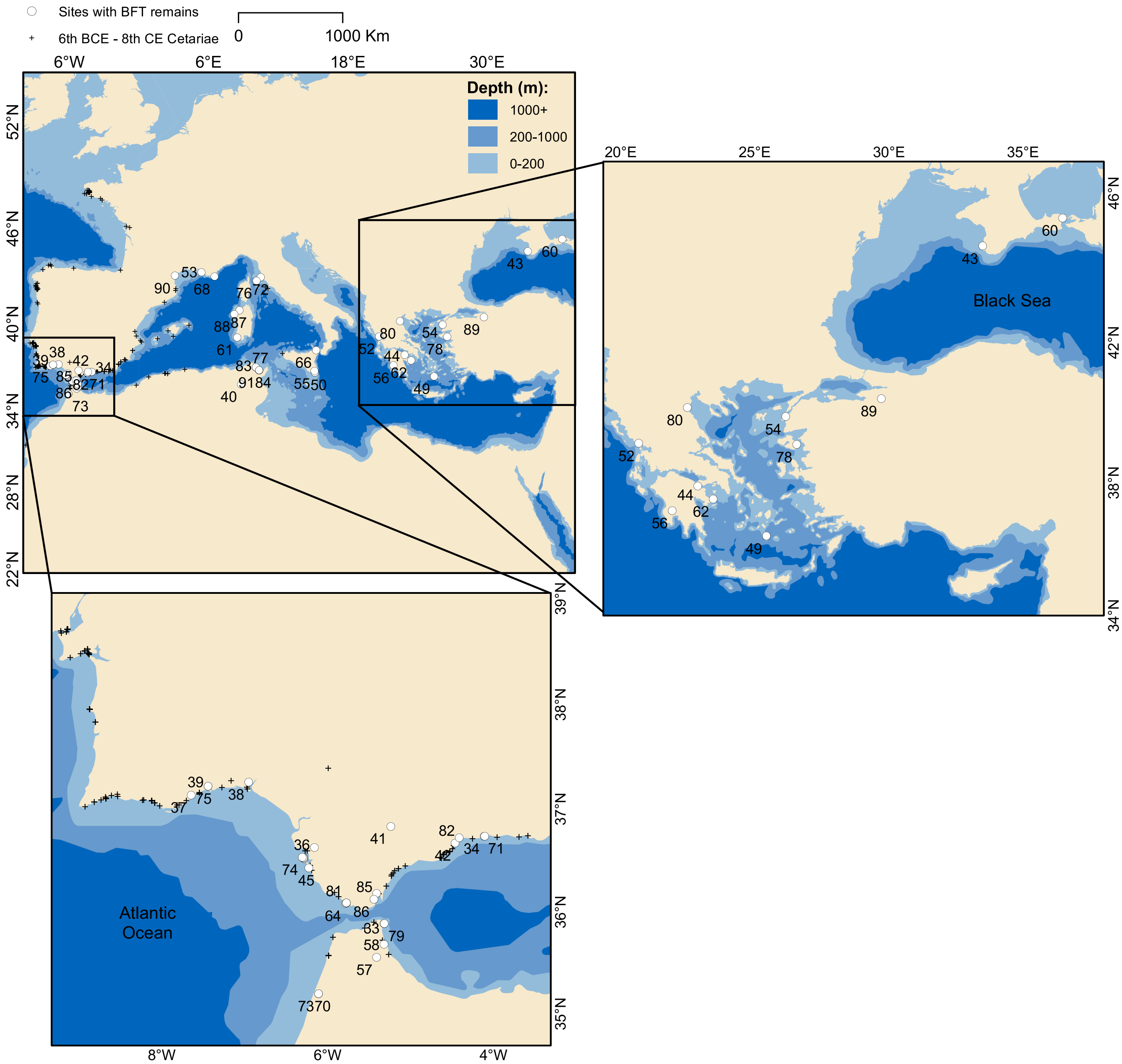

Figure 2. Map of Atlantic bluefin tuna (*T. thynnus*; BFT) archaeological remains recovered between the 9th century BCE and 7th century CE in reference to fish processing facilities (*cetariae,* from https://ramppa.uca.es/). For numbering refer to Supplementary Table .2S

Carthage (Nobis, 1999), and notably Tavira (Supplementary Table S2). During the same period, Greek BFT trade was developed as evidenced by archaeological finds from the Syracuse area (Bernal-Casasola *et al.*, 2021). Greek coinage from Cyzicus (Mysia, Sea of Marmara) depicting BFT imply that at least local trade of BFT was already well-established by the 6th century BCE (Di Natale, 2014). Undoubtedly, the combination of nets able to intercept spawning (and return) migrations, salting factories able to preserve catches, and amphorae able to transport catches, created the opportunity for commerce across the Mediterranean (Doumenge, 1999; Fromentin and Powers, 2005; Di Natale, 2012). Amphorae containing BFT remains, found in/or off Italy and Greece but originating from modern-day Spain and Morocco (Tailliez, 1961; Delussu and Wilkens, 2000; Zimmerman Munn, 2003; Theodoropoulou, 2014) exemplify this development, indicating that long distance trade of salted BFT (*salsamentum*) was taking place by at least the 5th century BCE (Supplementary Table S2).

BFT fishing methods developed in Greek and Roman times as variations of the *Almadraba* or *Tonnara* techniques (Sarà, 1998; García-Vargas and Florido Del Corral, 2010) that are often aggregated in the literature, and referred to as "tuna traps." Tuna traps varied, apparently originating as the non-static *Almadraba de tiro* (prototypes of beach-seines) before static/fixed *Almadrabas* (Spanish), *Tonnare* (Italian), or *Madragues* (French), developed, that were semi-permanently weighted to the sea floor, and became the dominant method of BFT exploitation from at least the 16th century CE onwards (García-Vargas and Florido Del Corral, 2010). It is not entirely clear which traps were used in antiquity. Oppian (177 years CE) reports the use of up to five boats, and watch towers (*thynnoskopeion*)—which identified the arrival of BFT (sometimes by orca sightings), in addition to instructing boats to encircle the catch. The same author appears to describe the "death-chamber" of fixed traps, where "nets like a city" with "gates" filled "the closing net with copious prey" (Oppianus, 1738). Testifying this, mosaics such as those from 3rd century CE Tunisia appear to portray BFT being dispatched inside a weighted net (Yacoub, 1995). Furthermore, the discovery of arranged anchor parts found off a Roman settlement in Morocco, which may have been fixing points for nets (Trakadas, 2010), suggest that both trap methods may in fact have been used in antiquity. The use of both methods enables the capture of BFT in various scenarios (at different migration distances from shores, bottom-types, and target sizes) that concurs with widespread zooarchaeological evidence (Figure 2) and indicates that exploitation rates had increased.

The importance of BFT to Greek and Roman societies between the 5th century BCE and 5th century CE can be clearly observed from coins minted in fishing settlements, which depicted BFT (Di Natale, 2014), multiple historical writings, notably from Aristotle (4th century BCE), Pliny the Elder (1st century CE), and Oppian (2nd century CE), and finds of salting factories (Figure 2). Factories not only produced *salsamentum* for trade but the fish sauce *garum* (or variations; *liquamen, muria, allec,* and *lymphatum*: Trakadas, 2005). Numerous BFT remains at factories in the Roman coastal settlements of 1st century CE Cadiz and 2nd century BCE–5th century CE Baelo Claudia (Strait of Gibraltar, Figure 2, Morales-Muñiz and Roselló-Izquierdo, 2007; Bernal-Casasola *et al.*, 2016, 2019) further indicate that large-scale BFT exploitation occurred. Salting factories in the eastern Mediterranean are seldom recovered, but classical writings document their existence (Roesti, 1966). Although, their scarce recovery may be the result of a lack of interest in such structures (Theodoropoulou, 2014), we suggest that less BFT exploitation occurred in the eastern Mediterranean than around the Strait of Gibraltar (Figure 1). This is corroborated by all amphorae containing BFT remains evidencing a west-to-east trade in Mediterranean antiquity (Supplementary Table S2).

According to the zooarchaeological remains, BFT exploitation in the eastern Mediterranean occurred mostly in the Aegean in antiquity (Figure 2, Supplementary Table S2). Though as in prehistory, this is likely to be skewed by uneven archaeological ef f ort. BFT migrations through the Dardanelles and Bosporus to/from the Black Sea were extensively documented by Aristotle, and Strabo (1st century CE in Roesti, 1966). Thus, we might have expected to ob-serve greater numbers of BFT remains around these straits. There is still uncertainty whether BFT migrations through this area were for feeding or spawning in the Black Sea (MacKenzie and Mariani, 2012; Di Natale, 2015). Zooarchaeological evidence of BFT from Greek times at Pantikapaion (Kerch, Ukraine; Morales-Muñiz *et al.*, 2007), and prior to that at Bronze Age Troy (~1000–2000 BCE, Sup-plementary Table S1: Rose, 1994; Uerpmann and Van Neer, 2000) might address this potential loss of population complexity via re-constructing past population structure and habitat use. BFT was highly valued there as noted from their appearance on coins from several Black Sea and Sea of Marmara fishing centers and classical writings on the scale of export to the Greek mainland (Roesti, 1966; Di Natale, 2014). This indicates the importance of this fishery historically, even if it was not conducted at the same scale as those in the western Mediterranean (Roesti, 1966; Bekker-Nielsen, 2005; Morales-Muñiz *et al.*, 2007).

We find it conceivable that BFT was exploited to sufficient extent across the Mediterranean in antiquity (Figure 2) to potentially have had some impact on population abundance and complexity, but the extent of this is currently unknown. In Roman times, people were aware that exploitation impacted at least inshore fishes (e.g. Gilthead seabream *Sparus aurata*) and cephalopods in the Tyrrhenian Sea, where they noted that by the 2nd century CE, they had decreased in size, were fewer, and therefore, efficient fishing techniques e.g. torch-fishing were purportedly banned (Trakadas, 2006). Hence, studies are warranted to address this theory as we currently do not have data to quantify the abundance and complexity of BFT populations in this period, and to which extent they might have been impacted by exploitation.

Middle age transition and intensification (8th–18th century CE)

Evidence of BFT fisheries is lacking between the 8th and 10th century CE. It is probable that the collapse of the Western Roman Empire gradually (over a few centuries) destabilized the parallel industries and trade (Horden and Purcell, 2000) on which BFT fisheries depended, and second, caused economic downturns which induced a greater dependence on localized exploitation throughout the Mediterranean (Montanari, 1979; Squatriti, 2002). The Eastern Roman Empire was revitalized, though there is no evidence that this promoted an increase in BFT exploitation. During the Islamic period in Iberia and Sicily (~8th–13th century CE), Al-Idrisi (1154a, b) wrote of BFT, and noted that in Ceuta (northern Africa), BFT were being caught with harpoons while traps were used elsewhere—specifically in Sicily. During the same century, Benjamin of Tudela noted the economic importance of salted BFT to Palermo (Sicily; Aniceti, 2019). In general, fish diets in Italy are perceived to have shifted to freshwater species between the 7th and 13th century CE (Montanari, 1979), though we doubt that this shifted the diets of coastal communities away from marine fish. In addition, the Spanish name for tuna traps (*Almadrabas*) is of Arabic Andalusian origin (deriving from ةبرضملا, a place to strike; or برض, knots) suggesting that some development of BFT exploitation occurred during this period.

Prior to a better documented period when tuna trap catch records were recovered, from 1512 CE onwards (Ravier and Fromentin, 2001; Pagá García *et al.*, 2017), the number and location of BFT remains ought to represent an opportunity to investigate historical exploitation. However, recoveries from the Middle Ages were lacking in comparison with antiquity (Supplementary Table S3, Figure 3). The few BFT remains recovered in this period likely do not represent a decline in exploitation but rather a lack of archaeological effort. One exceptional rescue (i.e. unplanned) excavation at Theodosius' Harbour, Istanbul (Turkey, Onar *et al.*, 2008), recovered 150 BFT vertebrae dating between the 4th and 15th century CE. Likewise, rescue excavations in Sicily recovered scores of BFT vertebrae from the 9th–13th century CE (Aniceti, 2019). This highlights a general lack of archaeological interest in Middle Age coastal contexts (Aniceti, 2019), where the two largest recoveries of this period were unplanned, suggesting that exploitation extent may be underestimated if using observations of BFT remains collated herein as a proxy.

Data on tuna trap presence before 1512 CE indicates that BFT exploitation around Sicily barely increased between the 5th and 12th century CE, from 20 to 25 traps (Pagá García *et al.*, 2018). It was not until the 13th century CE that Sicilian trap numbers noticeably increased, to 104 (Pagá García *et al.*, 2018), clearly documenting an increase in demand for BFT. This was probably spurred on by

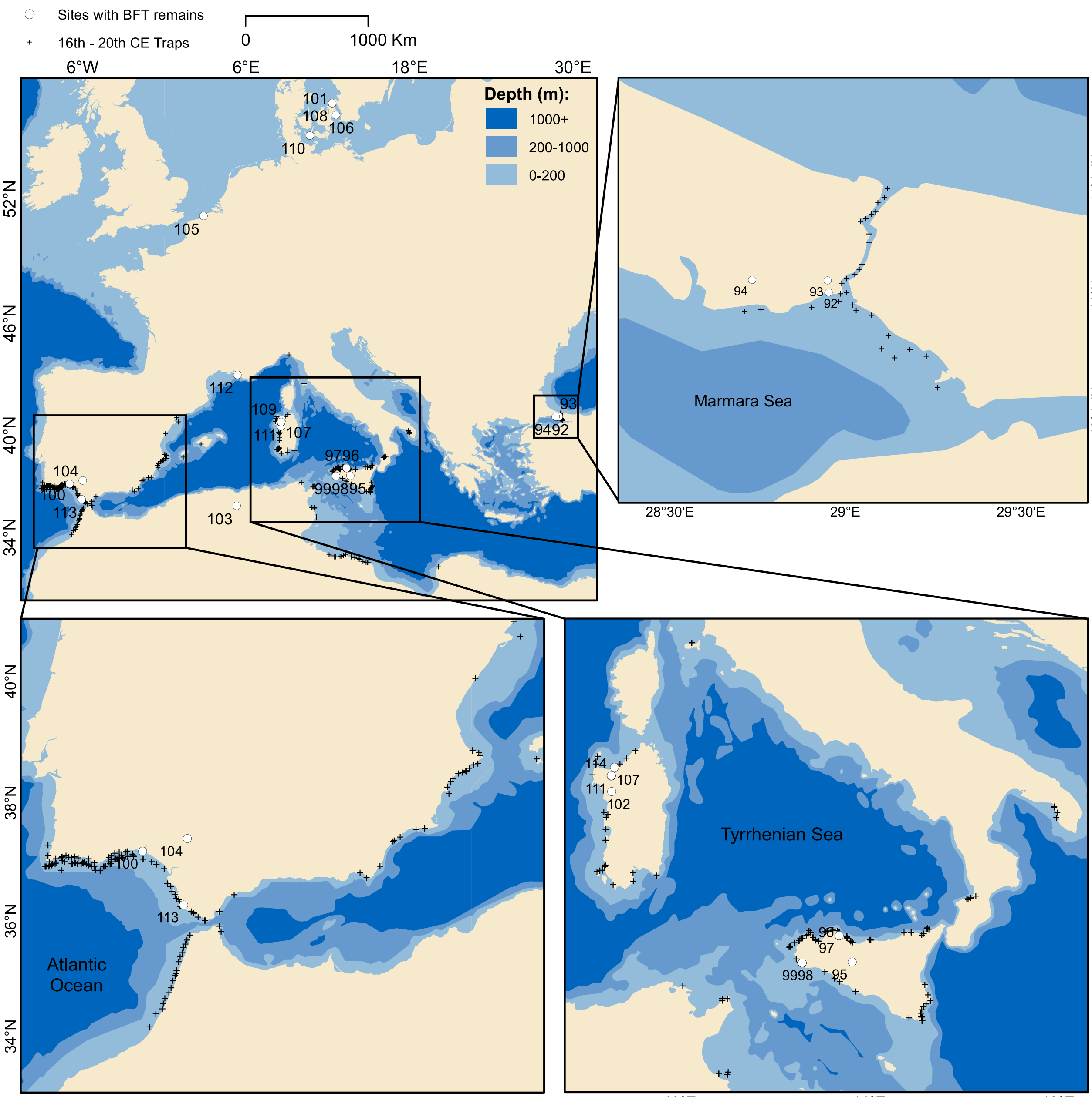

Figure 3. Map of Atlantic bluefin tuna (*T. thynnus*; BFT) archaeological remains recovered between the 8th and 19th century CE in relation to tuna trap locations (from Pavesi, 9881; Devedjian, 6219; Pagá García *et al.*, 7012). For numbering refer to Supplementary Table .3S

Christianism and aligns well with a Sicilian shift away from Islamic dietary practices. Likewise, from the 13th century CE, a plethora of literary works reference the Andalusian tuna traps (see Ladero Quesada, 1993; Bello León, 2005). This signifies a juncture when exploitation impacts likely increased after King Alfonso X of Castille gave the Knights of Santiago the license to these traps in 1248 CE once they regained (Christian) control in the most historically productive BFT fishing region of Iberia. This apparent increase in demand for BFT is comparatively late, e.g. in northern Europe, increased demand for marine fish had already occurred by the 10th century CE, predominantly for prevalent species, i.e. Atlantic herring (*Clupea harengus*) and cod (Barrett *et al.*, 2004; Oueslati, 2019). Investigation is warranted to clarify if exploitation impacts may have indeed increased from those during antiquity before the 13th century, for we do not know to which extent metrics such as the Sicilian trap numbers are influenced by pre-13th century data-gaps (Pagá García *et al.*, 2018).

During the 13th century CE, trap numbers probably increased due to more stable demand, in turn promoting the development of more efficient methods of BFT exploitation, i.e. the static traps. These traps (Figure 3) were certainly common by the 16th century CE, and perhaps the 14th century CE (Sarmiento, 1757; Ravier and Fromentin, 2001), and were more efficient because they could target BFT migrating further from the coast and were less dependent the effort of many personnel (Ravier and Fromentin, 2001). Therefore, catch variability probably decreased with well-designed static traps. Hence, we postulate that exploitation may have substantially increased between the 13th and 16th century CE, when traps also became more numerous (Ravier and Fromentin, 2001; Pagá García *et al.*, 2018).

In support of this theory, by the mid-16th century CE, it is estimated that Spanish traps alone caught 14000 tons of BFT (Ravier and Fromentin, 2001; Pagá García *et al.*, 2017). Spanish catches then decreased significantly between the mid-16th and 18th century CE, which Sarmiento (1757) attributed to their exploitation. García (2016) suggested that despite legislation in 1583 CE against it, prey and juvenile BFT were overexploited, and seabed disturbance close to the traps off the Atlantic coast of Andalusia altered the migration route of BFT further from shore. This would also explain the preva-lence of static traps that were able to reach further from shore with-out disturbing the seabed as a non-static trap/beach-seine would. The legislation reconstituted prescripts established in the 14th cen-tury CE (García, 2016), clearly then, exploitation impacts on BFT were evident by this time. Notably, catch variations over this period in Spain could only be explained minimally by climatic conditions (Ganzedo *et al.*, 2009). When looking at a greater temporal spread across the Mediterranean, Ravier and Fromentin (2001) noted 100-year fluctuation cycles in trap catches. These cycles were suspected to be mainly related to climate modifying migration patterns and/or recruitment (Ravier and Fromentin, 2001, 2004; Fromentin, 2009), which surely impacts the abundance and catches of pelagic species such as BFT. However, exploitation is expected to magnify fluctuations in abundance (Anderson *et al.*, 2008).

BFT remains from 15th century CE Belgium, and 13th–17th century CE Scandinavia (Supplementary Table S3, Figure 3) are a reminder that BFT exploitation was not only carried out by tuna traps in this era. This is also true for the Mediterranean where harpoon-ing in the Messina Strait has occurred for millennia (Di Natale *et al.*, 2005). Despite these likely being small-scale activities, they should be considered to avoid underestimating exploitation effort, and this extends to unreported/illegal fisheries which likely affected the historical trap catch records. Fishing, most probably by line and hook, even targeted BFT in the extremes of their modern-day range in 1671 CE East Greenland (Di Natale, 2012; Jansen *et al.*, 2021), and accounts of BFT fishing with harpoons off Norway date to 1762 CE (Lindquist, 1994). It is believed however that pre-20th century CE exploitation of BFT in the northeast Atlantic was sporadic and had negligible commercial value (Bennema, 2018).

From the 16th century CE onwards, the vast distribution of traps (Figure 3) and their catches (Ravier and Fromentin, 2001; Pagá García *et al.*, 2017) of f ers a more reliable indicator of the extent of exploitation, than the location, number, and size of zooarchaeological remains. Yet, BFT remains from this period are potentially useful to generate quantitative historical baselines (e.g. Alter *et al.*, 2012; Ólafsdóttir *et al.*, 2014) because they may of f er additional biological insights into life-history traits and adaptive responses not feasible with trap data. It must also be noted that trap catches were influenced by many factors and therefore do not necessarily reflect population abundance (Di Natale and Idrissi, 2012). The 16th–18th century CE trap locations of Pedras de Fogu (Italy), Conil (Spain), and Marseille Harbour (France) offer some of the most recent zooarchaeological remains (Figure 3). The scientific literature appears to well-understand the distribution of BFT fisheries during these centuries, but a knowledge gap exists in how impactful these fisheries were. Therefore, such pre-industrial remains might offer relevant baselines that could be achievable to return to with sustainable management (Schwerdtner Máñez *et al.*, 2014; Orton, 2016; Rodrigues *et al.*, 2019), in addition to elucidating the long-term drivers of population dynamics (Jackson *et al.*, 2001; Erlandson and Rick, 2010).

Industrialisation and expansion throughout the Atlantic (19th–20th century CE)

Only a single BFT remain was recovered from the 19th century CE (Supplementary Table S3), but many 20th century CE archived BFT specimens exist, which might allow for an extension of the application of biomolecular and morphometric tools on fish remains to this era. This is particularly important since 19th and 20th century CE overexploitation is more likely but currently, we lack quantitative metrics to identify what changes occurred to population abundance, structure, and life-history traits during these years. Archived collections, i.e. at public museums (which are not reported in this work), and private collections such as the Massimo Sella Archive are vital in this regard (Supplementary Table S3). Most of the bones in the Sella Archive represent BFT caught in central Mediterranean tuna traps (i.e. off Croatia, Italy, and Libya) between 1911 and 1926 (see Riccioni *et al.*, 2010), including those vertebrae studied by Sella on his seminal work on BFT size-at-age (Sella, 1929). Similar collections probably exist elsewhere and are of clear importance to locate since these specimens offer the potential to investigate the impact of exploitation during the 19th and 20th century CE, when exploitation was clearly intensive, yet remains remarkably understudied.

By 1880, tuna trap effort had increased, when only a fraction of the Spanish, Italian, Portuguese, and Tunisian traps believed to exist at the time landed a combined 22000 t (Ravier and Fromentin, 2001; Pagá García *et al.*, 2017). Therefore, together with missing trap catch data and other gear types, catches in the 19th century CE appear to be comparable to the most intensive decades of BFT exploitation, which occurred a century later with further advances in technology and effort. This coincided with declines in trap tonnage across the Mediterranean, particularly after 1960 (Cort and Abaunza, 2016; Pagá García *et al.*, 2017), in part due to the economic difficulties of re-establishing tuna traps following the World Wars (Roesti, 1966).

Several case studies exemplify this advance in technology and exploitation effort in the early 20th century CE. The first being the expansion of fishing on a large scale in the northeastern Atlantic. By the early 20th century, large (> 2 m TL, total length) BFT migrating during summer from the Mediterranean to feed (Hamre, 1958) near the north of their range in the Atlantic became subject to recreational fishing and by-catch in Norwegian, Danish and Swedish fisheries, which often targeted Atlantic mackerel (*Scomber scombrus*) and herring (MacKenzie and Myers, 2007). Advances in the robustness of the purse seine by 1930 allowed these three nations especially to develop this fishery, which peaked in 1952, when Norwegian catches alone exceeded 10 000 t (Hamre *et al.*, 1966). However, Norwegian catches became rare after 1970 (MacKenzie and Myers, 2007).

Second, commercial fisheries in the western Atlantic developed, especially between Cape Hatteras and Newfoundland (Mather *et al.*, 1995; Porch *et al.*, 2019; Di Natale *et al.*, 2020). By 1960, longlining in the western Atlantic escalated, primarily driven by Japanese demand. This caused the so-called “Brazilian episode”—an appearance of an intensive long-line and drift-gillnet fishery for large BFT off Brazil and the central-southern Atlantic, which then almost disappeared within a decade (Takeuchi *et al.*, 2009; Di Natale *et al.*, 2013, 2020). The provenance of BFT captured off Brazil is unknown. In total, two individuals tagged off the Bahamas in the 1960s were recaptured off South America (Mather *et al.*, 1995), yet some authors suggest that bite marks of the smalltooth cookiecutter shark (*Isistius brasiliensis*)—which is more common in the South Atlantic—on Mediterranean-caught BFT evidence an eastern Atlantic origin (Arena, 1988; Di Natale, 2010; Di Natale *et al.*, 2013; Quilez-Badia, *et al.*, 2013). Hence, BFT caught in the "Brazilian episode" may have falsely inflated western Atlantic population estimates and masked impacts on the eastern Atlantic and Mediterranean BFT population (Di Natale, 2019).

Third, by 1950, a fishery for juvenile BFT in the Bay of Biscay had developed that originated in the 1860s by handline (Bard, 1981). Here, as elsewhere, the retrofitting of echo sounders to vessels in the 1950s improved fishing efficiency. As a result, approximately 120 bait-boats operated from France and Spain in that decade, generating a historical peak in catch numbers that has not been surmounted since (Cort, 1990; Cort and Abaunza, 2019).

The final case study is that of the Black Sea. At the beginning of the 20th century, tuna traps (locally called *Dalians*) were operating in the Sea of Marmara (Örenç *et al.*, 2014) and Bosporus, supporting the economy of 26 salting factories (Parona, 1919; Ninni, 1923). Indeed, BFT remains indicate exploitation had occurred here and far into the northern Black Sea for millennia (Lebedev and Lapin, 1954; Lyashenko, 2006; Morales-Muñiz *et al.*, 2007). From 1909 to 1923 up to 500 t of BFT caught in Dalians were sold each year in Istanbul market alone (Devedjian, 1926), where most were large BFT caught between April and October (Karakulak and Oray, 2009). Here, exploitation also intensified during the 1950s through the development of a purse-seine fleet (Iyigungor, 1957). After the 1970s, poor catches forced BFT fishing fleets into the Sea of Marmara and the Aegean (Karakulak and Oray, 2009; Ulman *et al.*, 2020) while the ancient Dalian fishery ended completely (Karakulak, 2004). BFT are now rare in the Black Sea and in the Sea of Marmara but show signs of recovery (Di Natale, 2019).

There is a consensus that overexploitation was a primary factor driving each of these 20th century case studies (Karakulak and Oray, 2009; Fromentin, 2009; MacKenzie *et al.*, 2009; Di Natale, 2010; Worm and Tittensor, 2011; Di Natale, 2015; Cort and Abaunza, 2016, 2019; Porch *et al.*, 2019). However, studies have been limited in their ability to quantify exploitation impacts in this period because data is lacking prior to when ICCAT collected accurate statistics from the 1970s onwards (ICCAT, 2017), though some data on population status does exist for the 1950s and 1960s (MacKenzie *et al.*, 2009). Other explanations have been proposed, such that oceanographic changes induced poor recruitment and/or altered migration patterns away from Norway (Fromentin, 2009) and Brazil (Fromentin *et al.*, 2014). Yet, MacKenzie and Myers (2007) suggested that the Nordic catches were not driven by environmental conditions. A long absence of BFT from these areas until very recently (Di Natale *et al.*, 2019; Nøttestad *et al.*, 2020) indicates that a lack of prey was not the predominant factor. However, common to all, is that large individuals migrated to these areas (Pusineri *et al.*, 2002; Di Natale, 2010, 2015; Cort *et al.*, 2013) and although mixed size-classes were caught off 1950s Norway (Fromentin and Powers, 2005), only large individuals have returned (Nøttestad *et al.*, 2020). It is evident that both the western and eastern population of BFT was truncated (Fromentin, 2009; MacKenzie *et al.*, 2009; Siskey *et al.*, 2016), which is a symptom of overexploitation (Heino *et al.*, 2015). In support of this, population decline, and cohort loss is theorized to result in a loss of migratory behaviour or collective memory, which takes time to rebuild (Petitgas *et al.*, 2010; De Luca *et al.*, 2014; Mariani *et al.*, 2016). It is probable that climate, predator–prey dynamics, and overexploitation each contributed to the crashes of these fisheries. Multidisciplinary studies on fish remains offer the potential to disentangle these, thereby furthering the understanding the long-term drivers of population dynamics.

Discussion

Insights from traditional zooarchaeology

BFT bones recovered from archaeological excavations demonstrate that BFT exploitation had begun at 10000 years BCE. Despite large recoveries at sites such as Franchthi in the Aegean, basic fishing gear (Mylona, 2014), a lack of preservation facilities and demand suggest that it is unlikely BFT fishing was conducted on a large enough scale to impact population abundance or complexity until at least the Roman era onward. We hypothesize that because BFT are widely distributed and have a relatively large population size in the eastern Atlantic and Mediterranean, considerable exploitation intensity would be required to impact at the population level. It is remarkable that large ($>$ 2 m TL) BFT, commonly caught during the Modern Age, were seldom represented in the archaeological record. We suppose that large individuals would have been readily caught once nets that could intercept spawning migrations were commonly used, i.e. from antiquity. We stress that large BFT especially, but indeed all adults, are cumbersome and would, therefore, not be routinely transported to salting facilities or settlements where most excavations focused. Historically, fish were more often processed close to the shore, and their bones dumped or burnt on beaches (Morales-Muñiz *et al.*, 2007), therefore, we observe and report only a minor fraction of the actual remains. This is attested by refuse dumps at the 2nd century BCE beach site Punta Camarinal where many articulated vertebral columns of large BFT were recovered including fins and tails (Morales-Muñiz and Roselló-Izquierdo, 2007). In comparison, only scattered remains were found at the adjoining city and *cetariae* of Baelo Claudia (Morales-Muñiz *et al.*, 2004c). Indeed, this incomplete nature of zooarchaeological data hinders robust interpretations.

We urge caution when interpreting the distribution and quantity of the remains herein as a proxy of fishing effort or evidence of human behaviour. The aphorism "absence of evidence is not evidence of absence" certainly applies here, especially since Middle Age sites and coastal middens are clearly understudied. There were discrepancies between the estimated size of individuals and their species identifications—for example ~20% of studies reported individuals estimated $<$ 1.5 m in length (i.e. within the size range of albacore), while ~71% of studies did not report size estimations. It should be noted that reliable size reconstruction methods are yet to be established. Moreover, species identification from scales is contentious. Approximately 20% did not report the number of identified specimens (NISP), thus we suggest that NISP is not a good proxy for past population abundance or fishing effort. Another potential bias is that dating was estimated mostly by contextualizing stratigraphic units, with some records spanning multiple centuries, which clouds inferences of exploitation. Hence, further zooarchaeological study is required. The processing and trap locations presented here (from Pavesi, 1889; Devedjian, 1926; Pagá García *et al.*, 2017 and https://ramppa.uca.es/) offer plentiful locations for enquiry. In particular, the western Mediterranean *cetariae* collated by the RAMPPA Project, which date between 6th and 7th century CE, show no evidence of fish remains at ~90% of sites ($n = 303$). This further highlights gaps in the archaeological record, which are not attributed to poor recovery techniques, but specifically in this case, a lack of effort in excavating nearby coastal refuse dumps where BFT remains were discarded, rather than the settlements or *cetariae* themselves.

Unlocking the potential of fish remains

Considering challenges facing the robustness of traditional zooarchaeological data, the application of biomolecular or morphometric tools on fish remains is vital to unlock their potential to quantify past population abundance and complexity in ways that can reveal long-term ecological trends that are useful for management and conservation (see Orton, 2016). BFT remains are particularly promising for these aims since sites which provide ample material for analyses (NISP > 20) span from 6000 years BCE to the 20th century CE at various periods and locations (Figure 4). Periods and events marking developments in BFT exploitation intensity which should be the focus of future investigations, are; prior to overexploitation case-studies of the mid 20th century CE; prior to the late-19th century CE trap catch peak; prior to the 16th century CE trap catch fluctuations in Spain and shift towards fixed traps; prior to the 14th century CE Spanish fishing regulations and increase in Si-cilian trap numbers; and finally; pre-/post-BFT commercialization in antiquity.

Studies will be challenged in disentangling the influences of exploitation, and climate, which surely also effects BFT abundance and complexity (Fromentin, 2009; Reglero *et al.*, 2019), but exploitation is expected to increase with time and exacerbate fluctuations caused by climate (Anderson *et al.*, 2008). Indeed, a long time-series of samples is important in this regard to represent multiple stages of exploitation. Specifically, studies should focus on testing for the erosion of genetic diversity and effective population size as a proxy of abundance (e.g. Alter *et al.*, 2012; Ólafsdóttir *et al.*, 2014; Oosting *et al.*, 2019). The overexploitation of large individuals can be tested by investigating growth rate changes *via* morphometrics (e.g. Ólafsdóttir *et al.*, 2017) and the selection of genes related to maturation, and growth, as suggested by the theory of Fisheries Induced Evolution (Heino *et al.*, 2015; Hutchings and Kuparinen, 2021). Particularly for BFT, three important applications could be: first, testing for the loss of sub-populations as theorized for the Black Sea (Di Natale, 2015) using genomics to reveal past population structure and the selection of genes related to local adaptation (MacKenzie and Mariani, 2012), and isotopes to reconstruct past habitat use (e.g. Alter *et al.*, 2012; Guiry *et al.*, 2020). Second, investigating climate-mediated migration patterns or population components, that have been proposed to cause trap catch fluctuations of the 16th–20th century CE (Fromentin, 2009). These might be best studied using isotopic analyses on bulk bone collagen or individual amino acids to test for ecosystem-level and intra-species shifts in habitat use, and trophic structure (see Orton, 2016; Guiry *et al.*, 2020). Genomic studies on population structure are also expected to help here, and satisfy debate on various hypotheses (Fromentin, 2009; Karakulak and Oray, 2009; Di Natale, 2019; Cort andand Abaunza, 2019). Finally, the analyses of isotopes and elements might offer opportunities to assess the onset of heavy metal pollution and changes in migratory behaviour (see Calaprice, 1986; Orton, 2016; Blankholm *et al.*, 2020), as it is hypothesized that during the 20th century, (predominantly) noise pollution drove BFT further from shore and has since limited trap efficiency (Addis *et al.*, 2009).

The preservation of fish remains from the periods proposed is well within the range of success for biomolecular and morphome-tric studies to date (Orton, 2016; Oosting *et al.*, 2019). The preser-vation of ancient DNA is of most concern among the techniques proposed. Within fish remains, it is variable (Oosting *et al.*, 2019) and has proved to be poor in BFT bones from arid Iberian sites (Puncher *et al.*, 2019). This may limit the use of poorly preserved remains to demographic analyses only using mitochondrial DNA (Oosting *et al.*, 2019), which is a low-resolution marker for mod-ern population assignment (Carlsson *et al.*, 2004; Boustany *et al.*, 2008) but may offer utility toward genetic diversity changes. How-ever, in general, fish remains show good potential for whole genome applications (Ferrari *et al.*, 2020). In addition to genetics/genomics, bone collagen and amino acids constitutes an important biochemi-cal archive of stable isotopes and should not be hindered by preser-vation issues (Guiry and Szpak, 2021), at least for BFT remains from post-Roman periods. Element, e.g. heavy metals analyses on an-cient bones could also be explored (c.f. Calaprice, 1986; Blankholm *et al.*, 2020) with an awareness of diagenesis and soil bleaching. Fi-nally, studying growth rate changes from vertebrae is challenging, but it is still promising for the large vertebrae of BFT (Van Neer *et al.*, 1999). As a minimum, future studies engaged in BFT zooar-chaeology would benefit by applying ZooMS (Rick *et al.*, 2019), or genetic barcoding (Puncher *et al.*, 2019) to provide reliable species identifications from bone and scales.

The approach advocated herein is clearly also relevant for other species and populations subject to intensive fisheries, especially other inshore migrators, e.g. gadids and *Anguilla* spp. (Hoffmann, 2005; Kettle *et al.*, 2008; Barrett, 2019) and those with fragmented populations, e.g. salmonids and sturgeons (Hoffmann, 2005), as these may have been more vulnerable to fishing impacts in pre-industrial periods, and excavations readily reveal their remains (Kettle et al, 2008; Galik *et al.*, 2015; Barrett, 2019). This is particularly important for species which lack a rich base of literature and long-term datasets like the tuna trap catch series (which is often the case), those with populations yet to recover to mid-20th century CE baselines. Several studies have outlined their intent or begun to quantify historical exploitation on marine fishes (Orton, 2016; Morales-Muñiz *et al.*, 2018; Barrett, 2019; Ólafsdóttir *et al.*, 2014, 2017; Guiry *et al.*, 2020).

The need for historical baselines

Our review suggests that exploitation had the potential to impact BFT populations in the preindustrial era, as has been suggested for a host of f i sheries (e.g. Pauly, 1995; Jackson *et al.*, 2001; Hoffmann, 2005; Barrett *et al.*, 2004; Erlandson and Rick, 2010; Lotze *et al.*, 2014; Ólafsdóttir *et al.*, 2014; Morales-Muñiz *et al.*,2018; Oueslati, 2019). The increase in Sicilian trap numbers by the 13th century CE, the imposition of fishing regulations, and claims of overfishing in the 16th century CE (Sarmiento, 1757; García, 2016) corroborate this, but currently only climate was considered as a regulator of population dynamics in this period (Fromentin, 2009). Rather, we suppose that climate, predator–prey dynamics, and exploitation operated together (with minor other factors, Di Natale and Idrissi, 2012) to promote the fluctuations observed in trap catches from the 16th century CE onwards (see Ravier and Fromentin, 2001; Pagá García *et al.*, 2017). Indeed, it remains to be seen whether exploitation impacts may extend back to antiquity for BFT, as appears the case according to the spread of the zooarchaeological data and classical writings on the importance of tuna in Greek and Roman times.

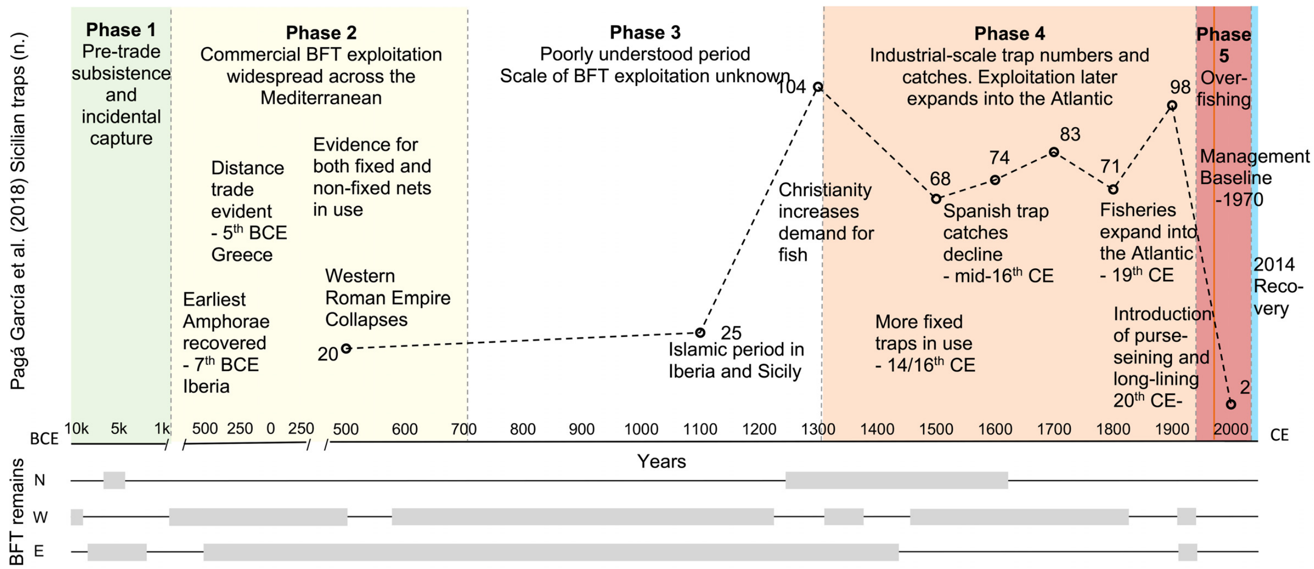

Figure 4. Schematic of major events related to the development of Atlantic bluefin tuna (*T. thynnus*; BFT) fisheries over time and the presence of tuna remains in time (grey bars) for three areas; N: northern Europe; W: western Mediterranean and Atlantic; and E: east of Sicily. k: thousand years. The line plot represents variation in the number of Sicilian tuna traps, as collated by Pagá García *et al.*.(2018)

By categorizing our observations on exploitation into broad periods (Periods 1–5, Figure 4) we clearly illustrate our theory, despite that changes would have occurred on a much finer scale than is often detectable through inferences on archaeological and historical data due to periods with sparse evidence. Moreover, we highlighted incomplete and biased qualitative archaeological and trap catch data that may underestimate fishing intensity in the Middle Ages (Pagá García *et al.*, 2017, 2018)—in addition to missing data on other gear than traps, i.e. in Scandinavia, the Bay of Biscay, the Sea of Marmara, the Black Sea, and artisanal fisheries, that increased the duration of BFT fishing season from at least the 16th century CE onwards (Devedjian, 1926; Di Natale, 2015; Cort and Abaunza, 2019).

Since recovery and resilience are dependent on exploitation intensity and duration (Pauly, 1995; Neubauer *et al.*, 2013), there is a need to better understand the exploitation history of BFT. Recovery will be overestimated, and resilience underestimated if we do not account for historical exploitation impacts. Even mid-20th century case studies of BFT overexploitation are not accounted for by the 1970s management baselines, despite being fully acknowledged (Fromentin, 2009; MacKenzie *et al.*, 2009; Porch *et al.*, 2019). We suggest that preindustrial exploitation impacts ought to be quantified, especially during the last few centuries, because these may offer more relevant baselines than those of the ancient past, for example (Lotze *et al.*, 2014; Schwerdtner Máñez *et al.*, 2014; Rodrigues *et al.*, 2019). In addition, more recent remains are more likely to be well-preserved, and thus readily provide data. Until these aims are achieved, the use of 1950s and 1960s fisheries catch data might be helpful to explore the current baseline (e.g. MacKenzie *et al.*, 2009) and allow for a greater degree of confidence in the sustainability of BFT catches.

Conclusion

BFT remains constitute a resource to investigate long-term population dynamics and exploitation impacts. The utility of traditional zooarchaeology toward this aim is limited due to biases, and spatiotemporal data gaps. Thus, the use of biomolecular and morphometric analyses should be promoted in tandem with increased zooarchaeological effort to understudied periods, i.e. Middle Ages; areas, i.e. coastal sites; and particularly fishing contexts, i.e. trap refuse dumps. Our review of literature provides clear evidence of BFT overexploitation during the mid-20th century CE from Norway (Hamre *et al.*, 1966), Brazil (Takeuchi *et al.*, 2009), the Bay of Biscay (Cort and Abaunza, 2019), and the Black Sea (Karakulak and Oray, 2009). Furthermore, a strong case could be made that the intensification of BFT exploitation extends back further to at least the 19th century CE, if not the 13th–16th century CE, in the eastern Atlantic and Mediterranean. However, a host of archaeological evidence would suggest that BFT exploitation may have been intensive since antiquity, according to the wide spatial extent of sites yielding zooarchaeological remains, among other archaeological evidence. Given this, the use of 1950s metrics as baselines for population status (MacKenzie *et al.*, 2009) might be tried to improve the currently used 1970s management baseline and decrease the uncertainty of future stock declines until quantitative historical baselines are produced for the preindustrial era.

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Data availability statement

The zooarchaeological records collated herein are available as Supplementary Information to this article. A constantly updated version is available at https://tunaarchaeology.org/database.

Supplementary data

Supplementary material is available at the ICESJMS online.

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