



Finding the right plaice at the right time: Multi-molecular analysis of flatfish reveals historical catch habitats

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Abstract

Flatfish are ecologically diverse species that commonly occur in marine environments, but also in estuarine and riverine habitats. This complicates the examination of the potential role of flatfish in the 'marine fish event horizon', an economic shift in human exploitation from freshwater to marine fish species during the 10–11th centuries CE around the southern North Sea. This study represents the first multi-disciplinary investigation of flatfish remains to make species-specific interpretations of flatfish exploitation. Peptide mass fingerprinting and multi-isotope analysis of carbon ($\delta^{13}\text{C}$), nitrogen ($\delta^{15}\text{N}$) and sulphur ($\delta^{34}\text{S}$) was performed on collagen from 356 archaeological flatfish and 120 comparative archaeological marine or freshwater species to explore the catch habitat of individual flatfish species between 600 and 1600CE from the North Sea area. European flounder show signals reflecting both freshwater and marine environments, while other flatfish show only those of marine habitats. A subtle shift towards more marine exploitation towards the end of the period is identified, corresponding to the observed transition in targeted species from flounder to plaice throughout the medieval period. Sites show slight differences in $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ within the same species, related to the local environments. Remarkable is the high abundance of marine plaice and flounder during the early medieval period, which shows clear marine or coastal exploitation of flatfish early on, well before the previously accepted onset of the marine fish event horizon. This indicates a gradual shift from coastal to open marine fish exploitation over the medieval period.

KEYWORDS

archaeology, fish remains, North Sea, Pleuronectiformes, stable isotopes

1 | INTRODUCTION

Archaeological sites around the southern part of the North Sea show a clear increase in northwest European marine fisheries

around the 10–11th century AD, the so-called "fish event horizon" (Barrett et al., 2004a, 2004b). The most marked increases are seen for Gadidae [e.g. cod (*Gadus morhua* (Linnaeus 1758)), haddock (*Melanogrammus aeglefinus* (Linnaeus 1758)), and whiting

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(*Merlangius merlangus* (Linnaeus 1758))), which were much less common in inland sites prior to this period. Meanwhile, freshwater species such as Cyprinidae and Salmoniformes became relatively less abundant in later periods (Barrett et al., 2004a, 2004b; van Neer & Ervynck, 2016). Flatfish (Pleuronectiformes) are significant within this dynamic, as certain species commonly caught by humans can reside in both marine and freshwater habitats. Flatfish have been uncovered from sites dated to well before the fish event horizon, but the representation of the whole order of Pleuronectiformes increases during and after the fish event horizon (Barrett et al., 2004a, 2004b; van Neer & Ervynck, 2016). These fish are still highly important in modern day fisheries, and many stocks have been overfished in the recent past (e.g. Cadrin et al., 2015; Rice & Cooper, 2003). The dynamics of flatfish exploitation through a longer time series has not been well investigated until now. This lack of baseline records limits the understanding of the health of the fish stocks in modern times. Understanding the occurrence of the earliest marine fisheries could further pinpoint the moment in time when humans began impacting marine ecosystems intensively.

Due to the changes in habitat choice and diet (Braber & de Groot, 1973; De Groot, 1971) throughout the life cycle of flatfish, simple species identification of flatfish remains from archaeological sites is not sufficient to tackle the question of where they have been feeding and might have been caught, which is key to understanding the role of these species in the freshwater/marine fishing dynamics during the fish event horizon. Pleuronectiformes are regarded as being primarily marine species. Some species, however, are known to occur, at least during a part of their lives, in brackish and freshwater systems, such as for example *Platichthys flesus* (Linnaeus 1758), or European flounder (e.g. Elliott et al., 1990; McGoran & Morrill, 2017; van Beek et al., 1989). Other commonly exploited species found in the North Sea area, such as *Pleuronectes platessa* Linnaeus 1758 (plaice), *Limanda limanda* (Linnaeus 1758) (dab), *Scophthalmus maximus* (Linnaeus 1758) (turbot), *S. rhombus* (Linnaeus 1758) (brill) and *Solea solea* (Linnaeus 1758) (Dover sole), are generally found in coastal or open marine environments as adults, although larvae and juveniles can occur in inshore waters or estuarine nurseries (e.g. Jager, 1999; Primos et al., 2013; Ramos et al., 2010; Russo et al., 2008). Stable isotope analysis of carbon ($\delta^{13}\text{C}$), nitrogen ($\delta^{15}\text{N}$) and sulphur ($\delta^{34}\text{S}$) can aid in differentiating between fish residing in different aquatic environments and potentially geographic regions (e.g. Fuller et al., 2012; Robson et al., 2016). Visual and morphological identification of flatfish species, such as flounder and plaice, is challenging, (e.g. Watt et al., 1997; Wouters et al., 2007) with identification made possible through molecular techniques (e.g. Dierickx et al., 2022).

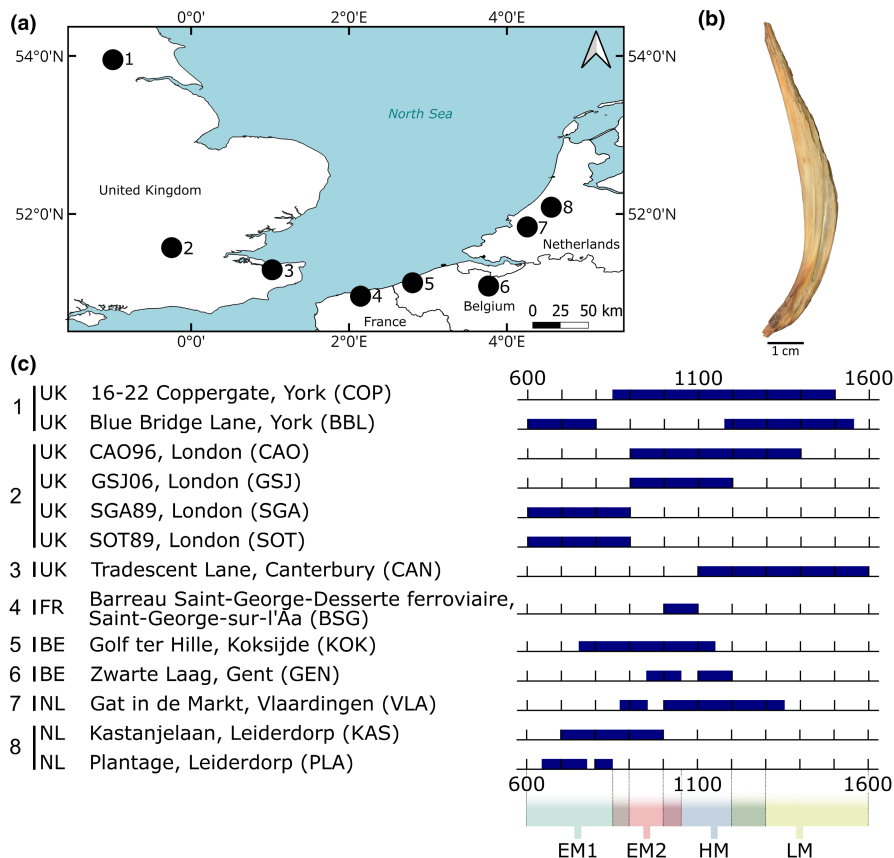
Many studies have analysed fish isotopic composition from western and northern Europe, mostly from Gadidae, and the number of dedicated European fish isotope studies is increasing (e.g. Barrett et al., 2008, 2011; Ervynck et al., 2018; Fuller et al., 2012; Häberle et al., 2016; Hutchinson et al., 2015; Nehlich et al., 2013; Ólafsdóttir et al., 2021; Orton et al., 2011; Robson et al., 2016). Only a handful of isotope studies have included archaeological flatfish samples as part of human dietary studies or general environmental studies of fish (Table S1 in the Supplementary Information S1,

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section 1). These studies reflect the wide variety of habitats flounder can occur in, as well as potential dietary changes throughout the life of a species and differences between Pleuronectid species (Antanaitis-Jacobs et al., 2009; Dahliwal et al., 2019; Ervynck et al., 2018; Fischer et al., 2007; Fuller et al., 2012; Göhring et al., 2016; Müldner & Richards, 2005, 2007; Robson et al., 2016), yet no in-depth time series for individual species has been investigated and the number of published flatfish data is low (only 29 samples for all time periods), preventing our understanding of targeted species and exploited habitats during and after the fish event horizon in the medieval period.

In this study, a large body of archaeological remains of multiple species within Pleuronectiformes ($n=356$) are analysed, together with comparative samples of marine and freshwater fish ($n=120$). An integrated biomolecular approach utilising multi-isotopic ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$, $\delta^{34}\text{S}$) and proteomic species identification techniques is used to investigate 13 sites from around the southern North Sea dating

FIGURE 1 Archaeological sites. (a) Map of the North Sea basin with the 13 archaeological sites in eight locations; (b) Example of an archaeological flatfish bone, os anale, analysed (BSG0104); (c) Chronological overview of the archaeological sites with the relevant phasings and their abbreviations used in the text: the numbers match those on the map. See [Table S2](#) for details on the used time periods.



to the medieval period (6th–16th century CE; [Figure 1](#)) and to reveal changes in flatfish fisheries in terms of targeted habitats and species.

2 | MATERIALS AND METHODS

2.1 | Archaeological site and sample selection

The sites were selected based on their location (i.e. southern North Sea area), dating of the features (between 600 and 1600 CE) and reported amount of Pleuronectiformes bones (minimum ca. 10 per family per dated phase). A detailed summary of each site is provided in the [Supplementary Information S1](#) (section 1). [Figure 1](#) shows the geographical location and the chronology of the sites respectively. From each site, a subset of flatfish samples was randomly selected, including various skeletal elements, for stable isotope analysis (see [Supplementary Information S2](#)) from each medieval phase/period (6th–16th century CE). To avoid repeated sampling of the same individual fish, only one sample was taken per combination of preliminary identified taxon, context, estimated size, element and side. Whenever available, samples from typical freshwater (Esocidae, Cyprinidae) and marine species (Gadidae) were also sampled to provide a local baseline for both habitats. These taxa were selected as they are common in archaeological sites from these regions, can feed on similar prey as flatfish do, and generally do not tend to migrate between habitat types. Seven modern commercially acquired flatfish samples were analysed alongside the archaeological samples as references for the analysis

for both quality criteria and habitat baselines. Site phases were categorised into time periods to discuss results ([Table S2](#)). Size estimations were done to bins of 10 cm standard length (SL) if possible, by visually matching to modern reference material of known sizes from the Royal Belgian Institute of Natural Sciences (RBINS) and the University of York Zooarchaeology Laboratory (YZL).

2.2 | Collagen extraction and stable isotope analysis

Collagen was extracted from 476 archaeological fish samples and seven modern flatfish samples and analysed using EA-IRMS (Elemental Analyser–Isotope Ratio Mass Spectrometer) at BioArCh, University of York, UK for carbon and nitrogen. Sulphur analysis was performed for a subsample of the dataset, those with high quality collagen (i.e. not excluded based on quality criteria for carbon and nitrogen; see below) and representing a good overall distribution of species, size, time period and site ($n=223$ archaeological and 7 modern) at SUERC, UK. Whole bones were preferentially used for analysis to avoid biases with growth layers. See [Supplementary Information S1](#) (section 2), for details on the extraction and analysis protocols.

2.3 | Species identification

Each selected sample was identified to family level and, where possible, species level using available identification keys

(e.g. Watt et al., 1997; Wouters et al., 2007). As morphological approaches are not always sufficient to distinguish between species of Pleuronectiformes, collagen peptide mass fingerprinting (PMF, also known as ZooMS, Zooarchaeology by Mass Spectrometry) was carried out, following the methodology from Dierickx et al. (2022) (also see [Supplementary Information S1](#), section 2). All samples were identified by following the biomarkers and methodology described in Dierickx et al. (2022) for flatfish and Harvey et al. (2018) for other fish taxa, except for Cypriniformes due to a lack of published peptide biomarkers.

2.4 | Quality criteria

For carbon and nitrogen stable isotope analysis, species-specific quality criteria were developed by analysing the collagen composition of Pleuronectiformes species reconstructed using LC-MS/MS data from Dierickx et al. (2022; also see [Supplementary Information S1](#), sections 2, 3, and 4). Samples with C:N > 3.5 were excluded from the analysis for plaice, flounder and dab, and those with C:N > 3.4 for turbot, brill and Dover sole. A dynamic cut-off value was used for Gadidae, following Guiry and Szpak (2021) (see [Supplementary Information S1](#), section 3). For sulphur, a discrepancy has been noticed between the mass spectrometry measured and calculated sulphur content (this study; Nehlich & Richards, 2009). Therefore, rather than relying on species-specific criteria, the quality criteria defined by Nehlich and Richards (2009) were followed: %S between 0.40% and 0.85%, C:S between 125 and 225 and N:S between 40 and 80.

2.5 | Radiocarbon dating

Radiocarbon dating was performed on material of the site of Barreau Saint-George in order to confirm dating obtained from pottery at the site. Three bovine samples from different pits, from where most fish material was obtained, were selected and dated at SUERC, UK. Results can be found in the [Supplementary Information S1](#), section 1, [Figure S1](#).

2.6 | Data analysis and availability

The distinction between marine and freshwater habitats using $\delta^{13}\text{C}$ was performed using well-established criteria (e.g. Fuller et al., 2012; Robson et al., 2016) and by looking at the comparative taxa analysed in this study to set baselines for marine and freshwater habitats in the North Sea region. These showed a cut-off point near -20‰ $\delta^{13}\text{C}$. Classification of habitat types using sulphur stable isotope values followed Nehlich et al. (2013) and Nehlich (2015), which uses data of fish taxa from the same hydrogeographic region, in which the freshwater signal for sulphur has an upper limit of around 15‰ , and $\delta^{13}\text{C} < -20\text{‰}$. Flatfish samples defined as marine

($\delta^{13}\text{C} > -20\text{‰}$; see results) have $\delta^{34}\text{S}$ values between 0 and 20‰ , with $\delta^{34}\text{S} < 10\text{‰}$ as estuarine, $10\text{‰} < \delta^{34}\text{S} < 15\text{‰}$ as estuarine/southern North Sea marine, while samples with $\delta^{34}\text{S} > 15\text{‰}$ are defined as strongly open marine (i.e. oceanic water without a substantial freshwater influence), following Nehlich et al. (2013) and Nehlich (2015). Data was analysed using R (R Core Team (2022), version 4.1.1 (2021-08-10)—“Kick Things”). Data was visualised using `ggplot()` (`ggplot2` package; Wickham, 2016) in R. A Chi-square test was performed using `chisq.test()` to assess if there is a significant association between two categories. Further associations between size, period, site and isotopic values in flounder and plaice were explored using Bayesian ANOVA. Full details and results are presented in the [Supplementary Information S1](#), section 6. Additional results and archaeological site background can be found in the [Supplementary Information S1](#). The data table with all the results can be found in [Supplementary Information S2](#) and raw isotopic data in [Supplementary Information S3](#). R code, photographs and peptide mass spectra of the archaeological samples can be found on Zenodo by following this link: <https://doi.org/10.5281/zenodo.10418711>.

3 | RESULTS

3.1 | Shifting species presences through time

From the archaeological samples, 356 were identified as Pleuronectiformes using PMF (two *L. limanda* or dab, 91 *P. flesus* or European flounder, 237 *P. platessa* or plaice, 13 *S. maximus* or turbot, three *S. rhombus* or brill, seven *S. solea* or Dover sole, and three Pleuronectidae), while the remaining samples were identified as the following: 30 Cypriniformes, 19 *Esox lucius* Linnaeus 1758 (pike), 2 *Conger* (Linnaeus 1758) (conger eel), 1 cf. *Salmo trutta trutta* Linnaeus 1758 (trout), 33 *Gadus morhua* (Atlantic cod), 34 *Melanogrammus aeglefinus* (haddock), 1 *Merlangius merlangus* (whiting). Of the modern samples, three were identified as plaice and four as flounder.

Considering only archaeological Pleuronectiformes samples confidently dated to a specific period, that is early medieval 1 (EM1), early medieval 2 (EM2), high medieval (HM) and late medieval (LM) (see [Figure 1](#) and [Table S2](#) for definitions), the relative species abundance shows a clear shift with plaice becoming more abundant compared to flounder throughout the medieval period ([Figure 2](#)). The difference in species abundance between the periods is significant (Chi-squared test: $p = .0001356$, $X^2 = 59.178$). The same trend is especially noticeable in some sites, for example, those in York, and less so in others ([Supplementary Information S1](#), section 5). In some of the other settlements, such as London and Koksijde, plaice can be just as abundant as flounder during the EM period, while in other settlements such as Gent and Vlaardingen, flounder remains present during the LM period. Other Pleuronectiformes species were only identified from a handful of samples in York, Canterbury, Barreau Saint-George, Koksijde, Gent and Vlaardingen ([Supplementary Information S1](#), section 5).

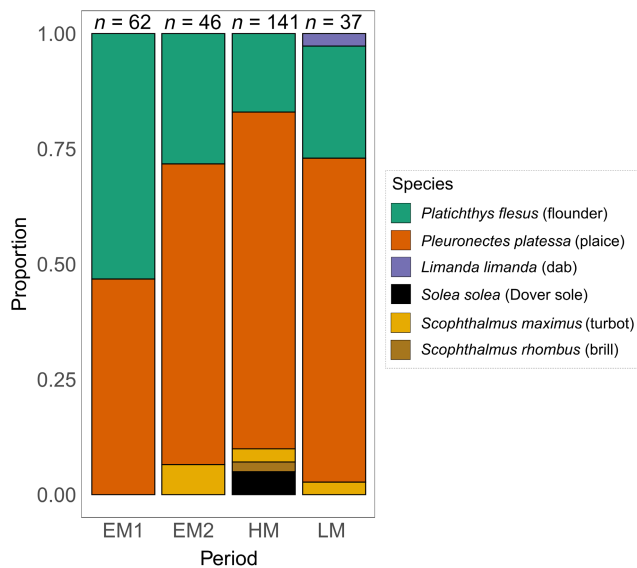


FIGURE 2 Proportional species abundance per period, as identified using peptide mass fingerprinting. Total number of samples per chronological period is listed above each bar.

3.2 | Habitat preferences and ecology reflected in isotope values

Freshwater species and marine species are generally clearly distinct in $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$, except for one Cypriniformes sample with a high $\delta^{13}\text{C}$ value (Figure 3). Most flatfish have similar $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ values to the marine species, except for eight flounder samples with $\delta^{13}\text{C}$ values below -20‰ , making them fall within the freshwater group. Flatfish have a rather restricted range for $\delta^{15}\text{N}$. Only a few samples have higher $\delta^{15}\text{N}$ values (14.0‰ – 17.5‰), identified as the more piscivorous species such as turbot and brill. The marine Gadidae also have elevated $\delta^{15}\text{N}$ values (13.5‰ – 18.5‰). Comparative freshwater species have a wide range of $\delta^{15}\text{N}$. The distinction between habitat types is less distinct for $\delta^{34}\text{S}$. Flatfish samples that were identified as freshwater by $\delta^{13}\text{C}$ ($<-20\text{‰}$) all have $\delta^{34}\text{S} < 9\text{‰}$, which corresponds to the delineation of habitat groups by Nehlich (2015) and Orton et al. (2011), although some freshwater specimens have $10\text{‰} < \delta^{34}\text{S} < 15\text{‰}$.

3.3 | Isotopic trends

The general trends for the two most numerous species, plaice and flounder, are described here. For detailed results on other species and effects of chronology, geography and size, see the Supplementary Information S1, section 6. The relative abundances of each habitat type in the early (EM; EM1 and EM2 joined here to increase sample size per species), high (HM) and late medieval (LM) periods are compared for both species (Figure 4). In each time period, freshwater and estuarine samples are mostly identified as flounder, while southern and open marine samples are mostly identified as plaice. For both species, there is an increase in southern

North Sea marine samples during the HM period and a decrease in estuarine samples compared to the EM period. Although not a strong relationship, this change is also confirmed by Bayesian ANOVA (see Supplementary Information S1, section 6; also see Figure S11). During the LM period, no estuarine plaice have been observed. There are clear differences observed between different size classes, in particular for $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$, with larger size classes having fewer samples with low values for $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$, as supported by Bayesian ANOVA (see Supplementary Information S1, section 6; also see Figure S9). No clear chronological or site effects were noticed between size classes (Supplementary Information S1, section 6, Figures S15–S20).

4 | DISCUSSION

Species specific timelines of medieval catch locations of Pleuronectiformes have been reconstructed through combining collagen PMF and stable isotope analysis.

4.1 | Species dynamics

Between the two species that are most abundant and heavily exploited in the southern North Sea, there is a clear relative decrease in consumption of flounder and a relative increase in consumption of plaice throughout the medieval period around the North Sea. This shift is especially noticeable during the second half of the EM and HM periods (10–11th century), when marine fishing increased around the North Sea (Barrett et al., 2004a, 2004b). This trend is observed at most sites and is very noticeable in York (see also Dierickx et al., 2022). A few sites show a slightly different trend or timing in the shift, which can be related to their specific historical context (see Supplementary Information S1, section 5). Settlements with easy access to the North Sea (e.g. coastal Koksijde) and with early maritime trade connections (e.g. London), have a high abundance of plaice during the EM period. Settlements with nearby estuaries (e.g. Barreau Saint-George, also see Dierickx et al., 2022, Gent, Vlaardingen, Leiderdorp) have relatively large numbers of flounder throughout the medieval period.

Only a handful of other flatfish species (turbot, brill, Dover sole and dab) have been identified. This matches most archaeological reports on fish remains from around the North Sea, which find flounder and plaice (or Pleuronectidae in general) to be most abundant (e.g. Enghoff, 1999; Ervynck & van Neer, 1992; Harland et al., 2016; Nicholson, 2009; Oueslati, 2019; Reynolds, 2015). Turbot and brill are only present at sites close to the coast and/or during the HM and LM periods, where marine fishing is ongoing. The presence of Dover sole in Tradescent Lane in Canterbury is explained both by its location at the southernmost part of the North Sea, where this species is more common (Heessen et al., 2015), and by the elite nature of the site with consumption of Dover sole linked to for example, monasteries (Ervynck & van Neer, 1992).

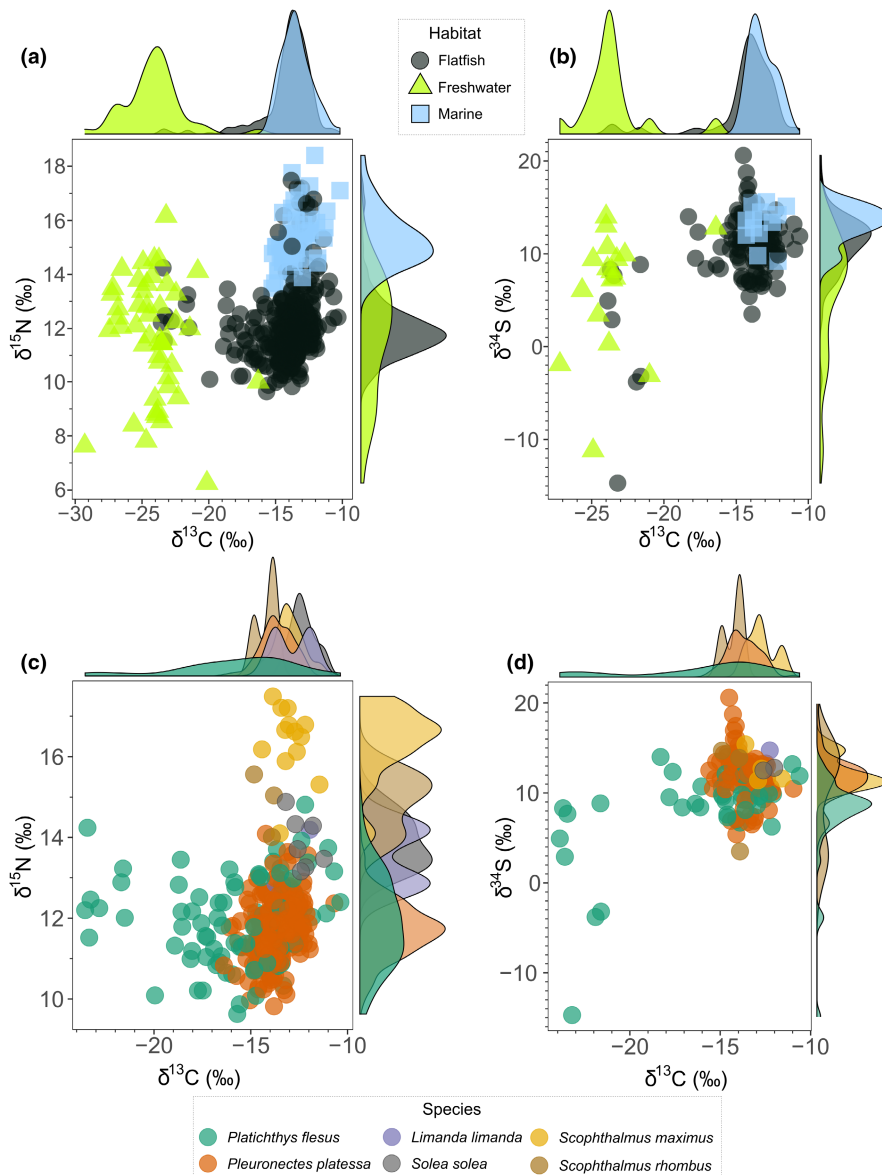


FIGURE 3 Scatter and density plots showing habitat distinctions. (a) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of all archaeological fish samples, coloured and shaped to the broad ecological group; (b) $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ of all archaeological fish samples, coloured and shaped to the broad ecological group; (c) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of Pleuronectiformes samples, coloured by species; (d) $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ of Pleuronectiformes samples, without *S. solea* in the density plots for clarity, coloured by species.

Other Pleuronectiformes species were less targeted and have mostly been recorded as by-catch during the post-medieval and modern periods (Bennema & Rijnsdorp, 2015; Walsh et al., 2015) or occur in more northern areas or neighbouring waters, making it less likely these were exploited on a regular basis in the selected sites.

4.2 | Quality criteria

This study further confirmed the need for species-specific quality criteria for isotope analyses, as proposed by previous research (e.g. Guiry & Szpak, 2020, 2021). In case species data is unavailable, phylogenetically closely related species should be used as a proxy, rather than ecologically similar species, as phylogeny is a strong determinant of the collagen composition, since this protein is coded by several genes (*COL1A1*, *COL1A2*, and sometimes *COL1A3*). For sulphur, it was not possible to define species-specific

criteria, due to an observed discrepancy (see [Supplementary Information S1](#), section 3).

4.3 | Inferences by habitat, size, location and chronology

4.3.1 | Habitat and size distinctions

The isotope values from different species of archaeological fish correspond to the expected isotope niches based on their modern ecologies, with freshwater and marine species being clearly distinct in $\delta^{13}\text{C}$ while the diet and trophic level is reflected by $\delta^{15}\text{N}$. Although the distinction between marine and freshwater habitats based on the comparative taxa seems to be quite clear in this case study (cut-off point of -20‰ $\delta^{13}\text{C}$), this might not be the case or be the same value for other taxa or in other regions (see Guiry, 2019). For example, the single Cypriniformes with a higher $\delta^{13}\text{C}$ value may have lived close to

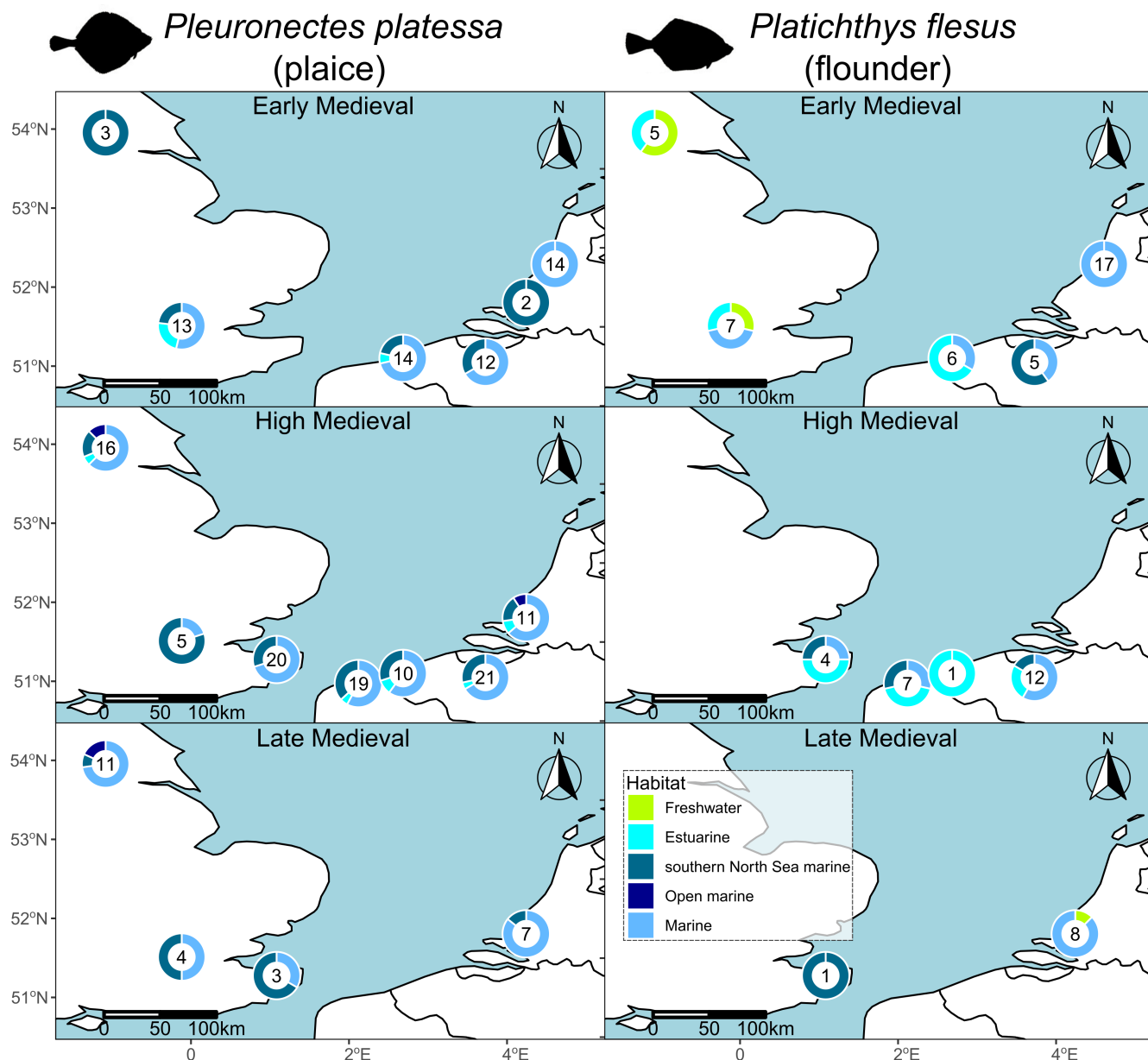


FIGURE 4 Summary of isotope data for European flounder (left) and plaice (right) for the three main time periods, early (top), high (mid), and late (bottom) medieval period. The number in the pie charts represents the total sample number per locality. Samples are categorised into five habitat types based on the isotope data. Freshwater: $\delta^{13}\text{C} < -20\text{‰}$; Marine: $\delta^{13}\text{C} > -20\text{‰}$; and where $\delta^{34}\text{S}$ data are available marine samples are further divided into the following three categories: Estuarine: $\delta^{34}\text{S} < 10\text{‰}$; southern North Sea marine (or freshwater influenced marine): $10\text{‰} < \delta^{34}\text{S} < 15\text{‰}$; and Open marine: $\delta^{34}\text{S} > 15\text{‰}$.

estuaries or could potentially reflect a higher cut-off point between marine and freshwater environments in a particular locale. As this is only one sample in a large dataset, we draw upon the overwhelming data for freshwater versus marine signatures. Both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for Gadidae match with data for central and southern North Sea Gadidae (Barrett et al., 2008; Orton et al., 2011). The correlation observed between $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ confirms $\delta^{34}\text{S}$ as a proxy for marine-freshwater habitats (e.g. Leakey et al., 2008; Nehlich, 2015; Nehlich et al., 2013).

Fewer individuals with estuarine and freshwater habitat isotopic signatures were observed for larger size classes (>30 cm SL). As flatfish grow larger, they tend to move out from estuaries and near-coastal habitats to more marine environments, which could result in

an overall increase in $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ values. The samples of flounder with a freshwater signature in this study all originate from small-sized individuals (10–30 cm SL), which can be expected as this species can often be found in freshwater environments when they are young, while moving towards the estuaries and marine habitats when they get bigger (Russo et al., 2008). Identifying those flounder with freshwater isotopic signatures as having been caught in freshwater habitats is complicated by the lifecycle of this species that can migrate to coastal areas for spawning or display ontogenetic changes in habitat preferences, and may retain their original freshwater signatures if having recently entered a marine environment (e.g. Aarnio et al., 1996; Russo et al., 2008; Selleslagh & Amara, 2008, 2015; Sims et al., 2004).

While changing their habitat as they grow larger, Pleuronectidae do not change the nature of their diet and generally eat similar prey from the same trophic levels throughout their lives (Braber & de Groot, 1973; De Groot, 1971), thereby explaining the lack of patterning of $\delta^{15}\text{N}$ values with increasing size class. Smaller sized (20–30 cm SL) flounder can sometimes show higher $\delta^{15}\text{N}$ values compared to larger size classes (>30 cm SL) (Figure S9; also see Ervynck et al., 2018).

4.3.2 | Location differences

Site location has a significant impact on the isotope composition of flatfish, which can in most cases be explained by the respective local environment (Supplementary Information S1, section 6). Coastal sites exclusively rely on marine flatfish ($\delta^{13}\text{C} > -20\text{‰}$), whereas samples with lower $\delta^{13}\text{C}$ values ($< -20\text{‰}$), indicating freshwater (influenced) habitats, were found in inland and peri-coastal sites (i.e. sites close to the coast where rivers are still under tidal influence), alongside marine samples. Vlaardingen and Leiderdorp are located close to the estuarine region of the southern Netherlands, which could explain the lower $\delta^{13}\text{C}$ values on average for both flounder and plaice at these sites.

Plaice samples with very high $\delta^{34}\text{S}$ values (>15‰) from Coppergate in York date to the 12th–13th century which stand apart from other sites included in this study. These individuals may have originated some distance from York as during this time marine fishing was well established and York had ready access and trade connections to the northern North Sea, where such high $\delta^{34}\text{S}$ values have been observed (Barrett et al., 2011; Nehlich et al., 2013). However, a closer origin for these fish is also possible due to high local bedrock $\delta^{34}\text{S}$ signatures in the North of England in particular (Bataille et al., 2021; St-John-Glew et al., 2018) combined with this region receiving more oceanic water from the Atlantic (Otto, 1983), which could cause a particular isotopic niche for this species at this time period.

In a few instances, human economic, dietary, and culinary choices could be driving the observed isotopic variation. The relatively high abundance of freshwater samples in York and London could indicate that fishing in the rivers Ouse and Thames for flounder was more common practice than it was in mainland Europe. Isotopic data from London fits nicely with historical sources indicating that fresh plaice was brought inland to London from coastal areas, while flounder was caught in the Thames (Reynolds, 2015; Galloway, 2017). Humans clearly made conscious choices about the habitat from which they fished specific flatfish and traded different species over longer distances.

4.3.3 | Chronological changes

No clear trends were observed for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data for either plaice or flounder, but a slight increase is observed for $\delta^{34}\text{S}$

throughout the medieval period, especially for plaice (see also Supplementary Information S1, section 6, Figure S11). During the EM period, most of the fish originated from marine habitats, most likely close-coastal and estuarine or freshwater-influenced marine habitats ($\delta^{13}\text{C} > -20\text{‰}$ and $5\text{‰} < \delta^{34}\text{S} < 15\text{‰}$). This high abundance of marine plaice and flounder during this EM period is remarkable, with southern North Sea exploitation occurring from as early as the 7th century (Figure 4). Humans were exploiting and transporting estuarine, coastal and marine flatfish inland to settlements such as York, London, Vlaardingen and Leiderdorp four centuries earlier than expected from the picture provided predominantly by Gadidae at the marine fish event horizon of the 11th century (e.g. Barrett et al., 2004a, 2004b, 2011). One previous isotopic study has alluded to a slightly earlier date for the increase in exploitation of marine environments with a single marine Clupeidae identified in early medieval York (Müldner & Richards, 2005). This early find of marine Clupeidae is unsurprising, as herring were already exploited in large numbers during the EM period and this fishery was identified as becoming dramatically more intensive during the HM period and LM period (Barrett et al., 2004a, 2004b).

Conversely, during the HM period, there is a relative decrease in flatfish originating from an estuarine/coastal environment and relative increase in those from the southern North Sea (marine $\delta^{34}\text{S} > 10\text{‰}$). This increasingly marine trend continues where by the LM period, no estuarine fish appear, while both southern North Sea and open marine fish are present. The shift towards more open sea fisheries is most apparent for plaice. This outward expansion of fisheries corresponds to the observed shift in species, as humans increasingly exploited the open seas for herring and cod, they also fished for plaice more frequently. Close coastal fisheries might have become less important and sustainable economically, therefore reducing the exploitation of flounder. No evidence was found here that indicates that flatfish fisheries expanded beyond the North Sea during the medieval period. This contrasts with the continuous geographical expansion that occurred during the HM and LM periods onwards for Gadidae and Clupeidae fisheries (e.g. Holm et al., 2021; Orton et al., 2014).

4.4 | Impact on our understanding of the marine fish event horizon

Flatfish exploited from inshore marine environments, such as estuarine and coastal areas, appear during the EM period not only in the coastal site of Koksijde, where it might be expected, but also in inland and peri-coastal settlements such as York, London, Gent, Vlaardingen and Leiderdorp, some as early as the 7th century CE. With most of the marine flatfish from these sites being larger than 20 cm SL (and about half even bigger than 30 cm SL), the chance of them being stomach contents from Anguillidae (eels) or other animals is slight (see Barrett, 2016), making it very likely these fish were intentionally brought to the site for human consumption. All these settlements were of local political significance, and were part of

active trade networks across the North Sea (Dijkstra et al., 2016; Loveluck & Tys, 2006; van Loon & de Ridder, 2006). It is possible that these maritime trade connections were linked to this early marine fish exploitation.

The cause of this early onset of marine exploitation of flatfish during the medieval period, however, remains to be explored. Being ecologically diverse and easy to exploit, flatfish may have served as a stepping stone taxon to more outward marine fisheries. Flatfish can be easily caught using nets (e.g. seine nets) either standing on the shore or from a boat, occasionally using hook and line, and even by flounder tramping. These methods were readily available during the early medieval period (e.g. van Neer & Ervynck, 2016). They could then have paved the way to more intense marine exploitation of other economically significant fish such as, Gadidae and Clupeidae, making the change from riverine and coastal exploitation to open marine fishing a gradual transition, alongside early herring exploitation.

A clear outward movement of marine flatfish fisheries is observed in London, York, and Gent during the HM period, as seen from $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ values, contemporary with the marine fish event horizon (Barrett et al., 2004a, 2004b). This outward movement resulted from the interplay of various socio-economic changes (Barrett et al., 2004a, 2004b) such as the expansion of trade networks, Scandinavian influence, growing population and urbanisation in these cities, and increased importance of Christian practices (Barrett et al., 2004a, 2004b). The potential decrease in freshwater quality (e.g. in York, O'Connor, 1989) combined with a collapse of freshwater fish stocks, as attested by historical sources from across Europe (Hoffmann, 1996), strengthened these changes. It is perhaps unsurprising that a shift towards more open marine environments is only detected here in larger cities, such as York, London and Gent, at the start of the HM period, while the smaller cities and coastal areas relied on more close-coastal focused flatfish fishing throughout the medieval period. These major cities, having a larger population and established connections in long-distance trade, had greater demand and opportunities to import marine fish from the specialised open marine fisheries that had developed by this point (also see Barrett et al., 2004a, 2004b; van Neer & Ervynck, 2016). The exploitation of estuarine and freshwater flatfish, however, remains active in sites across the southern North Sea during the HM and LM periods to a minor extent.

Recent isotopic research on archaeological human remains has been interpreted as indicating that, contrary to evidence provided by finds of fish remains from archaeological sites, an increase of marine foods in the diet in England did not occur until the 11th century (Leggett, 2022). However, modelling human diets using bulk stable isotopes is challenged by the visibility of different food groups contributing to collagen values. Marine fish consumption is difficult to detect when it comprises less than ca. 20% of the diet (Hedges, 2004; Leggett, 2022; Müldner & Richards, 2007; Prowse et al., 2004). Therefore any increase in marine fish consumption between 0 and 20% of the diet would be invisible in bulk bone collagen

isotope values. The evidence from flatfish presented here reveals the earlier, perhaps more subtle dynamics of marine fish consumption.

Molecular analysis of archaeological fish remains has enabled a species-specific multi-isotope approach to flatfish, revealing a detailed history of flatfish fisheries around the southern North Sea during the medieval period. In summary, we detected an early onset of inland trade in marine-caught flatfish, occurring from at least the 7–9th century CE and possibly earlier, and predating the marine fish event horizon by a few centuries. A clear shift in targeted flatfish species throughout the medieval period and an outward movement of the flatfish fisheries correspond with the increase in marine Gadidae and Clupeidae in the zooarchaeological evidence.

AUTHOR CONTRIBUTIONS

KD: Conceptualisation, Formal analysis, Investigation, Data Curation, Writing—Original Draft, Writing—Review & Editing, Visualisation. PS: Formal analysis, Writing—Review & Editing. JH: Resources, Writing—Review & Editing. AP: Resources, Writing—Review & Editing. TO: Resources, Writing—Review & Editing. AL: Resources, Writing—Review & Editing. AE: Resources, Writing—Review & Editing. WW: Resources, Writing—Review & Editing. MVT: Investigation, Writing—Review & Editing. DO: Conceptualisation, Writing—Original Draft, Writing—Review & Editing, Supervision. MA: Conceptualisation, Writing—Original Draft, Writing—Review & Editing, Supervision.

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CONFLICT OF INTEREST STATEMENT

There are no competing interests.

DATA AVAILABILITY STATEMENT

Additional results and archaeological site background can be found in the [Supplementary Information S1](#). The data table with all the results can be found in [Supplementary Information S2](#) and raw isotopic data in [Supplementary Information S3](#). R code, photographs and peptide mass spectra of the archaeological samples can be found on Zenodo by following this link: <https://doi.org/10.5281/zenodo.10418711>.

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SUPPORTING INFORMATION

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

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