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**Neanderthal foraging in freshwater ecosystems: A reappraisal of the Middle Paleolithic archaeological fish record from continental Western Europe.**

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**Abstract**

The prevalence of large game found in association with Middle Paleolithic tools has traditionally biased our ideas of Neanderthal subsistence practices. Studies document the exploitation of small mammals, birds, and plants by Neanderthals, whereas data on aquatic resources are still scarce and data on fish are almost non-existent. This article presents a review of fish remains from 11 Middle Palaeolithic fish bone assemblages from well contextualized sites in Belgium, France and Spain. It explores the nature of the evidence in order to determine whether Neanderthal fished and if so, whether fishing was a casual, opportunistic activity or a systematic practice. The first issue to address is whether archaeological fish remains at any given site represent human activity or not. Our study tests that assertion while enhancing our understanding of the diversity of food alternatives available to Neanderthals at any given site, and their ability to adapt to them. Methodological protocols include quantification, body mass and length estimations, and, whenever possible, spatial distribution of fish remains, taphonomic analyses and inference of the season of death. This methodology constitutes an analytical protocol to assess the contribution of fish to the human diet during the Paleolithic and set apart human-generated

fish deposits from those generated by alternative fish accumulators. The evidence gathered so far points essentially to circumstantial fishing by Neanderthals, and the question must necessarily remain open for the moment. Nevertheless, some of the evidence, in particular the presence of large (> 1 kg) fish in anthropogenic deposits and the absence of animal digestive traces and gnawing marks on fish bones in such deposits, seems compelling and suggests that Neanderthals could have played a role in the accumulation of some of these remains.

Keywords: Neanderthal; Fishing; Middle Paleolithic; Western Europe; Zooarchaeology; Taphonomy

## 1. Introduction

Western Europe constitutes a key area for investigating Neanderthal subsistence practices due to the quantity and quality of sites available for study. The most recent investigations in this region have significantly expanded our knowledge on the chronology (e.g., Richard et al., 2015; Guérin et al., 2017), environmental conditions (e.g., Britton et al., 2011; Moncel et al., 2015; Discamps and Royer, 2017), and subsistence strategies of Neanderthals (e.g., Delagnes and Rendu, 2011; Cortés-Sánchez et al., 2011, 2019; Niven et al., 2012; Daujeard et al., 2012, 2019; Gaudzinski-Windheuser et al., 2018). These data have contributed to establishing a reliable framework for interpreting the profound biological and cultural changes that occurred from Marine Isotopic Stages (MIS) 11–9 to 3 (Moncel et al., 2016). Traditionally, Neanderthals have been considered as big-game hunters (i.e., top-level carnivores; Bocherens, 2009; Gaudzinski-Windheuser and Niven, 2009; Richards and Trinkaus, 2009; Jaouen et al., 2019). However, over the past decade, studies have evidenced a diversified spectrum of subsistence strategies, with a significant contribution of small game (e.g., Blasco and Fernández Peris, 2012; Cochard et al., 2012; Morin et al., 2019). Archaeozoological and archaeobotanical analyses provide evidence of the exploitation of small mammals, birds, shellfish and plants (Laroulandie, 2000; Cortés-Sánchez et al., 2011, 2019; Hardy et al., 2012, 2013; Laroulandie et al., 2016; Estalrich et al., 2017), yet the role played by aquatic-vertebrate resources in Neanderthal diets has barely been documented, and Neanderthal fishing remains a controversial issue (Le Gall, 1992, 2000; Roselló-Izquierdo and Morales-Muñiz, 2005). Evidence exists that hominins practiced river or lake fishing during the Lower Paleolithic (Braun et al., 2010; Stewart, 1994) and the Middle Paleolithic in Africa, where specialized technologies such as barbed bone points have been developed by ca. 90 000 BP (Brooks et al., 1995; Yellen et al., 1995). However, in Western Europe, there is

currently no evidence that the exploitation of aquatic vertebrates was significant before the Upper Paleolithic period, especially the Magdalenian period (Cleyet-Merle, 1990). For most of the Middle Paleolithic, the sea level was lower than it is today, except during MIS 11 and 5e when sea levels were about 6 to 13 m above present levels (Dutton et al., 2015). For this reason, the vast majority of coastal archaeological sites, where hominins may have left traces of fishing activities, are currently submerged, often at great depths (Cleyet-Merle, 1990). Although a Neanderthal coastal adaptation, including fishing activities, that would have increased their dietary breadth is possible (see Brown et al., 2011; Zilhão et al., 2020), no such evidence has been found for the exploitation of continental freshwater ecosystems. Hence, the study of inland fishing activities, close to rivers or lakes, remains one of the only possibilities for studying Neanderthal fishing.

Middle Paleolithic fish bones are occasionally documented in inland caves close to rivers, often mixed with stone tools and faunal remains. These remains can only be considered as evidence of fishing by humans when other fish predators, in particular cave-dwelling carnivores and raptors, are ruled out as alternative accumulators. At the time of writing, few studies have been published on how to reliably diagnose fish deposits produced by most of these predators and set them apart from those produced by humans. In Europe, most of these papers focus on the Eurasian eagle-owl (*Bubo bubo*) and the Eurasian otter (*Lutra lutra*; Nicholson, 1991, 2000; Le Gall, 1999; Russ and Jones, 2011, Guillaud et al. 2017a, 2018).

This paper explores the role that Western European Neanderthals played in accumulating fish remains. The question “were Neanderthals freshwater fishers?” will also aim to determine whether fishing was an opportunistic or a systematic activity for this hominin. The

91 issue has far-reaching consequences since shifts in prey selection by Neanderthals and  
92 anatomically modern humans (AMH) are hotly debated issues. Small terrestrial faunas  
93 contributed to the Neanderthal diet as a fallback resource and as staples, yet small game  
94 became more frequent in the European Upper Paleolithic (UP), and this suggests that a non-  
95 overlap of niches between the two hominins might have existed (Stiner, 1994; Patou-Mathis,  
96 2000; Costamagno et al., 2005; Blasco and Fernández-Peris, 2012; Rufá et al., 2016; Balter  
97 and Simon, 2009; Hardy et al., 2013; Wißing et al., 2019). Fish and shellfish also appear in  
98 European Middle Paleolithic (MP) sites, but data on the use of aquatic vertebrates by  
99 Neanderthals are still scarce and aquatic faunas are rarely taken into account in studies of  
100 Neanderthal consumption patterns (Stringer et al., 2008; Cortés-Sánchez et al., 2011). This  
101 scarcity may simply reflect a time-mediated taphonomic bias; fish bones are unlikely to be  
102 preserved in archaeological archives because their chemical composition makes them much  
103 more susceptible to degradation (Szpak, 2011). This would explain why the earliest  
104 exploitation of marine mollusks by Neanderthals, dated to 166 ka cal BP (Bajondillo Cave,  
105 Málaga, Spain), is in keeping with that documented for AMH at Pinnacle Point in South Africa  
106 (Marean et al. 2007; Cortés-Sánchez et al., 2011, 2019), or on the Atlantic coast of North  
107 Africa (Campmas et al., 2016; Chakroun et al., 2017). Later MP deposits from Vanguard (ca.  
108 41.8 ka cal BP) and Gorham's Cave (ca. 30–32 ka cal BP) in Gibraltar document dolphins,  
109 seals and fish, in addition to marine mollusks (Stringer et al., 2008). Additional lines of  
110 evidence for the exploitation of aquatic resources by Neanderthals include residue analyses  
111 on stone tools, tooth use wear, and anthropological studies (Puech and Puech, 1993; Hardy  
112 et al., 2013; Trinkaus et al., 2019). Another potential line of inquiry is isotopic analyses. No  
113 isotopic studies have yet focused on the consumption of aquatic resources by Neanderthals,  
114 perhaps because if these did not make up a significant fraction of their diet, they may not be

discernible using current analytical procedures (Patou-Mathis, 2000; Drucker and Bocherens, 2004; Drucker et al., 2005; Stringer et al., 2008). For this reason, the development of sulfur or zinc isotope analyses seems promising for directly assessing fish consumption on Neanderthal bones (Privat et al., 2007; Nehlich et al., 2010; Jaouen et al., 2018).

Evidence of the use of aquatic resources helps to explain why Neanderthals settled in marine and freshwater areas and lends weight to the proposal that fishing was a well-established Neanderthal practice or an occasional, opportunistic activity. To explore this issue, our paper analyzes and reviews a series of MP fish collections from Belgium, France and Spain that span from MIS 11 to MIS 3 by applying a battery of protocols in order to define a methodology for assessing the contribution of fish to the human diet during prehistoric times.

## **2. Materials and methods**

### *2.1. Materials*

This study examines ichthyoarchaeological collections from 11 faunal assemblages (**Table 1; Fig. 1**), totalizing 3,159 fish remains (**Table 2**), and comprises new ichthyoarchaeological analyses from Scladina Cave (Belgium), Abri des Pêcheurs, Baume-Vallée Cave, and Baume Moula-Guercy (France). These analyses are combined with a reassessment of previously published fish assemblages from Caverne Marie-Jeanne and Walou Cave (Belgium), Vaufray Cave, Abri du Maras and Barasses II Cave (France), Cueva Millán and Áridos-1 (Spain; Gautier and Heinzelin, 1980; Morales, 1980; Le Gall, 1988, 2008; Roselló-Izquierdo, 1992; Van Neer and Wouters, 2011; Hardy et al., 2013; Béarez and Guillaud, 2019; Daujeard et al., 2019). The sites are dated from MIS 11-9 to MIS 3 (ca. 400 000 to 40 000 years ago) and all of them are cave sites, except Áridos-1 (**Table 1**). Diverse types of excavations are represented in our

corpus. The analysis of some assemblages may be biased due to the paucity of the samples (Caverne Marie-Jeanne, Abri des Pêcheurs and Baume-Vallée), while other sites contain more abundant ichthyoarchaeological collections and are therefore probably more reliable (Scladina Cave, Walou Cave, Vaufrey Cave, Abri du Maras, Barasses II Cave, Baume Moula-Guercy, Cueva Millán, Áridos-1). The representativeness of the fish series also varies depending on the time and extension of excavations, and the number of archaeological levels. Detailed data (location, sequence, chronology, biostratigraphy and lithic remains) on the sites and layers concerned by this analysis are given in the SOM.

## *2.2. Methods*

Due to the diversity of excavation methods and deposits, a preliminary inspection was conducted prior to the faunal analyses from each site to check for potential biases affecting sample size, bone distribution, etc. The fish material was recovered by sieving (dry and wet sieving). Data from each site, in particular data pertaining to the stratigraphy and taphonomy of the deposit, were thus examined in detail.

The anatomy and taxonomy of each of the newly studied and reviewed specimens were identified or confirmed in the laboratories of the countries of origin where the reference collections are housed (i.e., the Muséum national d'histoire naturelle (MNHN), France; the Laboratorio de Arqueozoología from Universidad Autónoma of Madrid, Spain; and the Royal Belgian Institute of Natural Sciences, Belgium). Archaeological studied samples are curated in these laboratories, except for Scladina Cave, which is at the Centre archéologique de la grotte Scladina (Andenne, Belgium), the collections of the French sites of the Rhône Valley, which are at the Musée d'Ornac (Ornac-l'aven, France), or at the Lazaret laboratory (Nice, France), and Vaufrey Cave, which is at the Musée national de Préhistoire (Les Eyzies, France).



Whenever possible, the spatial distribution of fish remains was examined to check for correlations with other faunal and lithic data. Bone surfaces were examined for taphonomic clues. Traces of human activities (butchery, cooking, burning), animal-induced modifications (gnawing marks, grooves, pits), as well as environmental alterations were recorded following established protocols (Jones, 1986; Nicholson, 1991; Lyman, 1994; Broughton et al., 2006; Erlandson et al., 2007, Fernández-Jalvo and Andrews, 2016). Bone surface damage was observed under a binocular microscope and some vertebrae were observed with a scanning electron microscope (SEM). Bone surface damage was allocated into five digestion categories: null, light, moderate, heavy and extreme (Andrews, 1990; Fernández-Jalvo and Andrews, 2016). Based on the methodology from a previous study (Guillaud et al., 2017a), the percentage of preserved bone surfaces from all elements was recorded, starting from 0–20% (very altered surface) and extending up to 80–100% (complete or mostly intact). Percentages were calculated following Dodson and Wexlar (1979) and adapted to fish osteology.

For each faunal assemblage, the number of identified specimens (NISP) and the minimum number of individuals (MNI) were determined. The MNI of the newly studied collections was obtained from the most abundant skeletal part in each site (Poplin, 1976; Grayson, 1984; Reitz and Wing, 1999).

Several fish studies highlight the relationship existing between vertebra size and body dimensions, but such information is lacking for most species (Casteel, 1976; Desse and Desse-Berset, 1996; Granadeiro and Silva, 2000; Guillaud et al., 2017b). For this reason, in addition to regression equations (Thieren et al., 2015 for sturgeon), fish size (i.e., total length, TL) and body mass (BM) were visually estimated through direct comparisons with specimens of known weight and length data from the reference collections when

osteometric models were not available. Size and body mass may provide information on fishing techniques or the habitats in which the fish was caught. However, quantification can be affected by excavation methods and by the potential action of multiple accumulators.

To determine the season of death (seasonality), the sclerochronological method was used (Van Neer et al., 1999; Le Gall, 2003; Guillaud et al., 2017b). Indeed, this method based on the study of the cyclical growth increments archived on skeletal parts, in this case, the fish vertebrae, generally enables to determine the period of the year when fishing took place. This information can then be used to infer the permanent or transient nature of the human occupation (Desse and Desse-Berset, 1993). When humans are identified as the sole accumulating agent, this information can be compared with data on the biology of the species (e.g., spawning periods, timing of fish migrations, etc.) to enhance our understanding of human mobility and settlement patterns (Casteel, 1972; Wheeler and Jones, 1989; Van Neer et al., 1999).

Inferences about biotopes and climate can often be made from faunal assemblages. On our sites, environmental conditions were first inferred from the data reported in the literature for terrestrial macrovertebrates (i.e., ungulates; Daujeard and Moncel, 2010; Hernandez et al., 2014) and microvertebrates (Alvarez et al., 1992; Damblon, 2011; Blain et al., 2014), including anurans (Ballmann et al., 1980), birds (Gala et al., 2005; Rufá et al., 2017) and rodents. Additional environmental data were gathered from the biology of freshwater fishes, as these can help to ascertain which specific predators may have generated a given fish assemblage. For example, salmonids (Salmonidae) require oxygen-rich water and a specific temperature for hatching and growing. Today, they are usually found in running water with temperatures ranging from 0–20 °C (Jonsson and Jonsson, 2009; Elliott and Elliott, 2010), which generally corresponds to the trout (*Salmo trutta*) and grayling

(*Thymallus thymallus*) zones (Huet, 1954). Burbot is a nocturnal fish, and prefers large rivers in a very cold environment (< 5 °C). It is mainly active in winter (Keith et al., 2011). Cyprinids (Cyprinidae) live in temperatures of 10–25 °C (Tissot and Souchon, 2010). Some cyprinids reported in our assemblages (e.g., chubs) can be found in the salmonid zonation, as they also thrive in running water. Barbels (*Barbus barbus*), on the other hand, prefer slow-flowing water, although they can also live in running water. Other species, such as stone loach (*Barbatula barbatula*) and bullhead (*Cottus gobio*) may also be found in cold, running water. In present-day terms, this zone would be similar to pre-mountain river sections of Western Europe.

### 3. Results

Scladina Cave (Belgium) Seventy-four fish remains were studied. These represent less than 2% of the faunal NISP (**SOM Tables 1 and 2**). European sturgeon (*Acipenser sturio*) was the dominant species but unfortunately, its remains were discovered in a disturbed zone (**Fig. 2**). Thus, although the origin of the sturgeon remains in Scladina is likely to be anthropogenic, since individual size estimates range from about 95 to 165 cm and exclude transport by a non-human predator, we cannot be sure of their attribution to the MP, and we preferred not to take them into consideration in this study. Perch (*Perca fluviatilis*) scales ( $n = 34$ ) were also present in level 4A but no size-related information could be obtained from them. Three pike (*Esox lucius*) remains were also found in levels 4B and 6A. Finally, level 4A comprised some unidentified fish remains. All species preferentially thrive in the lower courses of rivers, as in the bream zone (Huet, 1954). No visible traces of bone modification were recorded.

Walou Cave (Belgium) The 416 remains from the original study by Van Neer and Wouters (2011) were re-examined. This is the largest archaeological fish collection from Belgium. In levels CI-8 and CI-6, the assemblage is dominated by brown trout (*Salmo trutta*), followed by grayling (*Thymallus thymallus*), stone loach (*Barbatula barbatula*), pike (*Esox lucius*), burbot (*Lota lota*) and bullhead (*Cottus gobio*). Indeterminate salmonids and cyprinids—probably chub (*Squalius cephalus*) or dace (*Leuciscus leuciscus*)—are also present (**SOM Tables 3 and 4**). Fish remains represent 17.6% of the faunal NISP.

The estimated TLs ranged from a few centimeters for the bullhead to one meter for the largest salmonids, which can only be sea trout (*Salmo trutta*) or Atlantic salmon (*Salmo salar*). Most brown trout range around 20–40 cm. Cyprinids range around 5–10 cm. The presence of large salmonids points to a deep river, with running water. No bone modifications were observed. Fish bones from level CI-8 were clustered at the entrance of the cave. An accumulation of small fish (i.e., 5–10 cm) was recorded in square J17. Lithic artifacts and fauna were scattered all over the excavated area, mostly located outside the cave (i.e., E/F-24/25). The assemblage includes species that range from the trout to the barbel zones (Huet, 1954).

Caverne Marie-Jeanne (Belgium) A total of 14 fish remains, previously mentioned as Percomorphs by Gautier and Heinzelin (1980), were re-examined and determined. Species included barbel (*Barbus barbus*), bullhead, burbot and brown trout. Bullhead was the dominant species and level 4, an unspecified Mousterian level, yielded the largest number of remains (**SOM Tables 5 and 6**).

Except for brown trout, some of which reached 30 cm, TL ranged from 5–20 cm. These species range from the trout to the barbel zones. The detailed study of each bone did not reveal taphonomic traces of any kind. In general, vertebrae were better preserved (ca. 70–

90%) than skull bones, which were fragmented for the most part (ca. 10–30%). No traces of digestion were visible.

Vaufrey Cave (France) A total of 420 fish remains from the original study by Le Gall (1988) were re-examined. These represent about 12% of the faunal NISP. Species included Atlantic salmon, brown trout, grayling, pike, perch and eel (*Anguilla anguilla*), although the assemblage was dominated by unidentified cyprinids (**SOM Tables 7, 8 and 9**). Level VII (MIS 6) was the richest level in terms of taxonomic diversity and number of remains. From a biogeographical standpoint, brown trout and grayling abound in the upper river courses whereas perch, pike and eel are more frequent in the mid- or even lower courses (Huet, 1954). Salmonids range in size from 30 to 40 cm but a few vertebrae represent larger specimens, up to 50 cm. Eel and pike both range between 20 and 40 cm. All cyprinids are small (< 20 cm), whereas perch exhibit the widest size range of all (5–30 cm). Le Gall (1988) postulated that salmonids died in winter or early spring whereas cyprinids died in summer.

Alterations included a black coloration on some vertebrae, although it was not possible to assess whether this was due to manganese impregnation or burning. SEM images revealed taphonomic alterations (polishing) on the pharyngeal teeth of cyprinids, which may be due either to digestion or water dissolution.

Baume Moula-Guercy (France) With 1,307 remains, Baume Moula-Guercy Cave constitutes the largest collection in our study (**Tables 11 and 12**). Levels XVIII and XVII yielded more than 50% of the material. Fish represent about 14% of the faunal NISP. Species diversity is high and includes the agone shad (*Alosa agone*), eel, chub (*Squalius cephalus*), pike, burbot, Eurasian minnow (*Phoxinus phoxinus*), roach (*Rutilus rutilus*), brown trout and grayling. Burbot was the dominant species, followed by eel. Cyprinids range from 10–30 cm and salmonids from 10–20 cm, although some vertebrae represent specimens over 50 cm (> 1

kg). Shad measures 20-30 cm and eel includes small (ca. 20 cm) specimens and others over 70 cm (**SOM Table 11**). Incremental growth lines indicate that deaths occurred throughout the year. These species are mainly distributed in two distinct river zones: in the running waters of the grayling zone and in the slower flowing waters of the barbel zone. Although shad and burbot are more frequent in the lower courses of rivers, both species can migrate upstream into the barbel zone, and burbot being an arctic taxon, thrives in cold waters (see above). The high frequency of a demersal nocturnal fish seems intriguing and suggests the existence of a very particular predator and/or fishing technique. Some trout vertebrae present partly polished, smooth surfaces and a few other vertebrae may possibly have been crushed by teeth (**Fig. 3k**).

Abri du Maras (France) The study by Daujeard et al. (2019) revealed that only level 4.1 yielded fish (NISP = 167) remains, including 13 chub remains (ca. 35–40 cm TL, 550–850 g BM), unidentified cyprinids and perch scales (level 4; MIS 3; **SOM Tables 12 and 13**). Fish represent 12.5% of the faunal NISP. No evidence of digestion was observed on the bones. Chub is most frequent in the grayling zone whereas the perch optimum is in the slower flowing waters of the bream zone (Huet, 1954). The fish remains are located over an area of two square meters. However, although no evidence of subsequent burial is visible in the deposits to explain this spatial distribution, we have some doubts about the association between the fish remains and the archaeological layer. Direct dating of the fish bones did not provide reliable results.

Barasses II (France) Fish remains (NISP = 127) were only retrieved in the middle and lower parts of the sequence. Fish represent 7.7% of the faunal NISP. Salmonids—brown trout but especially grayling—dominate the assemblage (Béarez and Guillaud, 2019). Burbot, eel and perch are also present (**SOM Tables 14 and 15**). Salmonids range between 10–30 cm and

305 50–60 cm. The modal size category was 20–30 cm. Seasonality analyses showed that fish  
306 were captured throughout the year. The presence of salmonids reveals the existence of  
307 running waters. No bone surface modifications were recorded, although some remains were  
308 covered by manganese (**Fig. 3j**). The bone material was slightly fragmented (i.e., < 20% bone  
309 loss).

310 Abri des Pêcheurs (France) Only ten fish remains were studied, including eel, brown trout  
311 and grayling, the latter being the predominant species. Fish represent about 1% of the  
312 faunal NISP. Sector 2 (MIS 4) provided the largest number of remains. Eel may occasionally  
313 reach upper river courses where brown trout thrives (Huet, 1954). For salmonids, sizes  
314 ranged mostly between 10–30 cm, with a few remains representing an individual of about  
315 50 cm. Eels reached sizes of 50 cm. No remains bore visible traces of taphonomic  
316 modifications (**SOM Tables 16, 17 and 18**).

317 Baume Vallée (France) Of the 24 fish remains recovered, only the brown trout was  
318 identified. All the represented specimens are ca. 30 cm. Fish represent about 5% of the  
319 faunal NISP. Four trout vertebrae show traces of polishing (**SOM Tables 19 and 20**).

320 Áridos-1 (Spain) A total of 316 fish remains previously studied by Morales (1980) were re-  
321 examined. In terms of NISP, fish bones represent 16.5% of the faunal remains (> 20% when  
322 pulmonates are excluded). Species include eel, pike, twaite shad (*Alosa fallax*), barbel  
323 (*Barbus* sp.), Iberian nase (*Pseudochondrostoma* cf. *duriense*) and unidentified cyprinids  
324 (**SOM Tables 21 and 22**). Eel and pike are both around 20–30 cm, whereas cyprinids are  
325 around 30–40 cm with some specimens reaching 50 cm. Most species are consistent with  
326 slow running waters, such as those found in the barbel zone. No bone modifications were  
327 recorded, but it should be noted that some bones were still covered by a calcareous matrix.

Cueva Millán (Spain) A total of 284 fish remains previously studied by Roselló-Izquierdo (1992) were re-examined. These include brown trout (22–44 cm TL; 200–900 g BM), Iberian nase (21–31 cm; 150–300 g) and eel (43–67 cm; 300–600 g). Fish remains represent ca. 40% of the faunal NISP and are concentrated in Level 8I-1a (**SOM Tables 23 and 24**). Trout is the dominant species. All species occur in running waters, although eel thrives in many other biotopes. Some 20% of bones ( $n = 56$ ) present traces of black coloration but no other traces were recorded on the samples.

#### **4. Discussion**

Although it is questionable to compare faunal assemblages retrieved by different research strategies, excavation methods and retrieval techniques, a comparative overview of taphonomic issues can help to reveal non-evident aspects of the behavioral repertoire of a given bone accumulator agent. Our first observation is the generally well-preserved condition of these collections (**Fig. 4**), which allowed 75.3% of the items (2,380 remains) to be identified to at least the family rank. A second feature is related to the percentage of a fish assemblage that remains unidentified, as damage to bones varies from group to group. In our case, taken as a whole, 81% of the surveyed remains were identified to the anatomical and/or taxonomical level (**Table 2; Figs. 3, 4 and 5**). However, this average conceals substantial differences between samples, with the unidentified fish fraction ranging from 3.5 to 74.1%, which probably reflects diversified preservation conditions, among other factors.

It is therefore essential to examine reconstructions of fish size and mass, spatial distribution of bones and surface modifications, seasonality of catches, and ethological comparisons to explain the presence of fish in assemblages.



352

353 *4.1. Biological considerations and fish diversity*

354 It is difficult to translate the variety exhibited by these fish assemblages into  
355 straightforward patterns. These eleven collections combined, covering a temporal span of  
356 more than 300 ka (MIS 11–1), deriving from open-air and cave deposits and covering a  
357 latitudinal range of 10 degrees (ca. 40° to 50° north), have yielded 3,159 remains,  
358 representing 22 taxa (15 species if we concede that both salmon and brown trout are  
359 represented in the samples; **Table 2; Figs. 4 and 5**).

360 Biogeographical trends prove elusive since most taxa thrive in a rather wide range of  
361 environmental conditions. However, the best indicators show that the fish assemblages are  
362 strongly influenced by temperature. Only three species (burbot, bullhead and grayling)  
363 qualify as cold-water indicators, whereas only the eel represents a temperate water proxy  
364 given that it requires the Gulf Stream to transport its larvae to European rivers (Kettle et al.,  
365 2008.). Throughout the Upper Pleistocene, the Gulf Stream reached Iberian latitudes, and  
366 therefore the presence of eel in the two Iberian collections makes perfect sense, despite  
367 their very different ages (Áridos-1: MIS 11; Cueva Millán: MIS 3), and also explains why the  
368 eel is only recorded during temperate stages in French sites (Vaufrey, Baume Moula Guercy,  
369 Barasses II and Abri des Pêcheurs). In a similar way, the presence of burbot and bullhead at  
370 Walou and Marie-Jeanne, and of grayling in the former cave, is perfectly logical since these  
371 species reflect harsher conditions, in keeping with the tundra and cold steppe faunas from  
372 these Belgian sites (Damblon, 2011; Gautier, 1980). Burbot is a circum-Arctic species and  
373 would thus never have reached the Iberian Peninsula, where endemic temperate-water taxa  
374 are to be expected. However, as a rule, salmonids thrive in colder waters than cyprinids, and  
375 the two families form the bulk of western European freshwater fishes. As a result of their

high tolerance, they cannot be considered as good environmental proxies, despite attempts to do so (Le Gall, 2010).

From a chronological standpoint, the oldest fish assemblage (Áridos-1) corresponds to a climatic stage not very different from the current climate in the area and features a balanced fish fauna, which, except for the migratory shad and the now extinct (though artificially reintroduced) pike, can still be found in the area. This presence of species still extant today is a recurrent theme at all the sites, although the number and frequency of species shift through time. The only exception for France is the presence of grayling at Vaufrey Cave, since it disappeared from the Garonne Basin in modern times, before being reintroduced. Given the quantity and quality of available data, such differences cannot be explained by past abundances (i.e., 'availability'), or by the selectivity of the agent that caught the fish (i.e., 'choice'). Burbot and eel predominate in MIS 6 levels at Baume Moula Guercy. The fact that, despite other ecological differences, both species are bottom-dwellers and essentially crepuscular/nocturnal would narrow the range of potential (regular) predators to mammals. The highest number of records occur between MIS 5 and 3. MIS 5 collections, as paradigmatically evidenced by Walou Cave, show the highest taxonomical diversity with trout and grayling dominating the assemblages, followed by burbot and eel (**Table 2**). Fish taxa from MIS 5 do not reveal any major climatic differences, and fish assemblages correspond mainly to the grayling zone (i.e., pre-mountain river sectors with cold water; Huet, 1954). MIS 4 fish records are limited (**Table 2**; NISP = 14) although four sites represent this period (Walou, Baume Moula Guercy, Barasses II and Abri des Pêcheurs). The recorded species (chub, perch, eel and grayling) suggest more temperate water conditions, although water temperatures never exceed 23 °C for grayling (contrary to most salmonids, which are

399 winter spawners, grayling spawns in the spring once the water temperature reaches 9 °C;  
400 Persat, 1988; Keith, 1998).

401 MIS 3 sites are dominated by the brown trout, in France and in Spain, except for Áridos-1,  
402 where no single species is predominant. Brown trout is considered to be a cold-water  
403 species, as it thrives between 0–20 °C, but its flexibility and resilience, also in terms of water  
404 temperature, are reflected in the frequency of this species in the MIS 3 collections, and also  
405 in most of the remaining periods (Keith et al., 2011). To what extent such prevalence is also  
406 a reflection of choice on the part of potential predators remains an open question for now.

407 Although human intervention historically led to the depletion and local extinction of  
408 migratory species such as the sturgeon, Atlantic salmon, eel and shad, all of the Mousterian  
409 fish faunas studied here represent species still extant in Western Europe today. Likewise,  
410 although some of these species are alternatively recorded as Holarctic (e.g., Atlantic salmon,  
411 brown trout, grayling, burbot, bullhead), Palearctic (e.g., Eurasian minnow, stone loach),  
412 Euro-Siberian (e.g., roach, chub) or Iberian (Iberian nase and barbel), none of these taxa  
413 represent deviations from current biogeographical zones. On the other hand, on account of  
414 the spatiotemporal patchiness and scarcity of these ichthyofaunas, it is not possible to  
415 outline even a rough picture of the evolution of fish fauna through time in any given locality.  
416 As a result, the hypothesis that whoever was catching fish at any time during this temporal  
417 interval seems to have been constrained by availability, rather than making choices, must be  
418 discarded.

419 No comprehensive trend emerges from the inference of freshwater biotopes. Data show  
420 that MP fish derive from a wide variety of zones and freshwaters with diverse facies,  
421 currents, etc. This would help to explain the taxonomic diversity recorded in our corpus. As  
422 expected, due to the presence of fish species at different times and disparities in data, no

ecological information could be inferred regarding the persistence of fish communities in the same place over time in the rivers studied here. Scladina, for example, is the only site featuring sturgeon, whereas Baume Moula Guercy is the only Rhône Valley site containing pike, which could reflect a distinct paleohydrological context, as the latter species not only indicates clear water but also dense aquatic vegetation. The dominance of salmonids at Walou Cave, Barasses II Cave, Abri des Pêcheurs, Baume-Vallée and Cueva Millán, attests to the presence of running and oxygen-rich waters. The presence of grayling at Walou, Barasses II, Abri des Pêcheurs, Baume Moula-Guercy, and Vaufrey, indicates large rivers with deep zones, fast currents and gravel substrates. At Abri du Maras, Vaufrey and Áridos-1, the presence of cyprinids, such as chub and nase, indicates moderately-running waters, while the presence of perch attests to still waters. At Caverne Marie-Jeanne and Baume Moula-Guercy, the assemblages are dominated by benthic and/or nocturnal fish (e.g., bullhead, barbel, burbot and eel; Ojaveer et al., 2003; Bruslé and Quignard, 2011; Keith et al., 2011). At most sites, the only predators capable of negotiating such a wide array of fish taxa and biotopes under such different environmental conditions are humans.

#### *4.2. Fish bone representation and preservation*

The studied assemblages are characterized by a majority of complete elements (91%), but out of ca. 200 bone types potentially constituting the skeleton of a teleost, only 27 (13%) were recognized in our samples. Considering that no less than 230 individuals were identified in these assemblages, this constitutes an extremely low survival rate of anatomical portions (13.5%). This rate points to the role of time-related constraints, and not necessarily to the behavior of the bone accumulator in the retrieval of fragile fish bones from archaeological deposits.

Vertebrae (NISP = 2441; 77%) are the most common elements, whereas cranial bones (NISP = 132; 4%) are clearly underrepresented, and absent altogether from four sites (Scladina, Abri des Pechêurs, Baume Vallée and Barasses II). Scales, along with unspecified cranial and vertebral elements, such as neural and haemal processes, represented the remaining 19% (NISP = 586; scales were recorded at Scladina [38], Walou [100] and Abri du Maras [12]; only pectoral spines [7] and sturgeon dermal scutes [25] were recorded at Scladina; **SOM Table 24; Fig. 2, Fig. 3 and 4).**

Bone representation is characterized by high values in the cases of shad basioccipitals, which have a percentage of representation (PR) of 33.3%; burbot (PR = 19.5%) and eel (PR = 10.86%) caudal vertebrae, and pike (PR = 5%), bullhead (PR = 11.6%), salmonids (PR = 11.9%), stone loach (PR = 16.6%) and cyprinids (PR = 40.5%) precaudal vertebrae (**Table 2**). Precaudal vertebrae are overrepresented in perch (PR = 130%). Overall, the combined percentage of representation for all taxa is low, with disparate representation of cranial and post-cranial elements and low skeletal completeness.

Data relating to bone modification are very informative. In particular, no damage such as deformation, rounding, polishing or traces of digestion is visible on most remains, ruling out the action of carnivorans (**Table 3; Fig. 3a–i**). Very few traces are visible on bone surfaces: four salmonid vertebrae at Baume-Vallée and some at Baume Moula-Guercy presented smooth surfaces, while some pharyngeal teeth of cyprinids showed slight traces of digestion at Vaufrey Cave. The action of gastric juices results in a smooth and polished surface (Andrews, 1997), but prolonged transport of bones in water also produces rounding and polishing. Baume Moula-Guercy also contained some vertebrae possibly crushed by teeth (**Fig. 3k**). At Áridos-1, Barasses II and perhaps also Vaufrey, the crust of the matrix and manganese impregnations hamper the observation of traces on bones (**Fig. 3j**).

471

472       Following Dodson and Wexlar (1979) and Andrews (1990), the representation of  
473 anatomical elements, fragmentation, and the state of bone surfaces can be divided into five  
474 broad categories of modification—light, intermediate, moderate, great and extreme—  
475 depending on the intensity of digestion and the type of predator. Several experiments on  
476 the survival of fish skeletal elements during digestion in dogs, pigs and humans have been  
477 carried out (e.g., Jones, 1986; Nicholson, 1993). Modern carnivorans produce feces  
478 containing bones with varying degrees of damage and digestion. Among them, Mustelidae  
479 feces contain bones that tend to be less broken and digested (Andrews, 1990). Ingestion by  
480 other carnivorans shows higher digestion rates with extensive bone damage (Andrews,  
481 1990; Mallye et al., 2008; Russ, 2010; Mallye, 2011; Guillaud et al., 2017a).

482       Bone fragmentation by birds is more limited than by mammals. For diurnal birds, some  
483 pitting is observed, and broken edges are rounded (Andrews, 1990).

484       On the other hand, small fish are less likely to exhibit cut marks, and Willis et al. (2008)  
485 stated that cut marks—an indicator of human culinary preparation—are rarely visible on  
486 archaeological fish bones (but see Braun et al., 2010). Post-depositional taphonomic  
487 phenomena may also hide the presence of cut marks. Skeletal elements are often too  
488 damaged to differentiate between natural, human and non-human accumulations.

489

#### 490 *4.3. Fish size representation*

491       The studied archaeological fish span a wide spectrum of sizes ( $5 \leq TL \leq 165$  cm), with  
492 marked variations among groups. Modal values for salmonids range between 20–30 cm, but  
493 larger specimens, up to over 50 cm, are observed in Walou, Vaufrey, Baume Moula-Guercy,  
494 Barasses II and Abri des Pêcheurs. Cyprinids, comprising several species, range from 5–50

cm, with most individuals being either small (barbel) or large (chub, nase) for the species considered. Eels range from 20–70 cm, with most individuals being around 30–40 cm. Stone loach, minnow and bullhead all range from 5–10 cm. The estimated size range of the sturgeon from Scladina Cave is between 95 and 165 cm. Pike and burbot range between 10 and 40 cm, and perch between 5 and 20 cm. For shads, the sizes of the archaeological specimens are from 20–30 cm for *Alosa agone* and 40–50 cm for *Alosa fallax*.

It is highly unlikely that this range of sizes could be the result of the action of a single and identical bone accumulator. For the purposes of this work, three size categories are considered: (a) fishes with TL below 10 cm, (b) those with TL above 50 cm, and (c) specimens ranging between 10 and 50 cm TL. Body mass is difficult to estimate and often dependent on the shape and condition of the fish, but individuals from the first group normally average maxima of 10–15 g, whereas those from the second group seldom fall below 1 kg. It is very unlikely that fish from the first group, which in addition to stone loach and bullhead, include juveniles from other groups, could be caught by humans, except if these small fishes represent the stomach contents of larger-sized specimens brought to the archaeological deposit (Van Neer and Wouters, 2011). For fishes over 1 kg (e.g., salmon), humans are the only candidates liable to collect them on a regular basis in European freshwaters (see § 4.6). Fishes of intermediate sizes, in particular those ranging from 30 cm (i.e., 300–500 g) to 50 cm (i.e., 1 kg on average), constitute the bulk of contemporary freshwater catches and are of particular interest to us here, but these fishes can be caught by a wide range of predators. For this reason, for the purposes of this work, specimens near the maximum values of this range of intermediate sizes are of prime importance, including the aforementioned salmonids and the largest burbot (50 cm, ca. 1 kg) from Baume Moula-Guercy, for instance. Although they may potentially be captured by other predators, such as nocturnal and diurnal

birds of prey (Dodson and Wexlar, 1979; Laroulandie, 2002) or carnivorans (Andrews, 1990; Mondini, 2001), fishes in that intermediate range of size and body mass are also likely to be transported to caves by humans.

#### *4.4. Spatial distribution*

Different factors complicate the interpretation of spatial distribution. These include the lack of information on the spatial distribution of other kinds of remains (Caverne Marie-Jeanne, Vaufrey, Baume-Moula-Guercy, Cueva Millán, Áridos-1), restricted excavation areas (Barasses II), low sample sizes (Baume-Vallée, Abri des Pêcheurs), and fish remains with unclear stratigraphic provenience (Scladina). At Abri du Maras, the highest density of archaeological remains appeared next to the wall of the shelter where two squares (L-M6) yielded the greatest diversity of remains including mammals, lithics, birds and ash-lenses on different squares. Fish remains only appeared in layer 4.1, distributed over two square meters, although one square (I6) provided 90% of the fish remains, but the incorporation of fish with the archaeological level is unclear, so this distribution will not be discussed further. For such reasons, only Walou Cave was deemed appropriate to provide spatial information (Fig. 6).

The analysis carried out on level CI-8 from Walou Cave evidenced that although all kinds of remains were distributed throughout the excavated area, the highest density of lithics and fauna was found in squares E-F/24-25. This distribution pattern contrasted with that of fish, most of which were concentrated in square J17. No preferential distribution of the largest fish remains was observed (i.e., remains were scattered all over the excavated area). However, the square with the largest number of fish remains was located on the level from the cave's dripline and this sample only included small fish (i.e., bullhead, stone loach and



brown trout). In contrast, the scarce fish remains mixed with the archaeological material represented much larger individuals, mostly around 30–50 cm TL in the case of burbot, brown trout and grayling. This spatial distribution of fish remains could indicate the rejections of a nesting bird (**Fig. 3**).

#### *4.5. Season of capture*

Information on the season of capture can provide valuable clues for interpreting the behavior of a given fish predator. Except for the twaite shad, Atlantic salmon and sturgeon, all of the studied fish species, including eel, are permanent denizens of freshwater biotopes. All species congregate during the spawning season—which generally coincides with the spring except for salmon, trout and burbot—in restricted areas, often in shallow waters, which makes them more vulnerable and accessible to potential predators (**Table 4**).

The presence of some large migratory fish, therefore mature adults, such as Atlantic salmon in Vaufrey cave, shads in Baume Moula Guercy and Áridos-1, or sturgeon in Scladina, provides some indication of the fishing season. Indeed, these species, which frequent freshwaters only for reproduction, are present only during a few months of the year: from April to December for salmon (almost all adults die after reproduction) and shads, only from March to June for sturgeon (based on current data for France).

In most of the examined samples, the outer edges of the vertebral centra were eroded so that only the samples from Cueva Millán, Baume Moula-Guercy and Barasses II yielded reliable information. At Cueva Millán, brown trout, Iberian nase and barbel confirm the data from a previous analysis and show that although year-round mortality was observed, deaths occurred in a disproportionate manner during the ‘summer’ season, when natural mortality was at its lowest (Morales and Roselló, 1989). Given that, in principle, brown trout is a

winter spawner, its mortality cannot be readily associated with accessibility or vulnerability during the reproductive period, but this could well be the case for the two cyprinids. Data concerning the species from Barasses II and from Baume Moula-Guercy indicate that deaths also occurred throughout the year but a peak was recorded during autumn for burbot (**Table 4**), backing up the idea of catches peaking during the spawning season.

#### *4.6. Potential predators*

For most sites, it is difficult to identify the freshwater fish predators—and thus the extent of Neanderthal contribution—despite the close connection in all sites between fish remains, large faunal remains and lithic artefacts, except Caverne Marie-Jeanne. In most cases in our corpus, other potential predators exist beside Neanderthals. A wide diversity of faunal species, and of potential fish predators, such as Aves (Corvidae, Falconidae, Strigidae) or Carnivora (Canidae, Mustelidae, Ursidae) are also present in the assemblages (**Table 5**).

Many authors have studied the role of diurnal and nocturnal raptors (Mayhew, 1977; Dodson and Wexlar, 1979; Andrews, 1990; Laroulandie, 2002) and carnivorans (Andrews and Evans, 1983; Mondini, 2001; Campmas and Beauval, 2008) in modern bone accumulations. Erlandson and Moss (2001) investigated in detail diverse predator species that could potentially deposit fish remains in caves located close to shorelines, including canids (coyotes, foxes, wolves), river otters, bears (*Ursus* spp.) and birds (cormorants, condors, eagles, gulls and the Eurasian eagle owl). Canids, especially coyotes (*Canis latrans*), can sometimes take food to dens for their young or for later consumption. River otters rely on aquatic invertebrates and vertebrates but they often eat their prey on river banks, usually less than 20 m from the river. However, they can sometimes transport and accumulate fish bones or deposit spraints a few hundred meters from a river. Bears, essentially grizzly,

sometimes bury fish carcasses, but are not considered as bone collectors. The image of a bear waiting in the river for a salmon to fall into its mouth is familiar to everyone. However, this situation only occurs in Alaska or Kamchatka, where millions of Pacific salmon (*Oncorhynchus* spp.) seasonally return to the streams to spawn. While the two brown bear (*Ursus arctos*) subspecies, the grizzly bear (*U. a. horribilis*) and the Kamchatka brown bear (*U. a. beringianus*), are dependent on this resource (Hilderbrand et al., 1999), this is certainly not the case in Europe, where fish are virtually absent from the brown bear diet (Etienne and Lauzet, 2009; Niedzialkowska et al., 2019). Moreover, bears only consume the high-energy parts, i.e., the skin and gonads, sometimes the fillets, but fish carcasses are left on the banks and not dragged into dens. On the other hand, feeding experiments indicated that fish remains were rarely preserved after digestion by bears (Russ, 2010).

If the Etruscan bear (*Ursus etruscus*) was probably piscivorous (Medin et al., 2017), according to isotopic and microwear studies, the cave bear (*Ursus spelaeus*) is considered to be mostly herbivorous (e.g., Bocherens et al., 1997; Pinto-Llona et al., 2013; Jones and DeSantis, 2016; Naito et al., 2016; Ramírez-Pedraza et al., 2019). Therefore, it would not bring fish bones into caves. A primarily vegetarian diet was also probably the case for Deninger's bear (*Ursus deningeri*; Van Heteren et al., 2018) and the Asiatic black bear (*Ursus thibetanus*; Huyghens et al., 2003). Large felids, such as cave lions (*Panthera spelaea*), are not considered here since they are not known to eat fish (Bocherens et al., 2014).

Bird remains include raptors and corvids, such as the common kestrel (*Falco tinnunculus*) and raven (*Corvus corax*). Eagles and vultures occasionally scavenge on fish (Chaline et al., 1974), but do not frequent caves. Among strigids, the European eagle owl is often considered to be an accumulator. Other strigids are present, namely at Baume-Vallée and Caverne Marie-Jeanne, such as the tawny owl (*Strix aluco*) and eared owls (*Asio* spp.).

Finally, at Baume Moula-Guercy, the taphonomic study of micromammals suggests a contribution by owls, such as *Strix aluco* or *Asio otus* (see Desclaux et al., 2011). Studies of these predators indicate marginal fish remains in pellets (Wendland, 1984; Bouvier and Bayle, 1989). Strigids are opportunistic predators and would prey on the most abundant food in their habitat.

To date, the best-documented avian fish-consuming predators are the eagle owl (Guillaud et al., 2018; Nicholson, 1991; Le Gall, 1999; Russ and Jones, 2011), the barn owl (Broughton et al., 2006), the bald eagle (Erlandson et al., 2007), the European kingfisher (Frontin, 2017) and the yellow-legged gull (Guillaud et al., 2019). The eagle owl is identified as an agent of micromammal accumulation at several archaeological sites (Andrews, 1990; Laroulandie, 2002). Studies of the cormorant (*Phalacrocorax carbo*) indicate that it is one of the few predators of the common grayling (Suter, 1995; Suter and Morel, 1996). Although cormorants do not specifically select a narrow range of grayling sizes, they mainly consume small specimens. This fishing bird would be an ideal accumulator for most of the species identified in our corpus. However, ingested bones from pellets are often completely digested, and regurgitated fish are rare and only found in breeding colonies (Veldkamp, 1995). Moreover, although cormorants can be present on the continent, they are mainly found in coastal environments, and not in caves (Orta, 1992).

In sum, it would seem that none of the predators present at the sites of our corpus is piscivorous.

#### 4.7. Fish origin

The presence of grayling and burbot remains in the assemblages raises the question as to which predator could prey on them. Cormorants are one of their few predators, but humans

may have used composite tools or fishing traps to catch these species, knowing that these fish are easier to catch when they remain immobile near the shore or come to the surface, mainly during the spawning period.

The recurrence of species throughout the MP and UP, such as salmon, trout, grayling, is probably not a clear sign of selective fishing by human populations. As mentioned above, we do not have enough comparative sites to identify similar practices. For example, at Walou Cave, fish species remain unchanged throughout the sequence, from the MP to the UP. Following Van Neer and Wouters (2011) and Le Gall (2008), these species (grayling, trout and burbot) are also found in Magdalenian sites, such as Bois Laiterie, and in the same size ranges. Conversely, studies by Roselló-Izquierdo and Morales-Muñiz (2005) show an inverse proportion of fish remains at sites in the Iberian Peninsula. Upper Paleolithic sites (e.g., Arbreda and Amalda) contain smaller quantities of fish than the Cueva Millán site (Morales and Roselló, 1990; Muñoz and Casadevall, 1997). In France, the number of sites with fish remains (salmonids) of similar size increases throughout the Paleolithic, which confirms the practice of fishing, especially with the use of tools (e.g., fishhooks, traps), as is the case at the Pont d'Ambon Cave during the Azilian (Le Gall, 1984; Cravinho, 2009).

Finally, we can retain most of our corpus, except for Scladina and Abri du Maras, for which we are not totally sure about the origin of the fish assemblage. Most of the remaining sites are home to carnivorans and/or birds that could prey on fish (**Table 5**). However, six of the sites (Vaufrey, Baume-Vallée, Barasses II, Baume Moula-Guercy, Walou and Cueva Millán) comprise fish specimens of more than 1 kg and most of the sites show no bone modification of fish bones (**Table 6**). All the sites record anthropogenic activities, except Caverne Marie-Jeanne, and the majority of fish remains were found in deposits where human presence is clearly attested. Except for Áridos-1, all the deposits are located in caves,

which rules out the possibility that some fish remains were the result of natural deaths, whether cumulative or episodic, deposited on the river banks (Butler, 1993; **Table 6**). Also, although many of the non-piscivorous faunas from these sites incorporate species occasionally documented as fish predators, none of them are truly piscivorous, as would be the case of the otter or the cormorant (Dodson and Wexlar, 1979; Andrews, 1990; Orta, 1992; Suter, 1995; Suter and Morel, 1996; Erlandson and Moss, 2001; Mondini, 2001; Laroulandie, 2002). This is not to say that animals or natural processes did not generate some of the reported fish remains. Indeed, it has been argued that the presence of fish of less than 10 cm (10–15 g) cannot be attributed to human activity and that small fish accumulations such as that reported at the entrance of Walou Cave best conform with pellet deposition below the roosting place of an avian predator. For these reasons, it is important to stress that several of the studied deposits bear traces of several potential accumulators, but Neanderthals would also be on that list.

The issue is difficult to settle given the lack of straightforward evidence, such as fishing tackle. To our knowledge, no such instruments have ever been reported in Mousterian deposits. However, suggestive signs of Neanderthal action exist and become compelling when combined with other factors. The case of the only non-anthropogenic site of our corpus, the hyena den at Caverne Marie-Jeanne, is peculiar. Here, despite the extremely small fish sample within a huge faunal assemblage (itself a sign of non-anthropogenic fishing?), only tiny fishes (i.e., 5–20 cm TL) were retrieved, indicating that the scarcity of larger fish may not be a result of retrieval biases. More intriguing is the ‘dominance’ of the bullhead (43% of fish NISP; **SOM Table 6**) at Caverne Marie-Jeanne, Walou, Baume Moula-Guercy, Barasses II, and Áridos-1, as this indicates that fishing focused on adults of small species rather than on juveniles. Lastly, only a few bones (7%) could not be identified. This

suggests that these bones remained in good condition despite their fragility and only cranial elements exhibited fragmentation. As the remaining animal samples were not quantified, it is not possible to explore other aspects of these collections, although the abundance of carnivorans, microfaunas and birds indicates that predators, not just hyenas, might have been responsible for the accumulation of a substantial portion of the faunal assemblages. In contrast, the elephant butchery floor at Aridos-1, despite the importance of its microvertebrate and bird collections, features few raptors and carnivorans and a fish collection that represents 16.5% of the total NISP. Fish sizes there average around 50 cm (ca. 1 kg) and range from 20-70 cm TL. A full 75% of the 316 fish remains could not be identified, and the assemblage exhibited a balanced spectrum of taxa, without any single species being dominant (**SOM Table 21**).

Matters are more complicated when we seek parallels for Caverne Marie-Jeanne in Belgium, the only site of our corpus with no human activity, and where only very small fish were identified. This is completely different from our archaeological corpus where fish size is highly diversified. As far as we know, fish remains from medium to large-sized individuals are absent from non-anthropogenic deposits such as hyena dens (e.g., Enloe et al., 2000; Beauval et al., 2005; Enloe, 2012; Dusseldorp, 2013; Fourvel et al., 2014). The rare marks (polishing) on fish remains from Caverne Marie-Jeanne suggest that the potential predator could be a strigid, such as the European eagle owl.

For anthropogenic sites, faunal assemblages contain many remains of microvertebrates, birds, as well as a variety of animals that could have generated some of the small faunal deposits. Still, as previously stated, it would be difficult to reconcile the presence of the larger-sized salmonids and burbot with the activities of an avian or other type of cave-dweller predator. The mixed (faunal+anthropogenic+natural) nature of most of the studied

deposits makes it more difficult to detect clear-cut signals of any of the potential bone/fish accumulators, including Neanderthals (**Tables 5, 6**).

#### *4.8. Ethnographic data and archaeological contexts*

Ethnographic parallels are not always clear or applicable to archaeological sites, particularly in the case of a hominin whose very nature and cognitive processes are still a matter of debate (French, 2019).

Recent ethnographic data from North America and Canada shed light on the fish species caught, selected sizes, seasonality of catches, fishing methods, and modes of conservation and preparation. They also suggest fishing technology ideas for fish that died naturally and for live fish. These data can help to interpret the MP evidence.

Butler (1993) indicates that river transport may have deposited dead fish on river banks, as part of natural accumulations. In such contexts, complete carcasses are dispersed nearby, and spatial dispersion is limited. In a predation context, only parts of the carcass are found, with remains dispersed over a larger area farther from the river shore (Thomas, 1971; Butler, 1993). Russ (2016) argued that fishing behavior focused on the exploitation of anadromous forms during migration seasons. Data also suggest that when fishing was carried out on a year-round basis, it was a more significant economic activity during the summer months, when all groups intensified their fishing activities.

Nets were generally the most frequently used fishing method in Canada (Stewart, 1977). Most were of animal origin, including tendons (Stewart, 1977; Smith, 1984; Vanstone, 1984). The use of stone dams has been reported for capturing migrating Atlantic salmon (Smith, 1984; Taylor, 1984). Fish bones sometimes show traces of preparations, such as cut marks



caused by the removal of the head. Cordain et al. (2000) indicate that the exploitation of fish in hunter-gatherer groups is correlated with higher latitude.

At archaeological sites, most of the known instruments associated with fishing come from Mesolithic sites (Cleyet-Merle, 1990), such as the Azilian site of Pont d'Ambon (Dordogne) (see Le Gall, 1984). Several types of fishing tools may have been used during the Paleolithic period, while barb-tail spears may have been utilized during the Magdalenian period (Julien, 1982; Pétilion, 2009). Only proto-harpoons, with less prominent barbs, seem to be adapted to fishing practices (Cleyet-Merle, 1984).

Hooks were also observed toward the end of the UP period in Europe, developed after the Châtelperronian period or in the Azilian period in France. They may also have been used for bird hunting (Averbouh and Cleyet-Merle, 1995).

## **5. Conclusions**

For Neanderthals, even the use of aquatic resources was questioned up until a decade ago. The paradigm was that these humans were unable to gather stationary shellfish. In hindsight, the basis for the question as to whether Neanderthal practiced fishing relied on unstated assumptions and speculative grounds referring to debatable ideas about 'cognitive barriers' and the like. Indeed, ample evidence testifies to fishing practices by a wide range of terrestrial mammals, from bears to monkeys, which are not particularly well suited to the task. The long-standing, now redundant hypothesis that only modern humans are able to fish has led to some fascinating inconsistencies. One such inconsistency appears at Walou Cave and Cueva Millán, where the same fish species and sizes reported in the Mousterian levels are also recorded in the UP, where the issue of fishing is a foregone conclusion.

758 However, scientific hypotheses persist until new and reliable data debunk them and, for the  
759 moment, the only proof we have been able to muster is circumstantial, both in terms of site  
760 contexts and ethnographic parallels. Our data also show that fragile fish bones become  
761 increasingly rarer further back in time, thus chances of finding large collections diminish as  
762 the age of the site increases. A fortunate combination of factors would be required for a  
763 large freshwater fish assemblage to emerge on an archaeological site. From such a  
764 standpoint, addressing the issue of Neanderthal fishing in continental waters may not prove  
765 to be the best way to demonstrate the fishing abilities of this hominin, but in the absence of  
766 marine coastal sites, it seems to be the only solution.

767 This paper provides the first comprehensive presentation of freshwater fish data for the  
768 MP in Western Europe and endeavored to answer the key question: Were Neanderthals  
769 freshwater fishermen? The identification of small terrestrial game and marine remains in MP  
770 sites over the past decade indicates that the Neanderthal diet was diversified, depending on  
771 available resources, although to a lesser extent than for AMH.

772 A large corpus of European MP sites yielded freshwater fish remains dated from MIS 11  
773 to MIS 3. Ichthyofaunal assemblages revealed a varied fish spectrum with a common stock  
774 and some variations, depending on site location. These types of analyses should be  
775 approached cautiously since numerous factors must be considered, such as the  
776 incompleteness of excavation data, the absence of strict contemporaneity between sites,  
777 and the lack of actualistic references. No ecological changes were observed over time but  
778 the low number of remains in the different levels and sites limited our analysis of  
779 proportions throughout time. The combination of analyses presented here provides a  
780 detailed view of the fish species present at sites located close to a river with potential  
781 fishing.

The only non-human-occupied site, Caverne Marie-Jeanne, contains very small-sized fish probably accumulated by birds. Remains of clear piscivorous predators are lacking in most sites. Several criteria need to be considered for the sites with anthropogenic activities: bone representation, surface modification and fragmentation, fish size, species representation and the spatial distribution of bone accumulations. At these studied sites, all the layers with the highest lithic content provided fish remains, but these fish are medium-sized, and spatial distribution analyses were only reliable at Walou Cave. The results of these analyses suggest multi-accumulation: the number of fish remains at Walou Cave, large quantity of fish remains at Baume Moula Guercy, simultaneous presence of small and large specimens at Barasses II or Vaufrey Cave, and the absence of traces (digestion, beak marks and cut marks). The proportion of complete bone (91%) is very high, much higher than for most cave-derived assemblages, where the majority of the bone is fragmented, often heavily. This suggests that the bones themselves were not consumed or chewed, as would be expected if non-human predators, carnivorans and birds, had consumed the fish. This represents a clear signal in favor of hominins as possible predators. Moreover, if the black coloration of some fish bones is due to burning, it can be considered in MP sites (for instance Sclayn, Vaufrey Cave, Baume Moula-Guercy or Abri des Pêcheurs) with fireplaces or/and ash lenses that the fish bones were burnt as a result of human activities.

In all the anthropogenic sites with fish remains, avian predators may have contributed to their accumulation. However, except for Caverne Marie-Jeanne, Neanderthals are the common denominator of all these caves. This tends to suggest that Neanderthals probably played a significant role in the accumulation of some fish remains, particularly large fish.

Although it is difficult to postulate that Neanderthal populations fished regularly, and that fish significantly contributed to their daily diets, several of the sites studied here seem to

suggest more than opportunistic fishing. For sites where the occurrence of nocturnal birds is not attested by their remains, the presence of large fish (> 1 kg) with no digestive traces on their bones leads us to conclude that humans played a significant role in their accumulation. This pattern can be found at the sites of Vaufrey, Baume-Vallée, Barasses II, Baume Moula-Guercy, Walou and Cueva Millán. For the other sites, as well as smaller fish accumulations, it seems more likely that the abundance of fish results from both avian and human contributions.

The results presented here show that it is vital to continue these types of analyses in future excavations to enhance our understanding of Neanderthal fishing behavior (i.e., isotopes to identify fish consumption). We need to enlarge the scope of our survey to incorporate other Mousterian faunal collections where fish remains have been reported in order to confirm or refute these trends. This future survey needs to incorporate the faunal collections emerging on coastal Neanderthal sites from Southern Iberia and other localities along the Mediterranean shores, as these may bear evidence of marine fishing, an issue that has only been tangentially addressed in recent papers. In the meantime, we hope that the data and ideas put forward in this paper will encourage others to pursue the issue of Neanderthal fishing from alternative perspectives, as only a truly interdisciplinary perspective will eventually elucidate this crucial aspect of Neanderthal behavior.

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#### **Authors contributions**

EG, PB studied the fish material; EG, PB, CD, AD, ED, ERI, AMM, MHM wrote and edited the paper; CD, AB, ED, ERI, AMM, MHM provided part of the archeological material; PB, MHM obtained the fundings.

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1367 **Figure captions**

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1369 **Figure 1.** Location of sites of the corpus (red stars). Belgium: 1 = Scladina (Sclayn, Andenne);  
1370 2 = Walou (Trooz, province of Liège); 3 = Caverne Marie-Jeanne (Hastière-Lavaux, province  
1371 of Namur). France: 4 = Vaufrey (Cénac et Saint-Julien, Dordogne); 5 = Baume-Vallée  
1372 (Solignac-sur-Loire, Haute-Loire); 6 = Baume Moula-Guercy (Soyons, Ardèche); 7 = Barasses II  
1373 (Balazuc, Ardèche); 8 = Abri du Maras (Saint Martin d'Ardèche, Ardèche); 9 = Abri des  
1374 Pêcheurs (Casteljau, Ardèche). Spain: 10 = Cueva Millán (Hortigüela, province of Burgos); 11  
1375 = Áridos-1 (Arganda, Madrid). The black dots indicate other potential sites with some fish  
1376 remains.

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1378 **Figure 2.** Sturgeon pectoral spine and perch scale found at Scladina Cave.

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1380 **Figure 3.** a–i) SEM micrographs of fish remains: a) salmonid caudal vertebra from Walou  
1381 Cave; b) grayling caudal vertebra from Baume-Moula-Guercy; c) grayling caudal vertebra  
1382 from Barasses II; d) modern salmonid caudal vertebra eaten by Eurasian otter from Bugeat,

1383 France; e) modern cyprinid precaudal vertebra eaten by eagle owl from Tautavel, France; f)  
1384 modern eel vertebra eaten by yellow-legged gull from Chafarinas Islands, Spain; g) modern  
1385 salmonid premaxilla eaten by Eurasian otter from Bugeat, France; h) modern salmonid  
1386 dentary eaten by eagle owl from Tautavel, France; i) tooth from Baume-Moula-Guercy. j)  
1387 inclusion of manganese on salmonid vertebrae from Barasses II. k) deformation (beak  
1388 mark?) on a burbot precaudal vertebra from Baume Moula Guercy.

1389

1390 **Figure 4.** Distribution of fish species by site and chronology (NISP = Number of Identified  
1391 Specimens).

1392

1393 **Figure 5.** Chronological distribution of fish remains (adapted from Lisiecki and Raymo, 2005;  
1394 Kozłowski, 2017). The number in parentheses corresponds to the number of identified  
1395 specimens.

1396

1397 **Figure 6.** Spatial distribution of analyzed fish remains at: a) Walou Cave, level CI-8; b) Abri du  
1398 Maras, level 4.1.