



HAL
open science

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

Emilie Guillaud, Philippe Béarez, Camille Daujeard, Alban Defleur, Emmanuel Desclaux, Eufrasia Roselló Izquierdo, Arturo Morales-Muniz, Moncel Marie-Hélène

► To cite this version:

Emilie Guillaud, Philippe Béarez, Camille Daujeard, Alban Defleur, Emmanuel Desclaux, et al.. Neanderthal foraging in freshwater ecosystems: A reappraisal of the Middle Paleolithic archaeological fish record from continental Western Europe.. *Quaternary Science Reviews*, 2020, 252, pp.106731. 10.1016/j.quascirev.2020.106731 . hal-03035208

HAL Id: hal-03035208

<https://hal.science/hal-03035208>

Submitted on 2 Dec 2020

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

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

3 **Emilie Guillaud (1, 2), Philippe Béarez (1), Camille Daujeard (2), Alban Defleur (3), Emmanuel**
4 **Desclaux (4), Eufrasia Roselló-Izquierdo (5), Arturo Morales-Muñiz (5), Marie-Hélène Moncel (2)**

5
6 (1) Archéozoologie, Archéobotanique : Sociétés, Pratiques et Environnements (AASPE). UMR 7209,
7 CNRS, Muséum National d'Histoire Naturelle, 55 rue Buffon, 75005 Paris, France.

8 (2) Département Homme et environnement. UMR 7194, CNRS, Muséum National d'Histoire
9 Naturelle, Institut de Paléontologie Humaine, 1 rue René Panhard, 75010 Paris, France

10 (3) UMR 7264, CNRS, CEPAM, Université de Nice, Campus SJA3 24, avenue des Diabls Bleus, 06357
11 Nice Cedex 4, France

12 (4) Laboratoire départemental de Préhistoire du Lazaret. UMR 7264 CNRS, CEPAM, 33 bis boulevard
13 Franck Pilatte, 06300, Nice, France.

14 (5) Facultad de ciencias. Universidad Autónoma de Madrid, Madrid, Spain
15

16 **Abstract**

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

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

39

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

41 Taphonomy

42

43 **1. Introduction**

44 Western Europe constitutes a key area for investigating Neanderthal subsistence
45 practices due to the quantity and quality of sites available for study. The most recent
46 investigations in this region have significantly expanded our knowledge on the chronology
47 (e.g., Richard et al., 2015; Guérin et al., 2017), environmental conditions (e.g., Britton et al.,
48 2011; Moncel et al., 2015; Discamps and Royer, 2017), and subsistence strategies of
49 Neanderthals (e.g., Delagnes and Rendu, 2011; Cortés-Sánchez et al., 2011, 2019; Niven et
50 al., 2012; Daujeard et al., 2012, 2019; Gaudzinski-Windheuser et al., 2018). These data have
51 contributed to establishing a reliable framework for interpreting the profound biological and
52 cultural changes that occurred from Marine Isotopic Stages (MIS) 11–9 to 3 (Moncel et al.,
53 2016). Traditionally, Neanderthals have been considered as big-game hunters (i.e., top-level
54 carnivores; Bocherens, 2009; Gaudzinski-Windheuser and Niven, 2009; Richards and
55 Trinkaus, 2009; Jaouen et al., 2019). However, over the past decade, studies have evidenced
56 a diversified spectrum of subsistence strategies, with a significant contribution of small game
57 (e.g., Blasco and Fernández Peris, 2012; Cochard et al., 2012; Morin et al., 2019).
58 Archaeozoological and archaeobotanical analyses provide evidence of the exploitation of
59 small mammals, birds, shellfish and plants (Laroulandie, 2000; Cortés-Sánchez et al., 2011,
60 2019; Hardy et al., 2012, 2013; Laroulandie et al., 2016; Estalrich et al., 2017), yet the role
61 played by aquatic-vertebrate resources in Neanderthal diets has barely been documented,
62 and Neanderthal fishing remains a controversial issue (Le Gall, 1992, 2000; Roselló-Izquierdo
63 and Morales-Muñiz, 2005). Evidence exists that hominins practiced river or lake fishing
64 during the Lower Paleolithic (Braun et al., 2010; Stewart, 1994) and the Middle Paleolithic in
65 Africa, where specialized technologies such as barbed bone points have been developed by
66 ca. 90 000 BP (Brooks et al., 1995; Yellen et al., 1995). However, in Western Europe, there is

67 currently no evidence that the exploitation of aquatic vertebrates was significant before the
68 Upper Paleolithic period, especially the Magdalenian period (Cleyet-Merle, 1990). For most
69 of the Middle Paleolithic, the sea level was lower than it is today, except during MIS 11 and
70 5e when sea levels were about 6 to 13 m above present levels (Dutton et al., 2015). For this
71 reason, the vast majority of coastal archaeological sites, where hominins may have left
72 traces of fishing activities, are currently submerged, often at great depths (Cleyet-Merle,
73 1990). Although a Neanderthal coastal adaptation, including fishing activities, that would
74 have increased their dietary breadth is possible (see Brown et al., 2011; Zilhão et al., 2020),
75 no such evidence has been found for the exploitation of continental freshwater ecosystems.
76 Hence, the study of inland fishing activities, close to rivers or lakes, remains one of the only
77 possibilities for studying Neanderthal fishing.

78 Middle Paleolithic fish bones are occasionally documented in inland caves close to rivers,
79 often mixed with stone tools and faunal remains. These remains can only be considered as
80 evidence of fishing by humans when other fish predators, in particular cave-dwelling
81 carnivores and raptors, are ruled out as alternative accumulators. At the time of writing, few
82 studies have been published on how to reliably diagnose fish deposits produced by most of
83 these predators and set them apart from those produced by humans. In Europe, most of
84 these papers focus on the Eurasian eagle-owl (*Bubo bubo*) and the Eurasian otter (*Lutra*
85 *lutra*; Nicholson, 1991, 2000; Le Gall, 1999; Russ and Jones, 2011, Guillaud et al. 2017a,
86 2018).

87

88 This paper explores the role that Western European Neanderthals played in accumulating
89 fish remains. The question “were Neanderthals freshwater fishers?” will also aim to
90 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

115 discernible using current analytical procedures (Patou-Mathis, 2000; Drucker and Bocherens,
116 2004; Drucker et al., 2005; Stringer et al., 2008). For this reason, the development of sulfur
117 or zinc isotope analyses seems promising for directly assessing fish consumption on
118 Neanderthal bones (Privat et al., 2007; Nehlich et al., 2010; Jaouen et al., 2018).

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

126

127 **2. Materials and methods**

128 *2.1. Materials*

129 This study examines ichthyoarchaeological collections from 11 faunal assemblages (**Table**
130 **1; Fig. 1**), totalizing 3,159 fish remains (**Table 2**), and comprises new ichthyoarchaeological
131 analyses from Scladina Cave (Belgium), Abri des Pêcheurs, Baume-Vallée Cave, and Baume
132 Moula-Guercy (France). These analyses are combined with a reassessment of previously
133 published fish assemblages from Caverne Marie-Jeanne and Walou Cave (Belgium), Vaufray
134 Cave, Abri du Maras and Barasses II Cave (France), Cueva Millán and Áridos-1 (Spain; Gautier
135 and Heinzelin, 1980; Morales, 1980; Le Gall, 1988, 2008; Roselló-Izquierdo, 1992; Van Neer
136 and Wouters, 2011; Hardy et al., 2013; Béarez and Guillaud, 2019; Daujeard et al., 2019).
137 The sites are dated from MIS 11-9 to MIS 3 (ca. 400 000 to 40 000 years ago) and all of them
138 are cave sites, except Áridos-1 (**Table 1**). Diverse types of excavations are represented in our

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

147 *2.2. Methods*

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

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

162 Whenever possible, the spatial distribution of fish remains was examined to check for
163 correlations with other faunal and lithic data. Bone surfaces were examined for taphonomic
164 clues. Traces of human activities (butchery, cooking, burning), animal-induced modifications
165 (gnawing marks, grooves, pits), as well as environmental alterations were recorded following
166 established protocols (Jones, 1986; Nicholson, 1991; Lyman, 1994; Broughton et al., 2006;
167 Erlandson et al., 2007, Fernández-Jalvo and Andrews, 2016). Bone surface damage was
168 observed under a binocular microscope and some vertebrae were observed with a scanning
169 electron microscope (SEM). Bone surface damage was allocated into five digestion
170 categories: null, light, moderate, heavy and extreme (Andrews, 1990; Fernández-Jalvo and
171 Andrews, 2016). Based on the methodology from a previous study (Guillaud et al., 2017a),
172 the percentage of preserved bone surfaces from all elements was recorded, starting from 0–
173 20% (very altered surface) and extending up to 80–100% (complete or mostly intact).
174 Percentages were calculated following Dodson and Wexlar (1979) and adapted to fish
175 osteology.

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

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

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

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

199 Inferences about biotopes and climate can often be made from faunal assemblages. On
200 our sites, environmental conditions were first inferred from the data reported in the
201 literature for terrestrial macrovertebrates (i.e., ungulates; Daujeard and Moncel, 2010;
202 Hernandez et al., 2014) and microvertebrates (Alvarez et al., 1992; Damblon, 2011; Blain et
203 al., 2014), including anurans (Ballmann et al., 1980), birds (Gala et al., 2005; Rufá et al.,
204 2017) and rodents. Additional environmental data were gathered from the biology of
205 freshwater fishes, as these can help to ascertain which specific predators may have
206 generated a given fish assemblage. For example, salmonids (Salmonidae) require oxygen-
207 rich water and a specific temperature for hatching and growing. Today, they are usually
208 found in running water with temperatures ranging from 0–20 °C (Jonsson and Jonsson, 2009;
209 Elliott and Elliott, 2010), which generally corresponds to the trout (*Salmo trutta*) and grayling

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

219

220 **3. Results**

221 Scladina Cave (Belgium) Seventy-four fish remains were studied. These represent less than
222 2% of the faunal NISP (**SOM Tables 1 and 2**). European sturgeon (*Acipenser sturio*) was the
223 dominant species but unfortunately, its remains were discovered in a disturbed zone (**Fig. 2**).
224 Thus, although the origin of the sturgeon remains in Scladina is likely to be anthropogenic,
225 since individual size estimates range from about 95 to 165 cm and exclude transport by a
226 non-human predator, we cannot be sure of their attribution to the MP, and we preferred
227 not to take them into consideration in this study. Perch (*Perca fluviatilis*) scales ($n = 34$) were
228 also present in level 4A but no size-related information could be obtained from them. Three
229 pike (*Esox lucius*) remains were also found in levels 4B and 6A. Finally, level 4A comprised
230 some unidentified fish remains. All species preferentially thrive in the lower courses of
231 rivers, as in the bream zone (Huet, 1954). No visible traces of bone modification were
232 recorded.

233 Walou Cave (Belgium) The 416 remains from the original study by Van Neer and Wouters
234 (2011) were re-examined. This is the largest archaeological fish collection from Belgium. In
235 levels CI-8 and CI-6, the assemblage is dominated by brown trout (*Salmo trutta*), followed by
236 grayling (*Thymallus thymallus*), stone loach (*Barbatula barbatula*), pike (*Esox lucius*), burbot
237 (*Lota lota*) and bullhead (*Cottus gobio*). Indeterminate salmonids and cyprinids—probably
238 chub (*Squalius cephalus*) or dace (*Leuciscus leuciscus*)—are also present (**SOM Tables 3 and**
239 **4**). Fish remains represent 17.6% of the faunal NISP.

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

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

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

257 90%) than skull bones, which were fragmented for the most part (ca. 10–30%). No traces of
258 digestion were visible.

259 Vaufrey Cave (France) A total of 420 fish remains from the original study by Le Gall (1988)
260 were re-examined. These represent about 12% of the faunal NISP. Species included Atlantic
261 salmon, brown trout, grayling, pike, perch and eel (*Anguilla anguilla*), although the
262 assemblage was dominated by unidentified cyprinids (**SOM Tables 7, 8 and 9**). Level VII (MIS
263 6) was the richest level in terms of taxonomic diversity and number of remains. From a
264 biogeographical standpoint, brown trout and grayling abound in the upper river courses
265 whereas perch, pike and eel are more frequent in the mid- or even lower courses (Huet,
266 1954). Salmonids range in size from 30 to 40 cm but a few vertebrae represent larger
267 specimens, up to 50 cm. Eel and pike both range between 20 and 40 cm. All cyprinids are
268 small (< 20 cm), whereas perch exhibit the widest size range of all (5–30 cm). Le Gall (1988)
269 postulated that salmonids died in winter or early spring whereas cyprinids died in summer.

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

274 Baume Moula-Guercy (France) With 1,307 remains, Baume Moula-Guercy Cave constitutes
275 the largest collection in our study (**Tables 11 and 12**). Levels XVIII and XVII yielded more than
276 50% of the material. Fish represent about 14% of the faunal NISP. Species diversity is high
277 and includes the agone shad (*Alosa agone*), eel, chub (*Squalius cephalus*), pike, burbot,
278 Eurasian minnow (*Phoxinus phoxinus*), roach (*Rutilus rutilus*), brown trout and grayling.
279 Burbot was the dominant species, followed by eel. Cyprinids range from 10–30 cm and
280 salmonids from 10–20 cm, although some vertebrae represent specimens over 50 cm (> 1

281 kg). Shad measures 20-30 cm and eel includes small (ca. 20 cm) specimens and others over
282 70 cm (**SOM Table 11**). Incremental growth lines indicate that deaths occurred throughout
283 the year. These species are mainly distributed in two distinct river zones: in the running
284 waters of the grayling zone and in the slower flowing waters of the barbel zone. Although
285 shad and burbot are more frequent in the lower courses of rivers, both species can migrate
286 upstream into the barbel zone, and burbot being an arctic taxon, thrives in cold waters (see
287 above). The high frequency of a demersal nocturnal fish seems intriguing and suggests the
288 existence of a very particular predator and/or fishing technique. Some trout vertebrae
289 present partly polished, smooth surfaces and a few other vertebrae may possibly have been
290 crushed by teeth (**Fig. 3k**).

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

301 Barasses II (France) Fish remains (NISP = 127) were only retrieved in the middle and lower
302 parts of the sequence. Fish represent 7.7% of the faunal NISP. Salmonids—brown trout but
303 especially grayling—dominate the assemblage (Béarez and Guillaud, 2019). Burbot, eel and
304 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.

328 Cueva Millán (Spain) A total of 284 fish remains previously studied by Roselló-Izquierdo
329 (1992) were re-examined. These include brown trout (22–44 cm TL; 200–900 g BM), Iberian
330 nase (21–31 cm; 150–300 g) and eel (43–67 cm; 300–600 g). Fish remains represent ca. 40%
331 of the faunal NISP and are concentrated in Level 8I-1a (**SOM Tables 23 and 24**). Trout is the
332 dominant species. All species occur in running waters, although eel thrives in many other
333 biotopes. Some 20% of bones ($n = 56$) present traces of black coloration but no other traces
334 were recorded on the samples.

335

336 **4. Discussion**

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

349 It is therefore essential to examine reconstructions of fish size and mass, spatial
350 distribution of bones and surface modifications, seasonality of catches, and ethological
351 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

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

378 From a chronological standpoint, the oldest fish assemblage (Áridos-1) corresponds to a
379 climatic stage not very different from the current climate in the area and features a balanced
380 fish fauna, which, except for the migratory shad and the now extinct (though artificially
381 reintroduced) pike, can still be found in the area. This presence of species still extant today is
382 a recurrent theme at all the sites, although the number and frequency of species shift
383 through time. The only exception for France is the presence of grayling at Vaufrey Cave,
384 since it disappeared from the Garonne Basin in modern times, before being reintroduced.
385 Given the quantity and quality of available data, such differences cannot be explained by
386 past abundances (i.e., 'availability'), or by the selectivity of the agent that caught the fish
387 (i.e., 'choice'). Burbot and eel predominate in MIS 6 levels at Baume Moula Guercy. The fact
388 that, despite other ecological differences, both species are bottom-dwellers and essentially
389 crepuscular/nocturnal would narrow the range of potential (regular) predators to mammals.
390 The highest number of records occur between MIS 5 and 3. MIS 5 collections, as
391 paradigmatically evidenced by Walou Cave, show the highest taxonomical diversity with
392 trout and grayling dominating the assemblages, followed by burbot and eel (**Table 2**). Fish
393 taxa from MIS 5 do not reveal any major climatic differences, and fish assemblages
394 correspond mainly to the grayling zone (i.e., pre-mountain river sectors with cold water;
395 Huet, 1954). MIS 4 fish records are limited (**Table 2**; NISP = 14) although four sites represent
396 this period (Walou, Baume Moula Guercy, Barasses II and Abri des Pêcheurs). The recorded
397 species (chub, perch, eel and grayling) suggest more temperate water conditions, although
398 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

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

438

439 *4.2. Fish bone representation and preservation*

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

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

454 Bone representation is characterized by high values in the cases of shad basioccipitals,
455 which have a percentage of representation (PR) of 33.3%; burbot (PR = 19.5%) and eel (PR =
456 10.86%) caudal vertebrae, and pike (PR = 5%), bullhead (PR = 11.6%), salmonids (PR =
457 11.9%), stone loach (PR = 16.6%) and cyprinids (PR = 40.5%) precaudal vertebrae (**Table 2**).
458 Precaudal vertebrae are overrepresented in perch (PR = 130%). Overall, the combined
459 percentage of representation for all taxa is low, with disparate representation of cranial and
460 post-cranial elements and low skeletal completeness.

461 Data relating to bone modification are very informative. In particular, no damage such as
462 deformation, rounding, polishing or traces of digestion is visible on most remains, ruling out
463 the action of carnivorans (**Table 3; Fig. 3a–i**). Very few traces are visible on bone surfaces:
464 four salmonid vertebrae at Baume-Vallée and some at Baume Moula-Guercy presented
465 smooth surfaces, while some pharyngeal teeth of cyprinids showed slight traces of digestion
466 at Vaufrey Cave. The action of gastric juices results in a smooth and polished surface
467 (Andrews, 1997), but prolonged transport of bones in water also produces rounding and
468 polishing. Baume Moula-Guercy also contained some vertebrae possibly crushed by teeth
469 (**Fig. 3k**). At Áridos-1, Barasses II and perhaps also Vaufrey, the crust of the matrix and
470 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

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

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

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

522

523 *4.4. Spatial distribution*

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

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

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

547

548 *4.5. Season of capture*

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

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

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

567 winter spawner, its mortality cannot be readily associated with accessibility or vulnerability
568 during the reproductive period, but this could well be the case for the two cyprinids. Data
569 concerning the species from Barasses II and from Baume Moula-Guercy indicate that deaths
570 also occurred throughout the year but a peak was recorded during autumn for burbot (**Table**
571 **4**), backing up the idea of catches peaking during the spawning season.

572

573 *4.6. Potential predators*

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

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

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

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

610 Bird remains include raptors and corvids, such as the common kestrel (*Falco tinnunculus*)
611 and raven (*Corvus corax*). Eagles and vultures occasionally scavenge on fish (Chaline et al.,
612 1974), but do not frequent caves. Among strigids, the European eagle owl is often
613 considered to be an accumulator. Other strigids are present, namely at Baume-Vallée and
614 Caverne Marie-Jeanne, such as the tawny owl (*Strix aluco*) and eared owls (*Asio* spp.).

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

620 To date, the best-documented avian fish-consuming predators are the eagle owl (Guillaud
621 et al., 2018; Nicholson, 1991; Le Gall, 1999; Russ and Jones, 2011), the barn owl (Broughton
622 et al., 2006), the bald eagle (Erlandson et al., 2007), the European kingfisher (Frontin, 2017)
623 and the yellow-legged gull (Guillaud et al., 2019). The eagle owl is identified as an agent of
624 micromammal accumulation at several archaeological sites (Andrews, 1990; Laroulandie,
625 2002). Studies of the cormorant (*Phalacrocorax carbo*) indicate that it is one of the few
626 predators of the common grayling (Suter, 1995; Suter and Morel, 1996). Although
627 cormorants do not specifically select a narrow range of grayling sizes, they mainly consume
628 small specimens. This fishing bird would be an ideal accumulator for most of the species
629 identified in our corpus. However, ingested bones from pellets are often completely
630 digested, and regurgitated fish are rare and only found in breeding colonies (Veldkamp,
631 1995). Moreover, although cormorants can be present on the continent, they are mainly
632 found in coastal environments, and not in caves (Orta, 1992).

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

635

636 4.7. Fish origin

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

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

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

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

663 which rules out the possibility that some fish remains were the result of natural deaths,
664 whether cumulative or episodic, deposited on the river banks (Butler, 1993; **Table 6**). Also,
665 although many of the non-piscivorous faunas from these sites incorporate species
666 occasionally documented as fish predators, none of them are truly piscivorous, as would be
667 the case of the otter or the cormorant (Dodson and Wexlar, 1979; Andrews, 1990; Orta,
668 1992; Suter, 1995; Suter and Morel, 1996; Erlandson and Moss, 2001; Mondini, 2001;
669 Laroulandie, 2002). This is not to say that animals or natural processes did not generate
670 some of the reported fish remains. Indeed, it has been argued that the presence of fish of
671 less than 10 cm (10–15 g) cannot be attributed to human activity and that small fish
672 accumulations such as that reported at the entrance of Walou Cave best conform with pellet
673 deposition below the roosting place of an avian predator. For these reasons, it is important
674 to stress that several of the studied deposits bear traces of several potential accumulators,
675 but Neanderthals would also be on that list.

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

687 suggests that these bones remained in good condition despite their fragility and only cranial
688 elements exhibited fragmentation. As the remaining animal samples were not quantified, it
689 is not possible to explore other aspects of these collections, although the abundance of
690 carnivorans, microfaunas and birds indicates that predators, not just hyenas, might have
691 been responsible for the accumulation of a substantial portion of the faunal assemblages. In
692 contrast, the elephant butchery floor at Aridos-1, despite the importance of its
693 microvertebrate and bird collections, features few raptors and carnivorans and a fish
694 collection that represents 16.5% of the total NISP. Fish sizes there average around 50 cm (ca.
695 1 kg) and range from 20-70 cm TL. A full 75% of the 316 fish remains could not be identified,
696 and the assemblage exhibited a balanced spectrum of taxa, without any single species being
697 dominant (**SOM Table 21**).

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

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

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

713

714 *4.8. Ethnographic data and archaeological contexts*

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

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

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

730 Nets were generally the most frequently used fishing method in Canada (Stewart, 1977).
731 Most were of animal origin, including tendons (Stewart, 1977; Smith, 1984; Vanstone, 1984).
732 The use of stone dams has been reported for capturing migrating Atlantic salmon (Smith,
733 1984; Taylor, 1984). Fish bones sometimes show traces of preparations, such as cut marks

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

736 At archaeological sites, most of the known instruments associated with fishing come from
737 Mesolithic sites (Cleyet-Merle, 1990), such as the Azilian site of Pont d'Ambon (Dordogne)
738 (see Le Gall, 1984). Several types of fishing tools may have been used during the Paleolithic
739 period, while barb-tail spears may have been utilized during the Magdalenian period (Julien,
740 1982; Pétilion, 2009). Only proto-harpoons, with less prominent barbs, seem to be adapted
741 to fishing practices (Cleyet-Merle, 1984).

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

745

746

747 **5. Conclusions**

748 For Neanderthals, even the use of aquatic resources was questioned up until a decade
749 ago. The paradigm was that these humans were unable to gather stationary shellfish. In
750 hindsight, the basis for the question as to whether Neanderthal practiced fishing relied on
751 unstated assumptions and speculative grounds referring to debatable ideas about 'cognitive
752 barriers' and the like. Indeed, ample evidence testifies to fishing practices by a wide range of
753 terrestrial mammals, from bears to monkeys, which are not particularly well suited to the
754 task. The long-standing, now redundant hypothesis that only modern humans are able to
755 fish has led to some fascinating inconsistencies. One such inconsistency appears at Walou
756 Cave and Cueva Millán, where the same fish species and sizes reported in the Mousterian
757 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.

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

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

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

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

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

824

825 **Acknowledgements**

826 This work was supported by a grant from the Agence Nationale de la Recherche under
827 LabEx ANR-10-LABX-0003-BCDiv (direction P.B. and M.H.M.), as part of the program
828 “Investissements d’avenir” n° ANR-11-IDEX-0004-02. E.R.I. and A.M.M. were supported by
829 grants HAR 2014-55722-P and HAR 2017-88325-P from the Spanish Ministerio de Economía

830 y Competitividad, and by grant 19438/PI/14 from the Programa Séneca 2014. The authors
831 would like to thank the Muséum national d'histoire naturelle (Paris, France), the Institut de
832 Paléontologie Humaine (Paris, France), the Royal Belgian Institute of Natural Sciences, the
833 Universitat Autònoma de Madrid, the Laboratoire Départemental de Préhistoire du Lazaret,
834 the Cité de la Préhistoire de l'Aven d'Orgnac, and the Centre archéologique de la grotte
835 Scladina. We are grateful to the Programme Collectif de Recherche "Espaces et subsistance
836 au Paléolithique moyen dans le sud du Massif central" that supported fieldwork in France.
837 We would like to express our thanks to W. Van Neer, W. Wouters, J.-P. Raynal, G. Abrams
838 and C. Draily for collaborating with this project and for granting access to collections. We
839 also express our gratitude to the people who authorized the analysis of remains and
840 provided us with context information: N. Desse-Berset, P. Jacquement, S. Madelaine, J.-J.
841 Cleyet-Merle, P. Guillermin, F. Prud'homme, M. Rué, D. Bonjean, J. Rosell, A. Rufá, H.-A.
842 Blain, R. Blasco and C. Sesé. We would also like to thank G. Denys and H. Persat for providing
843 crucial information and modern specimens, F.J. Meunier (MNHN, Paris) and I. Doadrio
844 (Museo Nacional de Ciencias Naturales, Madrid) for their help with the identification of
845 tricky remains; and M. Lemoine (MNHN, Paris) and J. Cillis (Royal Belgian Institute of Natural
846 Sciences, Brussels) for the SEM pictures. We also thank L. Byrne for proofreading the English.

847 We would like to thank the two reviewers and the editor for their useful comments that
848 helped us to enhance this paper.

849

850 **Authors contributions**

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

854

855 **References**

856 Alvarez, M.T., Morales, A., Sesé, C., 1992. Mamíferos del yacimiento del Pleistoceno superior
857 de cueva Millán (Burgos, España). *Estudios Geológicos* 48, 193–204.

858 Andrews, P., 1990. *Owls, Caves and Fossils*. Natural History Museum Publications, London.

859 Andrews, P., 1997. What taphonomy can and cannot tell us. *Cuadernos de Geología Ibérica*
860 23, 53–72.

861 Andrews, P., Evans, E.N., 1983. Small mammal bone accumulations produced by mammalian
862 carnivores. *Paleobiology* 9, 289–307.

863 Averbouh, A., Cleyet-Merle, J.-J., 1995. Fiche hameçons. In: Camps-Fabrer, H. (Ed.), *Fiches*
864 *Typologiques de l'Industrie Osseuse Préhistorique: Paléolithique, Épipaléolithique,*
865 *Mésolithique, Néolithique. Cahier VII: Éléments Barbelés*. CEDARC, Treignes, pp. 83–99.

866 Ballmann, P., De Coninck, J., Heinzelin, J. de, Gautier, A., Geets, S., Rage, J.-C., 1980. Les
867 dépôts quaternaires ; inventaire paléontologique et archéologique. In: Gautier, A.,
868 Heinzelin, J. de (Eds.), *La Caverne Marie-Jeanne (Hastière-Lavaux, Belgique)*. Institut royal
869 des sciences naturelles de Belgique, Bruxelles, pp. 3–24.

870 Balter, V., Simon, L., 2009. Diet and behavior of the Saint-Césaire Neanderthal inferred from
871 biogeochemical data inversion. *Journal of Human Evolution* 51, 329–338.

872 Béarez, P., Guillaud, E., 2019. Ichtyofaune. In: Daujeard, C. (Ed.), *La grotte des Barasses II*
873 *(Balazuc, Ardèche) : entre néandertaliens, bouquetins et carnivores... Des occupations du*
874 *pléistocène supérieur en moyenne vallée de l'Ardèche*. *Documents d'Archéologie en*
875 *Rhône-Alpes et en Auvergne* 46, pp. 77-79.

876 Beauval, C., Maureille, B., Lacrampe-Cuyaubere, F., Serre, D., Peressinotto, D., Bordes, J.G.,
877 Cochard, D., Couchoud, I., Dubrasquet, D., Laroulandie, V., Lenoble, A., Mallye, J.-B.,

878 Pasty, S., Primault, J., Rohland, N., Pääbo, S., Trinkaus, E., 2005. A late Neandertal femur
879 from Les Rochers-de-Villeneuve, France. *Proceedings of the National Academy of Sciences*
880 of the United States of America 102, 7085–7090.

881 Blain, H.A., Santonja, M., Pérez-González, A., Panera, J., Rubio-Jara, S., 2014. Climate and
882 environments during Marine Isotope Stage 11 in the central Iberian Peninsula: the
883 herpetofaunal assemblage from the Acheulean site of Áridos-1, Madrid. *Quaternary*
884 *Science Reviews* 94, 7–21.

885 Blasco, R., Fernández Peris, J., 2012. A uniquely broad spectrum diet during the Middle
886 Pleistocene at Bolomor Cave (Valencia, Spain). *Quaternary International* 252, 16–31.

887 Bocherens, H., 2009. Neanderthal dietary habits: Review of the isotopic evidence. In: Hublin,
888 J.J., Richards, M. (Eds.), *The evolution of hominin diets: Integrating approaches to the*
889 *study of palaeolithic subsistence*. Springer, Dordrecht, pp. 241–250.

890 Bocherens, H., Baryshnikov, G., Van Neer, W., 2014. Were bears or lions involved in salmon
891 accumulation in the Middle Palaeolithic of the Caucasus? An isotopic investigation in
892 Kudaro 3 cave. *Quaternary International* 339-340, 112–118.

893 Bocherens, H., Billiou, D., Patou-Mathis, M., Bonjean, D., Otte, M., Mariotti, A., 1997.
894 Paleobiological implications of the isotopic signatures (^{13}C , ^{15}N) of fossil mammal
895 collagen in Scladina Cave (Sclayn, Belgium). *Quaternary Research* 48, 370-380.

896 Bouvier, M., Bayle, P., 1989. Le régime alimentaire de la Chouette hulotte *Strix aluco* dans le
897 Sud des Alpes françaises. *Bièvre* 10, 1–22.

898 Braun, D.R., Harris, J.W.K., Levin, N.E., McCoy, J.T., Herries, A.I.R., Bamford, M.K., Bishop,
899 L.C., Richmond, B.G., Kibunjia, M., 2010. Early hominin diet included diverse terrestrial
900 and aquatic animals 1.95 Ma in East Turkana, Kenya. *Proceedings of the National*
901 *Academy of Sciences* 107(22), 10002–10007.

902 Britton, K., Grimes, V., Niven, L., Steele, T.E., McPherron, S., Soressi, M., Kelly, T.E., Jaubert J.,
903 Hublin, J.-J., Richards, M.P., 2011. Strontium isotope evidence for migration in late
904 Pleistocene *Rangifer*: Implications for Neanderthal hunting strategies at the Middle
905 Palaeolithic site of Jonzac, France. *Journal of Human Evolution* 61, 176–185.

906 Brooks, A.S., Helgren, D.M., Cramer, J.S., Franklin, A., Hornyak, W., Keating, J.M., Klein, R.G.,
907 Rink, W.J., Schwarcz, H., Smith, J.N.L., Stewart, K., Todd, N.E., Verniers, J., Yellen, J.E.,
908 1995. Dating and context of three Middle Stone Age sites with bone points in the Upper
909 Semliki Valley, Zaire. *Science* 268, 548-553.

910 Broughton, J.M., Cannon, V.I., Arnold, S., Bogiatto, R.J., Dalton, K., 2006. The taphonomy of
911 owl-deposited fish remains and the origin of the Homestead cave ichthyofauna. *Journal of*
912 *Taphonomy* 4, 69–95.

913 Brown, K., Fa, D.A., Finlayson, G., Finlayson, C., 2011. Small-game and marine resource
914 exploitation by Neanderthals: the Evidence from Gibraltar. In: Bicho, N.F., Haws, J.,
915 Davies, L.G. (Eds.), *Trekking the Shore. Changing Coastlines and Antiquity of Coastal*
916 *Settlement*. Springer, New York, pp. 247-272.

917 Bruslé, J.L, Quignard, J.P., 2011. *Biologie des poissons d’eau douce européens*. Lavoisier,
918 Paris.

919 Butler, V.L., 1993. Natural versus cultural salmonid remains: Origin of the Dallas Roadcut
920 bones, Columbia River. *Journal of Archaeological Science* 20, 1–24.

921 Campmas, E., Amani, F., Morala, A., Debénath, A., El Hajraoui, M. A., Nespoulet, R., 2016.
922 Initial insights into Aterian hunter–gatherer settlements on coastal landscapes: The
923 example of Unit 8 of El Mnasra Cave (Témara, Morocco). *Quaternary International* 413, 5-
924 20.

925 Campmas, E., Beauval, C., 2008. Consommation osseuse de carnivores : résultats de l'étude
926 de l'exploitation de carcasses de boeuf (*Bos taurus*) par des loups captifs. Annales de
927 Paléontologie 94, 167–186.

928 Casteel, R.W., 1972. Some archaeological uses of fish remains. American Antiquity 37, 404–
929 419.

930 Casteel, R.W., 1976. Fish Remains in Archaeology and Paleo-environmental Studies.
931 Academic Press, London.

932 Chakroun, A., Chahid, D., Boudad, L., Campmas, E., Lenoble, A., Nespoulet, R., El Hajraoui,
933 M.A., 2017. The Pleistocene of Rabat (Morocco): Mollusks, coastal environments and
934 human behavior. African Archaeological Review 34(4), 493-510.

935 Chaline, J., Baudvin, H., Jammot, D., Saint Girons, M.-C., 1974. Les Proies des Rapaces (Petits
936 Mammifères et leur Environnement). Doin, Paris.

937 Cleyet-Merle, J.-J., 1984. A propos de la pêche au Paléolithique supérieur en France : apport
938 des représentations réalistes de poissons dans l'art mobilier, premiers résultats.
939 Antiquités Nationales 16/17, 49–58.

940 Cleyet-Merle, J.-J., 1990. La Préhistoire de la Pêche. Errance, Paris.

941 Cochard, D., Brugal, J.-P., Morin, E., Meignen, L., 2012. Evidence of small fast game
942 exploitation in the Middle Paleolithic of Les Canelettes, Aveyron, France. Quaternary
943 International 264, 32-51.

944 Cordain, L., Miller, J.B., Eaton, S.B., Mann, N., Holt, S.H., Speth, J.D., 2000. Plant-animal
945 subsistence ratios and macronutrient energy estimations in world-wide hunter-gatherer
946 diets. American Journal of Clinical Nutrition 71, 682–692.

947 Cortés-Sánchez, M, Morales-Muñiz, A., Simón-Vallejo, M.D., Lozano-Francisco, M.C., Vera-
948 Peláez, J.L., Finlayson, C., Rodríguez-Vidal, J., Delgado-Huertas, A., Jiménez-Espejo, F.J.,

949 Martínez-Ruiz, F., Martínez-Aguirre, M.A., Pascual-Granged, A.J., Bergadà-Zapata, M.M.,
950 Gibaja-Bao, J.F., Riquelme-Cantal, J.A., López-Sáez, J.A., Rodrigo-Gámiz, M., Sakai, S.,
951 Sugisaki, S., Finlayson, G., Fa, D.A., Bicho, N.F., 2011. Earliest known use of marine
952 resources by Neanderthals. *PLoS One* 6, e24026.

953 Cortés-Sánchez, M., Simón-Vallejo M.D., Jiménez-Espejo, F.J., Lozano Francisco, M.C., Vera-
954 Peláez, J.L., Maestro González, A., Morales-Muñiz, A., 2019. Shellfish collection on the
955 westernmost Mediterranean, Bajondillo cave (~160-35 cal kyr BP): A case of behavioral
956 convergence? *Quaternary Science Reviews* 217, 284–296.

957 Costamagno, S., Beauval, C., Lange-Badré, B., Vandermeersch, B., Mann, A., Maureille, B.,
958 2005. Homme ou carnivores ? Protocole d'étude d'ensembles osseux mixtes : l'exemple
959 du gisement moustérien des Pradelles (Marillac-le-Franc, Charente). *Archeofauna* 14, 43–
960 68.

961 Cravinho, S., 2009. Les poissons d'eau douce à la fin du Paléolithique supérieur en France.
962 Réexamen et étude complémentaire du site de Pont d'Ambon (Bourdeilles, Dordogne).
963 Ph.D. Dissertation, Aix-Marseille University.

964 Damblon, F., 2011. Les analyses anthracologiques dans la séquence de la grotte Walou. In:
965 Draily, C., Pirson, S., Toussaint, M. (Eds.), *La Grotte Walou à Trooz (Belgique). Fouilles de*
966 *1996 à 2004. Vol. 2. Département du Patrimoine & Institut du Patrimoine wallon, Namur,*
967 *pp. 132–145.*

968 Daujeard, C., Fernandes, P., Guadelli, J.C., Moncel, M.H., Santagata, C., Raynal, J.P., 2012.
969 Neanderthal subsistence strategies in Southeastern France between the plains of the
970 Rhone Valley and the mid-mountains of the Massif Central (MIS 7 to MIS 3). *Quaternary*
971 *International* 252, 32–47.

972 Daujeard, C., Moncel, M.H., 2010. On Neanderthal subsistence strategies and land use: a
973 regional focus on the Rhone Valley area in southeastern France. *Journal of*
974 *Anthropological Archaeology* 29, 368–391.

975 Daujeard, C., Vettese, D., Britton, K., Béarez, P., Boulbes, N., Crégut-Bonnoure, E., Desclaux,
976 E., Lateur, N., Pike-Tay, A., Rivals, F., Allué, E., Chacón, M.G., Puaud, S., Richard, M.,
977 Courty, M.A., Gallotti, R., Hardy, B., Bahain, J.J., Falguères, C., Pons-Branchu, E., Valladas,
978 H., Moncel, M.H., 2019. Neanderthal selective hunting of reindeer? The case study of Abri
979 du Maras (south-eastern France). *Archaeological and Anthropological Sciences* 11, 985-
980 1011.

981 Delagnes, A., Rendu, W., 2011. Shifts in Neandertal mobility, technology and subsistence
982 strategies in western France. *Journal of Archaeological Science* 38, 1771–1783.

983 Desclaux, E., Hanquet, C., El Guennouni, K., 2011. Origine(s) des accumulations de
984 micromammifères dans quelques sites préhistoriques du Pléistocène moyen et supérieur
985 d'Europe méridionale. In : Laroulandie, V., Mallye, J.B., Denys, C. (Eds.), *Taphonomie des*
986 *Petits Vertébrés : Référentiels et Transferts aux Fossiles*. *British Archaeological Reports*,
987 Oxford, pp. 101 -118.

988 Desse, J., Desse-Berset, N., 1993. Les poissons. In : Colardelle, M., Verdel, E. (Eds.), *Les*
989 *Habitats du Lac de Paladru (Isère) dans leur Environnement. La Formation d'un Terroir au*
990 *XIe siècle*. *Documents d'Archéologie Française* 40, 116-120.

991 Desse, J., Desse-Berset, N., 1996. On the boundaries of osteometry applied to fish.
992 *Archaeofauna* 5, 171–179.

993 Discamps, E., Royer, A., 2017. Reconstructing palaeoenvironmental conditions faced by
994 Mousterian hunters during MIS 5 to 3 in southwestern France: A multi-scale approach

995 using data from large and small mammal communities. *Quaternary International* 433, 64–
996 87.

997 Dodson, P., Wexlar, D., 1979. Taphonomic investigation of owl pellets. *Paleobiology* 5, 275–
998 284.

999 Drucker, D., Bocherens, H., 2004. Carbon and nitrogen stable isotopes as tracers of change in
1000 diet breadth during Middle and Upper Palaeolithic in Europe. *International Journal of*
1001 *Osteoarchaeology* 14, 162–177.

1002 Drucker, D.G., Henry-Gambier, D., Lenoir, M., 2005. Alimentation humaine au cours du
1003 Magdalénien en Gironde d’après les teneurs en isotopes stables (¹³C, ¹⁵N) du collagène.
1004 *Paléo* 17, 52–72.

1005 Dusseldorp, G.L., 2013. Neanderthals and Cave hyenas: Co-existence, competition or
1006 conflict? In: Clark, J.L., Speth, J.D. (Eds.), *Zooarchaeology and Modern Human Origins*.
1007 Springer, Dordrecht, pp. 191–208.

1008 Dutton, A., Carlson, A.E., Long, A.J., Milne, G.A., Clark, P.U., DeConto, R., Horton, B.P.,
1009 Rahmstorf, S., Raymo, M.E., 2015. Sea-level rise due to polar ice-sheet mass loss during
1010 past warm periods. *Science* 349(6244), aaa4019.

1011 Elliott, J.M., Elliott, J.A., 2010. Temperature requirements of Atlantic salmon *Salmo salar*,
1012 brown trout *Salmo trutta* and arctic charr *Salvelinus alpinus*: predicting the effects of
1013 climate change. *Journal of Fish Biology* 77, 1793–1817.

1014 Enloe, J.G., 2012. Middle Palaeolithic cave taphonomy: Discerning humans from hyenas at
1015 Arcy-sur-Cure, France. *International Journal of Osteoarchaeology* 22, 591–602.

1016 Enloe, J.G., David, F., Baryshnikov, G., 2000. Hyenas and hunters: zooarchaeological
1017 investigations at Prolom II Cave, Crimea. *International Journal of Osteoarchaeology* 10,
1018 310–324.

1019 Erlandson, J.M., Moss, M.L., 2001. Shellfish feeders, carrion eaters, and the archaeology of
1020 aquatic adaptations. *American Antiquity* 66, 413–432.

1021 Erlandson, J.M., Rick, T.C., Collins, P.W., Guthrie, D.A., 2007. Archaeological implications of a
1022 bald eagle nesting site at Ferrelo Point, San Miguel Island, California. *Journal of*
1023 *Archaeological Science* 34, 255–271.

1024 Estalrich, A., El Zaatari, S., Rosas, A., 2017. Dietary reconstruction of the El Sidrón
1025 Neandertal familial group (Spain) in the context of other Neandertal and modern hunter-
1026 gatherer groups. A molar microwear texture analysis. *Journal of Human Evolution* 104,
1027 13–22.

1028 Etienne, P., Lauzet, J., 2009. *L'Ours Brun d'Europe, Biologie et Histoire, des Pyrénées à*
1029 *l'Oural*. Biotope, Mèze & MNHN, Paris.

1030 Fernández-Jalvo, Y., Andrews, P., (Eds.), 2016. *Atlas of Taphonomic Identifications*. Springer,
1031 Dordrecht.

1032 Fourvel, J.B., Fosse, P., Fernandez, P., Antoine, P.O., 2014. La grotte de Fouvent, dit l'Abri
1033 Cuvier (Fouvent-le-Bas, Haute-Saône, France) : analyse taphonomique d'un repaire
1034 d'hyènes du Pléistocène supérieur (OIS 3). *Paleo* 25, 79–99.

1035 French, J.C., 2019. The use of ethnographic data in Neanderthal archaeological research.
1036 Recent trends and their interpretative implications. *Hunter Gatherer Research* 4(1), 25–
1037 49.

- 1038 Frontin, D., 2017. Économie de pêche au Mésolithique et diversité piscicole à l'Holocène
1039 ancien dans le bassin hydrographique du Doubs. Ph.D. Dissertation, Université Paris 1
1040 Panthéon-Sorbonne.
- 1041 Gala, M., Raynal, J.P., Tagliacozzo, A., 2005. Bird remains from the Mousterian levels of
1042 Baume-Vallée (Haute-Loire, France): preliminary results. In: Grupe, G., Peters, J. (Eds.),
1043 Feathers, grit and symbolism. Birds and humans in the ancient Old and New Worlds.
1044 Verlag Marie Leidorf, Rahden, pp. 141–145.
- 1045 Gaudzinski-Windheuser, S., Niven, L., 2009. Hominin subsistence patterns during the Middle
1046 and Late Paleolithic in northwestern Europe. In: Hublin, J.-J., Richards M.P. (Eds.), The
1047 evolution of hominid diets: Integrating approaches to the study of Palaeolithic
1048 subsistence. Springer, pp. 97–109.
- 1049 Gaudzinski-Windheuser, S., Noack, E.S., Pop, E., Herbst, C., Pfleging, J., Buchli, J., Jacob, A.,
1050 Enzmann, F., Kindler, L., Iovita, R., Street, M., Roebroeks, W., 2018. Evidence for close-
1051 range hunting by last interglacial Neanderthals. *Nature Ecology & Evolution* 2, 1087–
1052 1092.
- 1053 Gautier, A., 1980. Notes sur les mammifères. In: Gautier, A., Heinzelin, J. de (Eds.), La
1054 caverne Marie-Jeanne (Hastière-Lavaux, Belgique). Institut royal des sciences naturelles
1055 de Belgique, Bruxelles, pp. 25–42.
- 1056 Gautier, A., Heinzelin, J. de (Eds.), 1980. La Caverne Marie-Jeanne (Hastière-Lavaux,
1057 Belgique). Institut royal des sciences naturelles de Belgique, Bruxelles.
- 1058 Granadeiro, J.P., Silva, M.A., 2000. The use of otoliths and vertebrae in the identification and
1059 size-estimation of fish in predator-prey studies. *Cybium* 24, 383–393.

1060 Grayson, D.K., 1984. Quantitative Zooarchaeology: Topics in the Analysis of Archaeological
1061 Faunas. Academic Press, Orlando.

1062 Guérin, G., Frouin, M., Tuquoi, J., Thomsen, K.J., Goldberg, P., Aldeias, V., Lahaye, C.,
1063 Mercier, N., Guibert, P., Jain, M., Sandgathe, D., McPherron, S.J.P., Turq, A., Dibble, H.L.,
1064 2017. The complementarity of luminescence dating methods illustrated on the
1065 Mousterian sequence of the Roc de Marsal: A series of reindeer-dominated, Quina
1066 Mousterian layers dated to MIS 3. *Quaternary International* 433, 102–115.

1067 Guillaud, E., Béarez, P., Denys, C., Raimond, S., 2017a. New data on fish diet and bone
1068 digestion of the Eurasian otter (*Lutra lutra*) (Mammalia: Mustelidae) in central France.
1069 *The European Zoological Journal* 84, 226–237.

1070 Guillaud, E., Elleboode, R., Mahé, K., Béarez, P., 2017b. Estimation of age, growth and fishing
1071 season of a palaeolithic population of grayling (*Thymallus thymallus*) using scale analysis. .
1072 *International Journal of Osteoarchaeology* 27, 683–692.

1073 Guillaud, E., Lebreton, L., Béarez, P., 2018. Taphonomic signature of Eurasian Eagle Owl
1074 (*Bubo bubo*) on fish remains. *Folia Zoologica* 67, 143–153.

1075 Guillaud, E., Morales-Muñiz, A., Roselló-Izquierdo, E., Béarez, P., 2019. Taphonomy of
1076 Yellow-legged Gull (*Larus michahellis* Naumann, 1840) pellets from the Chafarinas Islands
1077 (Spain). *Canadian Journal of Zoology* 97, 100–111.

1078 Hardy, K., Buckley, S., Collins, M.J., Estalrich, A., Brothwell, D., Copeland, L., García-
1079 Taberner, A., García-Vargas, S., de la Rasilla, M., Lalueza-Fox, C., Huguet, R., Bastir, M.,
1080 Santamaría, D., Madella, M., Wilson, J., Fernández-Cortés, A., Rosas, A., 2012.
1081 Neanderthal medics? Evidence for food, cooking, and medicinal plants entrapped in
1082 dental calculus. *Naturwissenschaften* 99, 617–626.

1083 Hardy, B.L., Moncel, M.H., Daujeard, C., Fernandes, P., Béarez, P., Desclaux, E., Chacon
1084 Navarro, M.G., Puaud, S., Gallotti, R., 2013. Impossible Neanderthals? Making string,
1085 throwing projectiles and catching small game during Marine Isotope Stage 4 (Abri du
1086 Maras, France). *Quaternary Science Reviews* 82, 23–40.

1087 Hernandez, M., Mercier, N., Rigaud, J.P., Texier, J.P., Delpech, F., 2014. A revised chronology
1088 for the Grotte Vaufrey (Dordogne, France) based on TT-OSL dating of sedimentary quartz.
1089 *Journal of Human Evolution* 75, 53–63.

1090 Hilderbrand, G.V., Schwartz, C.C., Robbins, C.T., Jacoby, M.E., Hanley, T.A., Arthur, S.M.,
1091 Servheen, C., 1999. The importance of meat, particularly salmon, to body size, population
1092 productivity, and conservation of North American brown bears. *Canadian Journal of*
1093 *Zoology* 77, 132–138.

1094 Huet, M., 1954. Biologie, profils en long et en travers des eaux courantes. *Bulletin Français*
1095 *de Pisciculture* 175, 41–53.

1096 Huygens, O.C., Miyashita, T., Dahle, B., Carr, M., Izumiyama, S., Sugawara, T., Hayashi, H.,
1097 2003. Diet and feeding habits of Asiatic black bears in the Northern Japanese Alps. *Ursus*
1098 14, 236–245.

1099 Jaouen, K., Colleter, R., Pietrzak, A., Pons, M.L., Clavel, B., Telmon, N., Crubézy, E., Hublin,
1100 J.J., Richards, M.P., 2018. Tracing intensive fish and meat consumption using Zn isotope
1101 ratios: Evidence from a historical Breton population (Rennes, France). *Scientific Reports* 8,
1102 5077.

1103 Jaouen, K., Richards, M.P., Le Cabec, A., Welker, F., Rendu, W., Hublin, J.J., Soressi, M.,
1104 Talamo, S., 2019. Exceptionally high $\delta^{15}\text{N}$ values in collagen single amino acids confirm

1105 Neandertals as high-trophic level carnivores. Proceedings of the National Academy of
1106 Sciences of the United States of America 116, 4928–4933.

1107 Jones, A.K.G., 1986. Fish bone survival in the digestive systems of the pig, dog and man:
1108 some experiments. In: Clayson, A.T. (Ed.), Fish and Archaeology. Studies in Osteometry,
1109 Taphonomy, Seasonality and Fishing Methods. British Archaeological Reports, Oxford, pp.
1110 53–61.

1111 Jones, D.B., DeSantis, L.R.G., 2016. Dietary ecology of the extinct cave bear: evidence of
1112 omnivory as inferred from dental microwear textures. Acta Palaeontologica Polonica
1113 61(4), 735–741.

1114 Jonsson, B., Jonsson, N., 2009. A review of the likely effects of climate change on
1115 anadromous Atlantic salmon *Salmo salar* and brown trout *Salmo trutta*, with particular
1116 reference to water temperature and flow. Journal of Fish Biology 75, 2381–2447.

1117 Julien, M., 1982. Les Harpons Magdaléniens. CNRS Éditions, Paris.

1118 Keith, P., 1998. Evolution des peuplements ichtyologiques de France et stratégies de
1119 conservation. Ph.D. Dissertation, Université de Rennes 1.

1120 Keith, P., Persat, H., Feunteun, E., Allardi, J., 2011. Les poissons d'eau douce de France,
1121 Inventaires et Biodiversité. Muséum national d'histoire naturelle, Paris.

1122 Kettle, A., Heinrich, D., Barrett, J. H., Benecke, N., Locker, A., 2008. Past distributions of the
1123 European freshwater eel from archaeological and palaeontological evidence. Quaternary
1124 Science Reviews 27, 1309–1334.

1125 Kozłowski, J.K., 2017. L'impact de l'environnement sur l'évolution biologique et culturelle
1126 dans les périodes de transition en Préhistoire : Paléolithique ancien/moyen et
1127 Paléolithique moyen/supérieur. Comptes Rendus Palevol 16, 200–217.

- 1128 Laroulandie, V., 2000. Taphonomie et archéozoologie des oiseaux en grotte: applications aux
1129 sites paléolithiques du Bois-Ragot (Vienne), de Combe Saunière (Dordogne) et de la Vache
1130 (Ariège). Ph.D. Dissertation, Université de Bordeaux I.
- 1131 Laroulandie, V., 2002. Damage to pigeon long bones in pellets of the Eagle owl *Bubo bubo*
1132 and food remains of peregrine falcon *Falco peregrinus*: zooarchaeological implications.
1133 Acta Zoologica Cracoviensia 45(special issue), 331–339.
- 1134 Laroulandie, V., Faivre, J.P., Gerbe, M., Mourre, V., 2016. Who brought the bird remains to
1135 the Middle Palaeolithic site of Les Fieux (Southwestern, France)? Direct evidence of a
1136 complex taphonomic story. Quaternary International 421, 116–133.
- 1137 Le Gall, O., 1984. L'exploitation de l'ichthyofaune par les Paléolithiques : quelques exemples.
1138 In: Desse-Berset, N. (Ed.), 2èmes Rencontres d'Archéo-Ichthyologie : Table Ronde Sophia
1139 Antipolis - Valbonne, 14–16 oct. 1983. CNRS: Paris, pp. 89–112.
- 1140 Le Gall, O., 1988. Les poissons de la grotte Vaufray. In: Rigaud, J.P. (Ed.), La Grotte Vaufray à
1141 Cénac et Saint-Julien (Dordogne): Paléoenvironnements, Chronologie et Activités
1142 Humaines. Mémoires de la Société Préhistorique Française 19, pp. 351–356.
- 1143 Le Gall, O., 1992. Poissons et pêches au Paléolithique. Quelques données de l'Europe
1144 occidentale. L'Anthropologie 96(1), 121–134.
- 1145 Le Gall, O., 1999. Ichtyophagie et pêches préhistoriques. Quelques données de l'Europe
1146 occidentale. State doctorate thesis, Université de Bordeaux I.
- 1147 Le Gall, O., 2000. Les Moustériens étaient-ils pêcheurs ? Bulletin de la Société
1148 d'Anthropologie du Sud-Ouest 34, 3–11.
- 1149 Le Gall, O., 2003. La squelettochronologie appliquée aux poissons. Une méthode de
1150 reconnaissance des saisons de capture. Bulletin Préhistoire du Sud-Ouest 10, 9–24.

- 1151 Le Gall, O., 2008. Ichtyofaunes et pêches à la grotte Walou. In: Dewez, M. (Ed.), Recherches à
1152 la grotte Walou à Trooz (Belgique). Second rapport de fouille. British Archaeological
1153 Reports, Oxford, pp. 57–68.
- 1154 Le Gall, O., 2010. Influences des glaciaires-interglaciaires sur les ichtyofaunes des eaux
1155 douces européennes. Quaternaire 21, 203–214.
- 1156 Lisiecki, L.E., Raymo, M.E., 2005. A Pliocene-Pleistocene stack of 57 globally distributed
1157 benthic $\delta^{18}\text{O}$ records. Paleoceanography 20, PA1003.
- 1158 Lyman, R., 1994. Vertebrate Taphonomy. Cambridge University Press, Cambridge.
- 1159 Mallye, J.B., 2011. Taphonomie et archéozoologie d'un animal fouisseur: méthode de
1160 caractérisation de restes de Blaireau. In: Laroulandie, V., Mallye, J.B., Denys, C. (Eds.),
1161 Taphonomie des Petits Vertébrés : Référentiels et Transferts aux Fossiles. British
1162 Archaeological Reports, Oxford, pp. 43–56.
- 1163 Mallye, J.B., Cochard, D., Laroulandie, V., 2008. Accumulation osseuse en périphérie de
1164 terriers de petits carnivores : les stigmates de prédation et de fréquentation. Annales de
1165 Paléontologie 94, 187–208.
- 1166 Marean, C.W., Bar-Matthews, M., Bernatchez, J., Fisher, E., Goldberg, P., Herries, A.I.R.,
1167 Jacobs, Z., Jerardino, A., Karkanas, P., Minichillo, T., Nilssen, P.J., Thompson, E., Watts, I.,
1168 Williams, H.M., 2007. Early human use of marine resources and pigment in South Africa
1169 during the Middle Pleistocene. Nature 449, 905–908.
- 1170 Mayhew, D.F., 1977. Avian predators as accumulators of fossil mammal material. Boreas 6,
1171 25–31.
- 1172 Medin, T., Martínez-Navarro, B., Rivals, F., Madurell-Malapeira, J., Ros-Montoya, S.,
1173 Espigares, M.-P., Figueirido, B., Rook, L., Palmqvist, P., 2017. Late Villafranchian *Ursus*
1174 *etruscus* and other large carnivorans from the Orce sites (Guadix-Baza basin, Andalusia,

- 1175 southern Spain): Taxonomy, biochronology, paleobiology, and ecogeographical context.
1176 Quaternary International 431, 20–41.
- 1177 Moncel, M.H., Allué, E., Bailon, S., Barshay-Szmidt, C., Béarez, P., Crégut, É., Daujeard, C.,
1178 Desclaux, E., Debard, É., Lartigot-Campin, A.S., Puaud, S., Roger, T., 2015. Evaluating the
1179 integrity of palaeoenvironmental and archaeological records in MIS 5 to 3 karst
1180 sequences from southeastern France. Quaternary International 378, 22–39.
- 1181 Moncel, M.H., Arzarello, M., Peretto, C., 2016. The Holsiteinian period in Europe (MIS 11-9).
1182 Quaternary International 409, 1–8.
- 1183 Mondini, M., 2001. Taphonomic action of foxes in Punta Rockshelters: a case study in
1184 Antofogasta de la Sierra (Province of Catamarca, Argentina). In: Kuznar, L.A. (Ed.),
1185 Ethnoarchaeology of Andean South America. Contributions to Archaeological Method and
1186 Theory. Berghahn, New York, pp. 266–295.
- 1187 Morales, A., 1980. Los peces fósiles del yacimiento achelense de Áridos-1 (Arganda,
1188 Madrid). In: Santonja, M., López-Martínez, N., Pérez-González, A. (Eds.), Ocupaciones
1189 achelenses en el Valle del Jarama (Arganda, Madrid). Servicios de Extensión Cultural y
1190 Divulgación de la Diputación Provincial de Madrid, Madrid, pp. 93–104.
- 1191 Morales, A., Roselló, E., 1989. Commentaires au sujet de la détermination de l'occupation
1192 saisonnière dans deux gisements paléolithiques du nord de l'Espagne. L'Anthropologie 93,
1193 831–836
- 1194 Morales, A., Roselló, E. 1990. La Ictiofauna de la Cueva de Amalda. In: Altuna, J., Baldeón, A.,
1195 Mariezkurrena, K. (Eds.), La Cueva de Amalda (Zestoa, País Vasco). Ocupaciones
1196 Paleolíticas y Postpaleolíticas. Eusko Ikaskuntza, San Sebastián, pp. 255–266.

1197 Morin, E., Meier, J., El Guennouni, K., Moigne, A. M., Lebreton, L., Rusch, L., Valensi, P.,
1198 Conolly, J., Cochard, D., 2019. New evidence of broader diets for archaic *Homo*
1199 populations in the northwestern Mediterranean. *Science Advances* 5, eaav9106.

1200 Muñoz, M., Casadevall, M., 1997. Fish remains from Arbreda Cave (Serinyà, Girona),
1201 Northeast Spain, and their paleoecological significance. *Journal of Quaternary Science*,
1202 12(2), 111–115.

1203 Naito, Y.I., Germonpré, M., Chikaraishi, Y., Ohkouchi, N., Drucker, D.G., Hobson, K.A.,
1204 Edwards, M.A., Wißing, C., Bocherens, H., 2016. Evidence for herbivorous cave bears
1205 (*Ursus spelaeus*) in Goyet Cave, Belgium: implications for palaeodietary reconstruction of
1206 fossil bears using amino acid $\delta^{15}\text{N}$ approaches. *Journal of Quaternary Science* 31, 598-
1207 606.

1208 Nehlich, O., Borić, D., Stefanović, S., Richards, M.P., 2010. Sulphur isotope evidence for
1209 freshwater fish consumption: a case study from the Danube Gorges, SE Europe. *Journal of*
1210 *Archaeological Science* 37, 1131–1139.

1211 Nicholson, R.A., 1991. An investigation into variability within archaeologically recovered
1212 assemblages of faunal remains: the influence of pre-depositional taphonomic factors.
1213 Ph.D. Dissertation, York University.

1214 Nicholson, R.A., 1993. An investigation into the effects on fish bone on passage through the
1215 human gut: some experiments and comparisons with archaeological material. *Circaea* 10,
1216 38–51.

1217 Nicholson, R.A., 2000. Otter (*Lutra lutra* L.) spraint: an investigation into possible sources of
1218 small fish bones at coastal archaeological sites. In: Huntley, J.P., Stallibrass, S. (Eds.),
1219 *Taphonomy and Interpretation*. Oxbow Books, Oxford, p. 55–64.

- 1220 Niedzialkowska, M., Hayward, M.W., Borowik, T., Jedrzejewski, W., Jedrzejewska, B., 2019. A
1221 meta-analysis of ungulate predation and prey selection by the brown bear *Ursus arctos* in
1222 Eurasia. *Mammal Research* 64, 1–9.
- 1223 Niven, L., Steele, T.E., Rendu, W., Mallye, J.B., McPherron, S.P., Soressi, M., Jaubert, J.,
1224 Hublin, J.J., 2012. Neandertal mobility and large-game hunting: The exploitation of
1225 reindeer during the Quina Mousterian at Chez-Pinaud Jonzac (Charente-Maritime,
1226 France). *Journal of Human Evolution* 63, 624–635.
- 1227 Ojaveer, E., Pihu, E., Saat, T., 2003. *Fishes of Estonia*. Estonian Academy publishers, Tallinn.
- 1228 Orta, J., 1992. Family Phalacrocoracidae (Cormorants). In: Del Hoyo, J., Elliott, A., Sargatal, J.
1229 (Eds.), *Handbook of the birds of the world*. Lynx Editions, Barcelona, pp. 280–289.
- 1230 Patou-Mathis, M., 2000. Neanderthal subsistence behaviours in Europe. *International*
1231 *Journal of Osteoarchaeology* 10, 379–395.
- 1232 Persat, H., 1988. De la biologie des populations de l'ombre commun *Thymallus thymallus* (L.
1233 1758) à la dynamique des communautés dans un hydrosystème fluvial aménagé, le Haut-
1234 Rhône français. *Éléments pour un changement d'échelles*. Ph.D. Dissertation, Université
1235 Claude-Bernard Lyon I.
- 1236 Pétilion, J.-M., 2009. Des barbelures pour quoi faire? Réflexions préliminaires sur la fonction
1237 des pointes barbelées du Magdalénien supérieur. *P@lethnologie* 1, 69–102.
- 1238 Philippart, J.C., Vranken, M., 1983. *Atlas des poissons de Wallonie*. Distribution, écologie,
1239 éthologie, pêche, conservation. *Cahiers d'Éthologie Appliquée* 3, 1–391.
- 1240 Pinto-Llona, A.C., 2013. Macrowear and occlusal microwear on teeth of cave bears *Ursus*
1241 *spelaeus* and brown bears *Ursus arctos*: Inferences concerning diet. *Palaeogeography,*
1242 *Palaeoclimatology, Palaeoecology* 370, 41–50.

- 1243 Poplin, F., 1976. A propos du Nombre de Restes et du Nombre d'Individus dans les
1244 échantillons d'ossements. Cahiers du Centre de Recherches Préhistoriques 5, 61–74.
- 1245 Privat, K.L., O'Connell, T.C., Hedges, R.E.M., 2007. The distinction between freshwater- and
1246 terrestrial-based diets: methodological concerns and archaeological applications of
1247 sulphur stable isotope analysis. *Journal of Archaeological Science* 34, 1197–1204.
- 1248 Puech, P.F., Puech, S., 1993. L'usure des dents de Banyoles. In: Maroto, J. (Ed.), *La mandíbula*
1249 *de Banyoles en el context dels fòssils humans del Pleistocè*. Centre d'Investigacions
1250 *Arqueològiques de Girona, Gerona*, pp. 105–115.
- 1251 Ramírez-Pedraza, I., Tornero, C., Pappa, S., Talamo, S., Salazar-García, D.C., Blasco, R., Rosell,
1252 J., Rivals, F., 2019. Microwear and isotopic analyses on cave bear remains from Toll Cave
1253 reveal both short-term and long-term dietary habits. *Scientific Reports* 9, 5716.
- 1254 Reitz, E.J., Wing, E.S., 1999. *Zooarchaeology*. Cambridge University Press, Cambridge.
- 1255 Richard, M., Falguères, C., Pons-Branchu, E., Bahain, J.J., Voinchet, P., Lebon, M., Valladas,
1256 H., Dolo, J.M., Puaud, S., Rué, M., Daujeard, C., Moncel, M.H., Raynal, J.P., 2015.
1257 Contribution of ESR/U-series dating to the chronology of late Middle Palaeolithic sites in
1258 the middle Rhône valley, southeastern France. *Quaternary Geochronology* 30, 529–534.
- 1259 Richards, M. P., Trinkaus, E., 2009. Isotopic evidence for the diets of European Neanderthals
1260 and early modern humans. *Proceedings of the National Academy of Sciences*, 106(38),
1261 16034-16039.
- 1262 Roselló-Izquierdo, E., 1992. La ictiofauna musteriense de cueva Millán (Burgos):
1263 consideraciones de índole biológica y cultural contrastadas con ictiocenosis paleolíticas
1264 cantábricas. *Estudios Geológicos* 48, 79–83.

1265 Roselló-Izquierdo, E., Morales-Muñiz, A., 2005. Ictiofaunas musterienses de la Península
1266 Ibérica: ¿Evidencias de pesca neandertal? *Munibe* 57, 183–195.

1267 Rufá, A., Blasco, R., Roger, T., Moncel, M.H., 2016. What is the taphonomic agent
1268 responsible for the avian accumulation? An approach from the Middle and early Late
1269 Pleistocene assemblages from Payre and Abri des Pêcheurs (Ardèche, France).
1270 *Quaternary International* 421, 46–61.

1271 Rufá, A., Blasco, R., Roger, T., Rué, M., Daujeard, C., 2017. A rallying point for different
1272 predators: the avian record from a Late Pleistocene sequence of Grotte des Barasses II
1273 (Balazuc, Ardèche, France). *Archaeological and Anthropological Sciences* 10, 1459–1476.

1274 Russ, H., 2010. A taphonomic approach to reconstructing upper Palaeolithic hunter-gatherer
1275 fishing strategies. Ph.D. Dissertation, Bradford University.

1276 Russ, H., 2016. To fish or not to fish? Using observations of recent hunter-gatherer fishing in
1277 the interpretation of Late Pleistocene fish bone assemblages. In: Broderick, L. (Ed.),
1278 *People with animals: Perspectives and studies in ethnozoarchaeology*. Oxbow Books,
1279 Oxford, pp. 87–102.

1280 Russ, H., Jones, A.K.G., 2011. Fish remains in cave deposits; how did they get there? *Cave
1281 and Karst Science* 38, 57–60.

1282 Smith, D.G., 1984. Mackenzie delta Eskimo. In: Damas, D. (Ed.), *Handbook of North American
1283 Indians, Arctic*. Smithsonian Institution, Washington, pp. 347–358.

1284 Stewart, H., 1977. *Indian Fishing. Early Methods on the Northwest Coast*. Douglas &
1285 McIntyre, Vancouver.

1286 Stewart, K.M., 1994. Early hominid utilisation of fish resources and implications for
1287 seasonality and behaviour. *Journal of Human Evolution* 27(1-3), 229-245.

- 1288 Stiner, M.C., 1994. Honor Among Thieves. Princeton University Press, Princeton.
- 1289 Stringer, C.B., Finlayson, J.C., Barton, R.N.E., Fernandez-Jalvo, Y., Caceres, I., Sabin, R.C.,
1290 Rhodes, E.J., Carrant, A.P., Rodriguez-Vidal, J., Giles-Pacheco, F., Riquelme-Cantal, J.A.,
1291 2008. Neanderthal exploitation of marine mammals in Gibraltar. Proceedings of the
1292 National Academy of Sciences of the United States of America 105, 14319–14324.
- 1293 Suter, W., 1995. The effect of predation by wintering cormorants *Phalacrocorax carbo* on
1294 grayling *Thymallus thymallus* and trout (Salmonidae) populations: two case studies from
1295 Swiss rivers. Journal of Applied Ecology 32, 29–46.
- 1296 Suter, W., Morel, P., 1996. Pellet analysis in the assessment of great cormorant
1297 *Phalacrocorax carbo* diet: reducing biases from otolith wear when reconstructing fish
1298 length. Colonial Waterbirds 19, 280–284.
- 1299 Szpak, P., 2011. Fish bone chemistry and ultrastructure: implication for taphonomy and
1300 stable isotope analysis. Journal of Archaeological Science 38, 3358–3372.
- 1301 Taylor, J.G., 1984. Historical ethnography of the Labrador coast. In: Sturtevant, W.C., Damas,
1302 D. (Eds.), Handbook of North American Indians. 5. Arctic. Smithsonian Institution,
1303 Washington, pp. 508–521.
- 1304 Thieren, E., Wouters, W., Van Neer, W., 2015. Guide for the identification of archaeological
1305 sea sturgeon (*Acipenser sturio* and *A. oxyrinchus*) remains. Cybium 39, 175–192.
- 1306 Thomas, D.H., 1971. On distinguishing natural from cultural bone in archaeological sites.
1307 American Antiquity 36, 366–371.
- 1308 Tissot, L., Souchon, Y., 2010. Synthèse des tolérances thermiques des principales espèces de
1309 poissons des rivières et fleuves de plaine de l’Ouest européen. Hydroécologie Appliquée
1310 17, 17–76.

- 1311 Trinkaus, E., Samsel, M., Villotte, S. 2019. External auditory exostoses among western
1312 Eurasian late Middle and Late Pleistocene humans. PLoS One 14(8), e0220464.
- 1313 Van Heteren, A.H., Arlegi, M., Santos, E., Arsuaga, J.L., Gómez-Olivencia, A., 2019. Cranial
1314 and mandibular morphology of Middle Pleistocene cave bears (*Ursus deningeri*):
1315 implications for diet and evolution. Historical Biology 31(4), 485–499.
- 1316 Van Neer, W., Lougas, L., Rijnsdorp, A.D., 1999. Reconstructing age distribution, season of
1317 capture and growth rate of fish from archaeological sites based on otoliths and vertebrae.
1318 International Journal of Osteoarchaeology 9, 116–130.
- 1319 Van Neer, W., Wouters, W., 2011. Les restes de poissons des niveaux du Paléolithique
1320 moyen et supérieur de la grotte Walou. In: Draily, C., Pirson, S., Toussaint, M. (Eds.), La
1321 Grotte Walou à Trooz (Belgique). Fouilles de 1996 à 2004. Vol. 2. Département du
1322 Patrimoine & Institut du Patrimoine wallon, Namur, pp. 68–82.
- 1323 Vanstone, J.W., 1984. Mainland Southwest Alaska Eskimo. In: Damas, D. (Ed.), Handbook of
1324 North American Indians, Arctic. Smithsonian Institution, Washington, pp. 224–242.
- 1325 Veldkamp, R., 1995. Diet of cormorants *Phalacrocorax carbo sinensis* at Wanneperveen, The
1326 Netherlands, with special reference to bream *Abramis brama*. Ardea 83, 143–155.
- 1327 Wendland, V., 1984. The influence of prey fluctuations on the breeding success of the Tawny
1328 owl *Strix aluco*. Ibis 126, 284–295.
- 1329 Wheeler, A., Jones, A.K.G., 1989. Fishes. Cambridge University Press. Cambridge.
- 1330 Willis, L.M., Eren, M.I., Rick, T.C., 2008. Does butchering fish leave cut marks? Journal of
1331 Archaeological Science 35(5), 1438–1444.
- 1332 Wißing, C., Rougier, H., Baumann, C., Comeyne, A., Crevecoeur, I., Drucker, D.G., Gaudzinski-
1333 Windheuser, S., Germonpré, M., Gómez-Olivencia, A., Krause, J., Matthies, T., Naito, Y.I.,
1334 Posth, C., Semal, P., Street, M., Bocherens, H., 2019. Stable isotopes reveal patterns of

1335 diet and mobility in the last Neandertals and first modern humans in Europe. Scientific
1336 Reports 9, 4433.

1337 Yellen, J.E., Brooks, A.S., Cornelissen, E., Mehlman, M.J., Stewart, K., 1995. A Middle Stone
1338 Age worked bone industry from Katanda, Upper Semliki Valley, Zaire. Science 268, 553-
1339 556.

1340 Zilhão, J., Angelucci, D.E., Araújo-Igreja, M., Arnold, L.J., Badal, E., Callapez, P., Cardoso, J.L.,
1341 d'Errico, F., Daura, J., Demuro, M., Deschamps, M., Dupont, C., Gabriel, S., Hoffmann, D.L.,
1342 Legoinha, P., Matias, H., Monge-Soares, A.M., Nabais, M., Portela, P., Queffelec, A.,
1343 Rodrigues, F., Souto, P., 2020. Last Interglacial Iberian Neandertals as fisher-hunter-
1344 gatherers. Science 367(6485): eaaz7943.

1345

1346

1347

1348

1349

1350

1351

1352

1353

1354

1355

1356

1357

1358

1359

1360

1361

1362

1363

1364

1365

1366

1367 **Figure captions**

1368

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.

1377

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

1379

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.