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Mesolithic Freshwater Fishing: A Zooarchaeological Case Study

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Abstract: In this article we investigate the importance of freshwater fishing during the Mesolithic in France, in inland sites where fishing was always associated with big game hunting. We present a review of Mesolithic sites that have yielded freshwater fish remains and focus on a case study from an occupation dated to the eighth millennium BC at Les Cabônes rock shelter, located near the Doubs River, that yielded over 9,300 fish remains. Cyprinid (including bream, roach, and minnow) remains are predominant; other taxa, such as salmonids (probably trout), grayling, burbot, perch, and eel, are represented by only a few remains each. Although small fish (about 15 cm) constitute the majority of the catch, we provide evidence that their accumulation in the shelter is mostly of human origin. These catches constituted a source of food throughout the year, particularly during the lean season. According to the ecological preferences of the fish species identified, it is highly unlikely that they were caught in a single location. The animals were probably caught with passive fishing equipment in shallow banks or side channels where large numbers of specimens could be captured. Fishing appears to have been optimised to maximise yield-to-effort ratios, together with other wetland resources. Finally, we question the presumed causal links between site micro-setting, site occupation, and increased dependence on aquatic resources and reduced group mobility.

Keywords: fishing techniques, season, fish size, food resource, Early Holocene

1 Introduction

Early on, Binford postulated that throughout the Old World, human societies became increasingly dependent on aquatic resources for food in the Terminal Palaeolithic and Mesolithic (Binford, 1968). He associated this with a higher degree of sedentism, population growth, and food storage. Since then, research has focused on discussing two economic characteristics of "post-Pleistocene" societies: a broadening of the range of exploited species and a markedly increased dependence on small, highly productive species. In France, investigation of prehistoric fishing was initiated by precursors of archaeo-ichthyology through the

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analysis of fish remains (Desse & Desse, 1976, 1983; Le Gall, 1982, 1984). Work by Le Gall, mainly in continental environments and in the South of France, has shown that systematic fishing for large migratory species (salmon and sea trout) developed during the Late Palaeolithic (Le Gall, 1991, 1992, 1993, 1999). Then, during the Azilian period, freshwater fishing tended to focus more on abundant perennial species, such as cyprinids and pike, though studies were limited to regions south of the Loire and in the Doubs basin (Cravinho & Desse-Berset, 2005; Cravinho, 2011; Frontin, 2017; Le Gall & Pannoux, 1994). The situation is not as clear for the Mesolithic: mixed documentation and a very limited number of archaeo-ichthyological analyses limit our understanding of fishing during the period. A decrease in fishing has even been suggested due to the scarcity of fish bones found in some cultural contexts. Even on the scale of Western Europe, with the exception of southern Scandinavia and northern Germany, there are few studies of large Mesolithic assemblages of fish bone from inland sites (Dauphin, 1989; Niekus, Brinkhuizen, Kerkhoven, Huisman, & Velthuizen, 2012; Wierer et al., 2018; Wijngaarden-Bakker, 1989). Stable isotope analyses of the Mesolithic diet tend to highlight a diversity of situations: diets that are exclusively terrestrial, with a low contribution of freshwater fish, or with mixed terrestrial/aquatic resources (Drucker et al., 2016; Drucker, Bridault, Ducrocq, Baumann, & Valentin, 2020; Schulting, Blockley, Bocherens, Drucker, & Richards, 2008), in both the Early and the Late Mesolithic. The question of freshwater fishing and its contribution to the economy of Mesolithic groups certainly needs to be examined on a case-by-case basis. The aim of this article is to discuss the importance of freshwater fishing in an economy largely based on large game hunting, using unpublished data from the study[1] of an assemblage of more than 9,300 fish remains from an occupation of the Ranchot site (Jura), dated to the eighth millennium BC.

2 Archaeological Context

2.1 Freshwater Fishing in Mesolithic France

A bibliographical search enabled us to identify 21 Mesolithic sites in France in which bones of freshwater ichthyofauna were identified. Six additional sites only mention the presence of unspecified fish remains, that were most probably of freshwater or migratory species given their geographic location. This corpus thus comprises a total of 27 sites, distributed mainly inland over a large part of the country, and 32 assemblages for the entire Mesolithic period (Figure 1). More than half of these (15 out of 27) contain less than 25 remains and only 3 assemblages comprise more than 1,000 remains: the Cabônes shelter at Ranchot (Jura), the open-air sites of Noyen-sur-Seine “Le Haut-des-Nachères” (Seine-et-Marne), and La Chaussée-Tirancourt “le Petit Marais” (Somme), and probably also the Montclus site (Gard) (Table S1). This disparity is striking, especially as fine mesh sieving was carried out on most of these sites, albeit not always exhaustively (Table S1). In the valleys of northern France, where Mesolithic groups regularly settled on dry land near rivers, the presence of fish remains is not systematic even though the mammalian fauna is well preserved and exhaustive sieving was carried out (e.g. Ducrocq et al., 2019). Fishing is only clearly attested at a small number of sites. This is the case at Noyen-sur-Seine where, in addition to eel and pike remains, a dugout log-boat and fish traps have been preserved (Deseine, Guéret, Vigne, Mordant, & Valentin, 2019; Marinval-Vigne et al., 1989; Mordant, Valentin, & Vigne, 2013), and stable isotope analysis demonstrates that freshwater aquatic resources made a significant contribution to the human diet (Drucker et al., 2016).

These findings motivated a detailed study centred on the ichthyofaunal assemblage of layer 3 of the Cabônes shelter at Ranchot in the Jura (Frontin, 2017), a region rich in Mesolithic sites with well-preserved faunal remains.

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[1] Carried out as part of a PhD thesis by Frontin (2017).

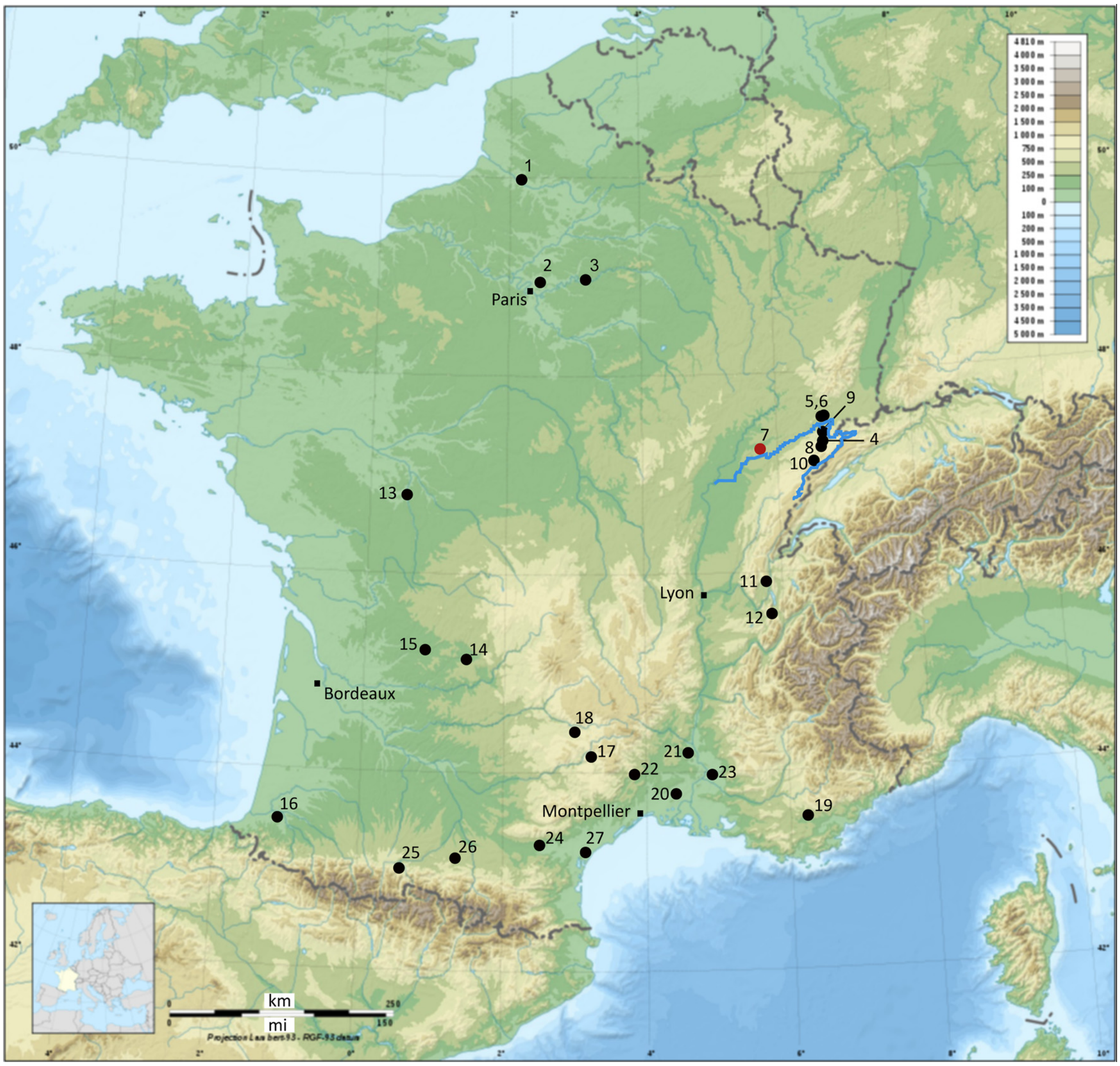

Figure 1: Location of French Mesolithic sites having yielded freshwater fish remains (map of France from cartesFrance.fr). (1) Le Petit Marais, (2) La Haute-Île, (3) Le Haut-des-Nachères, (4) Baume de Montandon, (5) Bavans, (6) Châtaillon, (7) Les Cabônes, (8) Gigot, (9) Rochedane, (10) La Roche-aux-Pêcheurs, (11) Sous Balme, (12) Jean-Pierre 1, (13) Abri des Rocs, (14) La Doue, (15) Le Peyrat, (16) Bourouilla, (17) La Poujade, (18) Roquemissou, (19) La Baume Fontbrégoua, (20) Le Plaisir, (21) La Baume de Montclus, (22) Grotte du Salpêtre, (23) Le Mourre de Sève, (24) Balma de l'Abeurador, (25) Moulin, (26) Buholoup, and (27) La Crouzade. The Doubs River is highlighted in blue. Please refer to Table S1 in the supporting information for the data.

2.2 Regional Context

Settlement intensified during the Early Mesolithic, from 8400 BC onwards. Then, during the Middle Mesolithic, between 7600 and 7000 BC, an increase in the number of sites is recorded at all altitudes, including large open-air sites (Cupillard et al., 2015); occupation levels are denser, richer, and attest to diversified activities. At the beginning of the Late Mesolithic, the number of sites in the region decreases, possibly due to a climatic deterioration (i.e. the 8200 cal. BP event), after which the number of occupations increases again from 6000 BC onwards (Cupillard et al., 2015).

Mesolithic sites with ichthyofaunal remains are distributed along the entire course of the Doubs. This river flows across the Central Jura for 453 km, crossing the Bourgogne Franche-Comté region in France as well as the cantons of Neuchâtel and Jura in Switzerland. It is supplied by some 15 tributaries, and is the main tributary of the Saône, which is itself the main tributary of the Rhône. The flow of the Doubs is irregular, of the pluvial to pluvial-nival type with severe low water in the summer; the flood period extends from September to the end of May due to feeding by the heavy rainfall that affects the Jura massif. While the extent of the Weichselian alluvial deposits is well established (Fleury, Farjanel, & Collin, 1982), our knowledge of the postglacial evolution of the river is incomplete (Rotillon, 2000; Séara, Rotillon, & Cupillard, 2002). It is known that the rapid warming phases of the Lateglacial–Holocene transition impacted hydrosystems all over Europe, increasing river bed incision and changing systems from laterally active braided flows to meandering single channels (Macklin & Lewin, 2003; Magny & Bravard, 2002; Pastre et al., 2000). According to a study conducted at Choisey near Dole (Rotillon, 2000), the Doubs first incised the valley at the beginning of the Lateglacial, then river dynamics slackened in the Preboreal and Boreal periods. The development of riparian vegetation may also have played a role in fixing river courses.

The impact of climate change can also be seen on fish populations. During the Last Glacial, only cryophilic and low-temperature breeding species, such as salmonids, burbot (*Lota lota*), or pike (*Esox lucius*) and, to a lesser extent, rheophilic cyprinids such as common dace (*Leuciscus leuciscus*), were able to survive north of refuge areas (Mediterranean fringe and Black Sea basin) (Le Gall, 2010). Opportunities for recolonisation arose during the deglaciation process, and fish populations attained their maximum expansion during the Lateglacial period, expanding along the natural channels formed by the Danube and the Rhone. Cryophilic species then dispersed rapidly, followed by thermophilic species (Le Gall, 2010; Persat & Keith, 1997, 2002; Persat, 2003).

2.3 The Cabônes Site at Ranchot

Les Cabônes rock shelter (or "abri du Colonel Martin") is situated in the last ranges of the Jura front. It is located on the right bank of the Doubs River at an altitude of 216 m, near the town of Ranchot (Jura), halfway between Besançon and Dole, in the lower Doubs valley (Figure 2). In this sector, the bed of the Doubs is wide and gently sloped (0.45%). The site is a small cave dug into a Lower Sequanian limestone ledge. It was probably formed by the joint action of the Doubs and a former karstic flow (Campy, David, & Cupillard, 1989; Cupillard & David, 1995). The opening of the cave forms a shelter about ten metres long. Following surveys carried out in the 1950s and 1960s, the site was extensively excavated from 1978 to 1989 under the direction of A. Thévenin, M. Campy, S. David, and C. Cupillard (Campy et al., 1989; Cupillard, 1998b; Cupillard & David, 1995).

The stratigraphy is fairly well preserved in the front part of the site, where three complexes can be identified (Campy et al., 1989) (Figure 3):

- A lower sterile complex consisting of pebbles lying on the limestone bedrock, corresponding to the Würmian alluvial deposits of the Doubs (layer 7).
- An intermediate complex consisting of Doubs overflow silts incorporating angular cryoclastic fragments and blocks from the dismantlement of the porch (layers 4, 5, and 6). The top part of this complex (layer 4a) marks the end of the lateglacial allochtonous contributions of the Doubs. These layers are contemporaneous with Upper-Final Magdalenian occupations (David, 1993). The fauna consists mainly of reindeer, with a date for one bone of 13965 ± 101 BP, while a cave lion remain was dated to 12565 ± 50 BP, i.e. 12620–13201 cal. BC (Cupillard et al., 2015; Stuart & Lister, 2007).
- An upper complex composed of clayey matrix with cryoclastic fragments, which is a local expression of the "groizes litées" resulting from the dismantling of the shelter. This complex is subdivided into two layers:

Layer 3 (formerly AOC, for Cryoclastic Organic Clay) is black and highly organic, rich in micro-charcoals of anthropic origin. It is 60–70 cm thick, thinning towards the Doubs around squares 6–8. It was excavated over 50 m^2 for a potential surface area of 80 m^2. The disturbances (burrows and ancient excavations) are generally located at the bottom of the shelter up to the porch. The outer zone of the site where material is very abundant probably corresponds to one or more discarding areas on the periphery of a dwelling area. However, little evidence of the latter subsists, apart from a hearth marked by a rubified zone in squares Z-A 14 (Figure 4). A lithic industry attributed to the Middle Sauveterrian forms most of the corpus; Early

Figure 2: General view of Les Cabônes site (Ranchot, Jura, France). The site is on the left, and the Doubs River is on the right. © C. Cupillard.

Mesolithic microliths such as crescents and oblique blunted points are also present at the base of the layer (Crotti & Cupillard, 2013; Cupillard et al., 2015; Roué, 2000). Isolated human remains were collected in this level, notably a skull fragment from square D9 dated to 8985 ± 40 BP (GrA-38019) belonging to a female individual related to haplogroup U5b1 (Posth et al., 2016) and the Villabruna cluster (Fu et al., 2016). Evidence from wild boar, red deer, and roe deer age-at-death data indicate a multi-seasonal use of the shelter (Leduc, Bridault, & Cupillard, 2015; Trémolières, 2020). The site might have been used (and reused) as a base camp as indicated by the abundance and diversity of the material recovered (Crotti & Cupillard, 2013; Cupillard, 2003). Layer 3 probably corresponds to an accumulation of several occupations dated between 8290 and 7060 cal. BC (2 sigma) (Table S2).

Layer 2 (formerly AC, for Cryoclastic Clay) is light-brown in colour and thickens towards the Doubs. It is largely disturbed by burrows and contains rare Mesolithic flints as well as Neolithic, Protohistoric, and Gallo-Roman remains. Radiocarbon analyses of two red deer bones yielded dates between 7570 and 7180 cal BC (2 sigma) (Cupillard et al., 2015; Drucker, Bridault, Hobson, Szuma, & Bocherens, 2008).

A sterile grey clay layer (Layer 1) and a surface layer (Layer 0) seal this complex.

It is noteworthy that the sedimentary nature of the upper complex (layers 0–3) points to a very weak or non-existent influence of the river in the formation of the Mesolithic archaeological levels. This contrasts with the lower silty levels (4, 5, and 6) which, however, did not yield any fish bones.

3 Materials and Methods

3.1 Materials

The ichthyofaunal remains were collected in layer 3, after fine-mesh sieving (nested sieves of 10–1 mm) of all the sediments extracted during the excavation. The studied sample comprises a total of 9,328 remains grouped into 2 differently sorted subsets:

- A first sample consists of 3,361 remains collected over a surface of 40 m^2 and sorted with the naked eye and/or under a magnifying glass (2–5×) by the archaeologists in the 1980s and 1990s. A preliminary study was carried out on 438 of these by P. Morel who identified the presence of at least five species (Morel in Cupillard, Auguste, Cupillard-Perrenoud, David, & Morel, 1988): brown trout (*Salmo trutta*),

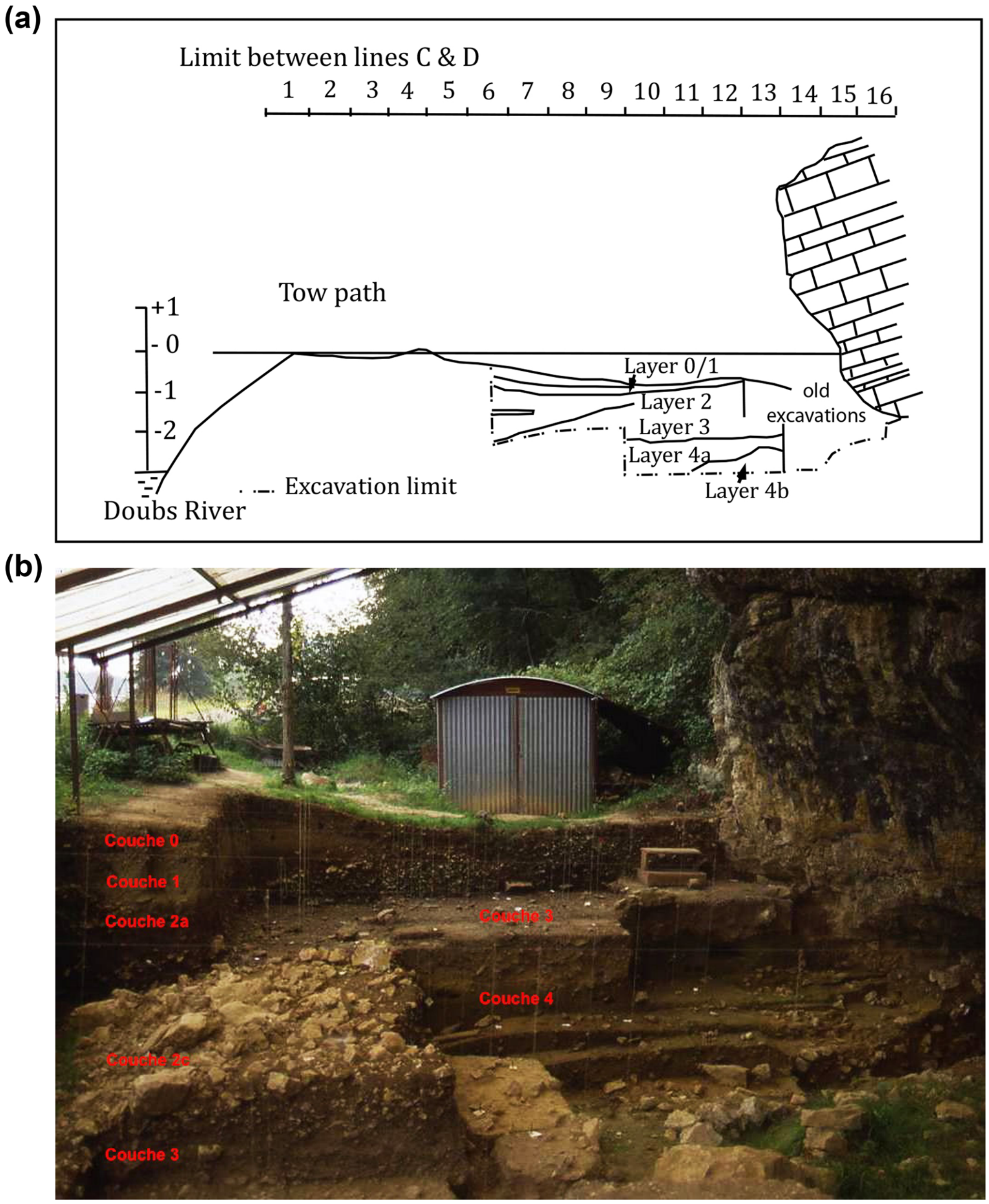

Figure 3: (a) Stratigraphy of Les Cabônes rock shelter. After S. Roué (2000). © N. Carquigny and (b) view of the excavation to the east with annotated stratigraphy. © C. Cupillard.

chub (*Squalius cephalus*), barbel (*Barbus barbus*), perch (*Perca fluviatilis*), grayling (*Thymallus thymallus*) and, possibly, burbot (*Lota lota*) and pike (*Esox lucius*). This sample also contains remains collected on sight, mostly large Salmonidae remains.

- The second sample was sorted by D. Frontin, a fish specialist, under a stereomicroscope (10–40×). It comprised 5,967 remains from five squares (H8/9, I9/10, and J10), equivalent to a volume of 13.63 L of sieving refuse resulting from the combined fractions of the sieving column (effective screen size 1 mm) (Figure 4). This area was selected because of the good preservation of the remains (Cupillard & David, 1995).

A small quantity of recent remains discarded on the site by a pair of kingfishers (*Alcedo atthis*) nesting in one of the shelter walls were mixed with these archaeological remains, but could be excluded from the

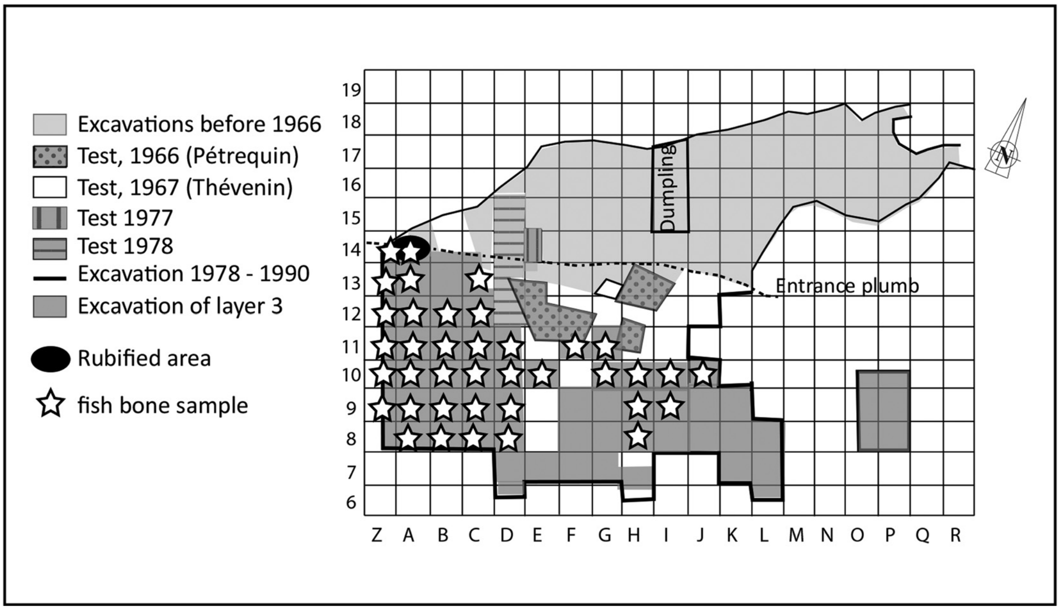

Figure 4: Excavation map of Les Cabônes shelter at Ranchot and sampling location of analysed fish remains from Layer 3; scale: a square represents 1 m^2. CAD A. Bridault, modified from Leduc and Carquigny (Leduc et al., 2015).

sample because of their "fresh" appearance. Because of this, particular attention has been focused on determining the origin – anthropic or otherwise – of the archaeological ichthyofaunal remains.

3.2 Methodology

3.2.1 Taxonomic Identification

Prior to identification, a collection of reference skeletons of 22 freshwater species was created, selected for their historical (Bruslé & Quignard, 2006; Keith & Allardi, 2001) and current (ONEMA, unpublished 2008) presence in the Doubs basin. Only indigenous species were retained. 1–5 specimens were prepared per species for a total of 53 individuals, the vast majority of which were obtained from scientific fishing carried out by the Jura departmental service of the National Office for Water and Aquatic Environments (ONEMA). Three additional species possibly present in the study area at the Lateglacial–Holocene transition complete the list of potential species, but do not appear in the reference collection as it was not possible to obtain adequate specimens. The spectrum of potential species thus amounts to 26 taxa (Table S3), of which no less than 16 belong to the Cyprinidae family.

3.2.1.1 Cyprinidae

The Cyprinidae family is widespread in French rivers and includes an exceptional diversity of species with varied biological and ecological characteristics. Identification at species level is therefore crucial for understanding the fishing economies of ancient societies. Unfortunately, the skeletal morphology of cyprinids is particularly constant from one species to another, and the existence of natural hybrids between species further complicates determination (Libois & Hallet-Libois, 1988). These species are therefore notoriously difficult to distinguish by morphoscopical analysis on archaeological remains. Radiographic analysis can, in some cases, facilitate identification (Desse & Desse, 1976, 1981, 1983), but the small size of the vertebrae found at Ranchot (85% of these elements measure less than 3 mm in diameter) rules out this option.

We therefore limited our identifications to the morphological analysis of the three most diagnostic bone elements present in our material: the pharyngeal arch, the basioccipital, and the second vertebra, applied only to elements over 50% completeness. Identification was based on the protocols and identification keys defined by Le Gall (1982, 1984), and supplemented with subsequently published observations (Bruslé & Quignard, 2006; Keith & Allardi, 2001) and a careful examination of our reference skeletons and individuals from photographic atlases (pharyngeal arch only) (Froese & Pauly, 2021; University of Nottingham, 2021). This allowed us to enrich the published keys with seven new species for the pharyngeal arch and basioccipital, and six new species for the second vertebra. The resulting identification keys are provided in the appendix of this article (Figures S1 and S2).

Due to the fragmented state of the cranial bones, it was however often impossible to observe, on a given bone, every criterion required for identification. A probabilistic approach was therefore implemented: remains not identifiable to species were classified by degree of morphological proximity to different groups of species, according to a resemblance gradient. Data were then summarised by skeletal part, and the three lists of species obtained were compared with each other, in order to obtain a final list of the cyprinid species present, probably present, and possibly present at Ranchot.

3.2.1.2 Salmonidae

Only one indigenous salmonid species,[2] the brown trout (*Salmo trutta*), is currently present in the Doubs basin today. It has, however, been hypothesised that salmon (*Salmo salar*) populations may have found refuge in the Mediterranean at the end of the Last Glacial, which implies the species might have reproduced in our study area. This hypothesis is based on the identification of salmon bone remains at a dozen French, Italian, and Spanish Palaeolithic and Mesolithic sites in the Mediterranean basin (Kettle, Morales-Muñiz, Roselló-Izquierdo, Heinrich, & Vøllestad, 2011), and on the presence of a salmon depiction at the Grande Grotte de Bize, in Aude (Le Gall, 2001). These identifications are controversial, and the remains have been alternatively attributed to trout or to specimens transported from the Atlantic basin (Desse & Desse-Berset, 2002; Desse-Berset, 1994; Kettle et al., 2011; Le Gall, 1999). However, recent ecological niche modelling tends to confirm that conditions in the Mediterranean during the Lateglacial period may have been favourable for the establishment of salmon (Kettle et al., 2011). Salmon could thus be potentially present at Ranchot.

Brown trout and salmon both belong to the *Salmo* genus, and present such skeletal similarities that it is only possible to distinguish them morphologically on two cranial elements (premaxilla and glossohyal) and on the first vertebra (Le Gall, 1982), bones which are almost absent from the Ranchot material. Researchers have adopted different approaches to address this long-standing difficulty: vertebral radiography (Desse & Desse, 1983), geometric morphometry (Guillaud, Cornette, & Béarez, 2016; Huber, Jorgensen, Butler, Baker, & Stevens, 2011; Moss, Judd, & Kemp, 2014), ancient DNA (Moss et al., 2014; Yang, Cannon, & Saunders, 2004). In addition, stable isotopes have been successfully used to differentiate sea-run from landlocked salmon (Sr/Ca ratio; Robinson, Jacobson, Yates, Spiess, & Cowie, 2009) and salmonid migratory ecotypes ($\delta^{13}C$ and $\delta^{15}N$; (Guiry et al., 2020) on archaeological material. For our part, we decided to approach trout/salmon determination by combining vertebral radiographs with ^{13}C and ^{15}N isotope analyses. Salmons are anadromous migrants, which, after spending part of their lives at sea, return to spawn in the river where they were born. As stable carbon and nitrogen isotope analyses can discriminate between marine and freshwater diets, spawning salmon[3] are expected to have a different isotopic signature than non-migratory trout (Bocherens, Polet, & Toussaint, 2007; Drucker & Bocherens, 2004; Robson et al., 2016). Isotopic analyses were conducted on ten salmonid vertebrae at the

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[2] The Arctic char *Salvelinus alpinus*, a species native to the lakes of the Alps and Savoy, is considered to have been introduced in the Jura and the Doubs basin (Machino, 2003). However, we considered that it could have been present in the Doubs Basin during the Mesolithic period.

[3] This is obviously not the case for juvenile salmon that have not yet left their native river.

Laboratory of Isotopic Biogeochemistry of the University of Tübingen, Germany, by D. Drucker. However, the collagen in the remains was too degraded to obtain reliable results, and frontal X-rays of the vertebrae did not yield better results. Given that the presence of salmon in the Doubs basin during the Mesolithic has not been confirmed to date, and that the only two first vertebrae of the *Salmo* sp. of the collection were both attributable to trout, we chose to assign all of the Ranchot salmonid bones to this latter species. However, the presence of salmon remains in our sample cannot be strictly excluded.

3.2.1.3 Other Species

The ranges of potential taxa for the other fish families present in Ranchot are limited to one or two species. Their identification was based on our reference collection and on reference publications (Desse, Desse-Berset, & Rocheteau, 1987, 1990; Le Gall, 1982, 1984; Libois, Hallet, & Rosoux, 1987; Picquès, 1998; Thieren, Wouters, Neer, & Ervynck, 2012).

3.2.2 Quantification

Teleost assemblages are typically quantified using indices initially developed for the study of terrestrial vertebrates. Some of these indices (number of specimens (NSP), number of identified specimens (NISP), Weight, etc.) are applicable to ichthyofaunal assemblages, whereas others, such as the minimum number of individuals (MNI), are more problematic. Indeed, many fish bone assemblages are dominated, sometimes very largely, by vertebral remains, and the most commonly used calculation for the MNI is based on counting the minimum number of elements of the most frequent single skeletal part (lateralised if necessary) in the assemblage. Yet teleost vertebral remains cannot be attributed to a single skeletal part. Not only do vertebra characteristics, which are not very variable along the vertebral column, limit anatomical determination to an anatomical type (“thoracic B”) and not to a precise rank (“12th thoracic vertebra”), but the very number of vertebrae within a type is variable for a given species, as are the numbers of vertebrae between individuals of the same species. However, the MNI is a useful index for understanding assemblages in terms of the acquisition and exploitation of individuals. An eel vertebra, a species with between 110 and 120 vertebrae, will not have the same significance in terms of the number of individuals caught as a roach vertebra, which has between 39 and 41 vertebrae (Froese & Pauly, 2021).

To overcome this difficulty, we chose not to carry out MNI calculations, as these would be based on a very limited number of cranial bones, and would only have yielded very low and biased results. We therefore opted for a weighted number of vertebrae relating all species to the same theoretical standard. This method was initially developed by Sternberg (Sternberg, 1989) and is based, for a given species, on the weighting of the number of its independent vertebrae (centrums with more than 50% preserved, i.e. more than 90% of the vertebrae at Ranchot) by a multiplier index representing the ratio between the average number of vertebrae of the most common species in the assemblage, taken as reference species, and the average number of vertebrae of the examined species. This weighted number of vertebrae, called Corrected Expected Number of Vertebrae (NVcor), makes it possible to establish a direct proportional relationship with the number of captured individuals, while avoiding the MNI. Furthermore, unlike cranial elements, which present inconsistent archaeological preservation depending on species, vertebrae are only slightly affected by differential preservation, and are thus ideal for assessing specific representation in the collection.

At Ranchot, the choice of standard species was complicated by the fact that while cyprinids represented over 96% of the assemblage, only a very small proportion of the remains could be attributed to a specific species. We therefore decided to calculate an average vertebra count for a standard “generic” cyprinid, based on the average of the minimum and maximum vertebra counts observed for each species in the assemblage. The calculated multiplier indices are presented in Supporting Information (Table S4). The abbreviations NV (number of vertebrae over 50% completeness) and NVcor will be used to present the results of the method.

3.2.3 Evaluation of Catch Size and Weight

The so-called continuous growth of teleosts makes it possible to establish a mathematically modelled relationship between bone dimensions and the size and weight of the specimen for most species. In order to reconstruct the size distribution of catches at Ranchot, each single vertebra was determined to the species, classified according to its anatomical type along the rachis, and then measured with an electronic calliper to an accuracy of one hundredth of a millimetre, in keeping with the conventional measurements defined by Morales and Rosenlund (Morales & Rosenlund, 1979). The size and weight of the individual were then estimated by applying linear or polynomial equations defined according to the species, vertebral type, and chosen vertebral measurement. The following references were used: Cravinho (2009) for cyprinids, Desse et al., (1990) for burbot, Desse et al., (1987) for perch, Picquès (1998); Thieren et al., (2012) for eel, and Hajkova, Roche, & Kocian (2003) for trout and grayling. The equations for roach, which is definitely present in the collection, were retained for the estimation of the size and weight of indeterminate cyprinids.

It should be noted that, depending on the species, the entire rachis or only certain sections can be used for these size reconstructions. In the case of eel and burbot, in particular, only the thoracic vertebrae can be used. This implies that catch weights calculated per species cannot be directly compared with each other. Again, a weighting of the results was applied: the total weight obtained for a given species was divided by the number of vertebrae used for the reconstruction, and this ratio was then multiplied by the NV of the species, and then related to the standard species (NVcor) by the use of the previously defined multiplier indices.

The catch weights obtained with this mathematical correction have no tangible certainty. On the other hand, they are proportional to the real weight of the catch, and this is appreciable, even if the latter remains inaccessible to us. The relative contributions of each fish species to the total amount of fish eaten on site, for example, can thus be reliably assessed.

3.2.4 Taphonomic Analysis and Nature of the Assemblage

Before interpreting the results of a faunal analysis in terms of past human behaviour, it is always necessary to ascertain the anthropogenic nature of the collection studied. Indeed, various natural phenomena can also lead to the formation of bone accumulations in rock shelters, namely, the action of fish-eating animal predators and trapping phenomena following a flood (Russ & Jones, 2011). The aim here is thus to compare the characteristics of the archaeological assemblage in terms of specific composition, size of remains, anatomical distribution, and taphonomic status with those typically observed in naturally occurring accumulations. Six piscivorous predators likely to produce rock shelter bone accumulations were identified in the study area, two mammals, the domestic dog *Canis familiaris* and the otter *Lutra lutra*, and four birds, the eagle owl *Bubo bubo*, the barn owl *Tyto alba*, the kingfisher *Alcedo atthis*, and the dipper *Cinclus cinclus*. References for the osteological characteristics of accumulations produced by the first four species existed in the literature and were used here, respectively, (Jones, 1986, 1984; Nicholson, 1993), (Guillaud, Béarez, Denys, & Raimond, 2014; Guillaud, Bearez, Denys, & Raimond, 2017; Nicholson, 2000), (Guillaud, Lebreton, & Béarez, 2018; Laroulandie, 2000; Russ, 2010), and (Broughton, Cannon, Arnold, Bogiatto, & Dalton, 2006). However, to our knowledge, no such references existed for kingfishers and dippers, so we set out to create our own. The bone remains accumulated during a season by a pair of kingfishers breeding in the Meuse basin in Belgium were collected and sieved. A 10 mL sample of sieve refusal was analysed, yielding 5,868 ichthyofaunal bone elements. Specific diagnosis was carried out on the 10 most diagnostic cranial elements of the assemblage, i.e. 552 remains, and the metric was carried out on a random sample of 500 vertebrae. The surface conditions of the latter were also examined in keeping with the work of Butler & Schroeder, 1998; Nicholson, 2000. A summary of the obtained results is presented later in this article. The detailed results of this work will be the subject of a specialist publication, in preparation. On the other hand, no bone from dippers' pellets could be obtained. In view of the very similar biological and ethological characteristics of the dipper to those of the kingfisher (size, feeding and dumping habits, nesting sites, etc.), we considered that the data from the latter species could constitute an acceptable proxy.

In order to undertake a comparison with the data of the accumulating agents, and to gain a better understanding of the taphonomic history of the collection, a survey of the surface conditions of all 9,328 remains of the Ranchot collection was carried out, noting for each the possible presence of pitting, rounding, deformation, and staining, as well as the presence of traces of fire marks and cutting marks, following the descriptions of Asmussen (2009); Butler & Schroeder (1998); Willis, Eren, & Rick (2008); Willis & Boehm (2014); Zohar, Ovadia, & Goren-Inbar (2016).

3.2.5 Seasonality of Catches

Finally, an assessment of fishing seasons was conducted through a skeleto-chronological analysis of a sample of 500 complete vertebrae selected for their excellent state of preservation. The method consists of the observation of growth rings on the articular faces of the vertebrae, which are presented in the form of alternating broad light-coloured annuli, corresponding to the growth of the individual during the warm season, and thin dark bands, corresponding to the cold season. The development stage of the ring on the outer edge of the vertebra allows us to assess the season of death of the individual. The protocol followed was adapted from the recommendations of Desse & Desse-Berset (1992); Le Gall (2003); Meunier (1988); Wheeler & Jones (1989). A comparative reference framework was established by analysing 183 vertebrae from the reference collection from the study area and from known capture seasons. Each archaeological vertebra was then examined three times, at intervals of several months, without taking note of the previously acquired results. Only data from elements that gave consistent results at all three appraisals were retained in our final results.

4 Results

4.1 Taxonomic Composition of the Studied Assemblage

The comparison of the faunal spectra resulting from the two sorting methods (by archaeologists and by the specialist) showed no difference in the representation of the identified species (Frontin, 2017). The results are therefore presented altogether.

Six families and seven species make up the Ranchot Layer 3 spectrum (Table 1). Cyprinid remains are largely predominant (96.6%), of which three species are attested with certainty – common bream, roach, and minnow.

Table 1: Relative abundance (Numer of Identified Specimens -NISP- values) of fish taxa from layer 3 of Les Cabônes

Taxa		NISP	%
Cyprinidae	Cyprinids	8,843	96.56
Abramis brama	Common bream	*18*	
Rutilus rutilus	Roach	*2*	
Phoxinus phoxinus	Minnow	*1*	
Salmo cf. trutta fario	Trout	243	2.65
Thymallus thymallus	Grayling	22	0.24
Lota lota	Burbot	20	0.22
Perca fluviatilis	Perch	23	0.25
Anguilla anguilla	Eel	7	0.08
Total identified		**9,158**	**100**
Unidentified		170	1.82
Total		**9,328**	

The latter were identified using several diagnostic elements (basioccipital, second vertebrae, and cranial elements), only slightly affected by fragmentation.

The other families are represented by only one species each - trout with 243 remains (i.e. 2.6% NISP), grayling, burbot, perch, and eel, with only a few remains each (i.e. less than 1% NISP).

The species making up this group have fairly similar ecological habits. They are mostly gregarious and diurnal, usually live close to the bottom or in open water, and circulate in rather cool, well-oxygenated, and relatively running waters. The eel, the only migratory species, also adapts to these diverse environments. The predominance of cyprinids in the assemblage undoubtedly reflects an environmental reality. It is the most represented family in the environment in terms of number of species (Keith & Allardi, 2001).

4.2 Fragmentation Rate of the Material

The state of fragmentation of the material is estimated using a percentage of completeness assigned to each specimen (Butler & Schroeder, 1998; Nicholson, 2000). For fish vertebrae, which are the most abundant bones in the assemblage, the condition of the centrum is recorded, as spines are often absent in archaeological material. Less than 10% of a sample of 1,184 vertebrae are less than 50% complete (Table 2). Consequently, fragmentation is low and has little effect on identification. On the other hand, the opposite configuration was observed for the pharyngeal arch, an element of a masticatory apparatus in cyprinids, which is quite resistant but often found fragmented. The presence or absence of teeth has not been taken into account, as they are easily detached. Only complete or well-preserved arches, which represent a minority (11 are 50% complete or more), were used in order to produce a reliable diagnosis.

Table 2: Completeness of cyprinid pharyngeal arches and vertebrae; sample of 1,971 layer 3 specimens

	1–24%	25–49%	50–74%	75–100%	*N*
Pharyngeal arch – cyprinids	390	308	68	21	787
Vertebrae – all taxa	58	51	97	978	1,184

4.3 Bone Modifications

Overall, bone surfaces are well preserved and only 13% of the remains show modifications (Table 3). No pitting marks, characteristic of the attack of bone surfaces by digestive juices, were recorded in the assemblage. Bone rounding caused by sediment abrasion is the most common modification found on any bone element, for all species and all sizes of specimens. It is clearly differentiated from rounding due to transit, on account of the absence of the characteristic rounded and glossy appearance of the latter (Llona & Andrews, 1999), which is more often confined to the extremities of elements and does not extend over entire surfaces. Only two types of deformations were found on vertebrae: “compression” and “undulations.” Compression of the articular faces, or even more rarely of the entire vertebral body, was only observed on small specimens ($N = 46$), mainly cyprinids and on a few salmonids. Two vertebrae presented

Table 3: Bone modification values recorded on fish remains in the Ranchot Layer 3 assemblage (complete sample)

	Pitting	Rounding	Deformation	Staining	All	NSP C3
N	0	727	90	368		9,328
% NSP C3	0	7.79	0.96	3.95	12.7	

crushing. The first shows crushing associated with a torsion of the vertebral body and the other displays crushing associated with a deformation of the lateral decoration. All of these deformations are related to traces of mastication described in the literature (Butler & Schroeder, 1998). These bones were chewed, but not ingested; instead, they were spat out after the flesh was consumed. This would therefore indicate that small fish were of dietary interest. The second type of deformation takes the form of “ripples” on the edges of articular faces ($N = 44$). This was only observed on white-coloured bones, which seem to result from heating to very high temperatures (calcination). Finally, changes in bone colour (from black to white) indicate different stages of heating, from carbonisation to calcination. These burn marks are observed on about 4% of the remains of all types of bones, all species, and all sizes of individuals taken together. They are probably not related to the cooking of fish but more logically to the burning of bone waste.

4.4 Representation of Skeletal Parts

The distribution of bones of all taxa into three anatomical units shows that axial skeleton bones are predominant (77.2%), mainly vertebrae. The presence of elements attached to the vertebral column (ribs, Weberian ossicles) is very marginal (Table 4). The appendicular skeleton is only documented by a few fin rays (0.1%). The cranial elements (basioccipital, pharyngeal arches, and teeth) account for 22.7%.

Table 4: Relative abundance (NISP) of fish skeletal elements grouped by anatomic unit (%) – Ranchot Layer 3 assemblage (complete sample, all taxa)

Anat. unit	Element	NISP	%
Head	Basioccipital	17	
	Frontal	1	
	Dentary	1	
	Quadrate	1	
	Premaxilla	1	
	Hyomandibular	1	
	Opercular	1	
	Pharyngeal arch	787	
	Teeth	1,304	
	Total	*2,114*	22.69
Appendicular skeleton	Pterygiophore	5	
	Acanthotriche	1	
	Total	*6*	0.06
Axial skeleton	Vertebrae	7,121	
	Ribs	62	
	Weberian ossicles	13	
	Total	*9,316*	77.22
Scales		3	0.03
	Total identified	*9,319*	*100.00*
	Unidentified element	9	

Only cyprinids are represented by different skeletal parts, including head bones. The perch is only represented by a few cranial remains, while the other species are only represented by their axial skeleton. The vertebrae are significantly more abundant at Les Cabônes (76.4% of NISP) than expected in a complete cyprinid skeleton (23%);[4] head and appendicular skeleton are significantly under-represented ($\chi^2 = 987.81$,

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[4] Observed values from Zohar and Biton (2011), Table 2.

$p < 0.0001$). How can this distribution of anatomical units be interpreted? As no traces of incision were observed on the bones, it is impossible to assess whether the fish were cut up before consumption. The under-representation of the cranial elements could reflect heading before being brought to the site, but in view of the small size of the catches (see below), this seems unlikely. On the other hand, their destruction *in situ* by trampling and/or weathering is plausible. Most of the cranial elements have a lower bone density than post-cranial elements (vertebrae in particular), and are not very resistant to destructive factors (Butler, 1996; Butler & Chatters, 1994). Teeth, the basioccipital, or pharyngeal arch are the most resistant cranial elements, and often survive best in archaeological material (Le Gall, 1982, 1984; Wheeler & Jones, 1989). The differences observed in the degree of fragmentation of pharyngeal arches and (more complete) vertebrae are consistent with this (Table 3). Moreover, the remains of salmonids and thymallids are more degraded here than the remains of other taxa, which is in keeping with taphonomic logic.

At Ranchot, the most resistant elements are thus the most abundant: vertebrae for all species, basioccipitals and pharyngeal arches for cyprinids, and teeth for cyprinids and percids. Consequently, it is likely that the differential representation of the skeletal parts of this assemblage results mainly from the *in situ* post-depositional destruction of preparation and/or consumption waste.

4.5 Characterisation of Captured Individuals

The relative representation of species in terms of the number of individuals caught was not assessed in MNI, due to the characteristics of the assemblage, but through %NVcor (refer methodology section) (Table 5). The method confirms the strong predominance of cyprinids (97%) established on the basis of the count in number of remains. In comparison, the other species, even the best represented species such as trout, represent an anecdotal number of catches.

This very large number of cyprinids is somewhat tempered by the small catch size. The reconstruction of the total length (TL) of individuals on a sample of 185 cyprinid vertebrae shows a distribution of values between 9.9 and 21.1 cm, with a median of 14.5 cm. Small cyprinids therefore appear to have been targeted. According to Fishbase (Luna, 2021b), the common size of a roach is 25 cm, and the average size of common cyprinid species potentially present in the assemblage is around 20 cm. The individuals from Ranchot therefore appear significantly smaller than expected. The size distribution of catches (Figure 5) forms a quasi-symmetrical bell curve, suggesting random recruitment of individuals.

This pattern also seems to be observed among certain rare species in the assemblage. Grayling shows a median size of 17.5 cm at Ranchot, for 17 vertebrae, whereas individuals caught today are commonly 30 cm in length (Luna, 2021c). Due to the small sample size, the distribution is not very precise, but shows a predominance of individuals between 10 and 25 cm, which is consistent with data for cyprinids (Figure 6). Similarly, the four reconstructed remains of burbot show sizes between 17.4 and 25.4 cm, for a median of 20.1 cm, well below the commonly expected size of 40 cm (Luna, 2021a). Finally, the only reconstructed perch remain is also from a small individual, estimated at 14.5 cm for a common species size of 25 cm.

Table 5: Relative abundance of fish taxa represented in the Ranchot Layer 3 assemblage: Nvert = number of vertebrae, NVcor = corrected number of vertebrae

	Nvert	% Nvert	NVcor	% NVcor
Cyprinids	4,997	95.7%	4,997	96.9%
Trout	192	3.7%	140	2.7%
Grayling	19	0.4%	14	0.3%
Burbot	7	0.1%	5	0.1%
Eel	5	0.1%	2	0.0%
Total	*5,220*	*100.0%*	*5,158*	*100.0%*

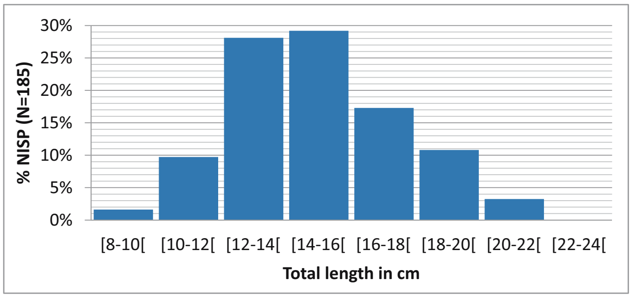

Figure 5: Reconstructed size distribution of cyprinids from layer 3 (*N* = 185 vertebrae).

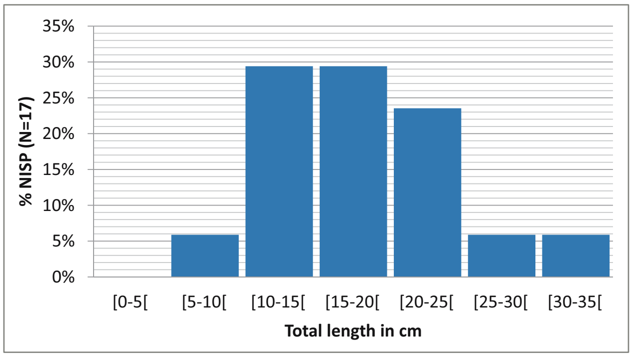

Figure 6: Reconstructed size distribution of grayling from layer 3 (*N* = 17 vertebrae).

Salmonids show a different pattern. On the one hand, reconstructed individuals (165 vertebrae) are larger and much closer to expected sizes, with TLs ranging from 6.6 to 64.2 cm, for a median of 33.5 cm. Today, the common size of a brown trout is 35 cm, even if record-breaking individuals can reach 1 m (Rochefort & Corolla, 2019). The reconstructed individuals are therefore consistent with these observations. On the other hand, size distribution here is anything but symmetrical (Figure 7). The curve gradually increases from 5 to 40 cm, reaches a mode in the [35–40 cm] class, which alone accounts for 22% of the catches, and then falls sharply beyond that, with only 6% of the catches measuring between 40 and 45 cm. There thus seems to be a threshold effect limiting the presence of large catches.

The eel could show a similar pattern. The sizes of the only two reconstructed individuals are 40.5 and 41.5 cm, in line with the common size of the species, 40 cm (Froese, 2021).

Based on data obtained for each species, we can also propose a reconstruction of catch sizes for the collection as a whole. To do this, we divided the NVcor of each species into size classes proportional to

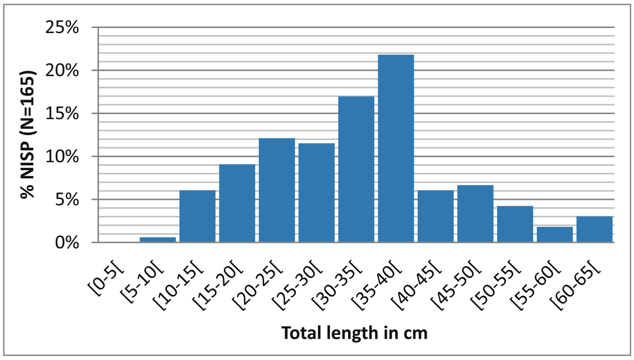

Figure 7: Reconstructed size distribution of salmonids from layer 3 (*N* = 165 vertebrae).

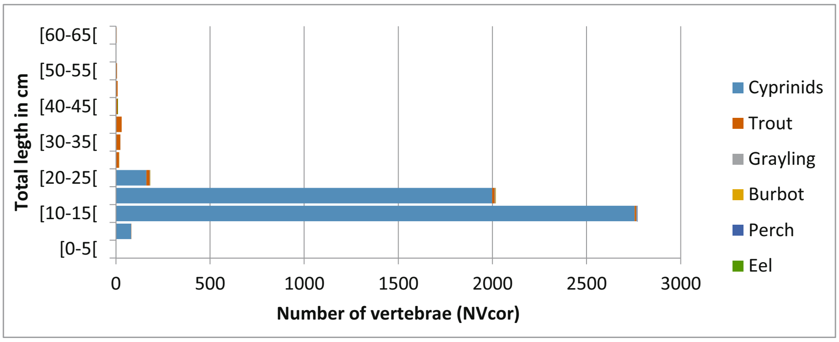

Figure 8: Projected size distribution of reconstructed fish sizes, all taxa, from layer 3, *N* = 5,158 (size distribution patterns observed for each species have been applied to total corrected number of vertebrae from the species).

those found in the samples used for size estimates, and then added them together. The resulting projection, shown below in Figure 8, clearly illustrates the predominance of small cyprinids in the assemblage: almost 94.5% of the catches are less than 20 cm in total length, 99.3% of which are cyprinids. Medium to large fish are thus very poorly represented, with only 2.1% of catches exceeding 25 cm, 95.4% of which are salmonids.

4.6 Food Contribution of Species

Using the measurements taken to reproduce catch size, it is also possible, on the same sample, to estimate weight. We were thus in a position to calculate an average specimen weight for each species in the assemblage, varying between 35.4 g for cyprinids and 495.7 g for trout, as presented in Table 6. In order to assess the relative contribution of species to the diet of the Ranchot occupants, these values were then multiplied by the NVcor of each species. The results of this transformation being strictly proportionate to the number of captured individuals, they allow the unbiased estimation of the part of each species in the fish eaten on site. The exact figures for the weight provided by each species are nonetheless theoretical constructs, and must not be taken at face value.

The results show that although cyprinids still dominate, trout made a significant contribution to the diet, accounting for more than a quarter (28%) of the consumed fish, despite the small number of remains (2.71% of NVcor).

Table 6: Estimated relative amount of each fish species in kilograms based on corrected number of vertebrae (NVcor); average weight of specimens calculated on vertebral measurements (samples in Figures 5–7)

	Average weight (g)	NVcor	% NVcor	Weight (kg)	Weight (%)
Cyprinids	35.4	4,997	96.88%	177.14	71.3
Trout	495.7	140	2.71%	69.39	28.0
Grayling	82.9	14	0.27%	1.16	0.5
Burbot	65.6	5	0.10%	0.33	0.1
Eel	124.0	2	0.04%	0.25	0.1
Total		*5,158*	*1*	*248.26*	*100.0*

4.7 Fishing Seasonality

Due to the very small size and state of preservation of remains, only 82 vertebrae had the required characteristics for a skeletal-chronological analysis of the season of capture. Of these, only 57 (70%) provided the three concordant readings required to ensure analysis reliability (sample details in Supporting

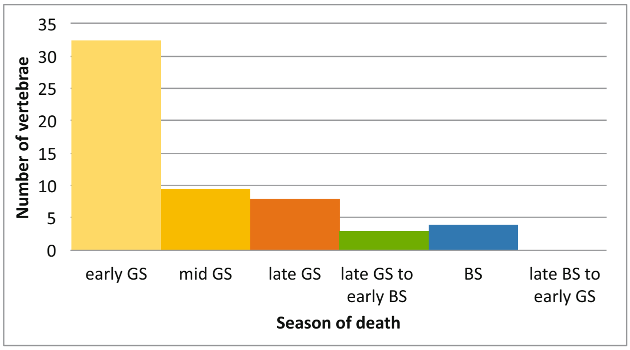

Figure 9: Distribution of identified season of death on a sample of 57 fish vertebrae from layer 3; GS = good season, BS = bad season.

Information, Table S4). Our study of catch seasonality is therefore based on a relatively limited sample. The results nevertheless show a strong structuring of the data (Figure 9): more than 57% of the catches occurred at the beginning of the good season. The number of catches then decreased rapidly as the summer season progressed, and only 7% of individuals appear to have been caught in the bad season. Thus, although fish could be caught all year round in Ranchot, it seems that this resource was mainly exploited in early spring, a period of food shortage known to be difficult and poor in resources.

No structuring of the data by species was observed.

5 Discussion

5.1 Origin of the Bone Accumulation

The question of the origin of the bone accumulation is central to any ichthyofaunal study, but was particularly central at Ranchot. The observation of present-day kingfisher pellets during the excavation immediately raised the possibility of a natural accumulator, and the unusually small size of the remains did not help to dismiss this hypothesis.

Specific attention was therefore paid to this problem during our study, in particular, through the analysis of a sample of remains from kingfisher pellets, leading to a better characterisation of this type of accumulation. A summary of the main results of our observations is presented in Table 7 below.

Table 7: Criteria for identifying a Kingfisher pellets assemblage

Criteria	Kingfisher accumulation characteristics
Skeletal part representation	Presence of complete skeleton, body-part representation similar to that of complete fish
Species identification	Broad spectrum, variable with species availability opportunistic fishing, favouring gregarious, benthic, and crepuscular/nocturnal species
Size of the remains	Centrum diameter always under 2 mm Range 0.41–1.94 mm; average 1.16 mm; 77.4% of remains between 0.8 and 1.4 mm
Prey size reconstruction (Cyprinids)	Range 5.4–13.5 cm TL; average 9.2 cm Most preys under 10 cm TL, but variable according to species (head diameter and body shape)
Vertebrae completeness	Excellent preservation, minimal breakage >90% of fully complete remains
Surface modifications	No modification of bone surfaces: no pitting, staining, rounding, or visible deformation of bones

Fortunately, these data exclude the intervention of this accumulating agent with almost complete certainty. If we consider the Ranchot assemblage as a whole, it is clear that all the larger individuals, with vertebrae larger than 2 mm in diameter and/or with a reconstructed size larger than 15 cm, could not have been the prey of such a small bird. However, a mixture of kingfisher regurgitation with another accumulation process remains possible, and we thus carried out a more detailed comparison between the characteristics of the cyprinids from Ranchot (which overwhelmingly dominate the smaller remains) and those of the fish consumed by the kingfisher. This comparison shows that although the cyprinid remains from Ranchot are small, their average diameter is significantly greater than those from the kingfisher pellets (Student's $t = 8.42$; $p \ll 0.001$), and it is statistically unlikely that they are of the same origin. Above all, the reconstruction of sizes based on this sample shows that the vast majority of cyprinids captured at Ranchot, with an average size of 14.9 cm, exceed the consumption capacity of the kingfisher. Out of a total of 185 fish for which size could be estimated, all but one[5] exceed 10 cm, the maximum size of prey listed in the literature (Hallet, 1985; Libois & Hallet-Libois, 1995), and 61.4% exceed 13.5 cm, the maximum size observed in the reference assemblage. Finally, the unimodal, symmetrical bell-shaped size distribution curve of the Ranchot cyprinids (Figure 5) is more suggestive of a single origin of the population than a mixture of two populations resulting from distinct selection processes.

It is also possible to exclude most of the other potential accumulative agents of bone concentrations. Relatively few piscivorous predators can be found in caves and rock shelters, and mammals give rise to very different assemblages from those of Les Cabônes. The catch size observed at Ranchot is not incompatible with otter habits (typically from 10 to 30 g for cyprinids and percids (~10–20 cm), and from 100 to 200 g for salmonids (~30 cm) Guillaud et al., 2014), but the remains consumed by this species are significantly marked by digestive processes, with 90% of the remains bearing acid attack marks, resulting in polishing, pitting or surface dissolution, and tooth marks and deformations affecting 3% of the remains (Guillaud et al., 2014). As no digestion marks are observed at Les Cabônes, otter action can therefore be excluded. The dog produces assemblages that are even more marked by taphonomic degradation, with very intense fragmentation of remains, and often unrecognisable surviving bones, reduced to corroded fragments and marked by traces of digestion (Jones, 1986, 1984; Nicholson, 1993). Again, this appears to be incompatible with the state of preservation of the Ranchot remains.

Fish bone assemblages generated by the Eurasian eagle-owl (*Bubo bubo*) similarly display features inconsistent with that of the Ranchot assemblage. First, the bones ingested by owls are marked by digestive processes, though to a lesser extent than by mammals: about 9% of the remains display moderate to intense digestive alterations (Guillaud et al., 2018). Second, the eagle owl tends to select prey significantly larger than those found in our archaeological assemblage: Guillaud notes that the predominant weight class in the eagle owl sample included fish estimated between 200 and 300 g (Guillaud et al., 2018), whereas the average weight in the Cabônes sample was no higher than 48 g. Finally, no piscivorous specialisation of the eagle owl has to our knowledge been described (Russ, 2010), and assemblages generated by the species should therefore include many remains of birds and small mammals, mostly absent from the archaeological sample.

Finally, there remains the case of the barn owl (*Tyto alba*). This nocturnal raptor has an opportunistic diet that can in specific circumstances become primarily piscivorous. The bird shows a general preference for prey weighing 10 and 70 g (Broughton et al., 2006), consistent with most of the fish consumed at Ranchot. Pitting and deformations are observed on less than 5% of the remains, but 19% show traces of rounding, which has not been observed in the archaeological collection. Moreover, the piscivorous specialisation of the barn owl has only been recorded in North America, in the case of the seasonal abundance of dead or dying fish stranded in the pools of an intermittent stream (Broughton et al., 2006). These environmental conditions are far different from those found on the banks of the Doubs, a deep and wide permanent river, and the estimated season of capture (early spring) is similarly conflicting. Therefore, a broader-

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[5] Estimated at 9.9 cm.

spectrum diet is to be expected for the barn owl, and, as for the eagle owl, the associated presence of small mammals should be expected were the accumulation produced by this species.

The inconsistencies between fish bone assemblages produced by animal accumulators and that of Les Cabônes appear therefore significant enough to exclude an animal origin of the archaeological collection. A natural origin can likewise be rejected: the stratigraphy of the shelter shows almost no influence of the Doubs River in the formation of the sediments of the Mesolithic levels having yielded fish remains. It seems therefore difficult to argue in favour of natural inputs of fish carried into the shelter during seasonal river flooding. Less importantly, the presence of the bream possibly upstream of its natural habitat also contradicts a natural fluvial origin. Finally, the size distribution pattern of salmonids, displaying a relatively brutal threshold for fish over 40 cm, appears inconsistent with a natural accumulation.

We therefore consider that an anthropogenic origin of the archaeological fish assemblage of Ranchot can be accepted, even though a marginal contribution by other accumulators cannot be ruled out entirely.

The spatial distribution analysis of fish bones shows a fairly homogeneous overall distribution of skeletal elements with, however, denser accumulation zones (Z-A-B 10–12, C10, H-I-J 8–10) coinciding with the preferential accumulation zones of lithic remains (Roué, 2000). Nevertheless, it is noteworthy that Salmonidae remains seem to be preferentially discarded near the hearth. Masticated and burnt remains are also preferentially located near the hearth.

5.2 Prey Acquisition

5.2.1 Fishing Environments

Fish are particularly sensitive to the physico-chemical and biological conditions of their living environment, and each species has specific environmental requirements. The slightest variation in these conditions influences its presence and demography in a given place. In a river environment, we observe a longitudinal organisation from the source to the mouth, in zones associating environmental conditions and well-defined fish populations. The most commonly used typology, proposed by Huet in 1949, defines five ecological zones with their associated species (Huet, 1949). Based on this range of species, it is thus possible to evaluate the capture zone(s) of individuals with an ichthyofaunal spectrum.

We thus plotted in Figure 10 the ecological preferences of the fish species identified at the site on the ecological zones of the Doubs (terminal zone not represented) (Verneaux, 1973).

The first observation is that, according to these data, it is highly unlikely that all the fish in the shelter were caught in a single location. The requirements of minnow and brown trout are incompatible with those

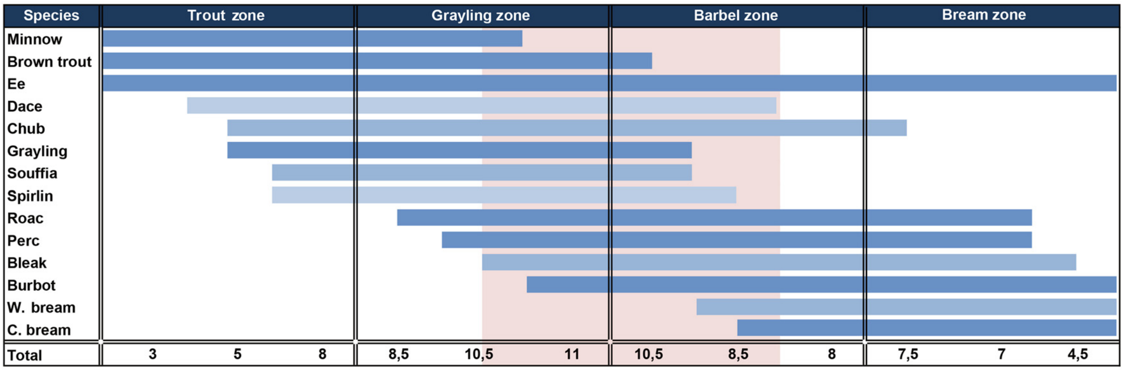

Figure 10: Ecological requirements of the fish species identified at Ranchot, plotted along the longitudinal zonation defined by Huet (1949), from upstream (Trout zone) to downstream (Bream zone). Total: number of Ranchot species present in sub-zone; pink area: minimal river area including all of the species documented at Ranchot.

of the two breams in terms of current, oxygen, and temperature. Fishing therefore seems to have been organised into river sections, with catches in different places. At the very least, for the capture of all the identified species, the fished area had to cover the downstream half of the grayling area and the upstream two-thirds of the barbel area. In addition, incursions into more distant fishing grounds cannot be excluded. Nevertheless, species composition remains consistent: 11 of the 14 determined species are typically present at the transition between the grayling and barbel zones, which could indicate a preferential fishing area.

The species identified in the corpus, and in particular cyprinids, generally prefer shallow waters with moderate currents. These species are therefore mainly found on the banks of the main channel or in secondary arms. Only grayling and the perch show divergent ecological preferences, favouring, respectively, the benthic zone of the main channel and slow-moving backwaters. These two minority species in the corpus may however move to secondary arms during the reproduction period. This points to the existence of a preferential catching environment for the whole assemblage.

5.2.2 Fishing Techniques

In France, during the Mesolithic, "obvious" fishing apparatus is rare. In continental and fluvial environments, only the "Haut-des-Nachères" deposit at Noyen-sur-Seine yielded exceptionally well-preserved remains of basketry traps made of privet and a wickerwork container in an anaerobic wetland environment (Mordant et al., 2013). In the European Mesolithic, numerous evidence of passive fishing securely dated exists. Fish traps, stakes, weirs, and wattle fences are recorded from Late Mesolithic contexts (e.g. McQuade and O'Donnell, 2007; Koivisto, 2017). At Ranchot, no such xylological remains were preserved, on account of deposition and conservation conditions, and the use of fishing tackle remains hypothetical. The Ranchot site did not yield any deer antler harpoons either, although these are known regionally during the Late Mesolithic (Cupillard, 1998a,c; Marquebielle, 2014). Some authors have suggested that certain types of microliths and armatures were used as arrow barbs for fishing (Rozoy, 1978), but there is no evidence for this at Ranchot.

The results of the ichthyological analysis described above shed light on the different fishing methods that may have been used at Ranchot. The use of traps (or nets) designed to capture small individuals is the most likely fishing technique to explain the observed cyprinid size (normal distribution around 14.5 cm). We cannot rule out the possibility that the graylings and burbots of the assemblage, which are slightly larger but more elongated than cyprinids, could have been caught in these same traps. Such traps could have been set in more or less deep water in diverse environments and could have captured both diurnal (bream, roach, minnow, and grayling) and nocturnal and crepuscular species (burbot).

However, larger trout could only have been caught with different traps and adapted baits, or by active fishing with harpoons, bows or arrows, or even by hand, which only targets specific individuals.

6 Conclusion

At Les Cabônes, small fish (around 15 cm) make up the majority of the catch, and provided food throughout the year, particularly during the lean season. Fishing seems to have been optimised to maximise yield-effort ratios. Passive fishing equipment could have captured large numbers of specimens "in shallow areas of rivers, perhaps those backwaters that gradually formed in large valleys in the early Holocene" (Marchand, 2020, p. 341, after Frontin, 2017, p. 274). There seems to have been little or no preparatory cutting. The food intake, which could have reached 258 kg of fish (mainly cyprinids and trout), at least, appears minor compared to food from ungulate hunting. Indeed, a minimum of 50 wild boar, 110 red deer, and 31 roe deer have been estimated from dental remains in layer 3 (Leduc et al., 2015; Trémolières, 2020). As these remains have been collected over the whole site, while fish remains have only been sampled from a selected number of contexts, a direct comparison of meat weight would not be relevant. Nevertheless, fishing in Ranchot could represent a key activity in the economy of the group(s), as it could be practised for most of the year, on a small scale, individually or by part of the group, in most river areas, and unlike hunting, could be combined with other activities.

No fish preparation activities, such as heading or smoking for later consumption, were detected by our analysis. The very small amount of burnt bones found may indicate that the fish were eaten raw, stewed, or boiled, as soon as they were captured. “Immediate” consumption of mostly small catches on the site would explain the presence of abundant vertebrae scattered over the entire studied surface, especially around the hearth.

The fish bone assemblage from Les Cabônes is remarkable, due to both the quantity of remains and the quality of the information it has yielded. Indeed, fishing does not seem to have been practised with the same intensity at all the sites in the Doubs River catchment (Abri Gigot 1, La Roche aux Pêcheurs, Rochedane, cf. Table S1) (Frontin, 2017). However, in the absence of a standardised protocol for the systematic collection of bones and the same volume of sediment study for all sites, this is difficult to demonstrate. But as we noted in the introduction, this is a pattern also observed at sites in the valleys of northern France. This suggests that the archaeological visibility of this activity is to some extent related to the settlement-system and/or site-function.

Interestingly, a fishing pattern remarkably similar to that at Les Cabônes is found at Galgenbühel in the Adige valley (south Tyrol, Italy), during the first two phases of the Sauveterrian occupation of the site, dated from 8600 to 7700 cal. BC: a fish spectrum dominated by cyprinids with a variety of species that live in slack and slow-moving streams; a similar dichotomy in the size of the catches, i.e. an abundance of medium to small sized individuals, and, for one species, larger individuals, all of which implies the use of non-selective passive fishing techniques (Wierer et al., 2018).

Thus, whether in the Adige, Doubs, or Seine valleys, analyses of the largest Mesolithic fish bone assemblages from inland sites provide converging information, namely, the capture of large quantities of small fish, through the use of traps set in areas adjacent to the main channel, and/or highly productive habitats. Moreover, in each of these sites, the exploitation of other wetland resources is well documented: pond turtle (*Emys orbicularis*) and beaver (*Castor fiber*), plus otter (*Lutra lutra*), and waterfowl in Noyen and Galgenbühel (Leduc et al., 2015; Marinval-Vigne et al., 1989; Wierer et al., 2018).

We interpret these results as evidence of Mesolithic occupations focused towards the exploitation of resource-rich wetlands. Such micro-settings offer the possibility of an embedded procurement of terrestrial and aquatic resources within a relatively circumscribed territory. If sites such as Les Cabônes were used repeatedly over many years, this may explain why they are large in size, include large assemblages of lithic and organic remains and display multi-seasonal signatures. It remains to be established whether there is a causal link between increasing dwelling sizes during some periods of the Mesolithic, multi-seasonal occupation, increased dependence on aquatic resources, and decreased group mobility.

The current state of the data does not yet allow us to assess whether the diet of Mesolithic groups from this period in the northern half of France is marked by an increased consumption of aquatic resources. Investigating subsistence strategies requires us to keep working at several scales of resolution and to enrich our database with complementary methods.

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