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Review

Is vertebral form a valid species-specific indicator for salmonids? The discrimination rate of trout and Atlantic salmon from archaeological to modern times

Emilie Guillaud [a, b, *], Raphaël Cornette [c, d], Philippe Béarez [a]

[a] UMR 7209, CNRS/MNHN "Archéozoologie, archéobotanique: sociétés, pratiques et environnement", Muséum national d'Histoire naturelle, Département Écologie et Gestion de la Biodiversité (EGB), 55 rue Buffon, CP 56, 75005 Paris, France
[b] UMR 7208, CNRS/MNHN/IRD/UPMC, Muséum national d'Histoire naturelle, Département Milieux et Peuplements Aquatiques (DMPA), 7 rue Cuvier, 75231 Paris Cedex 05, France
[c] UMR 7205, CNRS/MNHN/UPMC/EPHE, "Institut de Systématique, Évolution et Biodiversité" (ISYEB), Muséum national d'Histoire naturelle, Département Systématique et Évolution, 45 rue Buffon, 75005 Paris, France
[d] UMS 2700, "Outils et méthodes de la systématique intégrative", Muséum national d'Histoire naturelle, Département Systématique et Evolution, 57 rue Cuvier, 75231 Paris Cedex 05, France

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ABSTRACT

Salmonids, especially Atlantic salmon (*Salmo salar*) and trout (*Salmo trutta* sspp.), are ubiquitous throughout the European Upper Paleolithic archaeological context; however, as these species are morphologically similar, species identification can be difficult. Here we present (I) a species classification rate for the two species using modern reference specimens, and (II) an application on archaeological vertebrae of *Salmo* sp. recovered from the cave of Le Taillis des Coteaux (Vienne, France). This cave contains a rich archaeological sequence with an exceptionally well preserved stratigraphy, encompassing the Upper Paleolithic from the Aurignacian to the Middle Magdalenian. To discriminate both species, we used a geometric morphometric approach to analyse vertebral form using landmarks and sliding semi-landmarks, coupled with k-Nearest Neighbour classification method. Other quantitative approaches like Principal Component Analyses exist, but the k-NN method increases the power of these analyses. Linear Discriminant Analysis was also used; however, the k-NN method provided better results. This study presents the initial results of geometric morphometric discrimination of European salmonid bones. The success rate of reassigning these to the modern reference specimens ranged from 84 to 100%, depending on the vertebrae studied, with the data indicating that *S. trutta* sspp. were the dominant taxon on site. This study provides clear evidence that vertebrae morphology can be used to differentiate salmonid species, allowing archaeological specimens, even partially broken, to be identified.

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* Corresponding author. UMR 7209, CNRS/MNHN "Archéozoologie, archéobotanique: sociétés, pratiques et environnement", Muséum national d'Histoire naturelle, Département Écologie et Gestion de la Biodiversité (EGB), 55 rue Buffon, CP 56, 75005 Paris, France.
E-mail addresses: emilie.guillaud@edu.mnhn.fr (E. Guillaud), cornette@mnhn.fr (R. Cornette), bearez@mnhn.fr (P. Béarez).

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1. Introduction

In Western European Late Pleistocene sites fish remains are abundant, especially from the Magdalenian period (e.g. Cleyet-Merle, 1990; Le Gall, 1999). However, most remains consist of vertebrae, which make species identification difficult because of their closely related form and the lack of quantitative morphological studies (e.g. Desse and Desse, 1976; Meunier and Desse, 1978). Species identification is important as it allows us to understand fish consumption by hunter-gatherers during the Upper Paleolithic period. It also reveals important information about the rivers' physiography, water temperature and the distribution range of fish in the past. The Late Pleistocene is characterized by an alternating pattern of glacial and interglacial periods (Bond et al., 1993), including the Last Glacial Maximum (LGM 22000-18000 BP), during which the mean sea level was approximately 110–120 m lower than at present. The successive warmer period, the Tardiglacial, allowed fish (and humans) to come back from their refugia. As different fish species require particular temperature and oxygen levels (Jonsson and Jonsson, 2009; Elliott and Elliott, 2010; Tissot and Souchon, 2010), and because some of them migrate at distinct times of year, identified fish remains from Paleolithic cave sites are excellent climate and season markers.

During the Magdalenian period, salmonids, particularly Atlantic salmon (*Salmo salar*) and trout (*Salmo trutta* sspp.) are the most frequently recorded species in archaeological assemblages (Le Gall, 1999, 2008). For this reason, we chose to focus on these particular species, using morphology, in order to address important questions in archaeology, biogeography and salmon conservation.

Today, salmonids are an important group of both freshwater and anadromous fish distributed throughout the Holarctic region (Sanford, 2000). There are three recognized subfamilies: Salmoninae, Thymalllinae and Coregoninae. The Salmoninae comprises approximately 30 species in seven genera (Nelson, 2006). In Western Europe, the best studied species belong to the genus *Salmo*, represented in France by the Atlantic salmon (*S. salar*), the brown trout (*S. trutta fario*) and the sea trout (*S. trutta trutta*) (Charles et al., 2005; Keith et al., 2011). As a general practice among European archaeozoology, the size of vertebra is often the criterion used to separate salmon (when large) from brown trout (when small), overlooking the possible presence of sea-run trout. However, since sea trout is anadromous[1] and can grow almost as large as salmon, we chose to perform our study with the two sea-run salmonid form.

[1] Fish are born in freshwater, migrating to the ocean as juveniles where they grow into adults, before migrating back to freshwater to spawn.

Atlantic salmon occurs naturally along the coasts of the North Atlantic basin and European Arctic. It is an anadromous fish that spawns in rivers during autumn and winter. Juveniles spend between one and eight years in freshwater before reaching the sea, depending on latitude (Heland and Dumas, 1994). The marine phase lasts one to three years, after which the fish return to their natal rivers to spawn: a behaviour called “homing”. The spawners that survive (1–2%) may return, once or twice, back to sea. Both within and among populations, salmon and sea trout display variability in their length of stay in a freshwater habitat, while brown trout do not migrate and exhibit a more territorial behaviour.

During their freshwater residence, salmonids require well-oxygenated water and a specific temperature to grow and survive (Jonsson and Jonsson, 2009; Elliott and Elliott, 2010); both these parameters also determine their spatial distribution. Today, they are usually found in rivers where temperatures rise above 10 °C but do not exceed 20 °C (Keith et al., 2011).

The morphological similarity of salmonid vertebrae limits species identification (Desse, 1984; Butler and Chatters, 1994). Several criteria have been used to discriminate species and anadromous *vs. freshwater* resident populations in archaeological remains based on external morphological features (Desse and Desse, 1976): strontium/calcium ratios (Robinson et al., 2009) and X-ray of vertebrae (Desse, 1984); however, these methods are often unreliable or incomplete. With regards to morphological criteria, the lateral sides of the vertebrae appear less concave in *S. salar* than in *S. trutta* sspp. (but this is a continuous criteria with a high variability of form), and the vertebrae morphology varies along the column (Morales-Muñiz, 1984). As a consequence, distinguishing between modern salmonid species can be problematic using these criteria, and even more challenging with degraded bones. X-ray studies have provided positive results; however, different stages of growth must be taken into account and as X-ray profiles evolve over time, and are affected during migration, interpretation is problematic (Meunier and Desse, 1978; Cannon and Yang, 2006). Morphometric studies have also delivered promising results using ratios on distance (Moss et al., 2014), using previous geometric morphometric studies as suggested by Huber et al. (2011).

Recently, several cutting-edge projects have successfully extracted ancient DNA from salmonid remains in the Pacific Northwest of North America (Yang et al., 2004; Speller et al., 2005; Moss et al., 2014). Yang et al. (2004) are one of the few who have succeeded to extract DNA from ancient Pacific salmon vertebrae dating to 7000–2000 BP from archaeological sites in this region. They were able to distinguish four species: coho (*Oncorhynchus kisutch*), sockeye (*Oncorhynchus nerka*), pink (*Oncorhynchus gorbuscha*) and chum salmon (*Oncorhynchus keta*). However, this