Tracing Seaweed as Food and Fodder in Archaeology: A Review of Current Methods

Magdalena Blanz [a, b, c] *, Marie Balasse [d], Ingrid Mainland [e]
[a]*Austrian Academy of Sciences, Austrian Archaeological Institute, Vienna, Austria*
[b]*Vienna Institute for Archaeological Science (VIAS), University of Vienna, Vienna, Austria*
[c]*Human Evolution and Archaeological Sciences Research Network (HEAS), Vienna, Austria*
[d]*UMR 7209 Bioarchéologie, Interactions Sociétés environnements, CNRS/ MNHN Paris, France*
[e]*Archaeology Institute, University of the Highlands and Islands (UHI), Orkney College, Kirkwall, UK*

*Corresponding author: Magdalena.Blanz@univie.ac.at

This manuscript was published by the *Journal of Island and Coastal Archaeology* on 1st April 2026, available at doi.org/10.1080/15564894.2025.2576583.

Abstract

Seaweed is often overlooked as a potential food source for animals and humans in archaeological interpretations. However, plentiful historical and ecological evidence attests to seaweed consumption by humans and domesticated and wild animals (e.g. sheep, cattle, deer, coyotes). This literature review provides a summary of the use of seaweed as food and fodder by humans and terrestrial mammals more generally, and how seaweed consumption may be detected in archaeological contexts. It gives a detailed overview of currently available methods to identify seaweed consumption, including seaweed macrofossils and seaweed proxies such as small shells (which can indicate the past presence of seaweed at a site), and dental microwear and markers in dental calculus, as well as isotope ratios of skeletal material (which can give direct evidence of seaweed consumption). Several case studies are included to illustrate the implications of seaweed consumption by humans and animals in archaeological contexts, examining questions of food insecurity and adaptations to coastal environments.

Keywords:
kelp, palaeodietary reconstruction, marine foods, animal husbandry, fodder

1 Introduction

The consumption of seaweed, both past and present, by humans and animals is widely documented in coastal areas around the globe through historical, ethnographical, and ecological evidence (Abbott and Williamson 1996; Dumilag et al. 2022; Landsborough 1857; Martin 1716; Moore 2002; Newton 1951; Thurstan et al. 2018; Turner 2003); Fig. 1). Growing wild and requiring little labour to harvest, seaweeds provide fresh food even in the midst of winter and during droughts, when terrestrial resources are sparse. The potential importance of seaweed to past human and animal diets was first noted in an archaeological context over forty years ago (Aaronson, 1986; Bell, 1981).

Despite this, seaweed is generally an after-thought in archaeological dietary interpretations, following on from discussions of marine fish, marine mammals, and marine molluscs – if seaweed is even referenced at all. This is in part because the consumption of seaweed is difficult to identify in the archaeological record, since seaweed consumption is not evidenced by a food waste resistant to decomposition (e.g. bones, mollusc shells). Additionally, cases of seaweed preservation are rare, and its presence alone does not necessarily indicate that it was consumed due to its plurality of uses, ranging from insulation material to fuel to fertiliser (Fenton, 1997; Kenicer et al., 2000; Martin, 1716; Mooney, 2021; Sitzia et al., 2023). Combined with a general lack of seaweed in many western diets today, there is often little awareness that seaweed should be considered a possible food source for past humans and animals.

The aim of this review is to provide a practical guide for future research into the role of seaweed in past subsistence strategies, to provide an overview of the current state of research, and to highlight where additional information may be found. The review firstly provides a brief overview of seaweed as food and fodder around the world, with a focus on seaweed consumption by non-human terrestrial animals in Northern Europe. Additionally, health effects seaweed consumption may have on consumers are summarised. This is followed by an in-depth review of methods to identify seaweed consumption by terrestrial mammals (including humans) in archaeological contexts, encompassing the study of seaweed macrofossils and microfossils, as well as the analysis of dental microwear, biomarkers in dental calculus, and chemical and isotopic analyses of skeletal remains. The review then briefly explores the implications that seaweed consumption by humans and animals can have for archaeological interpretations worldwide.

2 Seaweed as Food and Fodder

2.1 What are Seaweeds?

Seaweeds are marine macroalgae, i.e. multicellular macroscopic algae. They are divided into green, red and brown algae according to their evolutionary pathway (rather than their colour). However, brown seaweeds are only distantly related to red and green seaweeds, which are more closely related to higher plants. The term seaweed is therefore not a biological classification, but rather used for convenience to group all types of marine macroalgae together. Seaweeds are non-vascular and generally have holdfasts instead of roots to fasten themselves to a hard substrate (e.g. rocks, other seaweeds, shells of live molluscs). They include kelp (a group of brown seaweeds, mainly Laminariales) and wrack (a term referring either to any seaweed washed up on the shore, or to certain brown seaweeds of the order Fucales), but exclude seagrass and samphire, which are vascular, true plants with roots, stems and leaves. Being neither true plants nor animals, but algae, seaweeds have so far received scattered attention across different archaeological disciplines, instead of being the focus of a single field.

Fig. 1 *Left: Seaweed-eating sheep on the island of North Ronaldsay, Orkney Islands, Scotland and right: seaweed-eating goats on the Isle of Mull, Inner Hebrides, Scotland. Pictures taken by Ingrid Mainland (left) and Jasmijn Sybenga (right), reproduced here with permission.*

2.2 Seaweed Consumption by Animals

A wide range of terrestrial mammals have been observed to consume seaweed, including sheep, cattle, horses, pigs, goats, but also various types of deer, elk, foxes, hares, bears and even coyotes (reviewed in Carlton and Hodder 2003; Moore 2002;). Seaweed foraging by terrestrial animals is likely widespread globally in areas where seaweed is available, but it is underrecognized and underreported (with most published mentions of visual observations occurring as incidental remarks) due to being rarely studied directly (Carlton and Hodder, 2003).

2.2.1 Seaweed consumption in cold environments

Although some animals have been observed to consume seaweed throughout the year (e.g. cattle in New Zealand, Kurrajong 1941; and North Ronaldsay sheep on the Orkney Islands, Scotland, H. R. Hansen, Hector, and Feldmann 2003; Fig. 1), most reports of seaweed-foraging are from Northern Europe in winter and spring (e.g. B. B. Hansen and Aanes 2012; Martin 1716;). This is likely a consequence of the shorter growing season in northern latitudes limiting terrestrial resource availability. For example, sheep in Iceland were reported to commonly feed solely on seaweed for 6-8 weeks (sometimes up to 18 weeks) a year, when terrestrial resources are covered by ice and snow (Hallsson, 1964). Historical and modern accounts have described animals eating seaweed in cold environments as a means of survival (Hansen and Aanes, 2012; Martin, 1716). However, in other cases animals are described to thrive, and even fatten on a winter diet of seaweed (e.g. Baldwin 2000; H. R. Hansen, Hector, and Feldmann 2003; Landsborough 1857; Martin 1716). Seaweed therefore serves as a reliable food source in coastal areas around the year, being available independently of terrestrial resources, which are more affected by ice and snow.

2.2.2 Seaweed consumption in hot/dry environments

Feral rabbits were observed to consume seaweed particularly in dry summers in South Africa, and similarly, porcupines have also been observed to consume seaweed on the country's west coast (Moore, 2002). However, in contrast to the many reports of seaweed consumption in Northern European winters, few other observations of seaweed consumption by terrestrial mammals have been made in hot or dry areas, where seaweed could fill a similar gap when terrestrial resources are scarce (droughts, dry seasons). It is unclear whether this is due to an absence of seaweed consumption in hot/dry environments, or bias in the literature (cf. Carlton and Hodder 2003).

2.2.3 Adaptations to seaweed consumption

In several studies red deer, sheep and cattle and were reported to have adapted their activity patterns to follow the tide times (as opposed to day and night), with animals observing the shore and moving to the seaweed as soon as the tide is out far enough (Conradt 2000; Hall 1975; Paterson and Coleman 1982; and own observations). Some animals even showed an awareness of the tidal rhythm when the sea was out of sight (Martin, 1716). In red deer and sheep, seaweed consumption appears to be a learned behaviour, with e.g. mother ewes teaching their young how to safely forage seaweed (Conradt 2000, and pers. comm. Kevin Woodbridge). The composition of the microbial populations in the guts of seaweed-eating sheep was found to be adapted to their diet, promoting seaweed-digestion, with major differences compared to pasture-fed sheep (Greenwood et al., 1983; Orpin et al., 1985). Additionally, sheep habitually consuming seaweed were also found to absorb more copper from their diet, likely as a result of adapting to the low amounts of bioavailable copper in seaweeds (MacLachlan and Johnston, 1982). Since the consumption of seaweed appears to require some degree of adaptation to be most beneficial to the consumers (behavioural, physiological, and even the need to 'develop a taste for seaweed'; Makkar et al., 2016), animals that regularly consume seaweed over generations appear to have an advantage over those that only turn to seaweed in times of extreme scarcity.

Historically, animal husbandry practices in some coastal areas were also adapted to support seaweed-consumption. For example, to prevent sheep from drowning, a refuge island called a "sheep fort" was constructed in the Orkney archipelago, Scotland, onto which foraging sheep cut off by the tides could rescue themselves (see Fig. 2; Berry 1985; Pollard, Gibson, and Littlewood 2016). On North Ronaldsay, also part of the Orkney archipelago, a drystone wall of 19 km was built in 1832 to keep sheep on the island's foreshore, where they have been roaming freely since then (Tulloch, 1974).

Fig. 2 *Sheep fort in the North Atlantic Ocean, South of Rusk Holm, Orkney Islands. A human-built island (made of stone) for sheep to rescue themselves onto when cut off from land by the incoming tide. Picture taken by Gunnie Moberg, reproduced here with permission from Orkney Library & Archive.*

2.2.4 Feeding livestock

Several early historical accounts describe seaweed being fed to animals by humans. The classical Greco-Roman literature of the 1st and 2nd century AD describes military forces feeding seaweed to their load-bearing livestock, such as horses (e.g. *Bellum Africum* and *Life of Caesar;* Müller 2001; Perrin 1919). Similarly, a set of Breton laws likely dating to the 6th-8th century AD (Dumville 1984) stipulated property/usage rights of woodlands and seaweed, and it specifically permitted the use of woodlands and seaweeds as fodder for oxen, regardless of land ownership (Excerpta de Libris Romanorum et Francorum, P61; Bieler 1963).

Over the last 300 years, several historical accounts from the United Kingdom describe providing livestock (primarily sheep, cattle and pigs) with fresh seaweed directly collected from the shore (Chapman, 1970; Fenton, 1997; Kenicer et al., 2000; Landsborough, 1857; Stephenson, 1968). In Iceland, seaweed was dried and stored in barns like hay for future use (Chapman, 1970; Hallsson, 1964). Along the European North Atlantic coast, seaweed was commonly given to pigs, sheep, and cattle boiled, often cooked together with coarse flour, oatmeal, bran, husks or hay as a milk producing, fattening, and/or winter fodder (Baldwin, 1994; Chapman, 1970; Fenton, 1997; Foslie, 1884; Hallsson, 1964; Kenicer et al., 2000; Sauvageau, 1920; Stephenson, 1968). Anecdotal evidence of mixing seaweed with bran and molasses to feed cows also exists from New Zealand (Kurrajong, 1941).The red alga dulse (*Palmaria palmata;* Baldwin, 2000; Hallsson, 1964; H. R.

Hansen et al., 2003; Landsborough, 1857; Paterson & Coleman, 1982; Sauvageau, 1920) and several brown algae (e.g. *Laminaria spp., Saccharina latissima, Alaria esculenta*; Chapman, 1970; Conradt, 2000; Hall, 1975; H. R. Hansen et al., 2003; Sauvageau, 1920) appear to be generally favoured*,* while only few accounts document the consumption of green algae (*e.g. Ulva spp.*; Carlton and Hodder 2003; H. R. Hansen, Hector, and Feldmann 2003) by seaweed-foraging terrestrial mammals. This is also supported by traditional local names for dulse translating to e.g. "cow seaweed", "cattle weed", "sheep's weed" and "horse seaweed" (French: *goémon à vache*; Sauvageau 1920; Breton: *bijin-saout*; Arzel 1984; Norwegian: *sauesoll*; Landsborough 1857; Stephenson 1968). The brown seaweed *Ascophyllum nodosum* was also known as "pig-weed" (Norwegian: *grisetang;* Orkney Norn: *paddy tang*; Chapman 1970), and *Pelvetia canaliculata* and *Alaria esculenta* were referred to as „sheep weed", "calf weed", "cow weed" and "pig weed" (Chapman 1970; Mooney 2018; Stephenson 1968). These names show the historical importance of seaweeds for animal husbandry in coastal areas.

Meat of seaweed-eating animals has been reported to have a slightly fishy, salty, gamey or even "bad" flavour, but this taste was and still is also highly esteemed by others (Chapman, 1970; Fenton, 1997; Kenicer et al., 2000; Lightfoot, 1777; Newton, 1951). For example, in 2012, mutton from seaweed-eating sheep was served as a delicacy to Queen Elizabeth II and guests at her Diamond Jubilee celebrations (Orkney Sheep Foundation, 2012).

2.3 Seaweed Consumption by Humans

Seaweed is well-known to be a common part of coastal East Asian cuisines (García-Poza et al., 2022), particularly in the form of sushi and seaweed salads, but numerous historical and ethnographical sources describe human consumption of seaweed in coastal areas world-wide (reviewed in e.g. Abbott and Williamson 1996; Ainis et al. 2019; Anggadiredja 2016; Dumilag et al. 2022; Kenicer, Bridgewater, and Milliken 2000; Kurokura 2004; Mouritsen et al. 2023; Naar 2020; Pérez-Lloréns 2019; Thurstan et al. 2018; Turner 2003; which are briefly summarised here). A myriad of historical recipes from around the world exist for specific seaweeds, which were to be eaten raw, roasted, fried, cooked, pickled, fermented, mashed, with soy sauce, potatoes, chillies, milk, butter, vinegar, cocoa, as part of salads, soups, ragouts, baked into bread, desserts (jellies), as snacks, or for breakfast, among others (reviewed in Kenicer, Bridgewater, and Milliken 2000; Mouritsen et al. 2023). Today, seaweed extracts are also consumed as part of ice-cream, plant-based milk, as dietary fibre supplements and as capsules to encase medicines.

In China, Japan and Korea, legal texts and historical accounts indicate a long history of consuming and valuing seaweeds: Edible seaweeds were given as gifts, and parts of taxes were paid in the form of seaweed (Batten, 1993; Hwang et al., 2020; Porterfield, 1922), with some of the earliest historical evidence dating to 2700 BC (Mouritsen et al., 2023). Ethnobotanical accounts from parts of the Philippines, Indonesia, Tonga, New Zealand and Hawaiʻi also indicate deeply-rooted local traditions of collecting seaweeds for consumption (Abbott and Williamson 1974; Anggadiredja 2016; Dumilag et al. 2022; Hurd et al. 2004; Ostraff 2006). In Australia, consumption of seaweeds by aboriginal populations has also been reported, but appears to have been limited in recent history (Thurstan et al., 2018), as seems to be the case in Africa.

There are rich, varied records of seaweed consumption in the Americas. In southern South America, seaweed had long been part of the diet of the Mapuche people when the Spanish first arrived, and its consumption was quickly adopted by the colonisers in the mid-sixteenth century (Pereira Salas, 1977). To this day, seaweeds can be bought on the streets in Chile. Seaweed is also part of traditional Peruvian dishes (Bradley, 2012), but it appears to have played a minor role as a food stuff the Caribbean (Pérez-Lloréns, 2019). In North America, seaweed features in the food traditions of many coastal indigenous people, including the Inuit, Kwakwaka'wakw, Haida, Delawarans, Iroquois, Wampanoag, Arcadians, Diegueno, Hupa and Towola (reviewed in Ainis et al. 2019; Mouritsen et al. 2023; Pérez-Lloréns 2019). Seaweed was also traded and gifted to people further inland, especially from the central and northern coasts of British Columbia and southern Alaska (Turner, 2003).

Seaweed was traditionally widely eaten in many coastal areas of Northern Europe, including Ireland, the British Isles, Iceland, Norway, and north-western France. For example, Iceland's oldest laws dating to the 12th century stated that it is permissible to eat berries and the red seaweed dulse on someone else's land, but not to take these away from the property without permission (see K § 186; Dennis, Foote, and Perkins 2000). Dulse was a common food for rich and poor in Iceland, with churches being issued licenses for its collection all around Iceland and dried dulse being transported to and traded with inland farmers throughout the last millennium (Hallsson 1964). Dulse was also traditionally toasted and served in Scottish and Irish pubs to stimulate beer consumption (Mouritsen et al., 2013). However, as in most of Europe, seaweeds declined in popularity, as Scottish Rev. Landsborough noted in 1849: "[Dulse] was much eaten by the Highlanders til it was supplanted by that nauseous herb, tobacco; and well would it have been for both purse and person if they had continued to prefer it to a costly narcotic" (Landsborough 1857, 54). Nevertheless, the same author also described seaweeds of the *Porphyra* species (laver) as a luxury food consumed by the affluent in Scotland (Landsborough 1857).

However, particularly in Ireland, seaweeds were also eaten as a last resort and poverty food (reviewed in Mouritsen et al. 2021). Nevertheless, traditional seaweed dishes such as laverbread and seaweed salads made mostly from wild seaweeds are still popular regional specialties in parts of Ireland, Iceland, Wales and Brittany today (Mouritsen 2023). Seaweed holds a more prominent place in everyday diets in Japan, Korea, Chile and parts of China and Peru, where it remains a widely consumed staple (Finucane et al., 2006; Minami et al., 2020; Peng et al., 2021) and is also cultivated commercially in aquafarms (Avila-Peltroche and Padilla-Vallejos, 2020; Kim et al., 2017).

2.4 Perceived and scientifically attested Health Effects of Seaweed Consumption

Numerous positive health effects have been ascribed to the consumption of seaweed (reviewed in detail in Pérez-Lloréns et al. 2023). Dulse, for example, was recorded in the early 18th century to have been used to treat various ailments in humans, including headaches, kill intestinal worms, improve one's sight, and to treat scurvy, colic and diarrhoea, with different preparations and ways of application for each desired effect (Kenicer et al., 2000; Martin, 1716). In the case of animals, seaweed was also fed to lambs as a remedy to inflamed stomachs caused by eating frosty grass (Fenton, 1997). Reports from the 20th century indicate that seaweed diets were thought to increase the fat content of cow's milk (Hallsson, 1964; Stephenson, 1968), increase winter wool production of sheep (Stephenson, 1968), help with calves' stomach problems when boiled with milk (Kenicer et al., 2000) and fatten animals and improve animal health in general (Hallsson, 1964).

Over the last decades, controlled nutritional studies have also linked seaweed consumption with improved health outcomes in humans, such as lowering mortality risk in patients humans with stomach and colorectal cancer (Minami et al., 2020), having favourable effects on blood glucose metabolism and blood pressure, and being inversely associated with cardiovascular disease mortality (reviewed in Cherry et al. 2019; Trigo et al. 2023). Controlled seaweed feeding experiments with terrestrial animals (including ungulates, rodents, and poultry) have confirmed some of the historically claimed beneficial effects of dietary supplementation with seaweed, such as improving gut health and preventing diarrhoea (Dierick et al., 2010, 2009; Heim et al., 2014; O'Doherty et al., 2010), improving immune function (Katayama et al., 2011; Saker et al., 2004), iodine status (Combet et al., 2014), reproductive performance (Okab et al., 2013) and meat quality (Moroney et al., 2015, 2012), among others (reviewed in Holdt and Kraan 2011; Makkar et al. 2016; Michalak et al. 2022). Consumption of several seaweeds (especially *Asparagopsis taxiformis)* was also shown to lower methane production in ruminants, which may be useful to lower the environmental impact of animal husbandry on the climate (Ross et al., 2023).

However, seaweed (extract) consumption also had negative results in several studies, including a depressing effect on food intake, growth and body weight (Erickson et al., 2012; Okab et al., 2013; Ventura et al., 1994). High concentrations of arsenic and iodine, and low concentrations of bioavailable copper in many seaweeds pose an additional concern (Cheney, 2016). In the case of sheep, it has been found that when nursing ewes subsist mostly on seaweed, their lambs are at risk of obtaining too little copper, leading to a neurological disorder ("seaweed stagger"; Ingimundarson 1995). To prevent this, mother ewes are commonly restricted from consuming seaweed, e.g. by taking them to inland pastures, during the lambing season (April to August; H. R. Hansen, Hector, and Feldmann 2003; Ingimundarson 1995). Therefore, using seaweed as animal food effectively and safely requires some experience or traditional knowledge.

Today, seaweed consumption is recommended as part of a balanced diet for humans (Lee et al. 2013), and as feed supplement for ruminants, poultry and pigs at low levels of up to 5 % of the total diet (Makkar et al., 2016), to make use of seaweed's beneficial properties, while avoiding negative effects. Higher amounts of seaweed may be safely included into animal diets, provided the animals are adapted to it: For example, North Ronaldsay sheep subsist nearly entirely on seaweed (with the exception of mother ewes and lambs, which graze on grass during the summer months) and seem to suffer from no significant adverse effects due to their diet, and are said by locals to gain in weight over winter (Hansen et al., 2003; Stephenson, 1968).

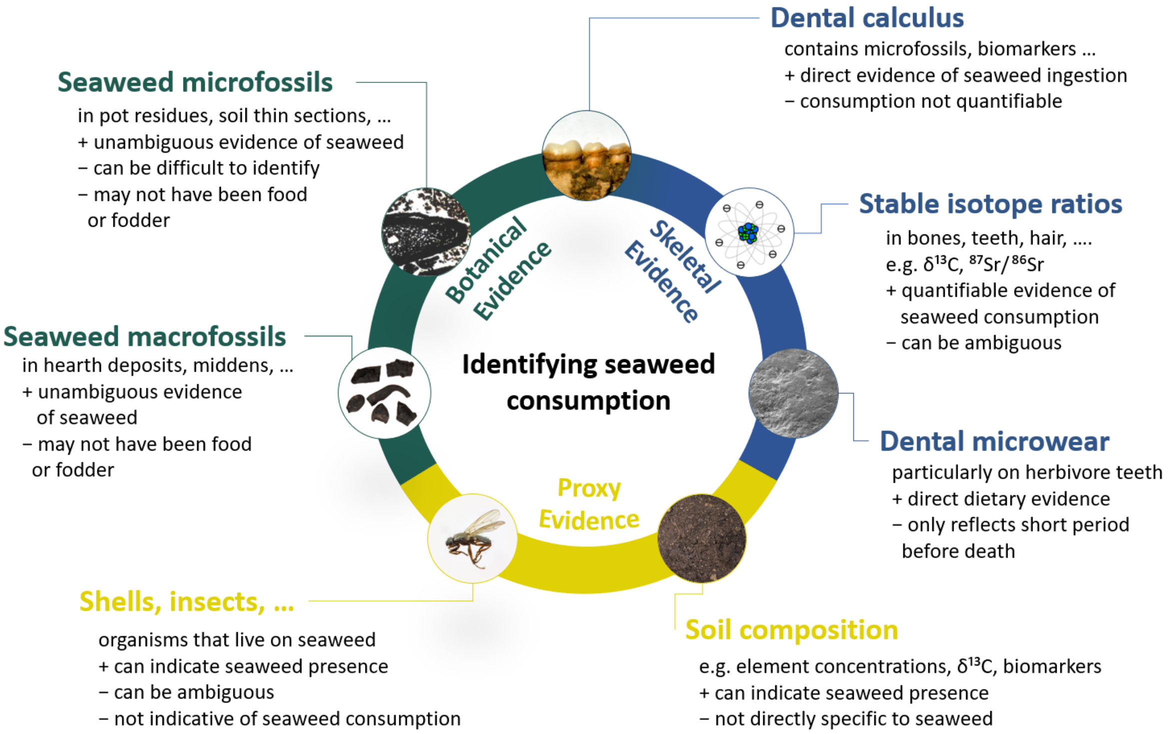

Fig. 3 *Overview of methods to identify the use of seaweed as food/fodder from the archaeological record. Where available, written records, images and oral histories can also provide insights into the use of seaweed as food and fodder. Diagram by M. Blanz, including images from Munro and Milek (2011), M. Blanz, Mainland (2000), M. Blanz, Janet Graham, and Dawn Mooney (clockwise from top-left; full image details and licenses in supplemental material).*

3 Identifying Seaweed Consumption in Archaeological Contexts: Methods and Findings

3.1 Seaweed Macrofossils and Microfossils

Seaweed is generally unlikely to be preserved at archaeological sites (Amorosi et al., 1998; Bell, 1981; Dillehay et al., 2008), but charring, waterlogging or freezing can prevent decomposition (Dillehay et al., 2008; Mooney, 2021). Seaweed remains at the Monte Verde II site in Chile, dated to between 12,270 and 12,030 cal BC, provide a notable example (Dillehay et al., 2008). These were preserved in hearth sediment fills, waterlogged beneath a peat stratum (Dillehay et al., 2008; Erlandson et al., 2008). They consist of ca. 125 g (dry weight) seaweed in the form of masticated cuds, partially burnt fragments, and were also found on the worked edge of a stone artefact (Dillehay et al., 2008)

When preserved at archaeological sites, seaweed fragments are usually found carbonised (e.g. Allison, Hall, and Kenward 1999; Becket et al. 2009; Bishop and Guðmundsson 2014; Toolis et al. 2007). Rarely, seaweed remains are also preserved as part of residues in ceramic vessels, e.g. in the Northern Patagonian archipelago (Belmar et al., 2023), or in kitchen middens on the coast of Peru (Lanning, 1967; Osborn, 1977). Since the preservation of seaweed is rare, so is their occurrence in soil micromorphological slides (Macphail et al., 2012) and their identification as seaweed is often difficult, as only a small transect of the seaweed is visible in thin section

(Mooney, 2021; Fig. 3). Raman spectroscopy may be used to distinguish terrestrial charcoal from carbonised seaweed (Sitzia et al., 2023). However, charred seaweed remains are not by themselves evidence of seaweed consumption, as charring may have occurred during its use as fuel, or when preparing seaweed ash for use as a food preservative (Martin, 1716), among other uses (reviewed in Mooney, 2018).

3.2 Dental Calculus Analysis: Seaweed Microfossils and Biomarkers

Dental calculus, i.e. hardened dental plaque also known as tartar, can entrap and preserve plant microfossils, microorganisms and molecules (Radini et al., 2017), including the remains of seaweeds and related organisms.

Grinding or dissolving dental calculus allows for the identification of trapped microfossils by microscope. The presence of germinal cells of bullkelp (*Durvillaea antarctica;* Belmar et al. 2024) and starch grains of dulse (*Palmaria palmata;* Murphy et al. 2022) in human calculus has been reported; however, due to a general lack of reference collections for identifying seaweed microfossils from archaeological calculus, such identifications remain putative and will require confirmation using purpose-built 3D reference collections. Additionally, the consumption of some seaweeds reduces calculus formation (van Dijken, Koistinen, and Ramberg 2015; Jun et al. 2018), which further lessens the likelihood of identifying seaweed microfossils in dental calculus.

Preserved biological marker compounds can be thermally extracted from dental calculus by thermal desorption and pyrolysis (i.e. heating without oxygen) and analysed by gas chromatography mass spectrometry (TD-GC-MS and Py-GC-MS). Buckley et al. (2023) identified a suite of diagnostic C_1 to C_6 alkyl pyrroles that indicate the likely presence of seaweed in calculus, and several alkyl pyrroles that are biomarkers for chlorophylls from *Chloroflexi* bacteria, which naturally occur in association with red seaweeds. These markers, paired with studies of the amino acid and alkene/alkane intensity patterns in the pyrolysis profile, provided evidence of seaweed inputs in human dental calculus from three Neolithic sites in Scotland and a Mesolithic site in Spain (Buckley et al., 2023). Metagenomic analysis of preserved DNA in dental calculus might also identify traces of seaweeds (and associated organisms), but this will require further methodological improvements to ensure robust interpretations (reviewed in Mann et al. 2023).

Most ingested seaweed was likely swallowed, but e.g. when used for medicinal purposes, chewed seaweeds may also have been spat out (see Pérez-Lloréns et al. 2023), with seaweed traces nevertheless becoming incorporated into dental calculus. The study of dental calculus thus provides a very promising new avenue to study seaweed consumption, and its presence in the mouth more generally.

3.3 Dental Microwear

Chewing foods can leave characteristic microscopic scratches and pits on tooth enamel, which can be studied using scanning electron microscopy (SEM) to identify past diets. In present-day sheep that predominantly ate fresh seaweed on the shore, distinct dental microwear patterns were identified that were unlike those of sheep that consumed grass (Mainland, 2000). Dental microwear may thus be helpful to identify seaweed consumption. However, chewing of sand and grit chewing of sand and grit associated with seaweed rather than the consumption of the seaweed itself likely also caused some of the observed dental microwear (Mainland, 2000). Therefore, the consumption of washed and dried seaweed would likely lead to different microwear patterns, as would seaweed consumption by humans - none of which have been studied so far. Additionally, continued use of teeth will lead to further wear, so that only the diet shortly prior to death is visible in dental microwear ("Last Supper phenomenon"; Grine, 1986). This is beneficial in terms of the study of short-term or seasonal dietary regimes but does not allow for an investigation of long-term diet. The complexity of dental microwear patterns likely also precludes its use to conclusively identify seaweed consumption in more diverse, human diets where seaweed was only a minor part of the diet.

3.4 Isotope Ratios in Tooth Enamel and Bone Collagen

Isotope ratios of carbon ($\delta^{13}C$), nitrogen ($\delta^{15}N$), oxygen ($\delta^{18}O$) and sulphur ($\delta\ ^{34}S$) in bodily tissues reflect the isotope ratios of consumed food and water with an offset. Under certain conditions, these can be used to identify and even quantify substantial seaweed consumption. This section outlines how this may be achieved, but also discusses how seaweed consumption can lead to misinterpretations in palaeodietary reconstructions using isotope ratios.

3.4.1 Carbon Isotope Ratios ($\delta^{13}C$)

Carbon isotope ratios in particular are useful to identify seaweed consumption. Most widely consumed seaweeds have $\delta^{13}C$ values generally between ca. −21‰ and −10‰ (with some red seaweeds having lower values; Raven et al. 2002; Szpak et al. 2013). In contrast, terrestrial plants following the C_3-photosynthesis pathway (around 95 % of green plants on earth; e.g. wheat, barley, rice, potatoes) generally have lower $\delta^{13}C$ values between ca. −31‰ and −24‰ (Kohn, 2010). In a C_3-environment, seaweed consumption by herbivores can therefore easily be identified by elevated $\delta^{13}C$ values in bone collagen, bone carbonate and tooth enamel, which was confirmed by study of present-day seaweed-eating sheep from the Orkney Islands in Scotland (Balasse et al. 2005; Balasse, Mainland, and Richards 2009; Blanz et al. 2020; Guiry and Szpak 2020; for comparison to archaeological data, present-day $\delta^{13}C$ data need to be adjusted by +1.5‰ to account for the Suess effect; Ambrose et al. 1997; Keeling 1979; McCarroll et al. 2009). Studies of archaeological remains from the Orkney islands have shown seaweed consumption by sheep to have been common in the area from the beginning of the 3rd millennium BC in the Neolithic, with elevated $\delta^{13}C$ values indicating around half of over 100 investigated Neolithic Orkney sheep from seven sites to have consumed seaweed (Balasse et al., 2005, 2006, 2009, 2019; Balasse and Tresset, 2009; Blanz et al., 2024a; Schulting et al., 2017).

As the enamel of a tooth is laid down over a set timeframe and is not remodelled after mineralization, sequential enamel sampling of teeth allows a chronological view into the diet and drinking water. Since $\delta^{18}O$ values of rain water are temperature-dependent and thus reflect seasonal changes, $\delta^{18}O$ values in combination with $\delta^{13}C$ values in tooth enamel can be used to study the time of year seaweed was consumed (Fig. 4; Balasse et al. 2005). Dental enamel data of sheep from Neolithic Orkney show that seaweed was predominantly eaten in winter (Balasse et al., 2006, 2009, 2019; Balasse and Tresset, 2009; Blanz et al., 2024a), indicating the importance of seaweed when terrestrial resources are sparse. This sequential method appears to be more effective in identifying seaweed consumption than bulk $\delta^{13}C$ analysis of bone collagen, which can miss smaller amounts of seaweed consumption (Blanz et al., 2020).

However, in more complex cases, including most human dietary reconstructions, the consumption of seaweed can be obscured by consumption of other foods with elevated $\delta^{13}C$ values, such as marine animals (shell fish, fish, marine mammals, marine birds), terrestrial plants following the C_4-photosynthesis pathway (e.g. millet, maize, other cereals adapted to dry conditions, and some saltmarsh plants), and CAM plants (e.g. cacti and pineapple). For example, in a study of human diet in the Marianas Archipelago in the western Pacific, it was not possible to distinguish whether elevated bone collagen $\delta^{13}C$ values originated from the consumption of seaweed, sugar cane or possibly even marine foods (Ambrose et al., 1997). Identifying seaweed consumption when C_4- or CAM-plants and other marine foods are also present in the environment (in addition to C_3-plants) is generally not feasible using bone collagen $\delta^{13}C$ values due to equifinality (Dufour et al., 2014).

This inability to source the consumed carbon's origin also affects the accuracy of radiocarbon-dating for individuals that may have consumed seaweed. As part of the marine reservoir effect, radiocarbon-depleted carbon can upwell in coastal areas (reviewed in Alves et al. 2018), and be incorporated into seaweed (Strokov, 2020). Consumers of such radiocarbon-depleted seaweed will then date older (in radiocarbon years) than their true age. This is a well-known issue for consumers of marine fish and marine mammals (Stuiver et al., 1986), where it can introduce offsets of over 1200 years (Ascough et al., 2005). The marine reservoir effect can be corrected for when the extent of marine-food consumption can be reconstructed (Sayle et al., 2014), but when the extent of marine food consumption is unknown (e.g. because it is not clear if C_4 plants or seaweed was consumed), this is not possible.

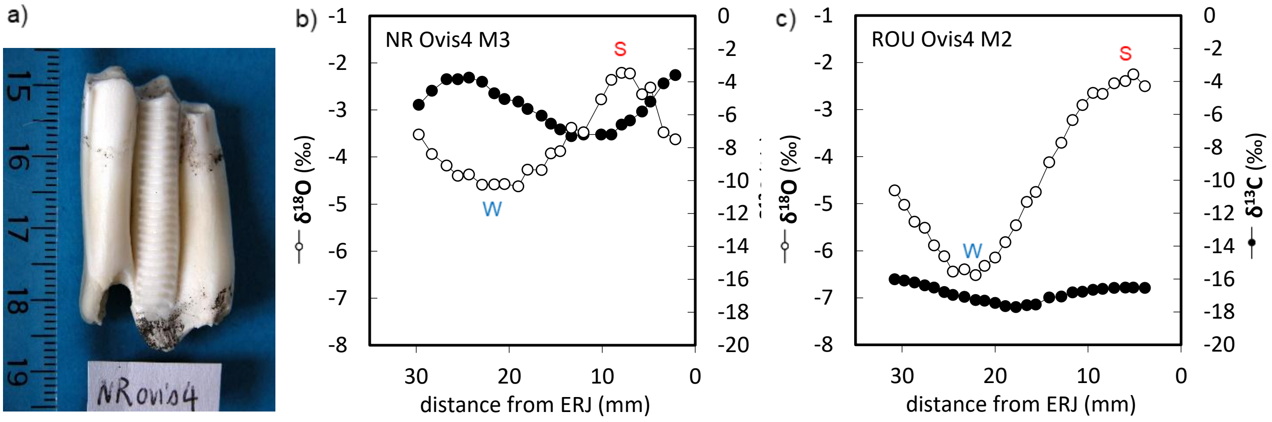

Fig. 4 *a) Sheep molar sequentially sampled for enamel; b) stable isotope ratio results of a sequentially sampled sheep molar that consumed substantial amounts of seaweed in winter, indicated by elevated $\delta^{13}C$ values when $\delta^{18}O$ values are low; c) stable isotope ratio results of a terrestrial feeding sheep. ERJ = enamel root junction; W = winter; S = summer. Data from Balasse et al. 2005 and Balasse, Mainland, and Richards 2009, picture taken by Marie Balasse.*

3.4.2 Sulphur Isotope Ratios ($\delta^{34}S$)

To study marine influences in terrestrial diets, $\delta^{34}S$ may also be used. Seawater sulphates have $\delta^{34}S$ values of ca. +20‰, whereas most values measured in freshwater, soil and minerals are lower (reviewed in Nehlich 2015). Therefore, elevated bone collagen $\delta^{34}S$ values (up to ca. +20‰) generally indicate marine influences in the diet. However, sea-spray and ocean-influenced rainwater as well as fertilisation with marine resources may influence soil and terrestrial plant $\delta^{34}S$ values in coastal areas to become elevated (Blanz et al., 2024b; Gröcke et al., 2021; Stack and Rock, 2011). On the Orkney Islands, elevated $\delta^{34}S$ values (14.4‰-18.0‰) were found both for sheep that did, and did not consume seaweed (Guiry and Szpak, 2020), showing that in coastal areas, sea-spray effects and ocean-influenced rain can fully mask the consumed diet. Therefore, elevated $\delta^{34}S$ values can be used to detect coastal/marine food consumption in non-coastal sites provided no other source of elevated $\delta^{34}S$ values is present, but they cannot specifically indicate seaweed consumption. In contrast, saltmarsh plants and seagrasses such as eelgrass (*Zostera marina*), can have much lower $\delta^{34}S$ values, around ca. +4‰ (Holmer and Hasler-Sheetal, 2014), so that in this case marine inputs can in fact lower consumer $\delta^{34}S$ values, allowing them to be distinguished from seaweed consumption (Guiry et al., 2021).

3.4.3 Strontium Isotope Ratios ($^{87}Sr/^{86}Sr$)

Seaweed generally contains large amounts of strontium compared to most terrestrial foods (Adams et al., 2011; Kabata-Pendias and Mukherjee, 2007; Schiener et al., 2015), with the oceanic $^{87}Sr/^{86}Sr$ ratio of 0.709 (Dungworth et al., 2019; Hess et al., 1986). Extensive seaweed consumption therefore leads to consumer $^{87}Sr/^{86}Sr$ ratios close to the oceanic $^{87}Sr/^{86}Sr$ ratio, as well as elevated Sr concentrations in tooth enamel (Blanz et al., 2022; Montgomery et al., 2007). However, consumption of other foods high in oceanic Sr, such as seaweed-fertilised terrestrial crops, would also lead to similar results (Blanz et al., 2019; Montgomery et al., 2007).

3.4.4 Nitrogen Isotope Ratios ($\delta^{15}N$)

To distinguish between consumption of seaweed and other marine resources, $\delta^{15}N$ values may be used. Seaweeds are primary producers, and tend to have lower $\delta^{15}N$ values than fish and marine mammals (Fredriksen, 2003; Hobson and Welch, 1992). Therefore, marine food consumption indicated by $\delta^{13}C$, $\delta^{34}S$ and/or $^{87}Sr/^{86}Sr$ combined with comparatively low $\delta^{15}N$ values can indicate seaweed consumption (Blanz et al. 2020), or possibly the consumption of molluscs (cf. Fredriksen 2003). Additionally, compound-specific stable isotope analysis of $\delta^{15}N$ in the amino acids glutamine/glutamate and phenylalanine in bone collagen have also been used to support interpretations of seaweed consumption in a Pleistocene caribou (Kubiak et al., 2021).

3.4.5 Oxygen Isotope Ratios ($\delta^{18}O$)

Since $\delta^{18}O$ values in consumer bioapatite are mainly affected by consumed water, including water contained in food, the consumption of fresh seaweed introduces large amounts of oceanic water to the consumer. In sheep that predominantly eat seaweed, this oceanic input was large enough to dampen the natural seasonal variation in $\delta^{18}O$ values in sequential samples of tooth enamel (Balasse et al., 2009). Therefore, where seaweed forms a large part of the diet (as evidenced e.g.

by $\delta^{13}C$), it can be possible to distinguish between seaweed being consumed fresh (with oceanic water) or after drying (without oceanic water). This was also the case for seaweed-eating Neolithic sheep on the Orkney Islands, which appear to have consumed fresh seaweed (Balasse et al., 2006). However, when reconstructing geographical origin using $\delta^{18}O$ values, changes to $\delta^{18}O$ induced by seaweed consumption are generally negligible, unless fresh seaweed was a main part of the diet.

3.4.6 Mixing Models

Mixing models are used to mathematically deduce relative contributions of different food sources (with different isotope ratios) to the consumer's diet using isotopic values of the consumer's tissues, their diet, and trophic offsets. By combining different types of isotopic evidence (e.g. $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$), it can sometimes be possible to identify a potential contribution of seaweed to the diet that would not have been possible using one isotopic system alone. Bayesian mixing models such as FRUITS, simmr, and MixSIAR thus offer a deceptively simple way of quantifying the extent of seaweed consumption for individual consumers. For example, strands of hair from an Inca child mummy from Quehuar volcano in today's Argentina were sequentially analysed for $\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$ and $\delta^{2}H$ values to reconstruct its diet using simmr (Poulallion et al., 2024). The model suggested a dietary contribution of 16.2%±12.9% from marine algae approximately 10 months prior to death, in addition to consumption of maize, beans and meat (Poulallion et al., 2024). Notably, the substantial margin of error reflects considerable uncertainty in this estimate.

All dietary models necessarily rely on estimations of the isotope ratios and elemental content of the different dietary sources and on estimations of the trophic enrichment factors, as these cannot be directly determined. Estimating these values is complex, and in the absence of archaeological food remains, can be associated with very large uncertainties. There is also a danger of employing incorrect trophic enrichment factors, e.g. by mistakenly using collagen-to-collagen enrichment factors instead of diet-to-collagen enrichment factors (Schulting et al., 2023). Additionally, in some cases, unknown food resources can affect isotope ratios in ways that cannot be modelled. Caution is therefore required when using mixing models to reconstruct palaeodiets from isotope ratio data (Schulting, MacDonald, and Richards 2022; Phillips et al. 2014; Phillips et al. 2014).

3.5 Trace Elements in Tooth Enamel

In general, trace element concentrations in skeletal tissues cannot be used to study dietary intake of these elements in archaeological contexts. This is because most elements are either not biologically incorporated into skeletal tissues, or their uptake is metabolically controlled, or because contamination from the soil and washing out alters the original elemental concentrations (Burton and Price, 2006). Concentration ratios of strontium, barium and calcium concentrations are exceptions to this, because they are taken up by the same biological pathway. Lower Ba/Sr values and elevated Sr/Ca values in tooth enamel can reflect seaweed consumption, or consumption of plants fertilised with seaweed (Blanz et al., 2022; Montgomery et al., 2007). Arsenic, vanadium and uranium concentrations were also found to be elevated in the tooth enamel of present-day seaweed-eating sheep, but cannot be used to identify seaweed consumption in most archaeological contexts, as contamination from soil also significantly elevates these concentrations in tooth enamel (to a much larger extent than for Sr and Ba due to concentration differences; Blanz, Stewart, et al. 2022).

3.6 Proxies and Soil Chemistry

Indirect evidence of the presence of seaweed can be obtained from proxy indicators that are associated with seaweeds that may preserve while the seaweed itself decays (depending on the burial conditions), for example mollusc shells, hydroids, bryozoans, insect remains, spirorbid shells, and potentially foraminifera and diatoms commonly found associated with or adhering to seaweed (Ainis et al., 2014; Alcalde et al., 2023; Amorosi et al., 1998; Bell, 1981; Kenward, 2009; Mooney, 2021; Reilly, 2003). Where these proxies are found away from past coastlines, this may indicate the transport of seaweed inland. In the case of insects, some caution is required, however, as they may change their ecological niche. For example, remains of the seaweed fly *Thoracochaeta zosterae*, which subsists on seaweed in modern day, were found in medieval inland terrestrial cesspits (Webb et al., 1998). Further study using $\delta^{13}C$ and $\delta^{15}N$ analysis revealed a terrestrial diet for the archaeological *Thoracochaeta zosterae,* indicating that they did not subsist on seaweed (Webb et al., 1998).

The likely past presence of seaweed can also be supported on the basis of soil chemistry, whereby elevated concentrations of potassium (Entwistle et al. 2007), phosphates, nitrates and other salts (Milek and Roberts, 2013), arsenic (Castlehouse et al. 2003), rare earth elements (Cook et al. 2006), as well as elevated $\delta^{13}C$ isotope ratios in HCl-insoluble soil (Simpson et al., 1998) and the presence of fucosterol (Bull et al., 1999) have been interpreted as indicative of the past presence of seaweed. However, these soil markers (with the exception of fucosterol) are not directly specific to seaweed, and leaching effects and marine inundation can cause changes to the soil chemistry, hindering geochemical studies of seaweed usage. Additionally, even where seaweed presence can be inferred, this does not provide evidence of its consumption, and may be due to e.g. fertilisation of crops with seaweed. Therefore, these indirect methods showing the presence of seaweed should be backed up by analysis of skeletal remains wherever possible, to clarify whether seaweed was consumed, or used for other purposes.

4 Implications of Seaweed Consumption

4.1 Subsistence Stress or Strategy?

Since our present-day perception of the desirability of food has the potential to greatly influence our interpretations of archaeological data, it is important to consider the current plurality of views on seaweed consumption. Particularly in historically poor countries like Ireland, where seaweed was consumed during the Great Famine that devastated the country in 1845–1849, many people have strongly associated eating seaweed with past poverty and starvation (reviewed in Mouritsen et al. 2021). However, seaweeds also played a significant role in coastal diets in times of abundance (Kenicer et al., 2000; Matsuda, 2001), being used “to make a truly delicious dish”, a food “light and nourishing for invalids” (Landsborough 1857, 56, 57). Clearly, the consumption of seaweed by itself does not indicate famine, resource scarcity or economic pressures. Instead, the use of seaweed as food particularly in coastal areas is simply the result of local resource availability, reflecting differences of coastal subsistence practices compared to inland farming traditions. But being available when terrestrial resources are not, seaweed is a food that may well have frequently been one of the last available foods in times of need, and thus prone to gaining stigma. This could lead to an avoidance of seaweed in times of abundance, depending on cultural and other societal factors, which may explain the geographical and cultural variability in popularity of seaweeds as foods today.

Similar to the case for seaweed as human food, it has also been suggested that seaweed consumption by sheep may have been only a fall-back strategy in years when not enough terrestrial resources were available (Schulting et al., 2017), and as a supplementary, rather than preferred resource for caribou (Kubiak et al., 2021). However, seaweed is consumed habitually by present-day sheep on the Orkney island North Ronaldsay, reported to be liked, and sheep even gain weight in winter when relying nearly solely on seaweed (H. R. Hansen, Hector, and Feldmann 2003; K. Woodbridge, personal communication, 2019). Seaweed-consumption by animals therefore also does not automatically indicate subsistence stress.

In cold climates, a key part of surviving winter and early spring was to assure the overwintering of core stock by acquiring sufficient fodder. At the beginning of every winter, the amount and type of animals that could be sustained with the available fodder supply and available wild resources had to be estimated, and animals were slaughtered accordingly (Amorosi et al., 1998). Ethnographical accounts from Iceland indicate that land without access to seaweed for feeding animals was valued less for this reason (Ingimundarson, 1995), and seaweed consumption was common every winter (Hallsson, 1964), providing a sustainable husbandry strategy.

However, when seaweed is consumed as a last resort by animals not adapted to its consumption, their already exhausted bodies may not be able to physiologically adapt to such a sudden dietary change, and they may die anyway. Such cases would not be visible in isotopic studies of tooth enamel, as incorporation of dietary carbon takes several months (Balasse, 2002), but would be visible in dental microwear (Mainland, 2000). This highlights the importance of integrating multiple analytical approaches, which allows for more complex interpretations of past palaeodiets.

4.2 Seaweed Consumption as an Adaptation

The consumption of seaweed is an adaptation to the coastal landscape, and its use can show the extent of adaptation to local resources and the local landscape. When seaweed is incorporated into a society's subsistence strategy, the availability of seaweed (alongside other coastal resources) can even influence colonisation routes. The "Kelp Highway Hypothesis", proposed by Erlandson et al. (2007), suggests a coastal route for the colonisation of the Americas from northern Asia along the North Pacific Coast. With the retreat of the ice sheets at the end of the Last Glacial Maximum (~16,000 years ago), the coast would have provided a linear coastal route adjacent to productive kelp forests, which provided a large variety of resources, including seaweed, but also shellfish, marine mammals, fish and seabirds. Once adaptations to these coastal resources have occurred, these could be exploited by migrating coastal peoples with little adjustment, while terrestrial ecosystems would have varied greatly, requiring further adaptations. This theory of a coastal migration route along the Pacific Ocean is supported by the seaweed finds at Monte Verde II, Chile, which was ca. 15 km from the sea during the late Pleistocene (Dillehay et al., 2008; Erlandson et al., 2015). Similar suggestions on the importance of coastal resources have also been made for the dispersion of early *Homo* along the Indian Ocean in East Africa, ~2.5 Mya (Verhaegen et al., 2002). However, seaweed consumption has not yet been proven in these cases, in part because a paucity of preservation, and because of an earlier lack of suitable methods.

Notably, evidence of seaweed was found in the dental calculus of an individual at the inland Mesolithic site La Corona, Spain, at a distance of 80 km from the sea today (Buckley et al. 2023). This points towards the high degree of adaptability of Mesolithic people, being able to exploit resources from a wide variety of environments as part of their (semi-)nomadic, broad spectrum subsistence strategies.

Seaweed was also shown to be part of human diets in the Neolithic in samples from mainland Scotland (Distillery cave, Oban) and the Orkney Islands (Isbister and Quanterness, to the north of mainland Scotland; Buckley et al. 2023). Evidence from stable isotope ratio analyses indicates a significant reduction of human consumption of marine resources from the Mesolithic to the Neolithic in the British Isles (Schulting and Richards 2002; Richards and Schulting 2006). Therefore, this new evidence of seaweed consumption from dental calculus in Neolithic Scotland confirms previous hypotheses that coastal resources were not fully abandoned as a human food source in the Neolithic in the British Isles (Milner et al., 2004; Richards and Schulting, 2006).

The continued reliance on marine resources in Neolithic Orkney despite the advent of agriculture is also clearly supported by stable isotope ratio evidence of sheep diets. On the Orkney Islands in Scotland, the absence of a significant woodland component as a potential source of tree-leaf fodder, as well as the difficulty of making dry hay due to ambient humidity, were regularly compensated by the use of seaweed. Particularly in winter, when snow cover reduced access to pastures, this resource may have been crucial to the earliest farming communities to establish sustainable farming in this insular context. Stable isotope results revealed the consumption of seaweed by some of the earliest sheep to arrive on the archipelago (around 3500 cal BC; Fig. 5) in small amounts at first, before it became more significant and recurrent in later contexts located on small islets as well as on the largest island, called Mainland (Balasse et al. 2019; Dockrill et al. 1994; Schulting et al. 2017). Combined with the evidence of Neolithic human consumption of seaweed from Isbister and Quanterness on Mainland Orkney and (Buckley et al. 2023), where sheep were also shown to have consumed significant amounts of seaweed (Schulting et al. 2017), these findings indicate a continued reliance on marine resources in Neolithic Orkney despite being undetectable by stable isotope ratio analyses of human remains. Evidence of seaweed consumption by sheep is also available from the Iron and Bronze Ages and the Viking/Norse period (Balasse et al., 2009) , but the contribution of seaweed did not increase or become ubiquitous in this time . Sheep relying all year round on seaweed, like today's North Ronaldsay sheep, have not been evidenced in the archaeological record to date. Seaweed consumption was also not evidenced in Neolithic cattle (Balasse et al., 2019; Jones and Mulville, 2016; Mainland et al., 2016; Schulting et al., 2017; Towers et al., 2017) or deer (Balasse and Tresset 2009; Blanz, Balasse, et al. 2022; Schulting et al. 2017) found on Orkney. Priority given to cattle over sheep for grazing on pastures, due to the greater socioeconomic value of the former, may explain these results (Schulting et al., 2017), while Neolithic deer on Orkney may have had limited coastal access or did not develop a taste for seaweed (Blanz et al., 2024a). Therefore, while adaptation to seaweed consumption was possible for sheep in Neolithic Orkney, it was not an inevitable outcome of a linear development, but rather a flexible response to local environmental and socio-economic conditions.

Seaweed consumption by humans may have followed similar non-linear trajectories, with seaweed's cultural perception being shaped over time by stigma and appreciation depending on economic, environmental and cultural circumstances. Local dietary adaptations to seaweed availability were thus likely complex and variable, reflecting both practical subsistence needs and shifting cultural attitudes.

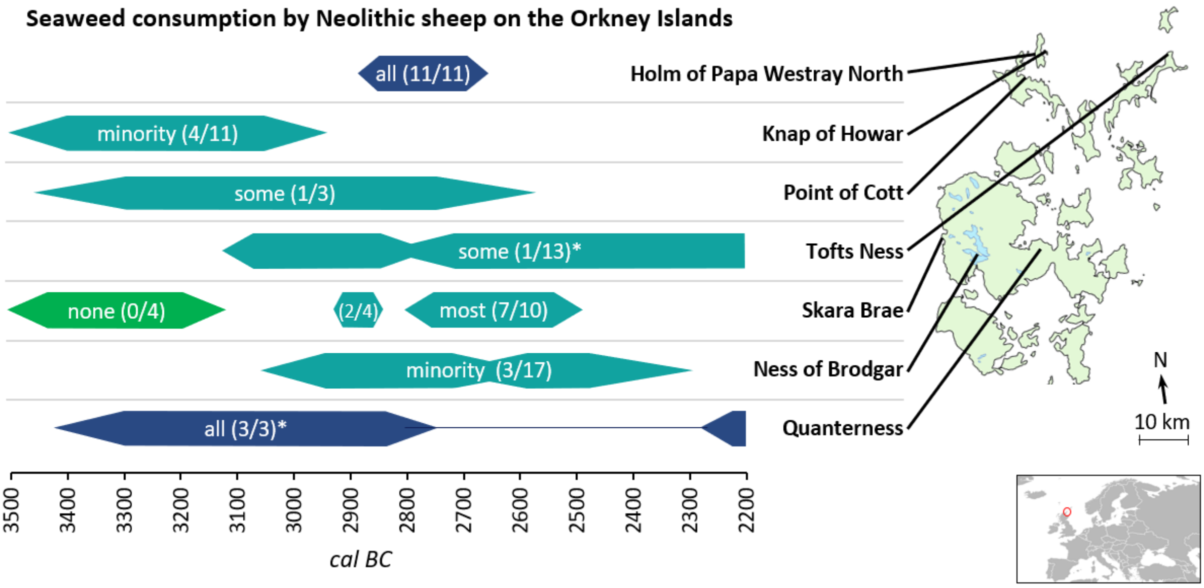

Fig. 5 *Seaweed consumption by sheep on Neolithic Orkney. Numbers in brackets indicate the number of sheep that consumed seaweed and the total number of sheep analysed. Blue = all analysed sheep ate seaweed, turquoise = some seaweed-eating sheep, green = no analysed sheep ate measurable amounts of seaweed. Unless noted otherwise, assessment of seaweed-consumption was made based on sequential enamel analyses of* $\delta^{13}C$ *and* $\delta^{18}O$ *(see main text for references). *data from bone collagen, which is less likely than tooth enamel to reflect seaweed consumption* (Blanz et al., 2020)*. The timeline is an approximation based on Bayliss et al. 2017, Schulting et al. 2010, Barber 1997, Card et al. 2018 and Schulting et al. 2017. Basemap from d-maps.com (public domain).*

5 Conclusion

This literature review has shown that seaweed was consumed in coastal areas around the world by both humans and terrestrial mammals, and should therefore not be neglected or even dismissed as a possible source of food in archaeological interpretations. Additionally, ecological, ethnographical and historical evidence indicates that while seaweed consumption may increase during food scarcity, seaweeds have also been desired for their taste, texture, nutrition value and medicinal properties in more plentiful times. Despite the growing recognition of the potentially significant role of seaweed as food, relatively little archaeological research has focused explicitly on seaweed, and many regions and periods remain unexplored in this regard. This may be partly due to seaweed's generally poor preservation in the archaeological record, as well as its absence in many contemporary Western diets, which may have influenced research priorities.

Additionally, due to the plurality of seaweed uses, seaweed consumption is difficult to identify in the archaeological record. When seaweed is the primary food, this can be identifiable and even quantifiable using stable isotope ratios in tooth enamel. However, when seaweed constituted only a minor part of the diet, as may be expected for most humans, the best way to identify seaweed consumption currently appears to be the analysis of in dental calculus due to its capability of detecting minor amounts of seaweed consumption. Future research, particularly the advancement and application of analytical techniques, will be crucial in further uncovering the extent and significance of seaweed consumption worldwide throughout (pre)history, offering valuable insights into past animal-human-environment interactions and subsistence practices.

6 Acknowledgments

This work was funded by the European Social Fund and Scottish Funding Council as part of Developing Scotland's Workforce in the Scotland 2014-2020 European Structural and Investment Fund Programme, and the Faculty of Historical and Cultural Studies at the University of Vienna. MB is grateful to Philippa Ascough, Jörg Feldmann and Mark Taggart for comments on an early version of this literature review and to Karen Milek and Dawn Elise Mooney for permitting the use of their images as part of Fig. 3. The authors are also grateful to Debora Zurro, Luca Sitzia, Ximena Power, Shalen Sadie Prado and Dawn Elise Mooney for their comments. Three anonymous reviewers are additionally thanked for their contributions.

7 Declaration of Interests

The authors report there are no competing interests to declare.

8 Author Contributions

Magdalena Blanz reviewed the literature, supplied images and data, prepared all figures, analysed and interpreted the data and wrote and revised the manuscript. Marie Balasse contributed data and images, and wrote parts of the manuscript and revised it. Ingrid Mainland supplied images and revised the manuscript. All authors read and approved the final draft prior to submission.

9 ORCID

Magdalena Blanz https://orcid.org/0000-0003-0195-6744
Marie Balasse https://orcid.org/0000-0003-1925-5110
Ingrid Mainland https://orcid.org/0000-0002-9701-8092

10 References

Aaronson, S., 1986. A role for algae as human food in antiquity. Food Foodways 1, 311–315. https://doi.org/10.1080/07409710.1986.9961891

Abbott, I.A., 1996. Ethnobotany of seaweeds: Clues to uses of seaweeds. Hydrobiologia 326–327, 15–20. https://doi.org/10.1007/BF00047782

Abbott, I.A., Williamson, E.H., 1974. Limu: An Ethnobotanical Study of Some Edible Hawaiian Seaweeds, in: Pacific Tropical Botanical Garden. Lawai, Hawaii.

Adams, J.M.M., Ross, A.B., Anastasakis, K., Hodgson, E.M., Gallagher, J.A., Jones, J.M., Donnison, I.S., 2011. Seasonal variation in the chemical composition of the bioenergy feedstock Laminaria digitata for thermochemical conversion. Bioresour. Technol. 102, 226–234. https://doi.org/10.1016/j.biortech.2010.06.152

Ainis, A.F., Erlandson, J.M., Gill, K.M., Graham, M.H., Vellanoweth, R.L., 2019. The Potential Use of Seaweeds and Marine Plants by Native Peoples of Alta and Baja California, An Archaeology of Abundance. University Press of Florida, Gainesville, Florida. https://doi.org/10.5744/florida/9780813056166.003.0005

Ainis, A.F., Vellanoweth, R.L., Lapeña, Q.G., Thornber, C.S., 2014. Using non-dietary gastropods in coastal shell middens to infer kelp and seagrass harvesting and paleoenvironmental conditions. J. Archaeol. Sci. 49, 343–360. https://doi.org/10.1016/j.jas.2014.05.024

Alcalde, V., Flores, C., Guardia, J., Olguín, L., Broitman, B.R., 2023. Marine invertebrates as proxies for early kelp use along the western coast of South America. Front. Earth Sci. 11, 1–12. https://doi.org/10.3389/feart.2023.1148299

Allison, E., Hall, A., Kenward, H., 1999. Technical Report. Living conditions and resource exploitation at the Early Christian rath at Deer Park Farms, Co. Antrim, N. Ireland: evidence from plants and invertebrates. Part 1: Text, Reports from the Environmental Archaeology Unit, York.

Alves, E.Q., Macario, K., Ascough, P., Bronk Ramsey, C., 2018. The Worldwide Marine Radiocarbon Reservoir Effect: Definitions, Mechanisms, and Prospects. Rev. Geophys. 56, 278–305. https://doi.org/10.1002/2017RG000588

Ambrose, S.H., Butler, B.M., Hanson, D.B., Hunter-Anderson, R.L., Krueger, H.W., 1997. Stable isotopic analysis of human diet in the Marianas Archipelago, western Pacific. Am. J. Phys. Anthropol. 104, 343–361. https://doi.org/10.1002/(SICI)1096-8644(199711)104:3<343::AID-AJPA5>3.0.CO;2-W

Amorosi, T., Buckland, P.C., Edwards, K.J., Mainland, I., McGovern, T.H., Sadler, J.P., Skidmore, P., 1998. They did not Live by Grass Alone: the Politics and Palaeoecology of Animal Fodder in the North Atlantic Region. Environ. Archaeol. 1, 41–54. https://doi.org/10.1179/146141096790605821

Anggadiredja, J.T., 2009. Ethnobotany Study of Seaweed Diversity and Its Utilization in Warambadi, Panguhalodo Areas of East Sumba District. J. Teknol. Lingkung. 10, 297. https://doi.org/10.29122/jtl.v10i3.1476

Arzel, P., 1984. Traditional management of seaweeds in the district of Leon. FAO Fish. Tech. Pap. 249, 1–49.

Ascough, P., Cook, G., Dugmore, A., 2005. Methodological approaches to determining the marine radiocarbon reservoir effect. Prog. Phys. Geogr. 29, 532–547. https://doi.org/10.1191/0309133305pp461ra

Avila-Peltroche, J., Padilla-Vallejos, J., 2020. The seaweed resources of Peru. Bot. Mar. 63, 381–394. https://doi.org/10.1515/bot-2020-0026

Balasse, M., 2002. Reconstructing dietary and environmental history from enamel isotopic analysis: Time resolution of intra-tooth sequential sampling. Int. J. Osteoarchaeol. 12, 155–165. https://doi.org/10.1002/oa.601

Balasse, M., Mainland, I., Richards, M.P., 2009. Stable isotope evidence for seasonal consumption of marine seaweed by modern and archaeological sheep in the Orkney archipelago (Scotland). Environ. Archaeol. 14, 1–14. https://doi.org/10.1179/174963109X400637

Balasse, M., Tresset, A., 2009. A key to the adaptation of Neolithic husbandry in the Orkneys: contribution of seaweed to the sheep diet at the Holm of Papa Westray, revealed through stable isotope analysis (δ13C and δ18O) of teeth, in: Ritchie, A. (Ed.), On the Fringe of Neolithic Europe. Society of Antiquaries of Scotland, Edinburgh, pp. 74–83.

Balasse, M., Tresset, A., Ambrose, S.H., 2006. Stable isotope evidence (δ13C, δ18O) for winter feeding on seaweed by Neolithic sheep of Scotland. J. Zool. 270, 170–176. https://doi.org/10.1111/j.1469-7998.2006.00104.x

Balasse, M., Tresset, A., Dobney, K., Ambrose, S.H., 2005. The use of isotope ratios to test for seaweed eating in sheep. J. Zool. 266, 283–291. https://doi.org/10.1017/S0952836905006916

Balasse, M., Tresset, A., Obein, G., Fiorillo, D., Gandois, H., 2019. Seaweed-eating sheep and the adaptation of husbandry in Neolithic Orkney: new insights from Skara Brae. Antiquity 370, 919–932.

Baldwin, J.R., 2000. Working with Seaweed in North-West Sutherland, in: Baldwin, J. (Ed.), The Province of Strathnaver. Scottish Society for Northern Studies, Edinburgh, pp. 116–141.

Baldwin, J.R., 1994. At the Back of the Great Rock: Crofting and Settlement in Coigach, Lochbroom, in: Baldwin, J.R. (Ed.), Peoples and Settlement in North-West Ross. Scottish Society for Northern Studies, Edinburgh, pp. 291–398.

Barber, J., 1997. The excavation of a stalled cairn at the Point of Cott, Westray, Orkney. Scottish Trust for Archaeological Research, Edinburgh.

Batten, B.L., 1993. Provincial Administration in Early Japan: From Ritsuryo kokka to Ocho kokka. Harv. J. Asiat. Stud. 53, 103. https://doi.org/10.2307/2719469

Bayliss, A., Marshall, P., Richards, C., Whittle, A., 2017. Islands of history: the Late Neolithic timescape of Orkney. Antiquity 91, 1171–1188. https://doi.org/10.15184/aqy.2017.140

Becket, A., Macgregor, G., Duffy, P., Finlay, N., Miller, J., Sheridan, A., 2010. Forest grazing and seaweed foddering: early Neolithic occupation at Maybole, South Ayrshire. Proc. Soc. Antiq. Scotl. 139, 105–122.

Bell, M., 1981. Seaweed as a prehistoric resource, in: Brothwell, D., Dimbleby, G. (Eds.), Environmental Aspects of Coasts and Islands (BAR International Series 94). British Archaeological Reports (BAR), Oxford, England, pp. 117–126.

Belmar, C.A., Reyes, O., Tessone, A., San Román, M., Morello, F., 2023. What is Cooking in the Pots of the Chiloé Archipelago?, in: Foodways of the Ancient Andes. University of Arizona Press, Tucson, Arizona, U.S.A., pp. 45–67. https://doi.org/10.2307/j.ctv37xg2bh.6

Belmar, C.A., Reyes, O., Tessone, A., Urbina, X., 2024. Plant Consumption in the Northern Patagonian Archipelago (41–47° S, Chile) Since 6000 Years BP to Historical Times: An Integrative Vision Through Ceramic Use Residues and Human Dental Calculus, in: Nature(s) in Construction Ethnobiology in the Confluence of Actors, Territories and Disciplines. https://doi.org/10.1007/978-3-031-60552-9

Berry, R.J., 1985. The natural history of Orkney; The New Naturalist No. 70. HarperCollins, London.

Bieler, L., 1963. The Irish Penitentials. The Dublin Institute for Advanced Studies, Dublin.

Bishop, R.R., Guðmundsson, G., 2014. The Archaeobotanical Remains from Aðalstræti.

Blanz, M., Ascough, P., Mainland, I., Martin, P., Taggart, M.A., Dieterich, B., Wishart, J., Sayle, K.L., Raab, A., Feldmann, J., 2019. Seaweed fertilisation impacts the chemical and isotopic composition of barley: Implications for analyses of archaeological skeletal remains. J. Archaeol. Sci. 104, 34–44. https://doi.org/10.1016/j.jas.2019.02.003

Blanz, M., Balasse, M., Card, N., Ascough, P., Fiorillo, D., Taggart, M.A., Feldmann, J., Mainland, I., 2024a. Life, Death and Teeth of Late Neolithic Sheep and Red Deer Excavated at Ness of Brodgar, Orkney Islands (UK). Environ. Archaeol. 6, 1–13. https://doi.org/10.1080/14614103.2022.2146320

Blanz, M., Gröcke, D.R., Martin, P., Church, M.J., 2024b. The effect of seaweed fertilisation on sulfur isotope ratios (δ34S) and grain size in barley: implications for agronomy and archaeological research. Front. Environ. Archaeol. 1–11. https://doi.org/10.3389/fearc.2024.1465082

Blanz, M., Mainland, I., Richards, M., Balasse, M., Ascough, P., Wolfhagen, J., Taggart, M.A., Feldmann, J., 2020. Identifying seaweed consumption by sheep using isotope analysis of their bones and teeth: Modern reference $\delta^{13}C$ and $\delta^{15}N$ values and their archaeological implications. J. Archaeol. Sci. 118. https://doi.org/10.1016/j.jas.2020.105140

Blanz, M., Stewart, S., Mainland, I., Ascough, P., Raab, A., Feldmann, J., Taggart, M.A., 2022. Trace element ratios in tooth enamel as palaeodietary indicators of seaweed consumption and coastal grazing, and their broader applicability. J. Archaeol. Sci. 139, 105551. https://doi.org/10.1016/j.jas.2022.105551

Bradley, R., 2012. Sudado de Raya: An Ancient Peruvian Dish. Gastronomica 12, 68–73. https://doi.org/10.1525/gfc.2012.12.4.68

Buckley, S., Hardy, K., Hallgren, F., Kubiak-Martens, L., Miliauskienė, Ž., Sheridan, A., Sobkowiak-Tabaka, I., Subirà, M.E., 2023. Human consumption of seaweed and freshwater aquatic plants in ancient Europe. Nat. Commun. 14, 1–11. https://doi.org/bag

Bull, I.D., Simpson, I.A., Dockrill, S.J., Evershed, R.P., 1999. Organic geochemical evidence for the origin of ancient anthropogenic soil deposits at Tofts Ness, Sanday, Orkney. Org. Geochem. 30, 535–556. https://doi.org/10.1016/S0146-6380(99)00020-0

Burton, J.H., Price, T.D., 2006. The Use and Abuse of Trace Elements for Paleodietary Research, in: Biogeochemical Approaches to Paleodietary Analysis. Springer US, Boston, MA, pp. 159–171. https://doi.org/10.1007/0-306-47194-9_8

Card, N., Mainland, I., Timpany, S., Towers, R., Batt, C., Ramsey, C.B., Dunbar, E., Reimer, P., Bayliss, A., Marshall, P., Whittle, A., 2018. To cut a long story short: Formal chronological modelling for the late neolithic site of Ness of Brodgar, Orkney. Eur. J. Archaeol. 21, 217–263. https://doi.org/10.1017/eaa.2016.29

Carlton, J.T., Hodder, J., 2003. Maritime mammals: terrestrial mammals as consumers in marine intertidal communities. Mar. Ecol. Prog. Ser. 256, 271–286.

Castlehouse, H., Smith, C., Raab, A., Deacon, C., Meharg, A.A., Feldmann, J., 2003. Biotransformation and accumulation of arsenic in soil amended with seaweed. Environ. Sci. Technol. 37, 951–957. https://doi.org/10.1021/es026110i

Chapman, V.J., 1970. Seaweeds and their uses, 2nd ed. by Methuen and Co. Ltd., London.

Cheney, D., 2016. Toxic and Harmful Seaweeds, Seaweed in Health and Disease Prevention. Elsevier Inc., Amsterdam, Netherlands. https://doi.org/10.1016/B978-0-12-802772-1.00013-0

Cherry, P., Hara, C.O., Magee, P.J., Mcsorley, E.M., Allsopp, P.J., 2019. Risks and benefits of consuming edible seaweeds 77, 307–329. https://doi.org/10.1093/nutrit/nuy066

Combet, E., Ma, Z.F., Cousins, F., Thompson, B., Lean, M.E.J., 2014. Low-level seaweed supplementation improves iodine status in iodine-insufficient women 753–761. https://doi.org/10.1017/S0007114514001573

Conradt, L., 2000. Use of a seaweed habitat by red deer (Cervus elaphus L.). J. Zool. Soc. London 250, 541–549.

Cook, D.E., Kovacevich, B., Beach, T., Bishop, R., 2006. Deciphering the inorganic chemical record of ancient human activity using ICP-MS: A reconnaissance study of late Classic soil floors at Cancuén, Guatemala. J. Archaeol. Sci. 33, 628–640. https://doi.org/10.1016/j.jas.2005.09.019

Dennis, A., Foote, P., Perkins, R., 2000. Laws of early Iceland: Grágás II. The University of Manitoba Press, Winnipeg, Canada.

Dierick, N., Ovyn, A., De Smet, S., 2010. In vitro assessment of the effect of intact marine brown macro-algae Ascophyllum nodosum on the gut flora of piglets. Livest. Sci. 133, 154–156. https://doi.org/10.1016/j.livsci.2010.06.051

Dierick, N., Ovyn, A., De Smet, S., 2009. Effect of feeding intact brown seaweed Ascophyllum nodosum on some digestive parameters and on iodine content in edible tissues in pigs. J. Sci. Food Agric. 89, 584–594. https://doi.org/10.1002/jsfa.3480

Dillehay, T.D., Ramírez, C., Pino, M., Collins, M.B., Rossen, J., Pino-Navarro, J.D., 2008. Monte Verde: Seaweed, Food, Medicine, and the Peopling of South America. Science (80-.). 320, 784–786.

Dufour, E., Goepfert, N., Léon, B.G., Chauchat, C., Jordán, R.F., Sánchez, S.V., 2014. Pastoralism in northern Peru during pre-Hispanic times: Insights from the Mochica period (100-800 AD) based on stable isotopic analysis of domestic camelids. PLoS One 9. https://doi.org/10.1371/journal.pone.0087559

Dumilag, R. V., Belgica, T.H.R., Mendoza, L.C., Hibay, J.M., Arevalo, A.E., Malto, M.A.D., Orgela, E.G., Longavela, M.R., Corral, L.E.H., Olipany, R.D., Ruiz, C.F.C., Mintu, C.B., Laza, B.O., San Pablo, M.H., Bailon, J.D., Berdin, L.D., Calaminos, F.P., Gregory, S.A., Omoto, A.T., Chua, V.L., Liao, L.M., 2022. Seaweed ethnobotany of eastern Sorsogon, Philippines. Algae 37, 227–237. https://doi.org/10.4490/algae.2022.37.8.16

Dumville, D.N., 1984. On the dating of the early Breton lawcodes. Etudes Celt. 21, 207–221.

Dungworth, D., Degryse, P., Schneider, J., 2019. Kelp in historic glass: The application of strontium analysis, in: Isotopes in Vitreous Materials. pp. 113–130. https://doi.org/10.2307/j.ctt9qdx40.10

Entwistle, J.A., McCaffrey, K.J.W., Dodgshon, R.A., 2007. Geostatistical and Multi-Elemental Analysis of Soils to Interpret Land-Use History in the Hebrides, Scotland. Geoarchaeology An Int. J. 22, 391–415. https://doi.org/10.1002/GEA

Erickson, P.S., Marston, S.P., Gemmel, M., Deming, J., Cabral, R.G., Murphy, M.R., Marden, J.I., 2012. Kelp taste preferences by dairy calves. J. Dairy Sci. 95, 856–858. https://doi.org/10.3168/jds.2011-4826

Erlandson, J.M., Braje, T.J., Gill, K.M., Graham, M.H., 2015. Ecology of the Kelp Highway: Did Marine Resources Facilitate Human Dispersal From Northeast Asia to the Americas? J. Isl. Coast. Archaeol. 4894, 1–20. https://doi.org/10.1080/15564894.2014.1001923

Erlandson, J.M., Braje, T.J., Graham, M.H., 2008. How Old is MVII?—Seaweeds, Shorelines, and the Pre-Clovis Chronology at Monte Verde, Chile. J. Isl. Coast. Archaeol. 3, 277–281. https://doi.org/10.1080/15564890802412098

Fenton, A., 1997. The Northern Isles: Orkney and Shetland. Tuckwell Press, East Linton.

Finucane, B., Agurto, P.M., Isbell, W.H., 2006. Human and animal diet at Conchopata, Peru: stable isotope evidence for maize agriculture and animal management practices during the Middle Horizon. J. Archaeol. Sci. 33, 1766–1776. https://doi.org/10.1016/j.jas.2006.03.012

Foslie, M., 1884. Die Laminarien Norwegens, Christiania vidensk.-selsk. forhandl. A. W. Bröggers, Christiania.

Fredriksen, S., 2003. Food web studies in a Norwegian kelp forest based on stable isotope (δ13C and δ15N) analysis. Mar. Ecol. Prog. Ser. 260, 71–81. https://doi.org/10.3354/meps260071

García-Poza, S., Cotas, J., Morais, T., Pacheco, D., Pereira, L., Marques, J.C., Gonçalves, A.M.M., 2022. Chapter 17: Global Trade of Seaweed Foods, in: Sustainable Global Resources of Seaweeds Volume 2. Springer, Cham, Switzerland, pp. 325–337. https://doi.org/10.1007/978-3-030-92174-3

Greenwood, Y., Orpin, C.G., Paterson, I.W., 1983. Digestibility of seaweeds in Orkney sheep. Proc. Physiol. Soc. 343, 121.

Grine, F.E., 1986. Dental evidence for dietary differences in Australopithecus and Paranthropus:

a quantitative analysis of permanent molar microwear. J. Hum. Evol. 15, 783–822. https://doi.org/10.1016/S0047-2484(86)80010-0

Gröcke, D.R., Treasure, E.R., Lester, J.J., Gron, K.J., Church, M.J., 2021. Effects of marine biofertilisation on Celtic bean carbon, nitrogen and sulphur isotopes: Implications for reconstructing past diet and farming practices. Rapid Commun. Mass Spectrom. 35. https://doi.org/10.1002/rcm.8985

Guiry, E.J., Noël, S., Fowler, J., 2021. Archaeological herbivore δ13C and δ34S provide a marker for saltmarsh use and new insights into the process of 15N-enrichment in coastal plants. J. Archaeol. Sci. 125, 105295. https://doi.org/10.1016/j.jas.2020.105295

Guiry, E.J., Szpak, P., 2020. Seaweed-eating sheep show that δ34S evidence for marine diets can be fully masked by sea spray effects. Rapid Commun. Mass Spectrom. 34, 1–10. https://doi.org/10.1002/rcm.8868

Hall, S.J.G.G., 1975. Some recent observations on Orkney Sheep. Mamm. Rev. 5, 59–64. https://doi.org/10.1111/j.1365-2907.1975.tb00187.x

Hallsson, S. V., 1964. The uses of seaweeds in Iceland, in: IV Congres International Des Sigues Marines 1961, Pergamon. Pergamon Press, Oxford, pp. 398–405.

Hansen, B.B., Aanes, R., 2012. Kelp and seaweed feeding by High-Arctic wild reindeer under extreme winter conditions. Polar Res. 31, 1–6. https://doi.org/10.3402/polar.v31i0.17258

Hansen, H.R., Hector, B.L., Feldmann, J., 2003. A qualitative and quantitative evaluation of the seaweed diet of North Ronaldsay sheep. Anim. Feed Sci. Technol. 105, 21–28. https://doi.org/10.1016/S0377-8401(03)00053-1

Heim, G., Sweeney, T., O'Shea, C.J., Doyle, D.N., O'Doherty, J. V, 2014. Effect of maternal supplementation with seaweed extracts on growth performance and aspects of gastrointestinal health of newly weaned piglets after challenge with enterotoxigenic Escherichia coli K88. Br. J. Nutr. 112, 1955–65. https://doi.org/10.1017/S0007114514003171

Hess, J., Bender, M.L., Schilling, J.G., 1986. Evolution of the ratio of strontium-87 to strontium-86 in seawater from cretaceous to present. Science (80-.). 231, 979–984. https://doi.org/10.1126/science.231.4741.979

Hobson, K.A., Welch, H.E., 1992. Determination of trophic relationships within a high Arctic marine food web using δ13C and δ15N analysis. Mar. Ecol. Prog. Ser. 84, 9–18. https://doi.org/10.3354/meps084009

Holdt, S.L., Kraan, S., 2011. Bioactive compounds in seaweed: Functional food applications and legislation. J. Appl. Phycol. 23, 543–597. https://doi.org/10.1007/s10811-010-9632-5

Holmer, M., Hasler-Sheetal, H., 2014. Sulfide intrusion in seagrasses assessed by stable sulfur isotopes-A synthesis of current results. Front. Mar. Sci. 1, 1–12. https://doi.org/10.3389/fmars.2014.00064

Hurd, C.L., Nelson, W.A., Falshaw, R., Neill, K.F., 2004. History, current status and future of marine macroalgal research in New Zealand: Taxonomy, ecology, physiology and human uses. Phycol. Res. 52, 80–106. https://doi.org/10.1111/j.1440-1835.2004.tb00318.x

Hwang, E.K., Choi, H.G., Kim, J.K., 2020. Seaweed resources of Korea. Bot. Mar. 63, 395–405.

https://doi.org/10.1515/bot-2020-0007

Ingimundarson, J.H., 1995. Of sagas and sheep: toward a historical anthropology of social change and production for market, subsistence and tribute in early Iceland (10th to the 13th century). University of Arizona.

Jones, J.R., Mulville, J., 2016. Isotopic and zooarchaeological approaches towards understanding aquatic resource use in human economies and animal management in the prehistoric Scottish North Atlantic Islands. J. Archaeol. Sci. Reports 6, 665–677. https://doi.org/10.1016/j.jasrep.2015.08.019

Jun, J.Y., Jung, M.J., Jeong, I.H., Yamazaki, K., Kawai, Y., Kim, B.M., 2018. Antimicrobial and antibiofilm activities of sulfated polysaccharides from marine algae against dental plaque bacteria. Mar. Drugs 16. https://doi.org/10.3390/md16090301

Kabata-Pendias, A., Mukherjee, A.B., 2007. Trace Elements from Soil to Human. Springer, Berlin.

Katayama, M., Fukuda, T., Okamura, T., Suzuki, E., Tamura, K., Shimizu, Y., Suda, Y., Suzuki, K., 2011. Effect of dietary addition of seaweed and licorice on the immune performance of pigs. Anim. Sci. J. 82, 274–281. https://doi.org/10.1111/j.1740-0929.2010.00826.x

Keeling, C.D., 1979. The Suess effect: ^{13}carbon-^{14}carbon interrelations. Environ. Int. 2, 229–300. https://doi.org/10.1016/0160-4120(79)90005-9

Kenicer, G., Bridgewater, S., Milliken, W., 2000. The ebb and flow of Scottish seaweed use. Bot. J. Scotl. 52, 119–148. https://doi.org/10.1080/13594860009441750

Kenward, H., 2009. Invertebrates in archaeology in the north of England, Northern Regional Review of Environmental Archaeology. English Heritage, Fort Cumblerand.

Kim, J.K., Yarish, C., Hwang, E.K., Park, M., Kim, Y., 2017. Seaweed aquaculture: cultivation technologies, challenges and its ecosystem services. Algae 32, 1–13.

Kohn, M.J., 2010. Carbon isotope compositions of terrestrial C3 plants as indicators of (paleo)ecology and (paleo)climate. Proc. Natl. Acad. Sci. 107, 19691–19695. https://doi.org/10.1073/pnas.1004933107

Kubiak, C., Mathewes, R., Grimes, V., Van Biesen, G., Richards, M.P., 2021. Evidence of a significant marine plant diet in a Pleistocene caribou from Haida Gwaii, British Columbia, through compound-specific stable isotope analysis. Palaeogeogr. Palaeoclimatol. Palaeoecol. 564, 110180. https://doi.org/10.1016/j.palaeo.2020.110180

Kurokura, H., 2004. The importance of seaweeds and shellfishes in Japan: Present status and history. Bull. Fish. Res. Agency Suppl. 1, 1–4.

Kurrajong, 1941. Feeding cows on seaweed. Examiner 2.

Landsborough, D., 1857. A popular history of British seaweeds. L. Reeve, London, Uk.

Lanning, D.P., 1967. Peru before the Incas. Prentice-Hall, Englewood Cliffs.

Lee, M., Chae, S.W., Cha, Y., Cho, M.S., Oh, H.Y., Kim, M.K., 2013. Development of a Korean Diet Score (KDS) and its application assessing adherence to Korean healthy diet based on the Korean Food Guide Wheels 7, 49–58.

Lightfoot, J., 1777. Flora Scotica; Vol 2. White, London.

MacLachlan, G., Johnston, W., 1982. Copper poisoning in sheep from North Ronaldsay maintained on a diet of terrestrial herbage. Vet. Rec. 111, 299–301.

https://doi.org/10.1136/vr.111.13.299

Macphail, R., Berna, F., Crowther, J., Linderholm, J., 2012. Integrated microstratigraphic investigations and the potential of coastal archaeological soils and sediments to record past land use and cultural activities in Norway and the UK, in: 14th International Working Meeting on Soil Micromorphology.

Mainland, I., 2000. A dental microwear study of seaweed-eating and grazing sheep from Orkney. Int. J. Osteoarchaeol. 10, 93–107. https://doi.org/10.1002/(SICI)1099-1212(200003/04)10:2<93::AID-OA513>3.0.CO;2-U

Mainland, I., Towers, J., Ewens, V., Davis, G., Montgomery, J., Batey, C., Card, N., Downes, J., 2016. Toiling with teeth: An integrated dental analysis of sheep and cattle dentition in Iron Age and Viking-Late Norse Orkney. J. Archaeol. Sci. Reports 6, 837–855. https://doi.org/10.1016/j.jasrep.2015.12.002

Makkar, H.P.S., Tran, G., Heuzé, V., Giger-Reverdin, S., Lessire, M., Lebas, F., Ankers, P., 2016. Seaweeds for livestock diets: A review. Anim. Feed Sci. Technol. 212, 1–17. https://doi.org/10.1016/j.anifeedsci.2015.09.018

Mann, A.E., Fellows, J.A., Fagern, Z., Austin, R.M., Nelson, E.A., Hofman, C.A., 2023. Do I have something in my teeth? The trouble with genetic analyses of diet from archaeological dental calculus. Quat. Int. J. 654, 33–46. https://doi.org/10.1016/j.quaint.2020.11.019

Martin, M., 1716. A description of the Western Islands of Scotland, 2nd ed. A. Bell, London, UK.

Matsuda, Y., 2001. History of fish marketing and trade with particular reference to Japan. Int. Inst. Fish. Econ. Trade 4, 23–38.

McCarroll, D., Gagen, M.H., Loader, N.J., Robertson, I., Anchukaitis, K.J., Los, S., Young, G.H.F., Jalkanen, R., Kirchhefer, A., Waterhouse, J.S., 2009. Correction of tree ring stable carbon isotope chronologies for changes in the carbon dioxide content of the atmosphere. Geochim. Cosmochim. Acta 73, 1539–1547. https://doi.org/10.1016/j.gca.2008.11.041

Michalak, I., Tiwari, R., Dhawan, M., Alagawany, M., Farag, M.R., Sharun, K., Emran, T. Bin, Dhama, K., 2022. Antioxidant effects of seaweeds and their active compounds on animal health and production – a review. Vet. Q. 42, 48–67. https://doi.org/10.1080/01652176.2022.2061744

Milek, K.B., Roberts, H.M., 2013. Integrated geoarchaeological methods for the determination of site activity areas: A study of a Viking Age house in Reykjavik, Iceland. J. Archaeol. Sci. 40, 1845–1865. https://doi.org/10.1016/j.jas.2012.10.031

Milner, N., Craig, O.E., Bailey, G.N., Pedersen, K., Andersen, S.H., 2004. Something fishy in the Neolithic? A re-evaluation of stable isotope analysis of Mesolithic and Neolithic coastal populations. Antiquity 78, 9–22.

Minami, Y., Kanemura, S., Oikawa, T., Suzuki, S., Hasegawa, Y., Nishino, Y., Fujiya, T., Miura, K., 2020. Associations of Japanese food intake with survival of stomach and colorectal cancer: A prospective patient cohort study. Cancer Sci. 111, 2558–2569. https://doi.org/10.1111/cas.14459

Montgomery, J., Evans, J.A., Cooper, R.E., 2007. Resolving archaeological populations with Sr-isotope mixing models. Appl. Geochemistry 22, 1502–1514.

https://doi.org/10.1016/j.apgeochem.2007.02.009

Mooney, D.E., 2021. Charred Fucus-Type Seaweed in the North Atlantic: A Survey of Finds and Potential Uses. Environ. Archaeol. 238–250. https://doi.org/10.1080/14614103.2018.1558805

Moore, P.G., 2002. Mammals in intertidal and maritime ecosystems: Interactions, impacts and implications. Oceanogr. Mar. Biol. Vol 40 40, 491–608.

Moroney, N.C., O'Grady, M.N., O'Doherty, J. V., Kerry, J.P., 2012. Addition of seaweed (Laminaria digitata) extracts containing laminarin and fucoidan to porcine diets: Influence on the quality and shelf-life of fresh pork. Meat Sci. 92, 423–429. https://doi.org/10.1016/j.meatsci.2012.05.005

Moroney, N.C., O'Grady, M.N., Robertson, R.C., Stanton, C., O'Doherty, J. V., Kerry, J.P., 2015. Influence of level and duration of feeding polysaccharide (laminarin and fucoidan) extracts from brown seaweed (Laminaria digitata) on quality indices of fresh pork. Meat Sci. 99, 132–141. https://doi.org/10.1016/j.meatsci.2014.08.016

Mouritsen, O.G., Cornish, M.L., Critchley, A.T., Pérez-Lloréns, J.L., 2023. History of seaweeds as a food, in: Hefft, D.I., Badmus, U., Adetunji, C.O. (Eds.), Applications of Seaweeds in Food and Nutrition. Elsevier, Amsterdam, Netherlands, pp. 1–17. https://doi.org/10.1016/B978-0-323-91803-9.00002-0

Mouritsen, O.G., Dawczynski, C., Duelund, L., Jahreis, G., Vetter, W., Schröder, M., 2013. On the human consumption of the red seaweed dulse (Palmaria palmata (L.) Weber & Mohr). J. Appl. Phycol. 25, 1777–1791. https://doi.org/10.1007/s10811-013-0014-7

Mouritsen, O.G., Rhatigan, P., Cornish, M.L., Critchley, A.T., Pérez-Lloréns, J.L., 2021. Saved by seaweeds: phyconomic contributions in times of crises. J. Appl. Phycol. 33, 443–458. https://doi.org/10.1007/s10811-020-02256-4

Müller, M., 2001. Das Bellum Africum: Ein historisch-philologischer Kommentar der Kapitel 1-47. Universität Trier.

Murphy, K., Deryck, S., Hardy, B., Zoëga, G., 2022. Preliminary dietary and behavioural insights from northern Iceland through the lens of dental calculus. Archaeol. Islandica 14, 137–163.

Naar, N., 2020. Appendix B: The Cultural Importance of Kelp for Pacific Northwest Tribes, in: Puget Sound Kelp Recovery Plan. Northwest Straits Commission, Bellingham, pp. 1–12.

Nehlich, O., 2015. The application of sulphur isotope analyses in archaeological research: A review. Earth-Science Rev. 142, 1–17. https://doi.org/10.1016/j.earscirev.2014.12.002

Newton, L., 1951. Seaweed Utilisation. Purnell and Sons, Paulton and London.

O'Doherty, J. V., McDonnell, P., Figat, S., 2010. The effect of dietary laminarin and fucoidan in the diet of the weanling piglet on performance and selected faecal microbial populations. Livest. Sci. 134, 208–210. https://doi.org/10.1016/j.livsci.2010.06.143

Okab, A.B., Samara, E.M., Abdoun, K. a., Rafay, J., Ondruska, L., Parkanyi, V., Pivko, J., Ayoub, M. a., Al-Haidary, A. a., Aljumaah, R.S., Peter, M., Lukac, N., 2013. Effects of dietary seaweed (Ulva lactuca) supplementation on the reproductive performance of buck and doe rabbits. J. Appl. Anim. Res. 41, 347–355. https://doi.org/10.1080/09712119.2013.783479

Orkney Sheep Foundation, 2012. Meat [WWW Document]. URL https://www.theorkneysheepfoundation.org.uk/the-meat/

Orpin, C.G., Greenwood, Y., Hall, F.J., Paterson, I.W., 1985. The rumen microbiology of seaweed digestion in Orkney sheep. J. Appl. Bacteriol. 58, 585–596. https://doi.org/10.1111/j.1365-2672.1985.tb01715.x

Osborn, A.J., 1977. Strandloopers, Mermaids, and Other Fairytales; Ecological Determinants of Marine Resource Utilization - The Peruvian Case, in: Binford, L.R. (Ed.), For Theory Building in Archaeology. Academic Press, New York, pp. 157–205.

Ostraff, M., 2006. Limu: Edible seaweed in Tonga, an ethnobotanical study. J. Ethnobiol. 26, 208–227. https://doi.org/10.2993/0278-0771(2006)26[208:LESITA]2.0.CO;2

Paterson, I.W., Coleman, C.D., 1982. Activity patterns of seaweed-eating sheep on North Ronaldsay, Orkney. Appl. Anim. Ethol. 8, 137–146. https://doi.org/10.1016/0304-3762(82)90139-0

Peng, J., Min, S., Qing, P., Yang, M., 2021. The impacts of urbanization and dietary knowledge on seaweed consumption in china. Foods 10. https://doi.org/10.3390/foods10061373

Pereira Salas, E., 1977. Apuntes para la historia de la cocina chilena. Editorial Universitaria, Chile.

Pérez-Lloréns, J.L., 2019. Seaweed Consumption in the Americas. Gastronomica 19, 49–59. https://doi.org/10.1525/gfc.2019.19.4.49

Pérez-Lloréns, J.L., Critchley, A.T., Cornish, M.L., Mouritsen, O.G., 2023. Saved by seaweeds (II): Traditional knowledge, home remedies, medicine, surgery, and pharmacopoeia. J. Appl. Phycol. https://doi.org/10.1007/s10811-023-02965-6

Phillips, D.L., Inger, R., Bearhop, S., Jackson, A.L., Moore, J.W., Parnell, A.C., Semmens, B.X., Ward, E.J., 2014. Best practices for use of stable isotope mixing models in food-web studies. Can. J. Zool. 92, 823–835. https://doi.org/10.1139/cjz-2014-0127

Plutarch, 1919. Life of Caesar. Translated by Bernadotte Perrin, Plutarch’s Lives, Volume 7. W. Heinemann, London.

Pollard, E., Gibson, J., Littlewood, M., 2016. Interpreting Medieval Inter-tidal Features at Weelie’s Taing on Papa Westray, Orkney, NE Scotland. J. Marit. Archaeol. 11, 299–322. https://doi.org/10.1007/s11457-016-9169-0

Porterfield, W.J., 1922. References to the Algae in the Chinese Classics. Torrey Bot. Soc. 49, 297–300.

Poulallion, E., Galván, V.A.K., Seldes, V., Zigarán, M.F., Browning, G.R., Fourel, F., Clauzel, T., Flandrois, J.P., Séon, N., Simon, L., Amiot, R., Lécuyer, C., 2024. The Inca child of the Quehuar volcano: Stable isotopes clue to geographic origin and seasonal diet, with putative seaweed consumption. J. Archaeol. Sci. Reports 59. https://doi.org/10.1016/j.jasrep.2024.104784

Radini, A., Nikita, E., Buckley, S., Copeland, L., Hardy, K., 2017. Beyond food: The multiple pathways for inclusion of materials into ancient dental calculus. Am. J. Phys. Anthropol. 162, 71–83. https://doi.org/10.1002/ajpa.23147

Raven, J.A., Johnston, A.M., Kübler, J.E., Korb, R., McInroy, S.G., Handley, L.L., Scrimgeour, C.M., Walker, D.I., 2002. Mechanistic interpretation of carbon isotope discrimination by marine macroalgae and seagrasses. Funct. Plant Biol. 29, 335–378. https://doi.org/10.1071/PP01201

Reilly, E., 2003. The contribution of insect remains to an understanding of the environment of Viking-age and medieval Dublin, in: Duffy, S. (Ed.), Medieval Dublin IV. Four Courts Press, Dublin, pp. 40–62.

Richards, M.P., Schulting, R.J., 2006. Touch not the fish: the Mesolithic-Neolithic change of diet: Against the grain? A response to Milner et al. (2004). Antiquity 80, 444–458.

Ross, F.W.R., Boyd, P.W., Filbee-Dexter, K., Watanabe, K., Ortega, A., Krause-Jensen, D., Lovelock, C., Sondak, C.F.A., Bach, L.T., Duarte, C.M., Serrano, O., Beardall, J., Tarbuck, P., Macreadie, P.I., 2023. Potential role of seaweeds in climate change mitigation. Sci. Total Environ. 885, 163699. https://doi.org/10.1016/j.scitotenv.2023.163699

Saker, K.E., Fike, J.H., Veit, H., Ward, D.L., 2004. Brown seaweed- (Tasco) treated conserved forage enhances antioxidant status and immune function in heat-stressed wether lambs. J. Anim. Physiol. Anim. Nutr. (Berl). 88, 122–130. https://doi.org/10.1111/j.1439-0396.2003.00468.x

Sauvageau, C., 1920. Utilisation des algues marines. O. Doin, Paris.

Sayle, K.L., Cook, G.T., Ascough, P.L., Gestsdóttir, H., Hamilton, W.D., McGovern, T.H., 2014. Utilization of δ13C, δ15N, and δ34S Analyses to Understand 14C Dating Anomalies within a Late Viking Age Community in Northeast Iceland. Radiocarbon 56, 811–821. https://doi.org/10.2458/56.17770

Schiener, P., Black, K.D., Stanley, M.S., Green, D.H., 2015. The seasonal variation in the chemical composition of the kelp species Laminaria digitata, Laminaria hyperborea, Saccharina latissima and Alaria esculenta. J. Appl. Phycol. 27, 363–373. https://doi.org/10.1007/s10811-014-0327-1

Schulting, R.J., MacDonald, R., Richards, M.P., 2023. FRUITS of the sea? A cautionary tale regarding Bayesian modelling of palaeodiets using stable isotope data. Quat. Int. 1–10. https://doi.org/10.1016/j.quaint.2022.02.012

Schulting, R.J., Richards, M.P., 2002. The Wet, the Wild and the Domesticated: the Mesolithic–Neolithic Transition On the West Coast of Scotland. Eur. J. Archaeol. 5, 147–189. https://doi.org/10.1177/14619571020050020201

Schulting, R.J., Sheridan, A., Crozier, R., Murphy, E., 2011. Revisiting Quanterness: New AMS dates and stable isotope data from an Orcadian chamber tomb. Proc. Soc. Antiq. Scotl. 140, 1–50. https://doi.org/10.9750/psas.140.1.50

Schulting, R.J., Vaiglova, P., Crozier, R., Reimer, P.J., 2017. Further isotopic evidence for seaweed-eating sheep from Neolithic Orkney. J. Archaeol. Sci. Reports 11, 463–470. https://doi.org/10.1016/j.jasrep.2016.12.017

Simpson, I.A., Dockrill, S.J., Bull, I.D., Evershed, R.P., 1998. Early Anthropogenic Soil Formation at Tofts Ness, Sanday, Orkney. J. Archaeol. Sci. 25, 729–746. https://doi.org/10.1006/jasc.1997.0216

Sitzia, L., Power, X., Zurro, D., Maalouf, J.P., Cárcamo, J., Chandía, K., Vega, J.M.A., Borie, C., Roa, C., Silva, C., Salazar, D., Vivanco, S., Hernández, V., Aliste, C., Ibacache, S., Lorca, R., 2023. Tracking kelp-type seaweed fuel in the archaeological record through Raman spectroscopy of charred particles: examples from the Atacama Desert coast. Archaeol. Anthropol. Sci. 15, 178–179. https://doi.org/10.1007/s12520-023-01860-y

Stack, P., Rock, L., 2011. A δ34S isoscape of total sulphur in soils across Northern Ireland. Appl. Geochemistry 26, 1478–1487. https://doi.org/10.1016/j.apgeochem.2011.05.021

Stephenson, W.A., 1968. Seaweed in Agriculture and Horticulture. Faber and Faber Limited, London.

Strokov, A.A., 2020. Phanagoria in the Great Migration Period: The First Radiocarbon Dates, Their Verification and Discussion. Mater. Archaeol. Hist. Ethnogr. Tauria XXV, 43–65.

Stuiver, M., Pearson, G.W., Braziunas, T., 1986. Radiocarbon Age Calibration of Marine Samples Back to 9000 Cal Yr BP. Radiocarbon 28, 980–1021. https://doi.org/10.1017/s0033822200060264

Szpak, P., White, C.D., Longstaffe, F.J., Millaire, J.F., Vásquez Sánchez, V.F., 2013. Carbon and Nitrogen Isotopic Survey of Northern Peruvian Plants: Baselines for Paleodietary and Paleoecological Studies. PLoS One 8. https://doi.org/10.1371/journal.pone.0053763

Thurstan, R.H., Brittain, Z., Jones, D.S., Cameron, E., Dearnaley, J., Bellgrove, A., 2018. Aboriginal uses of seaweeds in temperate Australia: an archival assessment. J. Appl. Phycol. 30, 1821–1832. https://doi.org/10.1007/s10811-017-1384-z

Toolis, R., Ceron-Carrasco, R., Engl, R., Hall, A., Hunter, F., Inglis, R., McSween, A., D.McLaren, Madella, M., O'Connor, T., Smith, C., 2007. Excavation of a burnt mound at Meur, Sanday, Orkney. Scottish Archaeol. J. 29, 31–49. https://doi.org/10.3366/E1471576708000193

Towers, J., Mainland, I., Montgomery, J., Bond, J., 2017. Calving seasonality at Pool, Orkney during the first millennium AD: an investigation using intra-tooth isotope ratio analysis of cattle molar enamel. Environ. Archaeol. 22, 40–55. https://doi.org/10.1080/14614103.2015.1116214

Trigo, J.P., Palmnäs-Bédard, M., Juanola, M.V., Undeland, I., 2023. Effects of whole seaweed consumption on humans: current evidence from randomized- controlled intervention trials , knowledge gaps, and limitations. Front. Nutr. https://doi.org/10.3389/fnut.2023.1226168

Tulloch, P.A., 1974. A Window on North Ronaldsay. The Kirkwall Press, Kirkwall.

Turner, N.J., 2003. The ethnobotany of edible seaweed (Porphyra abbottae and related species; Rhodophyta: Bangiales) and its use by First Nations on the Pacific Coast of Canada. Can. J. Bot. 81, 283–293. https://doi.org/10.1139/b03-029

van Dijken, J.W. V, Koistinen, S., Ramberg, P., 2015. A randomized controlled clinical study of the effect of daily intake of Ascophyllum nodosum alga on calculus, plaque, and gingivitis. Clin. Oral Investig. 19, 1507–1518. https://doi.org/10.1007/s00784-014-1383-2

Ventura, M.R., Castañon, J.I.R., McNab, J.M., 1994. Nutritional value of seaweed (Ulva rigida) for poultry. Anim. Feed Sci. Technol. 49, 87–92. https://doi.org/10.1016/0377-8401(94)90083-3

Verhaegen, M., Puech, P.F., Munro, S., 2002. Aquarboreal ancestors? Trends Ecol. Evol. 17, 212–217. https://doi.org/10.1016/S0169-5347(02)02490-4

Webb, S.C., Hedges, R.E.M., Robinson, M., 1998. The Seaweed Fly Thoracochaeta zosterae (Hal.) (Diptera: Sphaerocidae) in Inland Archaeological Contexts: δ13C and δ15N Solves the Puzzle. J. Archaeol. Sci. 1253–1257.

Supplemental Material:

Fig. 3 was created by Magdalena Blanz, including 7 images that were reproduced either with permission from the author, or are in the public domain. Starting from top-left going clockwise:

1) Soil micromorphological thinsection of seaweed *Ascophyllum nodosum* from Vatnsfjörður, Iceland. Reproduced from Munro and Milek 2011 with permission from Karen Milek.
2) Dental calculus on human teeth from Isbister, Orkney. Reproduced from Buckley et al. 2023 under http://creativecommons.org/licenses/by/4.0/
3) ^{12}C isotope schematic. Image created by Magdalena Blanz.
4) Scanning electron microscope image of microwear on a sheep's tooth. Reproduced from Mainland 2000 under a John Wiley and Sons License issued to Magdalena Blanz.
5) Soil. Photograph taken by Magdalena Blanz.
6) Seaweed fly. Image taken by Janet Graham and reproduced here under https://creativecommons.org/licenses/by/2.0/deed.en
7) Macrofossils of seaweed *Ascophyllum nodosum* from Lækjargata, Reykjavik. Photograph taken by Dawn Elise Mooney, reproduced here with permission.

All images were cropped to fit the new figure.

References for Supplementary Material

Buckley, S., Hardy, K., Hallgren F., Kubiak-Martens L., Miliauskienė Ž., Sheridan A., Sobkowiak-Tabaka I., and Subirà M. 2023. "Human Consumption of Seaweed and Freshwater Aquatic Plants in Ancient Europe." Nature Communications 14 (1): 1–11. https://doi.org/10.1038/s41467-023-41671-2.

Mainland, I. 2000. "A Dental Microwear Study of Seaweed-Eating and Grazing Sheep from Orkney." International Journal of Osteoarchaeology 10 (2): 93–107. https://doi.org/10.1002/(SICI)1099-1212(200003/04)10:2<93::AID-OA513>3.0.CO;2-U.

Munro, K. and Milek, K., 2011. Soil Micromorphology Assessment of Floor Deposits in Three Viking Age Outbuildings. Vatnsfjörður 2010: Framvinduskýrslur/Interim Report, pp.173-193.