Seasonal Migrational Behaviour in Irish Giant Deer
Megaloceros giganteus (Blumenbach, 1799)

An investigation of intra-tooth multi-isotope analysis application in palaeontological migration studies

Master Thesis by

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Abstract

The giant deer *Megaloceros giganteus* (Blumenbach, 1799) is an icon of the Ice Age due to their famous antlers, and is commonly found in Pleistocene marl deposits throughout Ireland. While the topic of their migrational behaviour has been suggested, mainly due to this behaviour being common in deer species today, it has never been researched. Similarly little research on the isotopic composition of giant deer has been conducted. Therefore, migrational behaviour and seasonal movement are suggested to be analysed in three giant deer from Ireland dating back to the Pleistocene Late Glacial through isotopic analysis. Analysis through sequential intra-tooth sampling for $^{87}Sr/^{86}Sr$ ratios is suggested and should be acquired from TIMS and MC-ICPMS on the giant deer's tooth enamel. Although issues are suggested for $^{87}Sr/^{86}Sr$ isotope research due to factors such as reservoir times of strontium in the body, studies on modern caribou suggest the validity of such analysis for the brachydont molars of cervids.

Possible reasons for migrational behaviour are explored. As a deer species, giant deer required a high nutrient uptake for antler growth and were not as well adapted for the cold-dry steppe environments of the Pleistocene glacials. These stresses would have made migrational behaviour beneficial for maximising nutrient uptake during the warmer months, and for avoiding the harshest winter conditions of the glacials by moving to sheltered, low lying areas. Giant deer from interglacials of the Pleistocene would have not been under the same stresses, as the closed environments of that period allowed for the mix-feeding strategies they likely employed. Irish giant deer may have been pushed to migrational behaviour especially by the onset of the Younger Dryas cold stage as the preferred lime-rich grasses and forbs they depended on disappeared from the island. Therefore, migrational behaviour and seasonal mobility strategies may have been paramount for giant deer during cold periods of the Pleistocene and should therefore be analysed through sequential sampling of enamel for $^{87}Sr/^{86}Sr$ ratios.

1. Introduction

The Giant Deer; *Megaloceros giganteus*

One of the largest cervids to have ever lived, *Megaloceros giganteus* (Blumenbach, 1799) sported a shoulder height of approximately 2.1 meters, and an even more impressive antler span of 3.6 m (Vislobokova, 2012; Monaghan, 2017). While often referred to as the "Irish elk", it is strictly neither Irish nor elk. The total range of this animal spanned much of Eurasia between 400,000 – 11,700 Before Present years ago (see Fig. 4) and is most genetically related to the extant fallow deer (*Dama dama*; Linnaeus, 1758) as opposed to any elk species (Lister et al., 2005; Lister & Stuart, 2019). Therefore, the term giant deer is more accurate.

The popularity of the *M. giganteus* is evident, as their skulls were collected as trophies by nineteenth centuries fossil enthusiasts and an astonishing amount of research has been conducted on their morphology (Gould, 1974; Adelman, 2012; Monaghan, 2017). Their popularity was also thriving during the Pleistocene, as they occur frequently in cave paintings such as in the Lascaux and Cougnac caves, France (Leroi-Gourhan, 1982; Clottes, 1999; see Fig. 1. B.). These cave paintings have given insights on the physical appearance and coat of this animal, which is incredibly difficult to decipher from fossil remains alone. It appears that this animal had a dark band running down the anterior and posterior sides, and had a large hump at the shoulder that has been suggested to function as a fat storage mechanism (Guthrie, 2005; Monaghan, 2017; see Fig. 1. D.).This thesis will discuss the possibility of migrational behaviour in *M. giganteus* and will explore the methodologies through which to investigate this, as well as the implications of such research. While migrational behaviour in *M. giganteus* has been suggested before by Vislobokova (2012), no specific research on the topic has yet been conducted. Such research may help shed light on the effects of climate change on large animal's migratory behaviour and as such help in understanding similar effects occurring in the present, such as in common wildebeest (*Connochaetes taurinus*; Burchell, 1823) and red deer (*Cervus elaphus*; Linnaeus, 1758) (Holdo et al., 2009; Moore, 2011; Seebacher & Post, 2015; Mysterud et al., 2016). As the Irish population of *M. giganteus* will be studied (dated between 14,700 – 11,700 BP; see Fig. 4), the possibility of land bridge connections between Ireland and Britain must also be explored as migration may have been possible between islands during the late glacial (Devoy, 1985; Brooks et al., 2011).
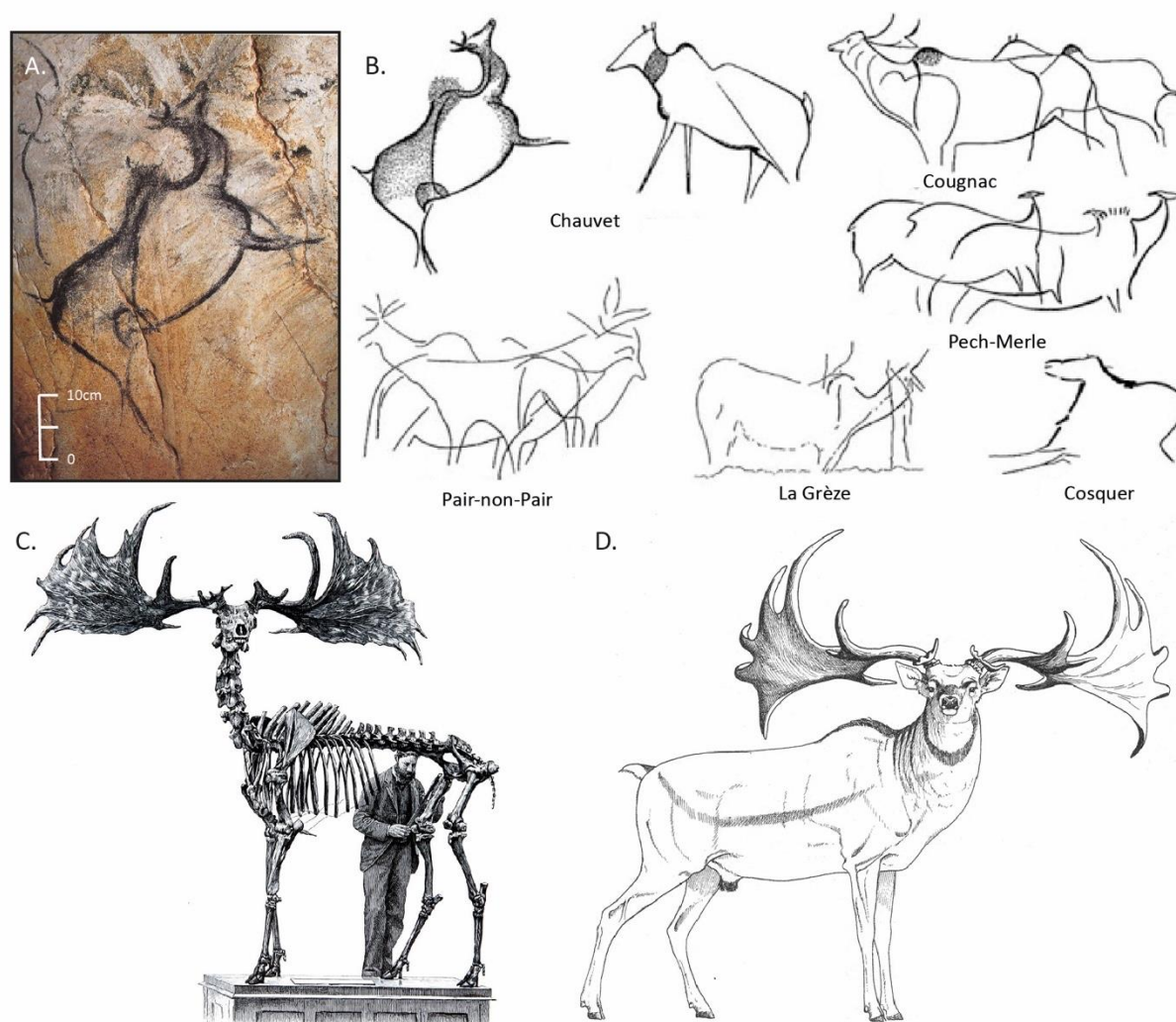
Fig. 1. (A.) "Panel of the *Megaloceros*" cave painting from Chauvet Cave, France (Delluc & Delluc, 1991). (B.) Cave paintings tracings of *M. giganteus* from multiple cave sites (Lemozi et al., 1969; Delluc & Delluc, 1991; Clottes & Courtin, 1995; Clottes, 1999). (C.) Mounted skeleton of *M. giganteus* (Millais, 1879; Gould, 1974). (D.) Coat reconstruction of *M. giganteus* based on the cave paintings in Fig. 1. B. (Geist, 1998; Guthrie, 2005).

1.1. *Systematic Palaeontology*

Order ARTIODACTYLA (Owen, 1848)
Family CERVIDAE (Gray, 1821)
Subfamily CERVINAE (Gray, 1821)
Tribe MEGACERINI (Viret, 1961)
Subtribe MEGACERINA (Viret, 1961)
Genus *Megaloceros* (Brookes, 1828)
Species *Megaloceros giganteus* (Blumenbach, 1799)

Systematic paleontological information obtained from Vislobokova (2013).

All deer species are classified under the family Cervidae, commonly referred to as cervids in literature (Geist, 1998). *Megaloceros giganteus* is a member of the Cervinae subfamily which refers to "Old World Deer" and is characterised by the foot structure as opposed to their geographic origin (Lister, 1994; Pitra et al., 2004). Other extant members in this subfamily include red deer and fallow deer (Brown & Chapman, 1991a,b; Lister et al., 2005).

M. giganteus is commonly grouped with the tribe Megacerini, and this tribe is suggested to only be currently represented by the fallow deer (Lister, 1994; Pitra et al., 2004). Characteristics of this tribe include an increase in the thickness of the lower jaw and the skull (pachyostosis and pachygnathy) (Lister, 1994; Vislobokova, 2012). Megacerini members ranged in size from species as small as extant roe deer (*Capreolus capreolus*; Linnaeus, 1758) to those like *M. giganteus* that rivalled the largest moose (*Alces alces*; Linnaeus, 1758) in size (Vislobokova, 2012). The size range of antlers has also varied through time, with early taxa such as *Praesinomegaceros* (Vislobokova et al, 1983) from the late Miocene (11.6 – 5.3 Million years ago) having relatively small antlers and Pleistocene taxa sporting their famously large antlers (Vislobokova, 2012).

The earliest members of this tribe date back to the late Miocene with species such as *Praesinomegaceros asiaticus* (Vislobokova et al, 1983) and *Neomegaloceros gracilis* (Korotkevich, 1971) being found in Inner Asia (Vislobokova, 2012). This region is thought to be the centre of origin for Megacerini, and all Megacerina (the subtribe to which *Megaloceros* belongs) are believed to have evolved from the genus *Cervavitus* (Vislobokova, 1990; Vislobokova, 2012; Vislobokova, 2013).

Moving into the Pliocene epoch (5.3 – 2.58 Ma), Megacerini become more common and widespread over much of Eurasia. Taxa such as *Arvernoceros* (Heintz, 1970)*, Orchonoceros* (Vislobokova, 1979) and *Sinomegaceros* (Dietrich, 1933) are found in regions such as the Mediterranean, Inner Asia and Russia respectively, displaying the range and diversity of Megacerini during the Pliocene (Vislobokova, 2012; Vislobokova, 2013).

The *Megaloceros* genus itself arose during the early Pleistocene (2.58 – 0.7 Ma) and is believed to be a sister group of *Praedama* (Portis, 1920), sharing the common ancestor *Arvernoceros* (Heintz, 1970; Van der Made & Tong, 2008; Vislobokova, 2013; see Fig. 2). It is distinguished from other members of the Megacerina subtribe by its large size and by the unique structure of the skull, antlers and dentition (Vislobokova, 2013). Early Pleistocene representatives of *Megaloceros* are only defined as *Megaloceros sp*. from the Taman Peninsula, although the morphology of the antler and antler base are similar to *M. giganteus antecedens* (Berckhemer, 1941; Vislobokova, 2013).

By the mid Pleistocene (770,000 – 126,000 BP) species such as *M. giganteus antecedens* are found in Asia and Europe (Lister, 1994; Vislobokova, 2013). *M. g. antecedens* is closely related to *M. g. giganteus*, even considered a paleosubspecies and may have been the forerunner of *M. g. giganteus* and *M. g. ruffii* (Nehring, 1891) (Vislobokova, 2013). The difference between the two being that *M. g. antecedents* has more compact antlers with larger more palmate basal tines compared to *M. g. giganteus* (Croitor et al., 2014; see Fig. 2).
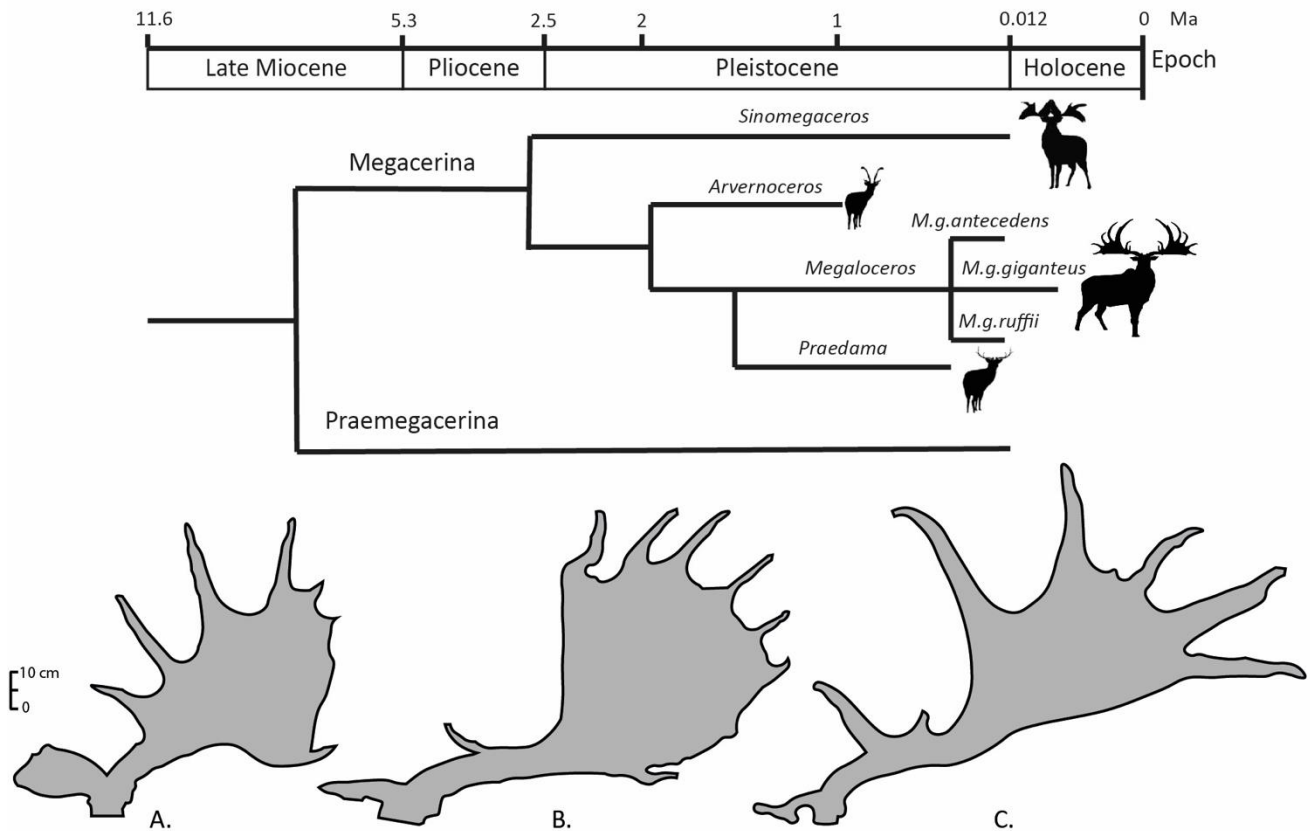
Fig. 2. Megacerini phylogeny and comparison of antler morphology in *Megaloceros giganteus* subspecies. (A.) *M. g. antecedens* (Vislobokova, 2013). (B.) *M. g. ruffii* (Vislobokova, 2013). (C.) *M. g. giganteus* (Titov & Shvyreva, 2016). Adapted from Vislobokova (2013) & Titov & Shvyreva (2016).

From the mid Pleistocene onward, *M. giganteus* becomes the most dominant and widespread megacerine, represented by subspecies such as *M. g. antecendens* and *M. g. ruffii*, but mainly *M. g. giganteus* (Vislobokova, 2013; Lister & Stuart, 2019). *M. g. giganteus* is considered the true "Irish elk" and specimens from Ireland are typically referred to as the species standard, sometimes referred to as *M. g. irlandicus* in the literature (Van der Made & Tong, 2008; Vislobokova, 2013). Throughout the remainder of this article, *Megaloceros giganteus* will refer to the true giant deer found throughout Europe, while Irish giant deer or Irish *M. giganteus* will specifically refer to the Late Glacial Irish population.

1.2. *Isotope Analysis in Palaeontology*

The use of isotopic analysis for understanding extinct species is common place in palaeontology, as it can help in solving questions regarding an animals diet, mobility and body temperature (Chritz et al., 2009; Eagle et al., 2011; Britton, 2017). The two most commonly analysed stable isotope ratios are carbon ($\delta^{13}C$) and oxygen ($\delta^{18}O$); other isotopes such as nitrogen, sulphur, lead and strontium to name a few have also been investigated and are discussed in detail later (McKechnie, 2004; Britton, 2017). Enamel tissue $\delta^{13}C$ or $\delta^{18}O$ values are obtained from the analysis of the mineral hydroxyapatite (bioapatite), but it is also possible to obtain hydroxyapatite isotopic values from bone and dentine material (Chritz et al., 2009; Britton, 2010; Kusaka, 2019). $\delta^{13}C$ and $\delta^{18}O$ can also be obtained from collagen, a protein present in bone and dentine, but not in enamel (Rucklidge et al., 1992; Jørkov et al., 2007; Salazar-Garcia et al., 2014). For the purposes of this thesis, the focus will be on enamel isotopic analysis. The isotopic composition of the carbonate substitutions within hydroxyapatite is determined by the lifestyle of the animal, essentially the philosophy of "you are what you eat" (Kohn, 1999; Schoeninger, 2010; Britton, 2010; Britton, 2017). Therefore, enamel or bone tissue can act as an archive of isotopic information on an animals diet and more. The values of isotopic ratios such as $\delta^{13}C$ and $\delta^{18}O$ are typically represented in parts per million (‰) due to

the low concentrations of the heavier stable isotopes. Fractionation is the partitioning of heavier and lighter isotopes of the same element in a natural system and occurs as two types, either equilibrium or kinetic fractionation. The fractionation that occurs through photosynthetic pathways or metabolic pathways are primarily kinetic fractionation (Krueger & Sullivan, 1984; Lee-Thorp et al, 1989; Cerling & Harris, 1999).

The $\delta^{13}C$ of carbonate in the hydroxyapatite of herbivores is related to the vegetation they consume, as certain types of plants (C_3 or C_4 plants) have distinct $\delta^{13}C$ ranges due to their differing photosynthetic pathways (Tieszen & Boutton, 1989; Bocherens, 2015). The $\delta^{13}C$ is calculated by comparing the ratio of the stable isotopes of carbon (^{13}C and ^{12}C) of the sample to a laboratory standard (denoted by the "δ" for light stable isotopes; Britton, 2010). Although consistent fractionation occurs from plant to animal this can be relatively easily corrected for by adding -14.1‰ hydroxyapatite $\delta^{13}C$ values to obtain the plant $\delta^{13}C$ ($\delta^{13}C_{diet}$; Lee-Thorp et al, 1989; Cerling & Harris, 1999).

The $\delta^{18}O$ of carbonate and phosphate in hydroxyapatite precipitates in equilibrium with body water, and $\delta^{18}O$ is known to be directly correlated to the meteoric water temperature they ingest (Dansgaard, 1964). The $\delta^{18}O$ is calculated by comparing the ratio of the stable isotopes of oxygen (^{18}O and ^{16}O) of the sample to a laboratory standard (Britton, 2010).

Sequential intra-tooth sampling of tissue such as enamel or dentine can be used to see relative changes in stable isotopes over time (see Fig. 8; Chritz et al., 2009). The relative chronological changes in $\delta^{18}O$ typically illustrates seasonality at mid to high latitudes, as higher $\delta^{18}O$ values correlate with summer temperatures and lower $\delta^{18}O$ values with winter (Dansgaard, 1964; see Fig. 8). In the same fashion, $\delta^{13}C$ relative variations can be used to see changes in diet of the animal through time, and $\delta^{13}C$ and $\delta^{18}O$ can be combined to see if these dietary shifts co-occur

with different seasons (Zazzo et al., 2002; Zazzo et al., 2006; Chritz et al., 2009). Such analysis has been conducted by Chritz et al. (2009) on *Megaloceros giganteus* from Ireland.

1.3. *Diet Preferences*

The exact dietary preferences of *Megaloceros giganteus* have been debated in the literature, with different populations yielding seemingly contrasting results. Microwear analysis of the molars can give contrasting results depending on the population studied, with Scandinavian giant deer believed to be primarily browsers while the Irish population being more dependent on grasses (Hayden, 2000; Aaris-Sørensen & Liljegren, 2004). Aaris- Sørensen & Liljegren (2004) further note that the similarities in the dentition between *M. giganteus* and *Alces alces* strengthens the case for browsing preferences. Rivals & Lister (2016) noting that *M. giganteus* specimens from Britain during the mid and late Pleistocene show an equal amount of browsing and grazing in their diet. Given these alternative suggestions for their diet, Stuart et al., (2004) suggests a generalist diet given their molar morphology.

Isotopic analysis of Irish *M. giganteus* specimens revealed that the $\delta^{13}C_{diet}$ was in the range of −21.9 to −24.6‰, suggesting a diet consisting of grasses and forbs, supplemented by browsing the leaves of trees and shrubs (Chritz et al., 2009). This type of generalist feeding is common amongst cervids as it allows them to obtain enough nutrients for their annual antler growth. Accumulating all of the $\delta^{13}C$ as well as nitrogen isotope ratio ($\delta^{15}N$, another commonly used isotope for diet reconstruction; Bocherens, 2015) of *M. giganteus* from multiple sites in Eurasia from Marine Isotope Stage 3 to the Holocene (57,000 – 7,600 BP) demonstrate the variability of this animal's diet through space and time (see Fig. 3). Collagen $\delta^{13}C$ and $\delta^{15}N$ were converted to their dietary isotopic values ($\delta^{13}C_{diet}$ & $\delta^{15}N_{diet}$) through the fractionation corrections suggested by Lee-Thorp et al. (1989) and Bocherens (2015).

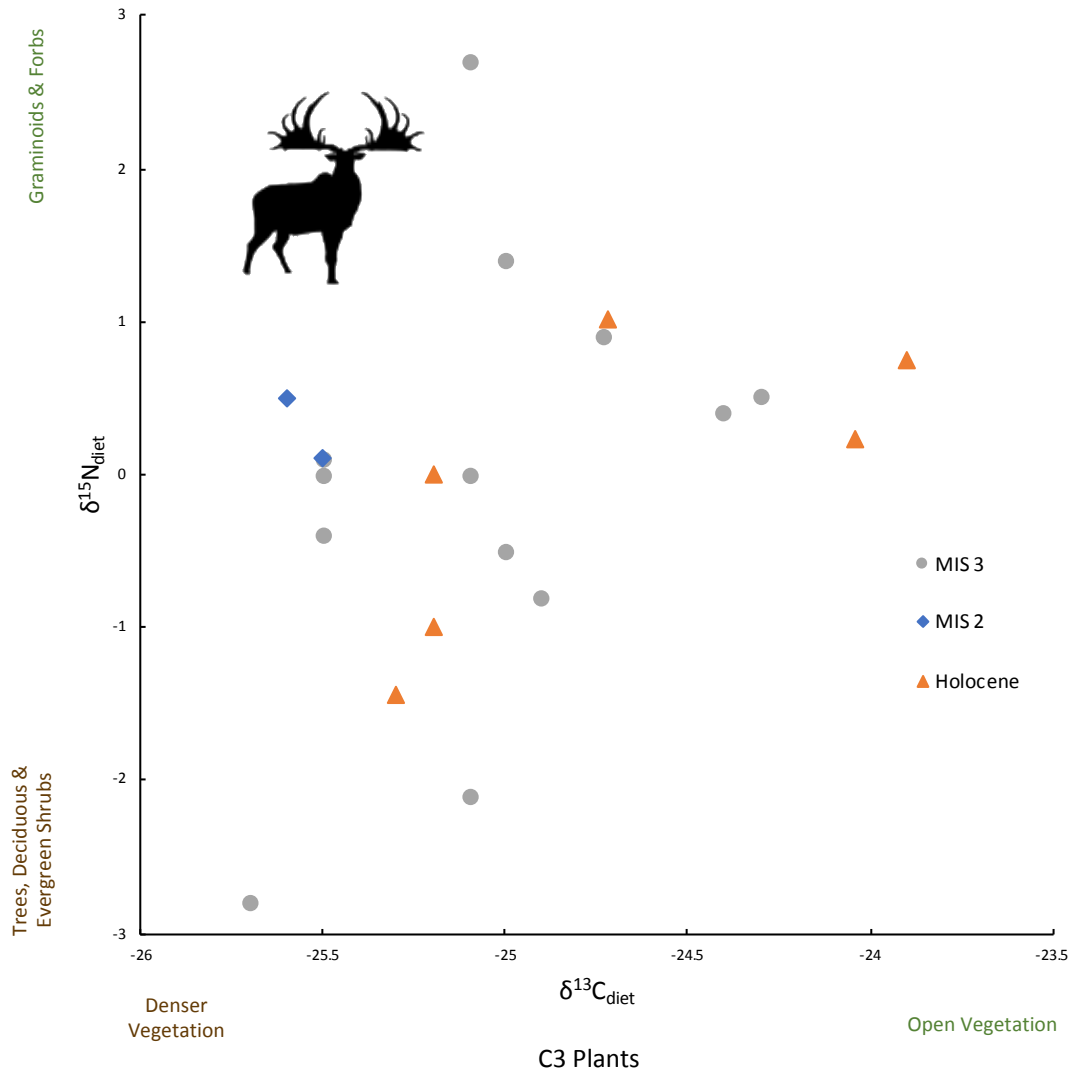**Fig. 3.** All $\delta^{13}C_{diet}$ and $\delta^{15}N_{diet}$ data from *Megaloceros giganteus* remains across Eurasia from MIS 3 to the Holocene (57,000 – 7,600 BP; n=22; see Appendix Table 1).

Van Geel et al. (2018) discovered botanical remains imbedded in the deep molar folds of a *M. giganteus* specimen dated to 42,800 – 42,370 calibrated (1σ) ^{14}C a BP from the Zandmotor, the Netherlands. The botanical remains were predominantly comprised of *Artemisia* and other Asteraceae. Van Geel et al. (2018) further suggests that this preference for *Artemisia* in the diet of *M. giganteus* was due to the selective diet of the animal, as it may have prioritized plants with a high nutrient content to fuel antler growth. *Artemisia* species, specifically *A. norvegica* have a high calcium content, calcium and phosphorus being the key nutrients required for antler growth (Moen et al., 1999). It has

been observed in other cervids that they will eat certain types or certain parts of plants during particular times of the year in order to meet the nutritional requirements at a specific point in time, as well as gnaw on bone and antler remains (Wika, 1982; Halls, 1984; Barrette, 1985). It is likely that *M. giganteus* shared this feeding behaviour in order to grow their impressive set of antlers. Geist (1998) calculated that to grow 45 kg antlers each year a *M. giganteus* stag would require a diet containing at least 3.45% protein, 0.44% CaO (0.32% Ca) and 0.37% P_2O_5 (0.15% P). This concentration of nutrients can be obtained if selective feeding strategies are employed, Geist (1998) suggested that eating specific parts of

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Betula would have sufficed for stags. Species of *Artemisia* are also known to have nutrient contents exceeding the requirements suggested by Geist (1998) (Klein, 1965; Ashraf et al., 2010; Van Geel et al., 2018).

1.4. *Range & Habitat Preferences*

Megaloceros giganteus remains can be found within Eurasia both in glacial and interglacial deposits (Bradshaw et al., 2003), therefore ascribing these animals to a particular biome is difficult. Lister & Stuart (2019) state that this animal cannot be described as a typical member of the mammoth steppe biome, the cold and dry high productivity grasslands that were widespread during the last glacial maximum (Zimov et al., 2012). *M. giganteus* is completely absent in the Siberian and northern Asian mammoth steppe, as opposed to the commonly found woolly mammoth (*Mammuthus primigenius*; Blumenbach, 1799), woolly rhinoceros (*Coelodonta antiquitatis*; Blumenbach, 1799) and steppe bison (*Bison priscus;* Bojanus, 1827). These animals being typically associated with the mammoth steppe (Kahlke, 1999). Instead, *M. giganteus* likely preferred what Lister & Stuart (2019) calls a "boreal parkland"*,* habitats where steppic-tundra conditions were present to the north and desert to semi-desert conditions to the south. Such conditions were present throughout the last glaciation and consisted of scattered *Pinus* or *Picea* (also possibly some boreal summergreen trees) in a relatively open environments supporting grasses, sedges, *Artemisia, Ephedra* and *Chenopodiaceae* (Allen et al., 2010). This type of habitat would have allowed for their generalist diet and would also allow for the selective feeding habits that is required for antler growth (Lister & Stuart, 2019).

In contrast, *M. giganteus* from interglacials such as the Eemian or Holstein, would have been surrounded by more closed environments that would allow for generalist feeding strategies (Brewer et al., 2008; Allen et al., 2010). *M. giganteus* from the Eemian interglacial (130,000 – 115,00 BP; MIS 5e) are also known to have had stouter limb bones and possibly more vertical antlers (Lister, 1994; Van der Made, 2006). This may have been an adaptation for coping with more closed forest conditions of the last Interglacial. Those of the Late Glacial had comparatively longer and slender limb bones and the more horizontal antlers that the species is famous for (Lister, 1994; Van der Made, 2006).

The evidence for the more vertical orientation of antlers in connection to more forested environments is limited by the lack of comparable specimens, as the different subspecies *M. g. giganteus* and *M. g. ruffii* have been suggested to be subspecies that inhabited more open and closed environments respectively (Lister, 1994; Vislobokova, 2013). *M. g. ruffii* specimens, while mainly found in Eemian interglacial deposits has also been observed in sediments alongside cold adapted species such as woolly mammoth and woolly rhinoceros (Lister, 1994; Vislobokova, 2013). Therefore, it is difficult to simply suggest one subspecies is associated with glacial or interglacial conditions, however such variation of antler morphology in response to vegetation density has been observed in *Alces alces* and *Rangifer tarandus* suggesting this response to environmental change is possible (Lister, 1994). It could also be possible that the extent of palmation was a response to warmer or colder climates as increased palmation would create wider surface area for heat loss for *M. g. ruffii* and less palmation in *M. g. giganteus* allowing for less heat to be loss, especially during velvet. While this relationship is observed between modern bovid horn morphology and temperature, Picard et al. (1996) finds this unlikely for cervids as they shed their antlers coming up to the coldest months of the year and thus are not affected by increased heat loss and with increased palmation.

Generally throughout the mid and late Pleistocene, *M. giganteus* would typically have been exposed to open or semi-open environments, judging by their molar microwear patterns (Saarinen et al., 2016).

1.5. *Irish population*

As mentioned previously, the "standard" for *Megaloceros giganteus* is the Irish population. Typically Irish *M. giganteus* specimens date back to the Late Glacial, specifically the late Allerød interstadial and onset of the Younger Dryas (approximately 13,600 - 12,600 BP) and are commonly preserved in marl deposits overlain by peat (Monaghan, 2017; Lister & Stuart, 2019; seeFig. 4).

It is unclear exactly how Ireland became populated with giant deer, one of the oldest *M. giganteus* specimens found in Ireland dates back to 41,859

(+5,099, -3,633) cal BP from Castlespook cave, Co. Cork (Woodman et al., 1997; Monaghan, 2017; Lister & Stuart, 2019) and suggests that Irish population was already present from the MIS 3 (57,000 - 29,000 BP) onwards. However, During the Last Glacial Maximum (23,300 – 17,500 BP) Ireland was probably completely covered by ice, thus this older Irish population surviving until the Late Glacial seems unlikely (Lister & Stuart, 2019). Therefore, it is suggested that the Late Glacial population recolonised Ireland as opposed to having persisted there. British *M. giganteus* date back to the Bølling (14,700 – 14,100 BP), and specimens found on the Isle of Man date to both the Bølling and Allerød (Lister & Stuart, 2019). Thus, it is suggested that the Irish *M. giganteus* population likely re-entered during the Allerød (13,900 – 12,900 BP) through Britain.

The dietary preferences of this population are noticeably different from that of other populations as mentioned previously. Saarinen et al. (2016) compared this Irish population to those from other parts of Europe, and noted that grazing was a far larger part of their diet. This is also suggested by the isotopic study by Chritz et al. (2009) with grazing being the primary diet, supplemented by browsing. This diet corresponds to the vegetation cover present in much of Ireland during the late Allerød, with *Betula* stands and *Helianthemum* being present in scattered assemblages with a predominance of open grasslands and herbs, corresponding to the "Gramineae Assemblage" (Watts, 1977; Van Asch & Hoek, 2012; see Fig. 4). This resembles the boreal parkland habitat discussed earlier where much of European *M. giganteus* specimens have been found, but with a higher dominance of open grasslands (Allen et al., 2010). However, as mentioned by Watts (1977) there is little evidence to suggest that *Betula* woodland established itself during the Late Glacial in Ireland. This may be due to *M. giganteus* being so common that they stripped establishing woodlands on the island, likely to eat specific parts of the plant for concentrated nutrient uptake. Watts (1977) also suggests that this may be due to the windy conditions present in Ireland, due to its exposure to the Atlantic Ocean. This may explain why although tree birch was present in Ireland during the Bølling and Allerød, there is still a predominance of grazing in the diet of Irish *M. giganteus* specimens.

During the subsequent cold period; the Younger Dryas (12,900 – 11,700 BP; see Fig. 4), the deterioration of vegetation cover over much of Western Europe lead to a peak of *Cruciferae* in Ireland, signalling the degradation of grasslands. The climate cooled towards arctic-alpine conditions, observed as an *Artemisia* phase (Watts, 1977; Barnosky, 1986). *Juniperus* and *Empetrum* disappear from the Irish pollen record, *Betula* and grasses become less abundance and dwarf *Salix* becomes dominant.
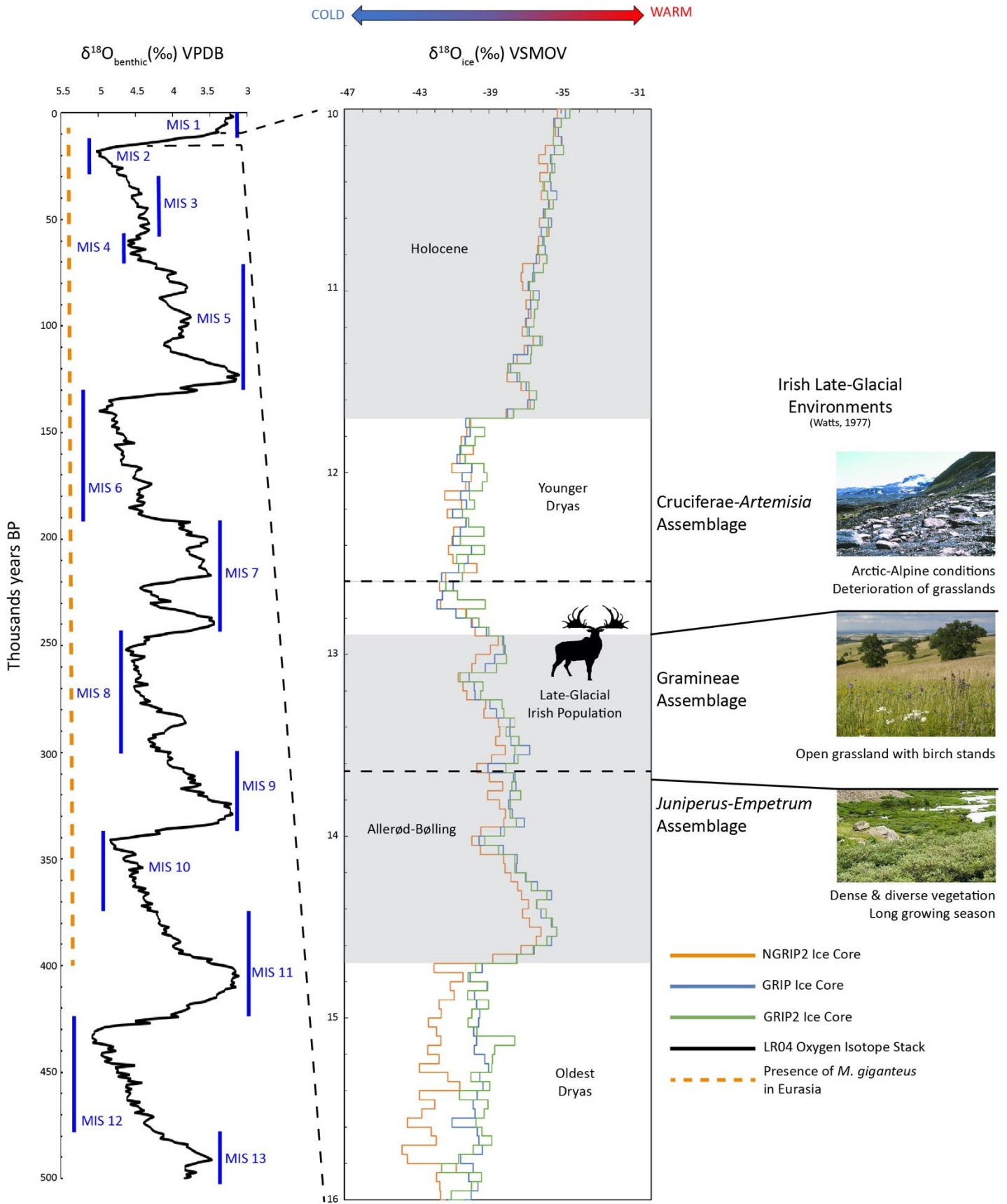
Fig. 4. Marine Isotope Stages (MIS) and benthic carbonate oxygen isotope data (Lisiecki & Raymo, 2005) and Greenland ice core chronology (Rasmussen et al., 2014) of the Pleistocene late-glacial with vegetation assemblages and environments described by Watts (1977) and Barnosky (1986). Shaded areas reflect interstadials and the Holocene defined by Rasmussen et al. (2014).

1.6. *Extinction*

The latest known *Megaloceros giganteus* found in Ireland dates back to the Younger Dryas, and the species as a whole is believed to have gone extinct in the Holocene about 7,600 cal BP in the Urals (Lister & Stuart, 2019). The expiration of the Irish population is likely caused by the climatic turndown of the Younger Dryas, where their preferred vegetation was no longer available. The generalist diets of *M. giganteus* would have made them particularly vulnerable to the onset of this cold phase, as the variety of palatable plants they required were not available to them (Chritz et al., 2009; Van Geel et al., 2018; Lister & Stuart, 2019). The semi-open mixed grasslands that *M. giganteus* thrived in during the Allerød were then replaced by arctic tundra environments in the Younger Dryas (Watts, 1977; Barnosky, 1986), which were not productive enough to support their high nutrient requirements (Chritz et al., 2009; Van Geel et al., 2018).

This lack of palatable plants would have made it difficult for *M. giganteus* stags to replenish the calcium and phosphorus needed for antler growth, and thus the large size that had been sexually selected for would have been a disadvantage (Moen et al., 1999). This contrast between smaller size selection and sexual selection may have caused the extinction of the Irish population. However, Worman & Kimbrell (2008) suggest that the situation may have been more dire for *M. giganteus* does, as the lower productivity and shorter growing season would have lowered fecundity by 50%, below the threshold of population survival. Barnosky (1985) compared *M. giganteus* specimens from Ballybetagh, Co. Dublin to giant deer from other Irish localities and noted a statistically significant size reduction of 2% in the Ballybetagh specimens. Barnosky (1986) suggests that this may represented the necessary downsizing of *M. giganteus* during the Younger Dryas. Lister & Stuart (2019) note that the dating of these specimens is not very accurate so ascribing them to the Younger Dryas specifically is difficult.

Under these lower nutrient conditions, downsizing would be the natural direction in order to cope. However, this natural selection of smaller individuals would have not been totally advantageous, as Worman & Kimbrell (2008) explain that the predators of Ireland during this time would have made it unfavourable to become smaller and therefore an easier target. Some of the predators that are known from Ireland during this time are wolves (*Canis lupus*; Linnaeus, 1758) and brown bears (*Ursus arctos*; Linnaeus, 1758) (Monaghan, 2017). Competition from other cervids such as reindeer (*Rangifer tarandus*; Linnaeus, 1758) would have also selected against downsizing (Monaghan, 2017).

Human hunting has also been suggested as a possible extinction cause, as it was until recently believed that humans did not arrive in Ireland until the 10,290 – 9790 cal BP (Bayliss & Woodman, 2009). However, the discovery of an brown bear patella with seemingly anthropogenic cut marks made by humans dating to 12,800 – 12,600 cal BP in Alice Cave, Co. Claire may suggest otherwise (Dowd & Carden, 2016). Dowd & Carden (2016) suggest that this group of humans was likely just "visitors" and represents a small scale human population event in Ireland. As well as this, no *M. giganteus* bones in the Natural Museum of Ireland demonstrate any signs of butchery, bar one worked antler dating to the Allerød which has been determined to have been found and altered by humans well after the Irish *M. giganteus* extinction (Barnosky, 1986; Tierney et al., 2010). Therefore, the influence of human activity on the Irish giant deer was likely insignificant to their extinction.

2. Evidence for Migrational Behaviour in *Megaloceros giganteus*

Migrational behaviour has been suggested previously by Vislobokova (2012), suggesting that during glacials, *Megaloceros giganteus* may have migrated north into periglacial tundra–steppe in the summer from southern boreal forests or forest-steppes and migrated to the southern part of their range in the winter. This migrational behaviour may have been sparked due to the preferred temperature range of this animal and more specifically, their dietary requirements of antler growth, female pregnancy and growth in general.

Regarding Irish specimens specifically, Barnosky (1985) notes that the low land topography of the Ballybetagh site would have been sought after by overwintering males after they separated from the females after the rutting season. This is because Ballybetagh was a sheltered lowland that also had accessibility to water at the time the *M. giganteus* were

present, and during the winter months this may have been more suitable for them as opposed to other, more open and exposed areas elsewhere.

Studies on the morphology of *M. giganteus* metapodia suggest that even the longer limbed *M. giganteus* from Ireland had relatively short limbs compared to other ungulates of a similar body size (Lister, 1994). Similar limb proportions can be observed in *Rangifer tarandus,* suggesting that *M. giganteus* may have been adapted for a cursorial lifestyle similar to *R. tarandus* (Geist, 1986; Vislobokova, 2012). The similarities in cursorial limb proportions may suggest that it was possible for *M. giganteus* to migrate considerable distances, as Grant's caribou (*R. tarandus granti*; Allen, 1902) are known to undertake the longest terrestrial migration of >4000km (Geist, 1986; Gunn et al., 2009).

2.1. *Temperature Stress*
Noted by Lister & Stuart (2019), judging by the range and faunal assemblages to which *Megaloceros giganteus* are discovered, it cannot be considered part of the typical "mammoth steppe" fauna. *M. giganteus* was not adapted for the cold conditions present during the coldest parts of the glacials compared to mammoth or woolly rhinoceros and was likely restricted to the semi-open boreal parklands found south of the steppe. In contrast to this, *M. giganteus* is more commonly found in interglacial deposits throughout Eurasia and typically found with interglacial fauna such as straight-tusked elephant (*Elephas/Paleoloxodon antiquus;* Falconer & Cauntley, 1847), hippopotamus (*Hippopotamus amphibius*; Linnaeus, 1758) and wild boar (*Sus scrofa*; Linnaeus, 1758); Vislobokova, 2012).

Migrational behaviour during the cold periods of the last glacial would have been a means for *M. giganteus* to avoid extreme winter temperatures by moving towards the southern extent of its range. Migrational behaviour during interglacials on the other hand may not have been as necessary. This temperature induced migration may be similar to what Barnosky (1985) mentions with low-land sheltered areas being sought after by *M. giganteus*.

2.2. *Dietary Stress*
As mentioned previously, the diet of *M. giganteus* varies depending on the population studied (see Fig.

3). The overarching conditions are a high nutrient diet that prioritises certain plants and/or certain parts of them (Geist, 1986; Van Geel et al., 2018). This highly selective diet may have caused *M. giganteus* to have to travel considerable distances to obtain enough of these high nutrient foods.

The seasonal loss of broad leaf forest vegetation would have likely forced *M. giganteus* to search for alternative sources of food, such as herbaceous plants like *Artemisia* (Vislobokova, 2012; Van Geel et al., 2018; Lister & Stuart, 2019). During the warmer months when productivity was highest, *M. giganteus* may have prioritised the budding parts of certain plants, which contain some of the highest concentrations of nutrients both from the boreal forest environments as well as in the more open border of the steppe (Vislobokova, 2012; Van Geel et al., 2018). This plasticity of diet would have allowed *M. giganteus* to more consistently obtain enough nutrients throughout the year. Similar strategies are seen in *Rangifer tarandus* and require a somewhat mobile lifestyle so that they can be there when the new, high nutrient food sources are available (Bjørkvoll et al., 2009; Vislobokova, 2012). Similar to *R. tarandus*, this mobility would allow them to infiltrate adjacent biomes and thus collect the dietary variety they require, from southern boreal forests to periglacial tundra–steppe (Vislobokova, 2012).

In the late Allerød and Younger Dryas onset, shifts in seasonality were more extreme then preceding interstadial conditions (Watts, 1977; Van Asch et al., 2012; see Fig. 4). This may have also forced *M. giganteus* to adopt a migratory behaviour, as the phenology of plants were likely more pronounced and thus be more spatially and temporally restricted (Martin et al., 2018).

2.3. *Isotope Research*
Intra-tooth isotopic research on *Megaloceros giganteus* tooth enamel sequential samples conducted by Chritz et al. (2009) displays sinuosity in the oxygen isotope ratio ($\delta^{18}O$) signal, likely reflecting seasonal changes the meteoric water temperature over time (see Fig. 8). It is noted that the sinuosity of specimen NMING:F7913 and NMING:F20514 is not as pronounced in comparison to the other specimen studied that displays a relatively stronger sinuosity in its $\delta^{18}O$ signal (between -5.4‰ and -1.8‰). This less

pronounced signal may be an effect of what Britton et al. (2009) describes as a "dampening" effect on the $\delta^{18}O$ signal. This occurs as the animal's rapid migration into different oxygen zones overprints the local seasonal $\delta^{18}O$ signal which is likely trending in the opposite direction, creating a smaller $\delta^{18}O$ range (Pilaar Birch et al., 2016). This may suggest that this particular specimen was migrating far enough to be in noticeably different $\delta^{18}O$ zones seasonally in Ireland, which are currently present across Ireland as $\delta^{18}O$ values become more depleted in a north easterly direction (Darling et al., 2003; Britton et al., 2009; Pellegrini et al., 2016). The less pronounced seasonal variation in certain specimens is also strange considering that the difference in seasonal temperatures during the late Allerød and Younger Dryas onset would have been quite large, perhaps more similar to the $\delta^{18}O$ produced by NMING:F21647 (Watts, 1977; Denton et al., 2005; Van Asch et al., 2012).

Analysis of $\delta^{18}O$ variations in individual molars of red deer and caprids from late Pleistocene deposits in Croatia demonstrate that migrational red deer display a $\delta^{18}O$ variation as low as 1-2‰, compared to non-migrational caprids with variation in the range of 3-4‰ (Pilaar Birch et al., 2016). Studies on non-migratory red deer from Scotland display a variation of around 3-4‰, while migrational caribou display variation as low as 1‰ (Britton et al., 2009; Stevens et al., 2011). Specimen NMING:F7913 $\delta^{18}O$ variation is 1.1‰ for M2 and 1.6‰ for M3, such low variation may suggest this particular individual's seasonal mobility. Specimen NMING:F20514 M2 range is only 0.8‰, but has a M3 range of 2.6‰ and makes it difficult to suggest this specimen underwent long distance migration. Such specimens would therefore be interesting to analyse further as they show a possible line of evidence for migrational behaviour.

The $\delta^{13}C_{diet}$ of these specimens was also researched by Chritz et al. (2009). The range of $\delta^{13}C_{diet}$ details a mainly C_3 plant diet. However, variations in the C_3 plant $\delta^{13}C_{diet}$ range may detail changes in the diet of these *M. giganteus* specimens through time. Typically woody C_3 vegetation contains lower $\delta^{13}C$ values than herbaceous C_3 vegetation in open environments (Tieszen & Boutton, 1989; see Fig. 3).

The case could be made that variations in the $\delta^{13}C$ may display a shift in diet seasonally, as more closed woody environments (with lower $\delta^{13}C$ values) may have been sought after during colder seasons of the year. Conversely, during the warmer seasons, the higher $\delta^{13}C$ values indicate a preference for open herbaceous environments, similar to the suggestion by Vislobokova (2012). This correspondence of $\delta^{13}C$ and $\delta^{18}O$ values can be observed in specimen NMING:F21647 and F7913 but not so expressively. It should be noted however that variations in $\delta^{13}C$ in C_3 plants can also be created through other means, such as C_3 plants growing in a water stressed environment which results in them having more positive $\delta^{13}C$ values (Farquhar et al., 1989) or lower temperatures causing less isotopic discrimination (Körner et al., 1991).

Nevertheless, the variation within the molar samples of specimens may still suggest a seasonal variation in the diet of 2 of the individuals studied by Chritz et al. (2009). This shift in diet may be linked to certain environments that they inhabit at certain times of the year, such as more closed and open habitats. Similar strategies are adopted by extant cervids such as red deer which move from woodlands to open areas seasonally (Bützler, 2001; Vislobokova, 2012; Trepet & Eskina, 2017). However, it should be noted that during the late Allerød and Younger Dryas onset Ireland likely did not have large forested areas, but rather sparse stands of *Betula* as opposed to woodland (Watts, 1977). Likely with minimum $\delta^{13}C$ values around -24.6‰, this movement was probably towards more shrubland or semi-open environments as opposed to unlikely closed forest environments as dense forest vegetation can have much lower values of -27‰ and lower (Tieszen & Boutton, 1989; Bocherens, 2015).

Due to the above mentioned stresses and isotopic evidence, the study of specimens from Irish localities is suggested. Specifically, the 3 specimens from Ireland (Table 1) from the Late Glacial population that were previously studied by Chritz et al. (2009) for $\delta^{13}C$ and $\delta^{18}O$ should be analysed further through different isotope systems in order to further uncover evidence of seasonal migrational behaviour. The base of knowledge built up by Chritz et al. (2009) on these

specific specimens would allow for more conclusions to be drawn on analytical results.

3. Materials & Methods
3.1. *Specimens and Localities*

All three *Megaloceros giganteus* specimens that are suggested to be analysed come from the National Museum of Ireland Natural History collection. These specimens have been previously analysed for both the $\delta^{18}O$ and $\delta^{13}C$ isotopic composition through sequential enamel samples by Chritz et al. (2009). The collection numbers of these specimens are NMING:F21647, NMING:F7913 and NMING:F20514. The use of these specimens will allow for the direct correlation between the previously analysed $\delta^{18}O$ signal and any

new isotopic signal from this study. These specimens were selected by Chritz et al. (2009) based on factors such as their age, quality of their enamel preservation and for minimal tooth wear although post eruption wear led to some tooth height loss. Upper molars were selected by the researchers as this research was interested in the annual cycle of antler shedding in males, thus upper molars were utilised to have a concrete connection between the molar's oxygen cycle, cementum accretion and antler cycle. Based on the analysis by Chritz et al. (2009), information such as the supposed age of death of the specimens can be given. Details on the specimens can be found in Table 1 and images in Fig. 5.

Table 1.

Information on the *Megaloceros giganteus* specimens previously analysed by Chritz et al. (2009) that are suggested for analysis. Age, season of first accretion and season of death interpreted from the M2 as the M2 is seen as more reliable compared to the M3 due to its formation at birth (Reimers & Nordby, 1968; Chritz et al., 2009; Klevezal, 2017). Images of the skulls Fig. 5 and locations in Fig. 6.

Specimen (NMING:)	County	Location No.	Locality	Antler Cycle	Age (months)	Season of first accretion	Season of Death
F7913	Dublin	1	Ballybetagh	Shed one antler, one partially shed	96-100	Summer	Early Summer
F20514	Wicklow	2	Castleruddery Lower Townland	Both antlers intact	126	Partial Summer	Late Summer/Autumn
F21647	Donegal	3	Mountcharles Townsland	Both antlers intact	84	Summer	Late Winter

As mentioned previously, most specimens from Ireland date to the late Allerød and beginning of the Younger Dryas and this age range is suspected for these specimens as well (Chritz et al., 2009; Monaghan, 2017; Lister & Stuart, 2019). This can be confidently said thanks to the environments in which they were found. As the older specimens (dating back to MIS 3) have only been found in cave deposits with other Pleistocene megafauna such as woolly mammoth and cave hyena (*Crocuta crocuta* (Erxleben, 1777); Woodman et al., 1997; Monaghan, 2017; Lister & Stuart, 2019). Considering all these specimens were found in marl deposits under peat, it is therefore assumed that all of these specimens range from the late Allerød to beginning of the Younger Dryas. However, no carbon dating has been conducted on these specimens thus making concrete conclusions is impossible. While the debate about whether these

specimens are from the late Allerød and start of the Younger Dryas is somewhat futile, exactly where within this time range is difficult to establish. The analysis of $\delta^{18}O$ conducted by Chritz et al. (2009) notes unusually high values compared to modern Irish fallow deer and red deer from the same study. Chritz et al. (2009) suggests this may be due to the meteoric water $\delta^{18}O$ signal being affected by longer residence times of lake water due to the particularly dry Younger Dryas conditions. Similar signals have been documented in soil sequences dating to the Younger Dryas in Ireland as well (O'Connell et al., 1999). $\delta^{13}C$ data from these specimens suggest a water stressed degrading environment which could further suggest an allocation to the colder Younger Dryas stadial (Farquhar et al., 1989; Chritz et al., 2009).

Fig. 5. All *Megaloceros giganteus* skulls used for analysis anterior view (left) and dorsal view (right). First row is NMING:F21647, second row NMING:F20514 and last row NMING:F7913.
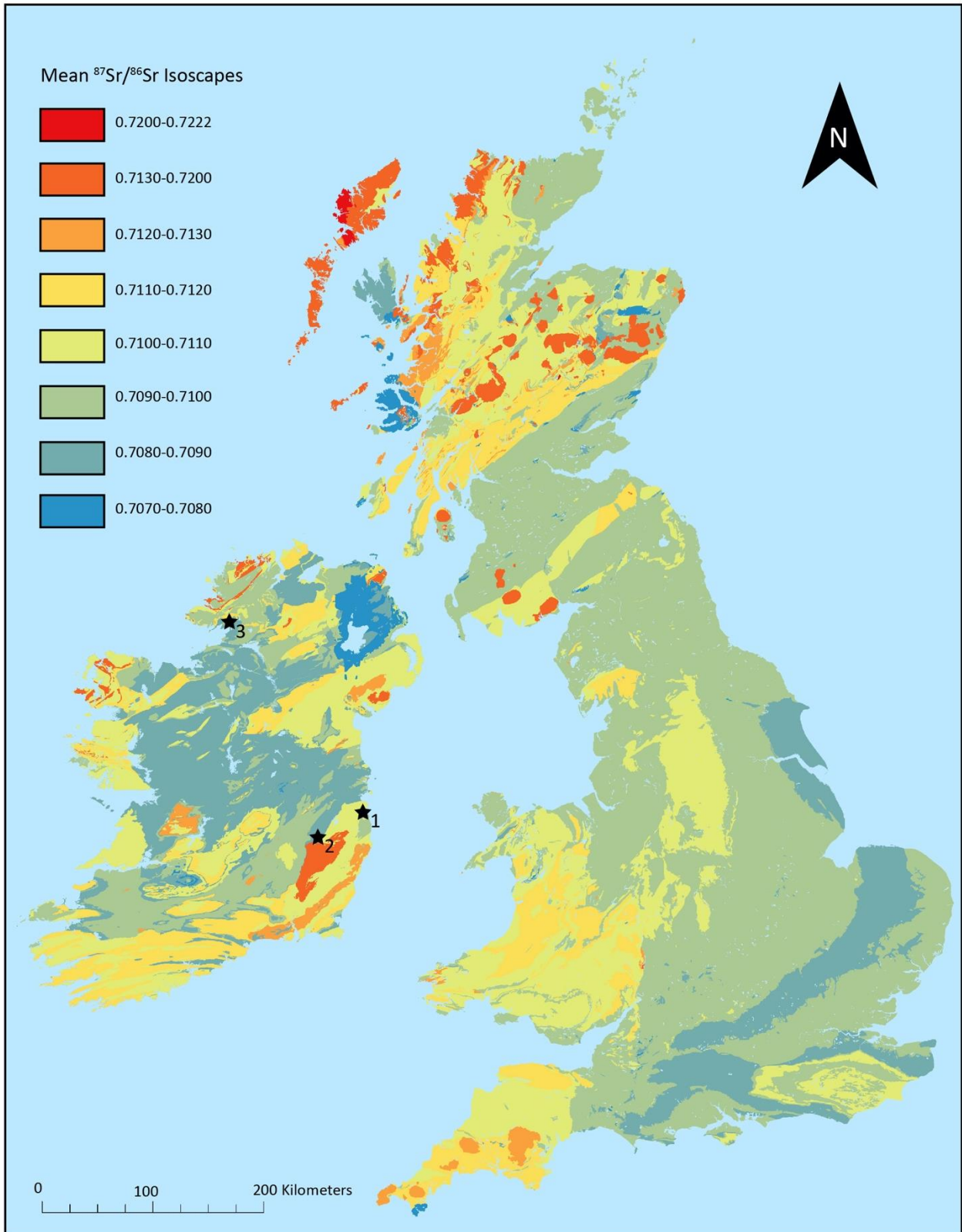
Fig. 6. Mean Bioavailable Strontium isotope ratio map (BASR map) of Ireland and Britain generated through ArcMap 10.8 including the locations of the three analysed specimens from Table 1. Location 1 is Ballybetagh, a famous location where more than 100 skulls have been excavated (Barnosky, 1985). Adapted from Evans et al. (2010), Snoeck et al. (2018) and Snoek et al (2020). British map based upon BGS Geology 625k, with the permission of the British Geological Survey.

3.2. *Methodologies*
3.2.1. *Strontium Isotope Analysis*

In order to observe possible migrational behaviour, the analysis of the strontium isotope ratio ($^{87}Sr/^{86}Sr$) is recommended. $^{87}Sr/^{86}Sr$ analysis has been implemented previously in order to study past migrational behaviour in Pleistocene megafauna such as woolly mammoths as well as Pleistocene and modern reindeer populations (Hoppe et al., 1999; Hoppe & Koch, 2007; Britton et al., 2009; Britton et al., 2011; Price et al., 2017; Gigleux et al., 2019). Strontium is taken up into the animal's body through the vegetation that they ingest, and the ratio between the two different isotopes does not fractionate as it moves through the food chain (Hurst & Davis, 1981; Slovak & Paytan, 2012). The $^{87}Sr/^{86}Sr$ ratio of the plant is mainly determined by the underlying geology, with the ^{87}Sr in rocks forming over time due to the radioactive decay of rubidium (^{87}Rb). This makes the relative content of ^{87}Sr to ^{86}Sr determined by both the age of the rock and how much Rb was originally present in the underlying bedrock (Faure, 1977). Thus, generally older geological structures will have a higher $^{87}Sr/^{86}Sr$ value. The Sr readily substitutes for calcium and is deposited in hydroxyapatite crystal in animal tooth enamel and bones when ingested (Comar et al., 1957; Slovak & Paytan, 2012; see Fig. 7).

In tooth enamel, the $^{87}Sr/^{86}Sr$ values are those that have been taken up during the infancy of the animal, as this is when the enamel forms. Once the enamel has been completely mineralised, the $^{87}Sr/^{86}Sr$ ratio is not altered (Hillson, 1996; Slovak & Paytan, 2012). In contrast, bone collagen is constantly remodelled through the lifetime of the animal, and the $^{87}Sr/^{86}Sr$ ratio from bone largely reflects the location that the animal lived at the final point of its life (Sealy et al. 1991).

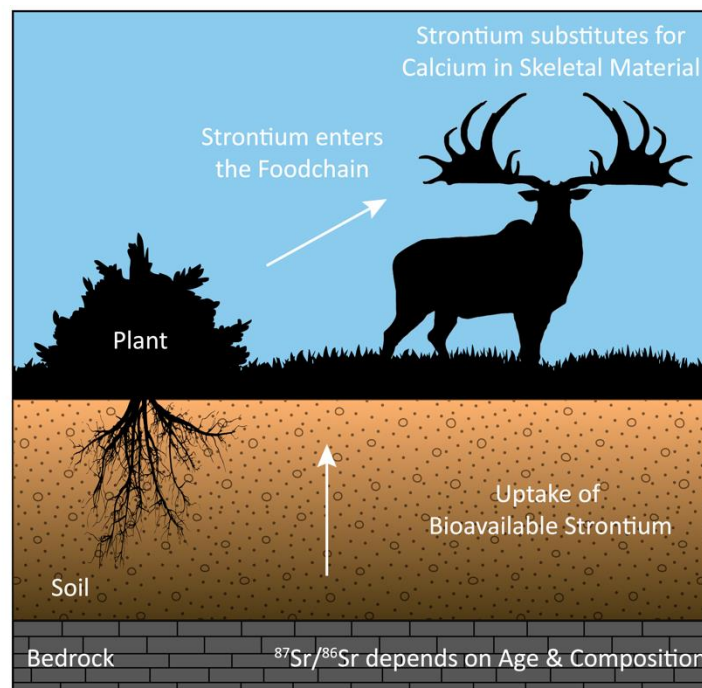**Fig. 7.** Summary of bioavailable strontium uptake in *Megaloceros giganteus*.

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Once a $^{87}Sr/^{86}Sr$ ratio is obtained from the *M. giganteus* enamel, this ratio can then be compared with the bioavailable $^{87}Sr/^{86}Sr$ map (BASr map) for Ireland. As mentioned previously the bioavailable $^{87}Sr/^{86}Sr$ values are a function of the underlying geology, and this can be seen in Fig. 6 however, rainfall, dust, and to a lesser extent surficial sedimentary deposits also likely affect these ratios (Snoeck et al., 2020). The bedrock of the island is mainly composed of Palaeozoic rock with some rare Mesozoic outcrops and with large lava flow basalt outcrops from the Tertiary in Co. Antrim (Holland & Sanders, 2009) where very low $^{87}Sr/^{86}Sr$ are found 0.7061-0.7070. Carboniferous limestones cover much of the island leading to large areas with a $^{87}Sr/^{86}Sr$ value between 0.7071-0.7080, while at the southern margins of Ireland Devonian "Old Red" Sandstone ranges between 0.7101-0.7110 (Holland & Sanders, 2009; Snoeck et al., 2020). All three specimens are found in locations with $^{87}Sr/^{86}Sr$ values in the range of 0.7071-0.7110, the famous Ballybetagh locality having a local signal of between 0.70906-0.710135 (lower range detected in grasses and higher range detected in shrubs), based on the $^{87}Sr/^{86}Sr$ signal from the closest locality being 2.58 kilometres away (53.22545^{o}N, -6.24517^{o}E; Snoeck et al., 2020 additional information).

Due to the availability of an Irish and British BASr maps, the possibility to analyse both enamel and collagen and the previously applicability of $^{87}Sr/^{86}Sr$ isotopes in enamel to record migratory behaviour in mammals, it is suggested that $^{87}Sr/^{86}Sr$ isotope analyse is conducted on these specimens. The current isotopic data of these specimens can be confidently correlated with the new $^{87}Sr/^{86}Sr$ isotope data created from the same sampling lines made by Chritz et al. (2009) (see Fig. 8).

3.2.2. Sulphur Isotope Analysis

Also suggested in the literature to study seasonal migrational movements isotopically is the study of the sulphur isotope ($\delta^{34}S$). While not as commonly employed for this type of analysis as the $^{87}Sr/^{86}Sr$ isotope ratio, it has been applied in a number of studies for archaeological material (Richards et al., 2001; Fornander et al., 2008; Drucker et al., 2011; Nehlich et al., 2014). Similarly to strontium isotopes, sulphur isotopes are taken up into the animals body through the vegetation they ingest and the vegetation gets its sulphur through groundwater and the atmosphere (Newton & Bottrell, 2007; Nehlich, 2015). Plants are able to convert the inorganic sulphur from the environment into organic compounds which can then be taken up by herbivores. There is little to no fractionation of the isotopic composition between plant and herbivore (Britton, 2010; Nehlich, 2015). The sulphur is taking into an animal's body for the building of certain amino acids such as cysteine and methionine (Brosnan & Brosnan, 2006).

Sulphur isotopic variation is a function of the local hydrology, as the main positive values for $\delta^{34}S$ originate from oceanic soluble sulphate, sulphate in evaporites and sulphides in the form of reduced pyrites FeS_2. The marine sources of sulphur can influence the terrestrial isotopic composition through sea-spray, coastal precipitation and aerosols (Böttcher et al., 2007; Britton, 2010; Nehlich, 2015). These marine influences can effect terrestrial signals many kilometres inland (O'Dowd et al., 1997; Britton, 2010). Similarly with strontium, sulphur isotopic composition is also controlled by the region's underlying geology, although in terms of bioavailable sulphur it is not as significant a factor as precipitation/ground water and atmospheric sources (Newton & Bottrell, 2007; Britton, 2010; Nehlich, 2015). The concentration of sulphur bearing minerals such as pyrite in the underlying regional geology is a controlling factor on the local $\delta^{34}S$ signal, as well as the presence of oceanic sulphate evaporites (Böttcher, 2001; Britton, 2010; Nehlich, 2015).

For the research of the *Megaloceros giganteus* specimens mentioned previously, this methodology is not as applicable as $^{87}Sr/^{86}Sr$ isotope ratio analysis. Firstly, $\delta^{34}S$ analysis can only be conducted on collagen, either from dentine or bone material (Britton, 2010; Drucker et al., 2011; Nehlich, 2015). While this does not mean that any *M. giganteus* specimen could not be analysed in this way, it would mean that the $\delta^{13}C$ and $\delta^{18}O$ data collected by Chritz et al. (2009) could not be correlated with $\delta^{34}S$ collagen data. Secondly, while there is a $^{87}Sr/^{86}Sr$ isoscape map available for Ireland and Britain (Evans et al., 2010; Snoeck et al., 2018; Snoek et al., 2020; see Fig. 6), there does not appear to be any $\delta^{34}S$ map available for the Republic of Ireland, only a Northern Ireland $\delta^{34}S$ isoscape map is currently available (Stack & Rock,

2011). The use of the $\delta^{34}S$ isotope for mobility could be utilised on bone/dentine material, in conjunction with other isotopes such as $\delta^{13}C$ and $\delta^{18}O$ to see if there are distinct differences between the area where the specimen was exhumed and the isotopic data, similar to some archaeological studies (Richards et al., 2001; Fornander et al., 2008; Drucker et al., 2011; Nehlich et al., 2014). However, in the case of the specimens in question, the use of the $\delta^{34}S$ isotope to investigates seasonal mobility is not suggested.

3.2.3. Nitrogen Isotope Analysis

The $\delta^{15}N$ has been used in paleoecological reconstructions in order to make interpretations on food web dynamics and dietary preferences (Balasse et al., 2001; Bocherens et al., 1997; Bocherens, 2015). $\delta^{15}N$ values have been retrieved for *Megaloceros giganteus* before, typically from specimens found in cave deposits as they have excellent preservation (Bocherens et al., 1997; Bocherens, 2015; see Appendix Table 1). An accumulation of $\delta^{15}N$ and $\delta^{13}C$ has been generated for *M. giganteus* specimens throughout Eurasia from MIS 3 to the Holocene (see Fig. 3) in order to show the variability of *M. giganteus* diet. However, no $\delta^{15}N$ values have yet been published concerning the Irish Late Glacial population.

Nitrogen is taken up by the herbivore through their dietary intake, and the plants they ingest obtain their nitrogen through the soil. Certain plants take up atmospheric nitrogen through symbiotic relationships with fungi that grow on their roots (mycorrhizae), and these plants have consistently lower $\delta^{15}N$ values compared to plants that do not have such a symbiotic relationship that obtain their nitrogen directly from the soil (Kohl & Shearer, 1980; Hobbie et al., 2009). Plants with lower $\delta^{15}N$ values include trees and deciduous and evergreen shrubs, while higher $\delta^{15}N$ values correspond with grasses, sedges and forbs (Bocherens et al, 2015). This fractionation between different plant functional groups can therefore be used to help reconstruct the dietary intake of an animal in conjunction with $\delta^{13}C$ data and has been conducted for many different species found in the Pleistocene mammoth steppe (Bocherens et al., 1997; Bocherens, 2015). Irish Late Glacial *M. giganteus* being likely predominantly grazers may have high $\delta^{15}N$ values and lower $\delta^{13}C$ values (Bocherens et al, 2015; Bocherens, 2015).

Nitrate (NO^{-}_{3}) is the largest reservoir of nitrogen in soils, followed by nitrite (NO^{-}_{2}) and ammonia (NH_3) and are then assimilated into amino acids in the organism's body (Yoneyama, 1995). The actual $\delta^{15}N$ analysis looks at the nitrogen composition in the collagen protein of the fossil remains, and thus requires a high post-mortem preservation quality (Van Doorn et al., 2012; Bocherens, 2015).

This isotopic data could perhaps be used in conjunction with $\delta^{13}C$ obtained from the specimens studied by Chritz et al. (2009) to better understand seasonal shifts in diet, which may be linked to seasonal mobility. However, $\delta^{15}N$ analysis cannot be conducted on tooth enamel, similar to $\delta^{34}S$ analysis, and therefore could not be directly compared to the $\delta^{13}C$ and $\delta^{18}O$ data (DeNiro & Epstein, 1981; Balasse et al., 2001). $\delta^{15}N$ is restricted to collagen and therefore could be done on the bone or dentine material of the specimens, however the question becomes what information would this analysis yield? As bone is constantly remodelled throughout the lifetime of the animal, it may help in determining the diet of the animals near the time of their death. The $\delta^{15}N$ values can then be compared season of death based on the cementum accretion analysis conducted by Chritz et al. (2009) (see Table 1). This $\delta^{15}N$ value could in theory be compared to dentine collagen, which is deposited early in the animal's life and is thought not to remodel once deposited (Balasse et al., 2001; Reynard & Tuross, 2015; Zazzo et al., 2006). It should be noted that this would be heavily affected based on which molar dentine is analysed. A suckling signal may be detected which would have cause an enrichment in $\delta^{15}N$ due to the higher protein milk compared to the normal herbivorous diet of the animal. With *M. giganteus's* brachydont molars (typical for cervids) the window of time that is preserved in dentine is smaller compared to a hyposodont molar, thus a longer suckling signal may be expected in the dentine of brachydont herbivores (Balasse et al., 2001). This may create complications for the comparison between the $\delta^{15}N$ values of bone collagen. Nevertheless, for the analysis of these particular molars, the applicability of the $\delta^{15}N$ isotope is limited and not suggested.

3.3. Analysis Procedures and Techniques
3.3.1. Sampling technique

Enamel is sequentially mineralised from the apex to the dentine-root junction (also known as the cervix), and once the enamel has been mineralised there is little or no remodelling (Gadbury et al., 2000; Balasse et al., 2003). By taking multiple samples through the enamel cusp of a tooth sequentially, short term isotopic variations can be seen throughout the tooth that reflect shifts in isotopic composition through time (Gadbury et al., 2000; Balasse et al., 2003; Britton et al., 2009; Chritz et al., 2009). This may be used in conjunction with the oxygen isotope ($\delta^{18}O$), allowing for the spatial variation demonstrated by the $^{87}Sr/^{86}Sr$ to be correlated with the summer/winter variation in the $\delta^{18}O$ values. Although it should be noted that phosphate group oxygen is less prone to diagenetic alteration than carbonate oxygen, but the carbonate group was utilised by Chritz et al. (2009) (Iacumin et al., 1996; Kohn et al., 1999). This combination has been utilised before for the study of reindeer migrations from the late Holocene and modern populations (Britton et al., 2009; Gigleux et al., 2019). Both $\delta^{18}O$ and $\delta^{13}C$ isotope values are given as permil (‰) and expressed as ratios of the heavier isotope to the lighter isotope, relative to Vienna Pee Dee Belemnite (V-PDB) for both carbon and oxygen by Chritz et al. (2009)
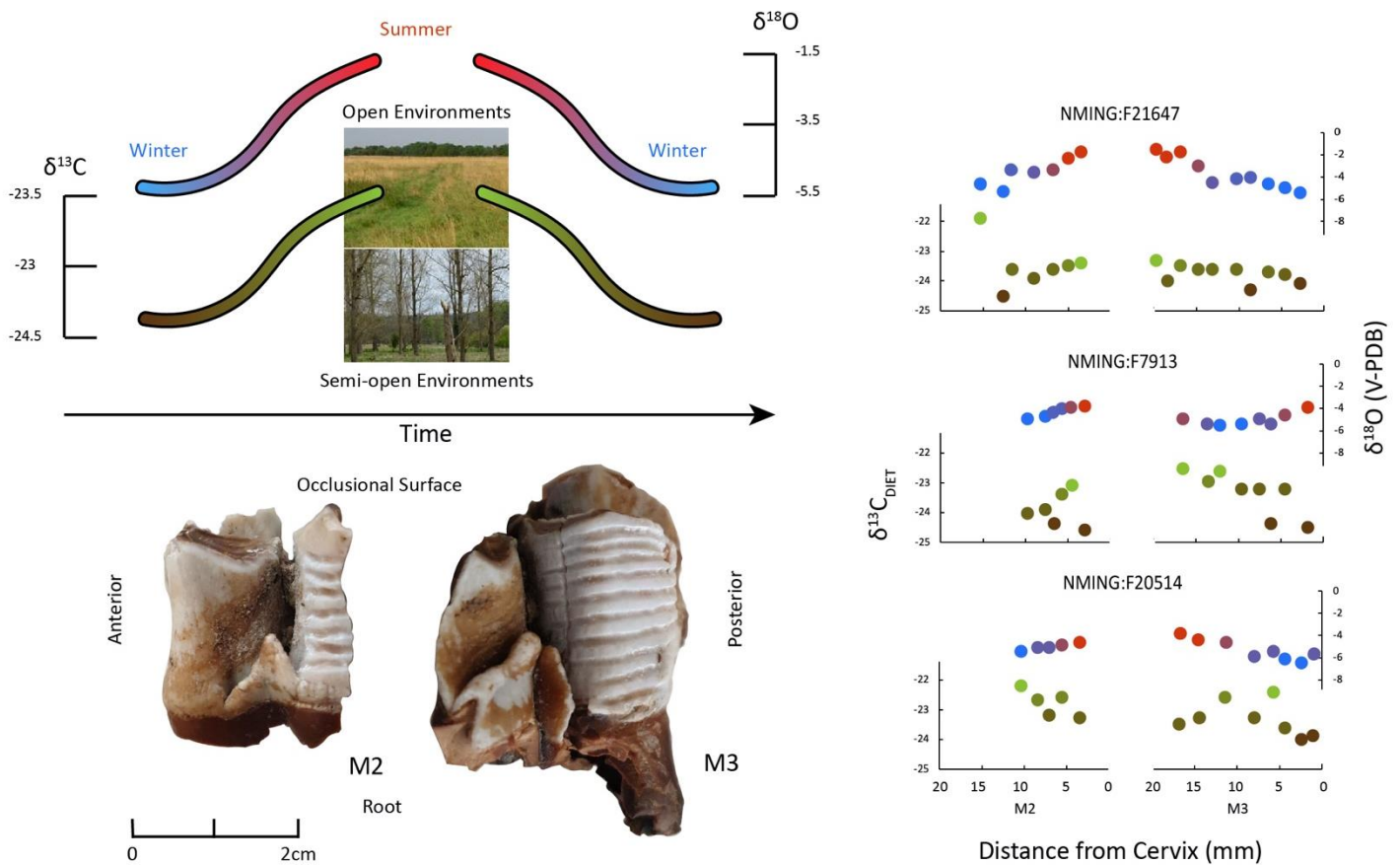

Fig. 8. Schematic diagram of the $\delta^{18}O$ (V-PBD) $\delta^{13}C_{diet}$ and record of a lingual view of the upper dextral M2 and M3 of *Megaloceros giganteus* specimen NMING:F21647 and where on the teeth samples were taken (left). $\delta^{18}O$ and $\delta^{13}C_{diet}$ of all specimens analysed by Chritz et al. (2009) (right).

Therefore, for this research, intra-tooth sequential sampling is suggested to observe the variations within the $^{87}Sr/^{86}Sr$ and $\delta^{18}O$ values within the growth period of *Megaloceros giganteus* molars. The second and third permanent molars (M2 and M3) should be utilised as they are formed during the first year or so of the animal's life, while the first permanent molar (M1) forms while the animal is *in utero* (Rees et al., 1966; Carter, 1998). The M1 thus will be affected by the maternal inputs and thus is problematic for $\delta^{18}O$ as it would contain a "weaning signal" (Wright & Schwarcz, 1998; Dupras & Tocheri, 2007). The

formation of the M2 takes place before the M3. By analysing both the M2 and M3 sequentially a longer life history isotopic signal can be extracted (Britton et al., 2009; Chritz et al., 2009). The timing of crown formation and the amount of time that an unworn molar represents is based on mandibular radiography studies of deer species like fallow deer and red deer by Brown & Chapman (1991a,b) as well as the isotopic data from Chritz et al. (2009) to be between 6 and 9 months.

For each specimen, both the second and third molar would be sampled for analysis, and these molars would be the same molars that were previously sampled by Chritz et al. (2009) which were already removed from the skulls. The sampling lines that were previously made by Chritz et al. (2009) would be sampled further, while making sure that samples are not drilled too extensively as to avoid dentine contamination (see Fig. 8). Chritz et al. (2009) states that the enamel surfaces were abraded using a dental drill with a diamond-tipped drill bit to clean the enamel surface and bands perpendicular to the growth axis were drilled sequentially from apex to cervix (occlusional surface to root), following the direction of mineralization. For sampling lines with insufficient enamel, new drilling transects will be created at similar intervals from cervix to apex while following the pattern of the previous sample lines. These areas would be abraded first with a diamond drill bit to remove any superficial enamel to expose a dull white enamel, as to minimize the collection of enamel that was possibly diagenetically altered. Between 5 and 7 milligrams of enamel powder will be collected using a handheld drill first onto weighing paper, then transferred into acid-cleaned polyethylene Eppendorf centrifuge tubes and weighed. The diamond drill bit would be cleaned between each sample using Milli-Q® ultrapure water, hydrochloric acid (HCl), Milli-Q® ultrapure water again and then ethanol (C_2H_5OH) and left to dry. Given the high costs associated with $^{87}Sr/^{86}Sr$, only certain points of the oxygen curve should be analysed (Price et al., 2017), likely points at both the lowest and highest points of the $\delta^{18}O$ curve.

3.3.2. Analysis

In order to obtain results from the enamel samples, mass spectrometry is required to differentiate between the heavier and lighter isotopes of strontium.

However, multiple options for what type of mass spectrometry procedure are available and come with their own strengths and weaknesses (Slovak & Paytan, 2012). Thus for generating sound results from the enamel samples, the decision will need to be made as to which technique should be utilised.

Thermal Ionizing Mass Spectrometry (TIMS) procedure has been more commonly and routinely used for $^{87}Sr/^{86}Sr$ in academia, this is likely due to its high reproducibility and precision (Slovak & Paytan, 2012). However, the main pitfall with this procedure being the time it takes to run analysis, which can be 1-2 hours per analysis (Montgomery et al., 2010; Slovak & Paytan, 2012).

Multi Collector Inductively Coupled Plasma Mass Spectrometry (MC-ICPMS) has also been discussed as an option for $^{87}Sr/^{86}Sr$ isotope ratio analysis in tooth enamel (Britton et al., 2009; Britton, 2010; Britton et al., 2011). Results can be almost as accurate from those analysed by TIMS and can be conducted in less time (approximately four samples per hour; Slovak & Paytan, 2012). However, more strontium is required compared to TIMS and backgrounds should be measured to correct for possible interferences on 84 and 86 masses, which come from the minute concentrations of krypton in the argon supply of the plasma (Slovak & Paytan, 2012; Ma et al., 2013).

Some authors have suggested the use of Laser Ablation MC-ICPMS (LA-MC-ICPMS) for $^{87}Sr/^{86}Sr$ isotope analysis (Copeland et al., 2008; Copeland et al., 2010; Scharlotta et al., 2012). However, some have observed major problems with this methodology, as significant deviations in the radiogenic $^{87}Sr/^{86}Sr$ ratio from values obtained by analysis of strontium chemically separated from the sample matrix have been observed by Vroon et al. (2008), and some authors have made suggestions against the methodology for migrational research (Simonetti et al., 2008; Neff & Lee, 2012). The exact reason for this is unclear, although isobaric interference as well as disruption in mass bias effects due to differential loading of the plasma have been suggested (Simonetti et al., 2008; Slovak & Paytan, 2012). However, this type of analysis only requires an incredibly small amount of sample to conduct analysis (Slovak & Paytan, 2012).

Typically for $^{87}Sr/^{86}Sr$ isotope analysis that is conducted in the Netherlands in specific universities

such as the Vrije Universiteit Amsterdam (VU), the use of thermal ionising mass spectrometry is utilised on the Thermo Finnigan MAT 262 RPQ TIMS at their Faculty of Earth and Life Sciences (Font et al., 2015; Laffoon et al., 2015; Kootker et al., 2016; Brusgaard et al., 2019). In the methodologies of such research conducted at the VU, strontium would then be extracted from the sample matrix through a Sr-specific crown ether resin (Eichrom©), which are loaded onto quartz cation exchange columns. This procedure is conducted in a class 100 clean lab under a laminar flowhood before being analysed. All measurements are referenced to the NBS987 standard which standardizes the mass spectrometer to 0.710240 (Brusgaard et al., 2019). Samples would be run to an internal precision of ± 0.000006 (1SE) or better at the VU (Kootker et al., 2016).

However, other mass spectrometry facilities are also available at the VU, specifically the Thermo Finnigan Triton TIMS and the Thermo Finnigan Neptune ICP MS. The Thermo Finnigan™ Triton TIMS was utilised in conjunction with the Thermo Finnigan MAT 262 RPQ TIMS at the VU in the study of Bronze Age livestock by Brusgaard et al. (2019), giving comparable results. Therefore, it is suggested that the use of either the Thermo Finnigan MAT 262 RPQ TIM, the Thermo Finnigan Triton TIMS or the Thermo Finnigan Neptune ICP should be utilised for this analysis. The uncertainties associated with LA-MC-ICPMS give enough concern to avoid this methodology unless used in a comparative manner.

4. Results and Discussion

If migrational behaviour was to be observed in these *Megaloceros giganteus* specimens, certain $^{87}Sr/^{86}Sr$ values would be expected at certain points of the $\delta^{18}O$ curve. For example, if the $\delta^{18}O$ curve is at its highest points, which would be associated with summer months, it would be expected that $^{87}Sr/^{86}Sr$ values from more northern parts of the country would be observed, such as those in Co. Antrim Tertiary flow basalts with distinctively low values (Snoeck et al., 2020; see Fig. 9).

At the low point of the $\delta^{18}O$ curve, which would insinuate winter months, it may be expected that specimens would migrate to southern parts of the country. $^{87}Sr/^{86}Sr$ values in the range of 0.7100 to 0.7120 may be expected, as they correlate with mid Devonian and lower Carboniferous Old Red Sandstones found in the south of the country (Holland & Sanders, 2009; Snoeck et al., 2020). Alternatively, signals from the Ballybetagh area (0.70906-0.710135; Snoeck et al., 2020 additional information) may be expected, given the suggestion that overwintering males would accumulate there to seek protection in the low land topography, as suggested by Barnosky (1985).

Other interesting $^{87}Sr/^{86}Sr$ signals are those that are extremely high, in the range of 0.7140 to 0.7200. Caledonian granites can be found as intrusive structures around Ireland such as in Co. Carlow, Wicklow and Donegal and have $^{87}Sr/^{86}Sr$ values in the range of 0.7140 – 0.7150 (Holland & Sanders, 2009). Even higher values up to 0.7222 can be found in areas of Britain, specifically in Proterozoic rocks found mainly in northern Scotland (Evans et al., 2010; Snoeck et al., 2018). If such high values were to be observed in the studied specimens, this may suggest that longer migrations crossing the Irish Sea and or the Northern Channel may have been possible for these animals. The highest $^{87}Sr/^{86}Sr$ values that have been observed by Snoeck et al. (2020) was 0.7164, thus values over this should be given special attention as being possibly British in origin.
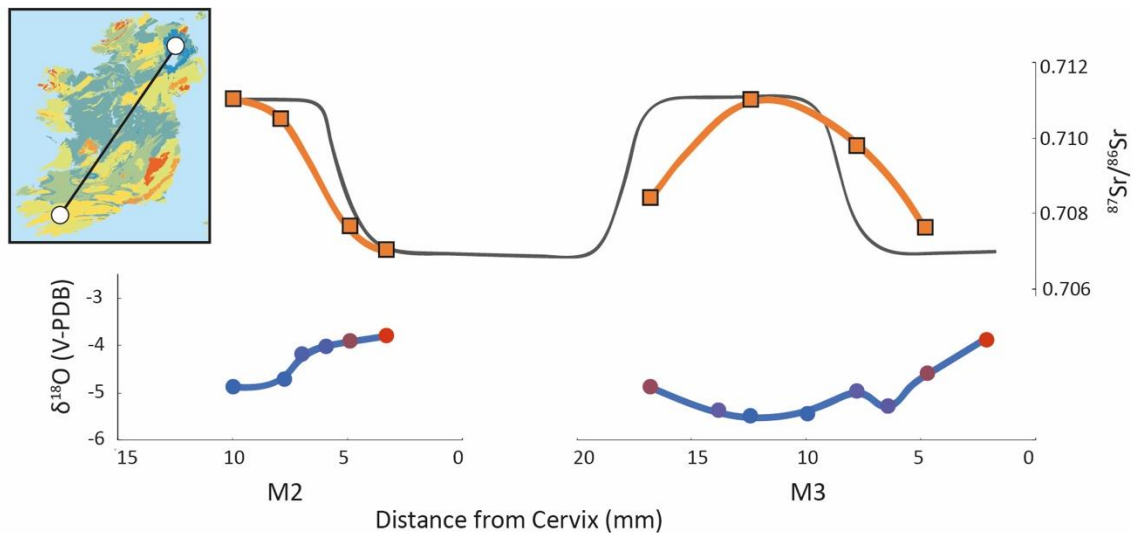
Fig. 9. Hypothetical variation in $^{87}Sr/^{86}Sr$ in a possible migrational specimen NMING:F7913 while migrating northeast to south west during summer and winter respectively. Grey line represents actual $^{87}Sr/^{86}Sr$ variation through the migration pathway. Orange points represents averaging and sampling effects on the $^{87}Sr/^{86}Sr$. Migration speed based on caribou migration speeds (approx. 80 km/week; Tape & Gustine, 2014) and residence time calculated based on Spaargaren (1983) and Britton et al. (2011) based on average giant deer stag body weight calculated by Geist (1998).

There has been discussion on the presence of land bridges in the Late Glacial between Ireland and Britain, with some authors claiming possible connections may have existed between Northern Ireland and Scotland or from southeast Ireland to southern Wales (Devoy, 1985; Lambeck & Purcell, 2001; see Fig. 10), while others claim any land connections during the Late Glacial were very unlikely (Brooks et al., 2011). Both Devoy (1985) and Lambeck & Purcell (2001) suggest that even if such connections were present, they were likely unreliable and unfriendly to migrating flora and fauna. However, even if such land connections were not so hospitable, *M. giganteus* specimens may have swam short distances of this land connection in order to find the right type of vegetation. Swimming behaviour has been observed in deer before, with red deer observed swimming distances of 7 km in marine waters and white-tailed deer (*Odocoileus virginianus*; Zimmermann, 1780) traveling up to 25 km between islands within the North American Great Lakes (Serjeantson, 1990; Reimchen et al., 2008; Mulville, 2010). Quigley & Moffatt (2014) states that given the lower sea level present during the last glacial maximum, this swimming behaviour may have implications on the introduction of deer species to Ireland. Perhaps the same could be said for introductions and transfers of *M. giganteus*

individuals between Ireland and England during the Late Glacial, or further seasonal movement from one island to another. While there are inconsistencies in the exact shift in sea level that can be observed during the Late Glacial, relative sea-level drops as low as -70 m have been modelled for the Wexford area from between 14,000 and 12,000 C^{14} years ago (Lambeck & Purcell, 2001), making swimming a possibility.
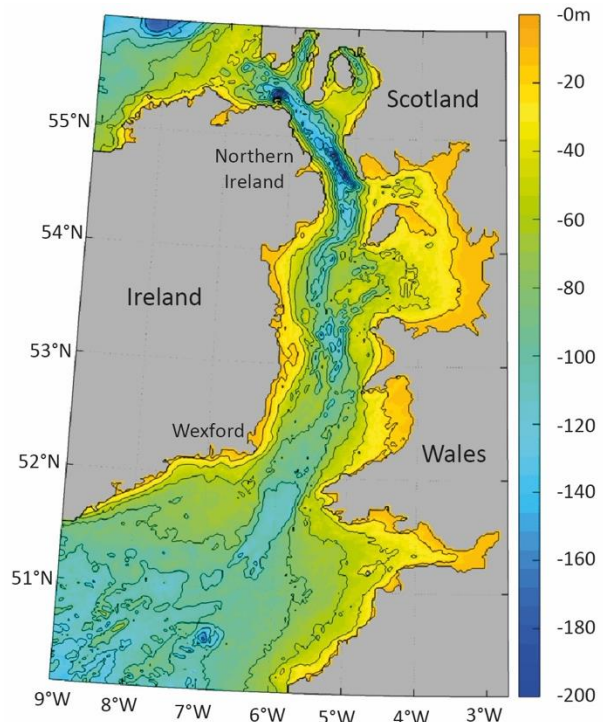

Fig. 10. Bathymetry map of the Irish and Celtic Sea, adapted from Bush et al. (2015).

If these specimens would not show any signs of migrational behaviour, it would be expected that the $^{87}Sr/^{86}Sr$ values throughout all of the molars would be at the same or similar values. If the values that were found in the molars is identical to the signature of the area, then it could be suspected that these specimens were diagenetically altered, taking in the $^{87}Sr/^{86}Sr$ signature of the surrounding area (Slovak & Paytan, 2012). However, diagenetic interference would be unlikely, given that these specimens were previously analysed and displayed $\delta^{13}C$ and $\delta^{18}O$ values that are to be expected from these animals.

If the $^{87}Sr/^{86}Sr$ values indicate no mobility in these specimens, it may suggest that *M. giganteus* did not adopt migrational behaviour. There could have been a number of reasons as to why the studied specimens do not display migratory behaviour. As suggested by Van Geel et al. (2018), due to the higher rate of evapotranspiration in the drier conditions of the late Pleistocene, water soluble minerals such as calcium were more concentrated in plants, as opposed to plants in moist conditions (Guthrie, 1990). This may have made it possible for *M. giganteus* to collect enough nutrients for antler growth in the dry late Pleistocene conditions without migrating long distances. This may be further suggested given that while it is common to find chewed antler and bone fragments in the Alaskan wilderness today as animals chew on the bone to ingest calcium, such chew marks are seldomly seen in late Pleistocene remains. Guthrie (1990) therefore suggests that the intake of essential nutrients was not an issue during the late Pleistocene. However, bone mastication by herbivores itself is a somewhat rare phenomenon as it can damage their teeth (Wika, 1982; Barrette, 1985; Cáceres et al., 2013). Furthermore, this lack of evidence may also be due to preservation potential, one could speculate that bone or antler material masticated by herbivores is not preserved well, as herbivores do not transport material to caves unlike some carnivores where preservation is high.

This line of reasoning can be extended to Late Glacial Ireland as well, especially given the dominance of Carboniferous limestone bedrock found across much of central Ireland. This calcium rich limestone would have helped make the vegetation in these areas particularly suited to a giant deer with high nutrient demands (Monaghan, 2017). Perhaps this abundance of lime rich vegetation would have made migrational behaviour unnecessary for *M. giganteus,* as nutrient demands were adequately met by the Late Glacial Irish vegetation. However, the presence of lime rich soils would suggest a low phosphorus concentration in plants, as the calcium reduces the availability of phosphorus in plants (Zohlen & Tyler, 2004; Reumer & Robert, 2005). Phosphorus being another key mineral for antler growth, perhaps this mineral would then be the driving factor for migrational behaviour.

It can be the case that some individuals display migrational behaviour, but some do not. This may be explained based on the lack of exact dating conducted on said specimens. It is unclear where exactly in the late Allerød and Younger Dryas onset these specimens come from, and migrational behaviour may only be a necessary behavioural adaptation during the colder conditions of the Younger Dryas (Van Asch et al., 2012; Vislobokova, 2012). Thus, the mix of studied specimens which may come from any point within this time period may create a mix of specimens that display migrational behaviour and those that do not.

Another possibility is that different individuals within the Late Glacial *M. giganteus* population conducted seasonal migrations and others did not. This can be seen with extant cervids such as reindeer and red deer, where populations can have co-occuring migrational and residence tactics (Chapman et al., 2011; Martin et al., 2018). This can be caused by a few reasons, being differences in topography in a region, density of individuals in a region or intraspecific competition (Chapman et al., 2011; Mysterud et al., 2011; Martin et al., 2018). Thus it could be suggested that the difference in individual's migration behaviour could be within a population itself and suggests that similar to many extant cervids (Ball et al., 2001; Cagnacci et al., 2011; Martin et al., 2018), seasonal migrational is expressed in some but not all individuals of the Irish giant deer population.

5. Pitfalls & Considerations
5.1. *Isotopic Metabolism*

Difficulties can arise in interpretation, as the relationship between the residence time of strontium in the body and its effects on enamel strontium is poorly understood (Montgomery et al., 2010). Studies on rats, monkeys and humans demonstrate that

strontium has a long residence time in the body in the range of 26 months (Dahl et al., 2001; Bärenholdt et al., 2009; Montgomery et al., 2010). This can naturally affect the strontium values of sequential samples, as it may be the case that strontium values between the molars studied may simply be from the same reservoir over the duration of formation, creating an averaging effect (Montgomery et al., 2010; Bower, 2017). However, the brachydont nature of the molars of *Megaloceros giganteus* mean that the molars are formed over a shorter amount of time as opposed to hypsodont molars (Brown & Chapman, 1991a,b; Britton et al., 2011). Thus mineralisation of the molars is finished sooner which suggests that mineralisation likely takes place in growing chemically-active bodies of young individuals, when averaging of the strontium signal is less pronounced due to quicker biomineralization causing body fluids to be flushed out quicker than in older animals (Montgomery et al., 2010). Britton et al. (2011) suggests that the problem of strontium residence times may be reduced in the study of brachydont herbivores for this reason. The successful application of sequential strontium isotope analysis may further suggest that residence times of strontium in the body during molar formation in brachydont herbivores is similar to that of oxygen, suggesting that it is not as grave an issue but should still be taken into account (Britton et al., 2009; Britton et al., 2011; Bower, 2017).

The association of the seasonality deduced by the δ^{18}O curve and the location implied by the ^{87}Sr/^{86}Sr values are core to understanding migratory patterns in *M. giganteus*. However, there is little understanding about the correspondence between the two signals, as the residence times of the two elements are extremely different and thus are likely not synchronous (Montgomery et al., 2010). However, the study of modern caribou ^{87}Sr/^{86}Sr and δ^{18}O data seems to suggest otherwise, that the two isotopic signatures co-vary as the summer and winter ranges' ^{87}Sr/^{86}Sr values corresponded with the summer and winter δ^{18}O variation (Britton et al., 2009; Britton et al., 2011). This again may be a similar situation with the averaging of ^{87}Sr/^{86}Sr values, as the molars form while the giant deer are young and have chemically active bodies and this drastically shortens the residence time of strontium in the animal (Britton et al., 2011). Therefore, similar residence times were utilised for

strontium in the hypothetical strontium variation in specimen NMING:F7913 enamel seen in Fig. 9.

5.2. *Sampling*

Fig. 8 displays the sample lines created by Chritz et al. (2009), these sampling lines were made with a dental hand drill and are thus not perfectly in a straight line. This may have implications for the accuracy to which one line represents the shortest period of time (Balasse, 2003). It should be noted however that when even taking perfectly linear sequential samples, it is very unlikely that one sample will only be representative of one sequential enamel layer, but rather of multiple (Balasse, 2003; Blumenthal et al., 2014; Bower, 2017). Therefore, it must be taken into account that these samples will likely represent strontium uptake from the animal's diet over an unprecise amount of time. However, although the sampling in this manner may not be perfectly representative of discrete time intervals, they are still chronological and are enough to obtain a relative change in an isotopic signature in response to environmental change (Balasse, 2003; Chritz et al., 2009; Britton, 2017).

Due to the brachydont nature of the molars being studied, less molar material can be sampled compared to hypsodont molars and thus a shorter window of time is available to be interpreted. The initial obstacle is that less seasonal fluctuations can be observed in a single specimen compared to a hypsodont herbivore (Brown & Chapman, 1991a,b; Balasse et al., 2001; Britton et al., 2011). Based on δ^{18}O data from the studied specimens it suggests that a span of approximately a year is recorded between both molars. While the δ^{18}O low points typically appear to be observed twice with the summer peak being present at only one point (Chritz et al., 2009; see Fig. 8), it suggests that the summer ^{87}Sr/^{86}Sr values would only be possibly recorded once with the winter ^{87}Sr/^{86}Sr values being recorder perhaps twice. This would allow for interpretations to be made about the return of specimens to certain locations in the winter, but not for the summer periods.

5.3 *^{87}Sr/^{86}Sr Value Interpretation*

Problems can arise when attempting to assign seasonal movement to ^{87}Sr/^{86}Sr values, as much of Ireland contains similar ^{87}Sr/^{86}Sr values due to the

large stretches of Carboniferous limestone (Holland & Sanders, 2009; Snoeck et al., 2020). The problem that similar values are found could imply that these animals did not seasonally migrate or that they simply travelled along geologically similar locations causing little to no change in $^{87}Sr/^{86}Sr$ values across the molars (Rogers et al., 2018). However, if there is truly a large difference between the summer and winter migrational ranges it would still be expected that some variation in the $^{87}Sr/^{86}Sr$ values would be found. If little $^{87}Sr/^{86}Sr$ variation is found with specimens with a particularly dampened $\delta^{18}O$ signal such as specimen NMING:F7913, it may suggest migration through similar geologic areas or that there may be issues with the sampling strategy employed (Hoppe et al., 2004; Zazzo et al., 2005; Zazzo et al., 2006).

As stated previously, the characteristic low or high $^{87}Sr/^{86}Sr$ values would allow us to suggest areas that may have been within the migratory range of the animal. However, if *M. giganteus* behaved similarly to reindeer and passed through areas quickly in the migration (Geist, 1986; Britton et al., 2009; Gunn et al., 2009), there may be a dilution effect of specific lithology's $^{87}Sr/^{86}Sr$ values and would make them difficult to distinguish. This effect has been observed by Britton et al. (2009) as the zones between summer and winter ranges were not preserved in the molar enamel of modern caribou. This is because the rapid movement of the caribou over the migration route's lithologies and the phasing of molar mineralisation. However, areas such as the northeast of Ireland where Tertiary lava flow basalts are present may possibly be near the final point of a migrational route, seeing as it is close to the coast. Therefore, these low $^{87}Sr/^{86}Sr$ values may still be preserved in the molar enamel. This may be more difficult is distinguishing possible British $^{87}Sr/^{86}Sr$ values such as those above 0.7164 (Evans et al., 2010, Snoeck et al., 2018), as these areas are relatively small and thus may be passed over quickly by giant deer during their migration.

Conclusion

This literature review concludes that the study of migrational behaviour in Irish giant deer *Megaloceros giganteus* should be conducted, as the results of such research would expand our understanding of these animals and may have implications for current large migratory mammals. The Irish Late Glacial population would be an ideal choice as they are abundantly found which lends itself to such destructive analysis and inhabited a presumably isolated island which limits the possibilities of migration. Specifically, three specimens should be further analysed as both carbon and oxygen isotopic data is already available for them and one particular specimen displays the oxygen dampening effects which may also suggest migration over large areas. However, specimens across Europe should ideally be analysed in the future in order to suggest that migrational behaviour was indeed common behaviour for these animals.

Based on the literature surrounding the reconstruction of migrational behaviour in mammals, the use of the strontium isotope ratio is suggested based on the availability of a BASr map for Ireland and Britain, the variation of lithologies present in Ireland and the fact that $^{87}Sr/^{86}Sr$ values can be extracted from the same enamel samples for carbon and oxygen data. Use of either the Thermal Ionizing or the Multi Collector Inductively Coupled Plasma (MC-ICP) Mass spectrometers is advised, as Laser Ablation MC-ICP has been suggested to interfere with the $^{87}Sr/^{86}Sr$ results.

The use of $^{87}Sr/^{86}Sr$ analysis brings complications, specifically to do with the residence times expected for strontium in the body as well as defining seasonal migrational behaviour through $^{87}Sr/^{86}Sr$ results. While $^{87}Sr/^{86}Sr$ results from modern caribou studies suggest that strontium analysis on brachydont herbivores such as giant deer would garner valid results, morphological and physiological differences between the two may have implications on this assumption. Nevertheless, the study of giant deer strontium signatures is suggested as it may help answer questions about the applicability of $^{87}Sr/^{86}Sr$ analysis in palaeontology and the paleoecology of giant deer. The study of large mammal's migratory behaviour during periods of abrupt climate change in the fossil record can and should be used to assess what implications there may be for modern large migratory mammals experiencing similar climatic changes.

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Appendix Table 1.

All δ^{13}C and δ^{15}N data from *Megaloceros giganteus* (Blumenbach, 1799) across Eurasia from Marine Isotope Stage 3 to MIS 1 (Holocene) used in Fig. 3. All isotopic data was extracted from collagen, (D) refers to tooth dentine.

Country	Location	Sample	δ13C	δ15N	Age	C14 Date	σ	Reference
Russia	Preobrazhenk	maxilla	-18.9	5.75	MIS 1	7889	38	Van der Plicht et al., 2015
Russia	Sopka	antler	-19.04	5.24	MIS 1	7925	40	Van der Plicht et al., 2015
Russia	Ust-Talaya	axis	-19.72	6.02	MIS 1	9235	45	Van der Plicht et al., 2015
Russia	Ust-Talaya	radius	-19.65	7.04	MIS 1	9235	45	Van der Plicht et al., 2015
Russia	Sosnovy Tushamsky	tibia	-19.925	5.825	MIS 1	9425	34	Van der Plicht et al., 2015
Russia	Ust-Tushama	axis	-20.3	3.56	MIS 1	10320	45	Van der Plicht et al., 2015
Germany	Hohlenstein Stadel cave	-	-20.7	2.2	MIS 2	12175	50	Immel et al., 2015
Germany	Hohle Fels	-	-20.1	2.9	MIS 2	12370	30	Immel et al., 2015
Germany	Ziegeleigrube Coenen	pelvis	-20.8	3.8	MIS 3	-	-	Wißing et al., 2015
Germany	Ziegeleigrube Coenen	mandibula	-20.6	4.7	MIS 3	-	-	Wißing et al., 2015
Germany	Ziegeleigrube Coenen	mandibula	-20.5	4.6	MIS 3	43190	510	Wißing et al., 2015
France	Jonzac; Charente-Maritime	-	-20	4.5	MIS 3	-	-	Richards et al., 2008
France	Jonzac; Charente-Maritime	-	-20.1	5	MIS 3	-	-	Richards et al., 2008
France	Saint-Césaire	maxillary	-20.5	5	MIS 3	-	-	Dusseldorp, 2011
France	Camiac	femur	-20	6.4	MIS 3	-	-	Dusseldorp, 2011
France	Camiac	long bone	-20.1	7.7	MIS 3	-	-	Dusseldorp, 2011
Poland	Perspektywiczna cave	metacarpal	-19.9	4.2	MIS 3	-	-	Krajcarz et al., 2016
Belgium	Scladina Cave	ectocuneiform	-20.2	4	MIS 3	-	-	Bocherens et al., 1997
Belgium	Scladina Cave	upper tooth (D)	-20.2	5	MIS 3	-	-	Bocherens et al., 1997
Belgium	Scladina Cave	premolar	-19.7	5.9	MIS 3	-	-	Bocherens, 2015
France	Abri du Maras	mandibula	-19.3	5.5	MIS 3	-	-	Daujeard et al., 2019
France	Abri du Maras	maxilla	-19.4	5.4	MIS 3	-	-	Daujeard et al., 2019