

RADIOCARBON



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WATERS**

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EDMARINE BIVALVE FEEDING STRATEGIES AND RADIOCARBON AGES IN NORTHEAST ATLANTIC COASTAL WATERS

Elena Lo Giudice Cappelli^{1*} • William E N Austin^{1,2}

¹School of Geography and Sustainable Development, University of St Andrews, St Andrews KY16 9AL, Scotland, UK

²Scottish Association for Marine Science, Scottish Marine Institute, Oban, Scotland, UK

Corresponding author. Email: elgc@st-andrews.ac.uk.

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ABSTRACT. Marine mollusk shells have been extensively used to provide radiocarbon (¹⁴C)-based chronologies in paleoenvironmental and archaeological studies, however uncertainties in age measurements are introduced because secondary factors such as vital effects and diet may influence ¹⁴C incorporation into these shells. Deep burrowing and deposit feeding mollusks, in particular, may incorporate “old” carbon resulting in apparently older ages than their contemporary environment. In this study, we present paired ¹⁴C and stable isotope ($\delta^{13}\text{C}$ and $\delta^{18}\text{O}$) measurements for nine species of known-age bivalves having different feeding strategies and collected in six localities around the NE Atlantic. We exclude potential “old” carbon contamination in these known-age mollusk shells, acquire a better understanding of local ecology and provide an improved context for the environmental interpretation of ¹⁴C ages. Our results indicate that, in the NE Atlantic, marine mollusk-derived ¹⁴C ages provide a reliable basis for environmental and archaeological investigation, independently of vital effects and differences in microhabitats, feeding strategies and sample location—all of which are apparent from stable isotopes.

KEYWORDS: diet, mollusks, paleoecology, radiocarbon.

INTRODUCTION

Marine mollusk shells can be a very useful source of palaeoarchives in coastal and continental shelf waters, particularly with regard to their stable isotopes ($\delta^{13}\text{C}$ and $\delta^{18}\text{O}$) (e.g. Simstich et al. 2005a, 2005b; McConnaughey and Gillikin 2008; Mettam et al. 2014; Reich et al. 2015) and trace metal composition (Mg/Ca, Sr/Ca) (e.g. Batenburg et al. 2011; Warter et al. 2015). The shell composition of many mollusk species is likely to represent ambient seawater conditions and can be used to trace the physical and chemical properties of the surrounding waters. Furthermore, mollusk carbonate can provide a direct chronology of environmental change through radiocarbon (¹⁴C) dating.

The disequilibrium between marine and atmospheric ¹⁴C concentrations requires that the resulting marine reservoir age must be taken into account when using marine sourced samples to construct a chronology. Marine reservoir ages have been generated for a number of sites (Cage et al. 2006; Rick et al. 2012; Hadden and Cherkinsky 2015, 2017a, 2017b) but further uncertainty is introduced as mollusks inhabit a range of ecological niches. The usual assumption is that shell carbonate is precipitated from dissolved inorganic carbon in seawater; however, shell formation can be influenced by secondary factors such as metabolic processes (vital effect) and feeding strategies (DeNiro and Epstein 1978; Tanaka et al. 1986; Gillikin et al. 2006; McConnaughey and Gillikin 2008). This may be

of significance in the case of deep burrowing and deposit feeding mollusks, as they can incorporate in their shells carbon from old calcareous sediments resulting in apparently older ages than the true age of seawater dissolved inorganic carbon (e.g. Cage et al. 2006; Mangerud et al. 2006). Additionally, a recent study reported that old, but bioavailable organic matter found in arctic aquatic environments due to thawing of permafrost (yedoma) can be a source of old carbon in the diet of aquatic organisms, causing an overall “aging” effect (Guillemette et al. 2017). Several studies purport to find apparent ^{14}C age differences between contemporaneous mollusk specimens (e.g. Forman and Polyak 1997; Hogg et al. 1998; Yoneda et al. 2000; Rick et al. 2012; England et al. 2013; Jull et al. 2013; Hadden and Cherkinsky 2015, 2017a, 2017b); whereas others claim that no significant age difference is observed between species from different ecological settings (Harkness 1983; Berkman and Forman 1996; Eiríksson et al. 2004; Ascough et al. 2005; Tisnérat-Laborde et al. 2010).

Similarly, the impact of vital effects and feeding strategies on stable isotopes is still under debate. Some studies report high internal variability in marine mollusk stable isotopes that would prevent their use as robust environmental proxies (e.g. Gillikin et al. 2006); whereas others used stable isotopes to identify palaeoenvironments and ecological processes within these environments (e.g. Mettam et al. 2014; Reich et al. 2015).

To assess the reliability of ^{14}C ages and stable isotopes, we analyzed 9 species of known-age marine bivalves collected in 6 localities around the NE Atlantic coast (Figure 1). By comparing live-collected pre-bomb marine bivalve ^{14}C ages and stable isotopes from (i) replicate samples of a single species from the same locality (ii) the same species at different localities and (iii) different species at the same locality, we examined *in situ*, intra-species and inter-species variability in a wider context than has been previously undertaken.

MATERIAL AND METHODS

Area of Study

The Fishery Board of Scotland conducted a survey of bottom fauna in the northern part of the North Sea and to the north and west of Scotland during the years 1922–1925 (Stephen 1934). The current study focuses on six of these sites: Shetland (Gruting Voe), Cromarty Bay, Forth (St Andrews Bay), Minch (Loch Erisort), Hebrides (Loch Leurbost) and Faroes.

Gruting Voe is located in the southwest of Shetland (Figure 1). Two main types of soil are present in this catchment: peat and organic soils, both poorly draining. A few rivers and streams discharge in Gruting Voe, however freshwater influence in the voe is generally very low. This, together with an overall small tidal range, leads to wind-driven currents locally, with wind typically blowing from the south (Cefas 2010a).

Figure 1 Location map of samples analyzed in this study (stars), and circulation map representing major current pathways after Austin et al. (2012) and Baxter et al. (2011). Black arrows indicate North Atlantic current, green arrows indicate coastal currents. Sea surface salinity and temperature data are from GIN sea regional climatologies (Seidov et al. 2018). (Please see electronic version for color figures.)

Cromarty Bay is a shallow, enclosed basin adjacent to the Moray Firth on the east coast of Scotland (Figure 1). Two types of soils are characteristic of the area: peaty soils and most predominantly humus iron podzols, the latter being freely draining and potentially reducing runoff. The catchment area includes one large river (River Conon) and smaller watercourses that seasonally supply freshwater to the Cromarty Bay. Predominant winds are from the north east and, in combination with density (freshwater) flows, can drive local currents. Tidal energy is strong in the Cromarty Firth, but tidal currents seems to slow down in proximity of the Bay where a sand bar is deposited (Cefas 2010b).

The Forth is situated on the eastern coast of Scotland bathing the city of St Andrews after which the Bay takes its name (Figure 1). Nowadays, this is an urbanized area and most of the land is arable, improved grassland. In proximity of the Forth Estuary, prevailing currents are tidal and freshwater inputs have a very marginal influence on local hydrography. Local currents are overall relatively weak and the Forth is more of a coastal/marine environment than an estuary (Cefas 2013).

The Minch bathes the eastern coast of the Isle of Lewis in the Outer Hebrides (Figure 1). The catchment area of Loch Erisort is dominated by peaty soils with the sparse presence of organic and brown forest soils. Currents can be highly impacted by seasonal freshwater inputs from local streams resulting in density flows, but are generally quite weak. The rough topography of the seafloor may enhance local currents close to constrictions, and wind-driven currents usually prevail over tidal energy (Cefas 2010c).

The Hebrides site, Loch Leurbost, is also situated on the eastern coast of the Isle of Lewis, just north of the Minch site (Figure 1). Two types of soils characterize this loch: brown forest soils (freely draining) on the northern coast and peaty soils (poorly draining) inland to the north of the loch and along the southern coastline. Currents are generally weak but can be channeled by changes in local bathymetry owing the presence of the island of Tannaraidh and other smaller islands at the mouth of loch as well as sills between the head, inner and outer basins. Additionally, density flows can occur seasonally following heavy rain periods and enhanced riverine inputs (Cefas 2011).

The Faroe Islands are situated between Iceland, Norway and Scotland (Figure 1), in a region where Atlantic Ocean waters enter the Nordic Seas. A persistent tidal flow encompasses Faroes' shelf waters separating this coastal environment from the open ocean. Faroes coast is jagged by many fjords and consists of steep cliffs and mountainous plateaus, which are part of the North Atlantic basalt region that formed in the Tertiary during a period of intense volcanism (Gillespie and Clague 2009).

Overall, these six sites are either calm depositional fjordic environments (Shetland, Minch and Hebrides) or low energy enclosed coastal basins sheltered from the open ocean (Cromarty, Forth and Faroes), with relatively stable annual sea surface temperatures and salinities (Figure 1). With the exception of the Forth, there are no limestones in the area of study which means that we can exclude potential "old" carbon contaminations due to ^{14}C -depleted dissolved inorganic carbon in all other sites. A fairly uniform water mass bathe the UK continental slope as its steepness limits the amount of deep North Atlantic waters entering the shelf (Inall et al. 2009; Baxter et al. 2011). To the west, the main water mass stems from the warm and saline Eastern North Atlantic Central Water, which travels northward along the west coast of Scotland (Inall et al. 2009). Similarly, the Scottish Coastal Current also travels northward carrying waters from the Irish and Clyde Seas and experiencing a slight freshening in proximity of the fjords peppering the coast of western Scotland (Inall et al. 2009; Baxter et al. 2011) (Figure 1). To the east, the circulation in the North Sea is typically anti-clockwise and fresh

and cool North Atlantic waters enter this region from Orkney and Shetland and along the Norwegian Trench (Baxter et al. 2011) (Figure 1).

Sampling Strategy

Samples were collected from both intertidal areas by hand-sampling a fixed volume ($0.5 \times 0.5 \times 0.15$ m), or from below the low watermark using a Petersen grab (0.1 m^3 volume). Material was washed through 2 mm (intertidal samples) and 1.5 mm (grab samples) mesh sieves, before counting and identification of the mollusk fauna. The collection now resides with the National Museum of Scotland (reg. no.: NMSZ 1951.19), and specimens are stored dry in airtight glass vials or sealed polyethylene bags. Table 1 lists the nine species analyzed in this study and their ecologies and habitats; Table 2 includes the samples available for stable isotopes and ^{14}C analysis. Five of the six sites contain more than one of these species, typically including a combination of suspension feeding, deposit feeding or mixed feeding species (Table 2). No records exist to conclusively indicate all specimens were live-collected, although this was certainly the intent of the original project, and so the remote possibility exists for some of the material to be reworked and potentially diagenetically altered. To improve the likelihood of the samples being live on collection, all samples analyzed were articulated bivalves with intact pereostracum, and frequently with internal organic matter still present.

[Insert Tables 1 and 2 about here.]

Stable Isotopes and Radiocarbon Analyses

Samples were weighed and placed in a 0.2M HCl solution overnight to ensure dissolution of about 20% of the outer carbonate. This pre-treatment also loosened any pereostracum adhering to the outer shell, which was mechanically removed along with any other surficial organic material attached to the shell. Samples were washed repeatedly with distilled water to remove any remaining acid, then freeze-dried and finally ground prior to analysis. Subsamples were taken for stable isotope mass spectrometry and ^{14}C analyses. Stable isotopes measurements were performed at the University of St Andrews in a Gasbench autosampler coupled to a ThermoScientific Finnigan Delta plus mass spectrometer. Standard reference materials (IAEA C2 travertine and Iceland Spar calcite) were analyzed along with the samples for quality control with a calcite acid fractionation factor of 1.01025 at 25°C (Sharma and Clayton 1965) and internal precision (zero enrichment test) of $\pm 0.05\%$ for $\delta^{13}\text{C}$ and $\pm 0.1\%$ for $\delta^{18}\text{O}$ measurements. For accelerator mass spectrometry ^{14}C (AMS ^{14}C) analysis, samples were hydrolyzed to CO_2 using 100% H_3PO_4 (phosphoric acid), and then gas cryogenically trapped into sealed quartz-glass tubes. Age measurements were made at the NERC Radiocarbon Laboratory, East Kilbride (SUERC).

Statistical Treatment of Data

We subdivided our dataset in three subsets to investigate: *in situ* variability (same species—same locality), intra species variability (same species—different localities) and inter species variability (different species—same locality). Note that replicate samples used to discuss *in situ* variability refer

to individual samples, not repeat measurements on the same shell. We used the method detailed in Ward and Wilson (1978) to test for homogeneity within groups of ^{14}C measurements.

To understand whether ages are comparable and thus can be combined together, we determined the pool mean (A_p) of each subset of measurements

$$A_p = \frac{\sum(A_i/S_i^2)}{\sum(1/S_i^2)}$$

and then calculated

$$T = \frac{\sum(A_i - A_p)^2}{S_i^2}$$

where A_i is the measured ^{14}C age and S_i is the associated 1σ error. When T was less than the critical value for $\alpha=0.05$, then ^{14}C ages are not statistically different and can be combined together.

RESULTS AND DISCUSSIONS

In situ Variability: Same Species—Same Locality

For the Shetland dataset, we have replicate samples only of *A. nitida* (Table 3). Based on three measurements (5 shells were measured in total), $\delta^{13}\text{C}$ varies from -0.1 to 0.1% , $\delta^{18}\text{O}$ varies between 2.7 and 3.2% and ^{14}C dates vary from 467 to 510 BP (Figures 2 and 3).

[Insert Table 3 about here.]

Figure 2 Stable isotopes discriminate between different ecological settings. Circles mark mixed feeders, squares suspension feeders, triangles deposit feeders and diamonds symbiont bearers. Samples from Shetland are in blue, from Cromarty in pink, from Forth in yellow, from Minch in green, from Hebrides in red, and from Faroes in black. Error bars represent the instrumental errors on $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$.

Figure 3 ^{14}C measurements. a) *In situ* variability. b) Spatial variability in *Abra* spp. c) Spatial variability in *Nucula* spp. d) Inter species variability; stars mark average ^{14}C age at each location regardless of species. Red lines mark the average ^{14}C age of each subset of data, empty symbols mean no replicate measurement was available. Error bars represent $\pm 1\sigma$ error of ^{14}C ages.

For the Forth dataset, duplicate samples of *A. alba* (5 shells), *C. gallina* (4 shells) and *N. turgida* (4 shells) were analyzed (Table 3). For *A. alba*, $\delta^{13}\text{C}$ varies between 0.1 and 0.3% , $\delta^{18}\text{O}$ varies from 2.1 to 2.4% and ^{14}C ages vary from 496 to 517 BP (Figures 2 and 3).

For *C. gallina*, $\delta^{13}\text{C}$ varies between 0.1 and 0.2% , $\delta^{18}\text{O}$ varies from 0.4 to 0.8% and ^{14}C dates vary between 417 and 464 BP (Figures 2 and 3).

For *N. turgida*, $\delta^{13}\text{C}$ varies between 0.3 and 1.3% , $\delta^{18}\text{O}$ varies between 2.0 and 3.0% , and ^{14}C ages vary between 447 and 462 BP (Figures 2 and 3)

For the Minch dataset, we have duplicate samples of *A. alba* (4 shells) and *T. flexuosa* (3 shells) (Table 3). For *A. alba*, $\delta^{13}\text{C}$ varies between -0.9 to -0.7% , $\delta^{18}\text{O}$ varies from 2.3 to 2.5% , and ^{14}C dates vary from 448 to 552 BP (Figures 2 and 3).

For *T. flexuosa*, $\delta^{13}\text{C}$ varies between -5.5 and -5.4% , $\delta^{18}\text{O}$ varies from 1.4 to 1.5% , and ^{14}C ages vary between 506 and 532 BP (Figures 2 and 3).

For the Faroes dataset, we have duplicate measurements only of *N. nucleus* (5 shells) (Table 3). $\delta^{13}\text{C}$ varies between 1.3 and 1.7‰, $\delta^{18}\text{O}$ varies around 2.8 ‰ (Figure 2) and no duplicate ^{14}C date is available for this sample.

In general, *in situ* variability in stable isotope measurements is low due to the precision of the measurements, yet statistically significant (Figure 2). In Figure 2 we reported individual stable isotope measurements to show the overall variability of the dataset. Four groups can be identified based on mollusks' feeding strategies and shells stable isotope composition: symbiont bearer, suspension feeders, mixed feeders and deposit feeders (Figure 2—different symbols shape). The highest *in situ* variability in $\delta^{13}\text{C}$ measurements was found in *N. turgida* and *N. nucleus* possibly because they are deposit feeders that can incorporate into their shells carbon from different sources (Yonge 1939; Ruppert et al. 2004; Cage et al. 2006; Mangerud et al. 2006). Notably, terrestrial organic matter is enriched in ^{12}C from soils resulting in lower $\delta^{13}\text{C}$ values than marine organic matter (e.g. Ficken et al. 1998; Balasse et al. 2005; Schmidt and Gleixner 2005; Marconi et al. 2011; Schiener et al. 2014). Similarly, *A. alba* $\delta^{13}\text{C}$ *in situ* variability is statistically significant albeit small (Figure 2). Most likely this is the result of *A. alba* being a mixed feeder that can process a large volume of sediments to feed on detritus when it does not suspension feed (Dame 1996). The presence of symbionts seems to drive the unique $\delta^{13}\text{C}$ of *T. flexuosa* (Mangerud et al. 2006), whereas no *in situ* variability is observed in the suspension feeder *C. gallina* $\delta^{13}\text{C}$ (Figure 2). *In situ* variability in $\delta^{18}\text{O}$ is significant in *A. alba*, *C. gallina* and *N. turgida* from Forth and in *A. nitida* from Shetland. We suggest that *in situ* changes in $\delta^{18}\text{O}$ could be either due to changes in microhabitats or to differences in time-averaging among individuals. These mollusks are infaunal burrowers able to move within the sediments depending on food availability and changes in environmental conditions. This implies that the measured $\delta^{18}\text{O}$ possibly reflects microhabitat preferences. Additionally, five specimens of *A. nitida* (Shetland), four of *C. gallina*, five of *A. alba* and four of *N. turgida* (Forth) were ground together before being measured, which means that the observed variability could also relate to seasonal changes in sea water conditions over a number of years, depending on the individual specimen's lifespan. While these are known to be short-lived species, no information is available on shells' lifespan, thus we have no means to check for differences in ontogenetic ages.

In contrast, no significant *in situ* variability is observed in ^{14}C ages and all shells are the same age within the $\pm 1\sigma$ error, with the exception of *A. alba* from Minch (Table 3). However, all shells are the same age when considering the $\pm 2\sigma$ error on ^{14}C ages, and no "old" carbon effect was observed in the Forth dataset suggesting lack of weathering of the Carboniferous limestone (Figure 3a).

Intra-Species Variability: Same Species—Different Location

The mixed feeder *Abra* spp. (*A. alba* and *A. nitida* together) is present at five of the six locations: Shetland, Cromarty, Forth, Minch and Hebrides (Figure 1), thus enabling inter-locality comparison of stable isotope and ^{14}C measurements. Based on all five localities, spatial variability is significant in *Abra* spp. stable isotopes (Figure 2—circles), whereas it does not affect ^{14}C ages within the $\pm 1\sigma$ level of uncertainty (Figure 3b; Table 4).

[Insert Table 4 about here.]

Nucula spp. is present at three of the six locations: Forth, Minch and Faroes (Figure 1), allowing to assess spatial variability of stable isotope and ^{14}C measurements in deposit feeders. Considering all three localities together, spatial variability is significant in *Nucula* spp. $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ (Figure 2—triangles), whereas it does not affect ^{14}C ages within the $\pm 1\sigma$ level of uncertainty (Figure 3c; Table 5).

[Insert Table 5 about here.]

In summary, marine bivalve stable isotopes record seasonal changes in local environments and can be a useful source of palaeoarchives in coastal and continental shelf waters (Figure 2). The spread in $\delta^{18}\text{O}$ measurements in *Abra* spp. seems to reflect the temperature gradient between the sites with colder temperature in Shetland (high $\delta^{18}\text{O}$) and warmer temperature at the Hebrides (low $\delta^{18}\text{O}$) (Figures 1 and 2). The range of $\delta^{13}\text{C}$ values most likely represent changes in local productivity often related with seasonal variations in freshwater and nutrient supplies (Figures 1 and 2). In contrast, ^{14}C ages do not change significantly with location, and all measured bivalves (*Abra* spp. and *Nucula* spp.) are the same age within the $\pm 1\sigma$ level of uncertainty (Figures 3b and 3c; Tables 4 and 5).

Inter-Species Variability: Different Species—Same Location

To discuss inter-species variability, in Shetland, we measured stable isotopes and ^{14}C ages in the shells of *A. nitida* (mixed feeder) and *T. ovata* (suspension feeder) (Table 6). Inter-species variability is significant in $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ measurements (Figure 2), whereas it does not affect ^{14}C ages, as the two species of bivalves are the same age within the $\pm 1\sigma$ level of uncertainty (Figure 3d; Table 6).

[Insert Table 6 about here.]

In Forth, we measured stable isotopes and ^{14}C ages in the shells of *A. alba* (mixed feeder), *C. gallina* (suspension feeder) and *N. turgida* (deposit feeder) (Table 6). Considering all three species together, inter-species variability is significant in $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ measurements (Figure 2), whereas it does not affect ^{14}C ages, as all samples are the same age within the $\pm 1\sigma$ level of uncertainty (Figure 3d; Table 6).

In Minch, we measured stable isotopes and ^{14}C in the shells of *A. alba* (mixed feeder), *T. flexuosa* (suspension feeder with chemosynthetic symbiont) and *N. nucleus* (deposit feeder) (Table 6). Considering all three species together, inter-species variability is significant in $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ measurements (Figure 2), whereas it does not affect ^{14}C ages, and all samples are the same age within the $\pm 1\sigma$ level of uncertainty (Figure 3d; Table 6).

In Faroes, we measured stable isotopes and ^{14}C in the shells of *Astarte borealis* (suspension feeder), *Astarte elliptica* (suspension feeder) and *N. nucleus* (deposit feeder) (Table 6). In this particular case, combining data from all three species, inter-species variability is significant for both stable and radiogenic isotopes (Figures 2 and 3d; Table 6).

In summary, stable isotopes in marine bivalve shells can be reliably used to identify feeding strategies and ecological settings (Figure 2). Only *A. elliptica* falls outside the corresponding “feeding box” (Figure 2; black square in triangles group), perhaps suggesting a problem with the measurements performed in this shell or its identification. In contrast, ^{14}C ages show no evidence of sensitivity to mollusk diets or microhabitats, as all analyzed shells are the same age within the $\pm 1\sigma$ level of uncertainty (Figure

3d; Table 6). This includes the measurements from Faroes that locally showed significant interspecies variability (Table 6). Nevertheless, we acknowledge that with higher precision dates ($\pm 1\sigma < 35$ yr) the difference in ^{14}C ages between specimens with different ecologies and feeding strategies might become significant.

Does Diet Affect Radiocarbon Ages?

Previously published ^{14}C ages, based on several species of mollusks and covering a range of environments, showed significant age differences between contemporaneous specimens (e.g. Forman and Polyak 1997; Hogg et al. 1998; Mangeroud et al. 2006; England et al. 2013; Petchey et al. 2013; Hadden and Cherkinsky 2017a; Rick et al. 2012; Rick and Henkes 2014). In these studies, older than expected ^{14}C ages were consistently measured in deposit feeding mollusks, as these species were argued to be able to incorporate old carbon in their shells. This apparent ‘aging effect’ can be due to two sources of “old” carbon: inorganic carbon from old calcareous sediments and/or terrestrial inputs (Forman and Polyak 1997; England et al. 2013), and old organic matter (yedoma) from the underlying sediments in samples coming from arctic regions (Forman and Polyak 1997; Guillemette et al. 2017). The latter source of old carbon could potentially explain the older ^{14}C ages reported in Mangeroud et al. (2006) and England et al. (2013) as their samples come from Svalbard, the Barents Sea and the Arctic Ocean. Additionally, high variability in ^{14}C ages within and between shells was found in samples collected in estuarine and brackish environments due to the mixing of marine and ^{14}C -depleted fresh waters and to carbon recycling (Hadden and Cherkinsky 2017a; Rick et al. 2012; Rick and Henkes 2014). As a consequence, several researchers have suggested to either (i) exclude deposit feeders from palaeoenvironmental reconstructions, (ii) recommended species-specific correction factors to calibrate ^{14}C ages measured in deposit feeders, or (iii) advocated for the calculation of regional and sub-regional reservoir ages (Forman and Polyak 1997; Petchey et al. 2013; Hadden and Cherkinsky 2017a; Rick et al. 2012; England et al. 2013; Rick and Henkes 2014).

In this study, we combine stable isotopes and ^{14}C measurements for a range of marine bivalves having different feeding strategies and inhabiting a variety of ecological niches in the NE Atlantic. By pairing stable isotopes and ^{14}C measurements, we were able to better understand the mollusks’ ecology (Figure 2) and thus better assess the reliability of ^{14}C ages (Figure 3). *In situ* variations of shell $\delta^{13}\text{C}$ may reflect changes in carbon source, namely whether a mollusk is feeding on marine or terrestrial organic matter or switching between feeding strategies (Figure 2). Spatial changes in shell $\delta^{13}\text{C}$ may indicate seasonal variations in marine productivity often related to freshwater input in fjordic and coastal systems (Figures 1 and 2). Similarly, *in situ* variations of $\delta^{18}\text{O}$ values can be due to differences in microhabitats and/or in shells time-average due to possibly different ontogenetic ages of the analyzed specimens (Figure 2), whereas spatial changes in $\delta^{18}\text{O}$ may relate to seasonal changes in seawater temperature and salinity (Figures 1 and 2). In contrast, no statistically significant variation in ^{14}C measurements has been recorded in the compiled dataset (Figure 3d) and we would argue that all studied species can be used to provide a robust ^{14}C chronology independently of their diet. We speculate that, given the oceanography and geology of these sites in the NE Atlantic, seawater dissolved inorganic carbon is fairly homogeneous and unaffected by “old” carbon derived from the weathering of older rocks, ultimately resulting in the robust ^{14}C ages we measured (Figure 3). As already proposed by Petchey et al. (2013), pairing stable isotopes and ^{14}C ages provides an opportunity

for a deeper understanding of environmental influences on ^{14}C dates, ultimately enabling an improved resolution of ^{14}C based chronologies.

CONCLUSIONS

The main conclusion that can be drawn from these results is that marine bivalve shells from the NE Atlantic can be used not only as reliable proxies for environmental and ecological change, but also for dating such reconstructions. As previously described in the literature, stable isotopes record changes in local environment, circulation (water mass) and ecology, being useful sources of palaeoarchives in coastal and continental shelf waters. Additionally, our results highlight that, in the NE Atlantic, mollusk carbonate provides a reliable basis for building the chronology of marine environmental change through ^{14}C dating, independently of vital effects and differences in microhabitats, feeding strategies and sample location. Reliable ^{14}C dating may still be compromised by the unknown incorporation of “old” carbon in mollusk shells in regions with “old” limestones. We therefore recommend the routine pairing of ^{14}C and stable isotopes ($\delta^{13}\text{C}$ and $\delta^{18}\text{O}$) measurements to provide an improved ecological context for interpreting ^{14}C ages.

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Table 1 Shells species, ecologies, and habitats.*

Species	Feeding strategy	Substrate	Depth habitat
<i>Abra alba</i>	Mixed feeder	Muds, silty sands and soft muddy gravel	From extreme low watermark to about 65 m water depth
<i>Abra nitida</i>	Mixed feeder	Muds, sandy muds, silty sands and muddy gravel	Offshore to depths of about 180 m
<i>Astarte borealis</i>	Suspension feeders	Sandy muds and gravel	Below 5 m water depth
<i>Astarte elliptica</i>	Suspension feeders	Sandy muds and gravel	Below 5 m water depth
<i>Chamelea gallina</i>	Suspension feeder	Clean sands and muddy sands—infaunal burrower	Above the low watermark to about 50 m water depth
<i>Nucula nucleus</i>	Deposit feeder	Coarse sediments	To about 140 m water depth
<i>Nucula turgida</i>	Deposit feeder	Fine sediments— infaunal	To 90 m water depth
<i>Thyasira flexuosa</i>	Symbiont barer and suspension feeder	Sandy muds	From 10 to 180 m water depth
<i>Timoclea ovata</i>	Suspension feeder	Sands, muddy sands, shell gravel and gravel— shallow burrower	From 4 to 180 m water depth

*Ecology and habitat information is from Tebble (1966).

Table 2 Sample list.*

Lab Identifier	AMS publication code	Location	Latitude (N)	Longitude (W)	Species	Feeding strategy
GR/7903	SUERC-11180	Shetland	60.2	1.51	SA1-Abra nitida (a)**	Mixed
GR/7904	SUERC-11181	Shetland	60.2	1.51	SA1-Abra nitida (b)**	Mixed
GR/7905	SUERC-11182	Shetland	60.2	1.51	SA1-Abra nitida (c)**	Mixed
GR/7906	SUERC-11183	Shetland	60.2	1.51	SA1-Timoclea ovata	Suspension
GR/7907	SUERC-11184	Cromarty	57.47	4.09	SA5-Abra nitida	Mixed
GR/7908	SUERC-11185	Forth	56.15	2.53	SA7-Chamelia gallina (a)**	Suspension
GR/7909	SUERC-11186	Forth	56.15	2.53	SA7-Chamelia gallina (b)**	Suspension
GR/7910	SUERC-11189	Forth	56.15	2.53	SA7-Abra alba (a)**	Mixed
GR/7911	SUERC-11191	Forth	56.15	2.53	SA7-Abra alba (b)**	Mixed
GR/7912R	SUERC-11192	Forth	56.15	2.53	SA7-Abra alba (c)	Mixed
GR/7913	SUERC-11193	Forth	56.15	2.53	SA7-Nucula turgida (a)**	Deposit
GR/7914	SUERC-11195	Forth	56.15	2.53	SA7-Nucula turgida (b)**	Deposit
GR/7915	SUERC-11196	Minch	58.18	6.13	SA30-Abra alba (a)**	Mixed
GR/7916	SUERC-11199	Minch	58.18	6.13	SA30-Abra alba (b)**	Mixed
GR/7917	SUERC-11200	Minch	58.18	6.13	SA30-Thyasira flexuosa (a)**	Suspension
GR/7918	SUERC-11201	Minch	58.18	6.13	SA30-Thyasira flexuosa (b)**	Suspension
GR/7919	SUERC-11203	Minch	58.06	6.29	SA30-Nucula nucleus	Deposit
GR/7920	SUERC-11204	Hebrides	58.12	6.46	SA31-Abra nitida	Mixed
GR/7921	SUERC-11205	Hebrides	58.12	6.46	SA31-Abra alba	Mixed
GR/7922	SUERC-11206	Faeroes	62.2	6.29	SA48-Astarte borealis	Suspension
GR/7923	SUERC-11209	Faeroes	62.2	6.29	SA48-Astarte elliptica	Suspension
GR/7924	SUERC-11210	Faeroes	62.2	6.29	SA48-Nucula nucleus (a)**	Deposit
GR/7925	—	Faeroes	62.2	6.29	SA48-Nucula nucleus (b)**	Deposit

* All samples come from coastal waters. Feeding strategies are largely based on the interpretations of Tebble (1966).

**Replicate analyses. Please note that replicates (a), (b), and (c) refer to individual samples, not repeat measurements on the same shell.

Table 3 *In situ* variability.*

Lab Identifier	AMS publication code	Locality	Species	Feeding	¹⁴ C age BP	1σ ¹⁴ C age error	Year of Collection
GR/7903	SUERC-11180	Shetland	SA1-Abra nitida (a)	Mixed	498	37	1924
GR/7904	SUERC-11181	Shetland	SA1-Abra nitida (b)	Mixed	510	35	1924
GR/7905	SUERC-11182	Shetland	SA1-Abra nitida (c)	Mixed	467	35	1924
					A_p = 491		
					T = 0.8		
					χ².05=6		
GR/7908	SUERC-11185	Forth	SA7-Chamelia gallina (a)	Suspension	464	35	1925
GR/7909	SUERC-11186	Forth	SA7-Chamelia gallina (b)	Suspension	417	35	1925
					A_p = 441		
					T = 0.9		
					χ².05=3.8		
GR/7910	SUERC-11189	Forth	SA7-Abra alba (a)	Mixed	517	35	1924
GR/7911	SUERC-11191	Forth	SA7-Abra alba (b)	Mixed	496	35	1924
GR/7912R	SUERC-11192		SA7-Abra alba (c)	Mixed	467	35	1924
					A_p = 493		
					T = 1.0		
					χ².05=6		
GR/7913	SUERC-11193	Forth	SA7-Nucula turgida (a)	Deposit	462	35	1924
GR/7914	SUERC-11195	Forth	SA7-Nucula turgida (b)	Deposit	447	35	1924
					A_p = 455		
					T = 0.1		
					χ².05=3.8		
GR/7915	SUERC-11196	Minch	SA30- Abra alba (a)	Mixed	552	35	1924
GR/7916	SUERC-11199	Minch	SA30- Abra alba (b)	Mixed	448	35	1924
					A_p = 500		
					T = 4.4		
					χ².05=3.8		
GR/7917	SUERC-11200	Minch	SA30-Thyasira flexuosa (a)	Symbiont	532	35	1924
GR/7918	SUERC-11201	Minch	SA30-Thyasira flexuosa (b)	Symbiont	506	39	1924
					A_p = 520		
					T = 0.2		
					χ².05=3.8		

*Red numbers indicate when *in situ* variability is statistically significant for α=0.05. (Please see electronic version for color.)

Table 4 *Abra* spp. (mixed feeder) inter-locality variability.

Lab Identifier	AMS publication code	Locality	Species	¹⁴ C age BP	1σ ¹⁴ C age error
GR/7903	SUERC-11180	Shetland	SA1- <i>Abra nitida</i> (a)	498	37
GR/7904	SUERC-11181	Shetland	SA1- <i>Abra nitida</i> (b)	510	35
GR/7905	SUERC-11182	Shetland	SA1- <i>Abra nitida</i> (c)	467	35
GR/7907	SUERC-11184	Cromarty	SA5- <i>Abra nitida</i>	475	35
GR/7910	SUERC-11189	Forth	SA7- <i>Abra alba</i> (a)	517	35
GR/7911	SUERC-11191	Forth	SA7- <i>Abra alba</i> (b)	496	35
GR/7912R	SUERC-11192	Forth	SA7- <i>Abra alba</i> (c)	467	35
GR/7915	SUERC-11196	Minch	SA30- <i>Abra alba</i> (a)	552	35
GR/7916	SUERC-11199	Minch	SA30- <i>Abra alba</i> (b)	448	35
GR/7920	SUERC-11204	Hebrides	SA31- <i>Abra nitida</i>	476	35
GR/7921	SUERC-11205	Hebrides	SA31- <i>Abra alba</i>	477	35
				A_p = 489	
				T = 6.9	
				χ².05=18.3	

Table 5 *Nucula* spp. (deposit feeder) inter-locality variability.

Lab Identifier	AMS publication Code	Locality	Species	¹⁴ C age BP	1σ ¹⁴ C age error
GR/7913R	SUERC-11193	Forth	SA7- <i>Nucula turgida</i> (a)	462	35
GR/7914	SUERC-11195	Forth	SA7- <i>Nucula turgida</i> (b)	447	35
GR/7919	SUERC-11203	Minch	SA30- <i>Nucula nucleus</i>	452	35
GR/7924	SUERC-11210	Faroës	SA48- <i>Nucula nucleus</i> (a)	554	35
				A_p = 479	
				T = 6.2	
				χ².05=7.8	

Table 6 Inter-species variability.*

Lab Identifier	AMS publication code	Locality	Species	¹⁴ C age BP	1σ ¹⁴ C age error
GR/7903	SUERC-11180	Shetland	SA1-Abra nitida (a)	498	37
GR/7904	SUERC-11181	Shetland	SA1-Abra nitida (b)	510	35
GR/7905	SUERC-11182	Shetland	SA1-Abra nitida (c)	467	35
GR/7906	SUERC-11183	Shetland	SA1-Timoclea ovata	507	35
				A_p = 495	
				T = 0.9	
				χ².05=7.8	
GR/7908	SUERC-11185	Forth	SA7-Chamelia gallina (a)	464	35
GR/7909A	SUERC-11186	Forth	SA7-Chamelia gallina (b)	417	35
GR/7910	SUERC-11189	Forth	SA7-Abra alba (a)	517	35
GR/7911	SUERC-11191	Forth	SA7-Abra alba (b)	496	35
GR/7912R	SUERC-11192	Forth	SA7-Abra alba (c)	467	35
GR/7913R	SUERC-11193	Forth	SA7- Nucula turgida (a)	462	35
GR/7914	SUERC-11195	Forth	SA7- Nucula turgida (b)	447	35
				A_p = 467	
				T = 5.1	
				χ².05=12.6	
GR/7915	SUERC-11196	Minch	SA30- Abra alba (a)	552	35
GR/7916	SUERC-11199	Minch	SA30-Abra alba (b)	448	35
GR/7917	SUERC-11200	Minch	SA30-Thyasira flexuosa (a)	532	35
GR/7918	SUERC-11201	Minch	SA30-Thyasira flexuosa (b)	506	39
GR/7919	SUERC-11203	Minch	SA30-Nucula nucleus	452	35
				A_p = 498	
				T = 7.1	
				χ².05=9.5	
GR/7920	SUERC-11204	Hebrides	SA31-Abra nitida	476	35
GR/7921	SUERC-11205	Hebrides	SA31-Abra alba	477	35
				A_p = 477	
				T = 0.0	
				χ².05=3.8	
GR/7922	SUERC-11206	Faroës	SA48-Astarte borealis	414	35
GR/7923	SUERC-11209	Faroës	SA48-Tridonta elliptica	540	35
GR/7924	SUERC-11210	Faroës	SA48-Nucula nucleus (a)	554	35
				A_p = 503	
				T = 9.7	
				χ².05=6	
GR/7907	SUERC-11184	Cromarty	SA5-Abra nitida	475	35
			All shells together	A_p = 485	
				T = 26.7	
				χ².05=32.7	

*Red numbers indicate when inter species variability is statistically significant for α=0.05.

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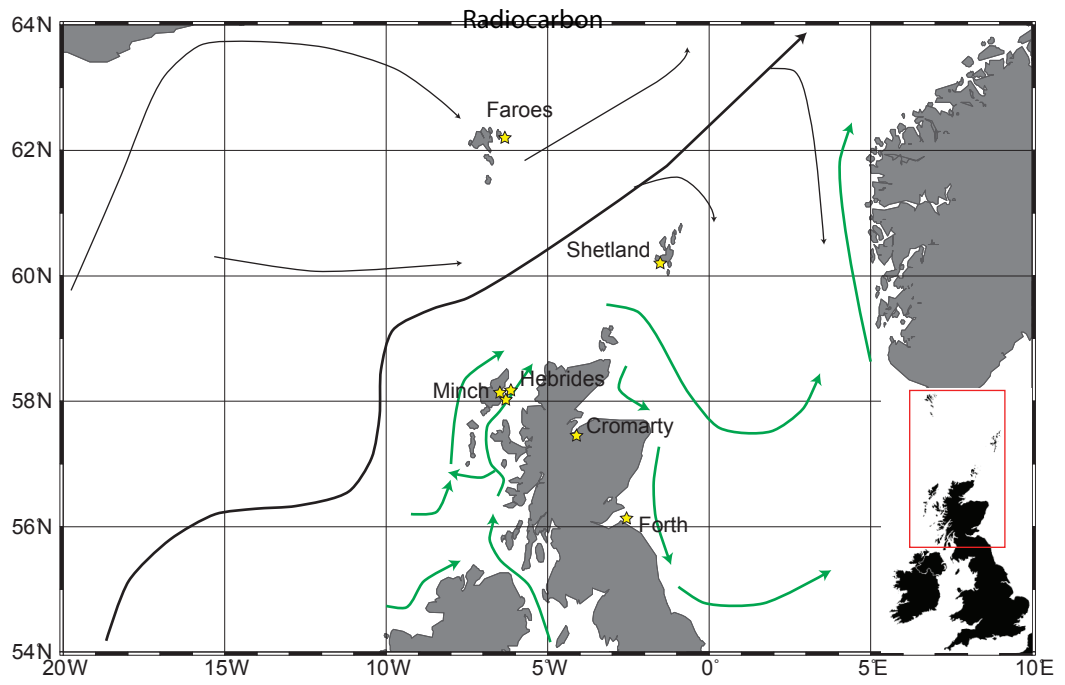
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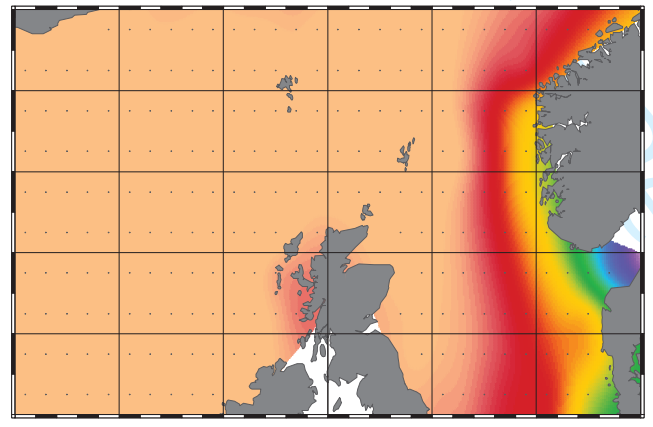
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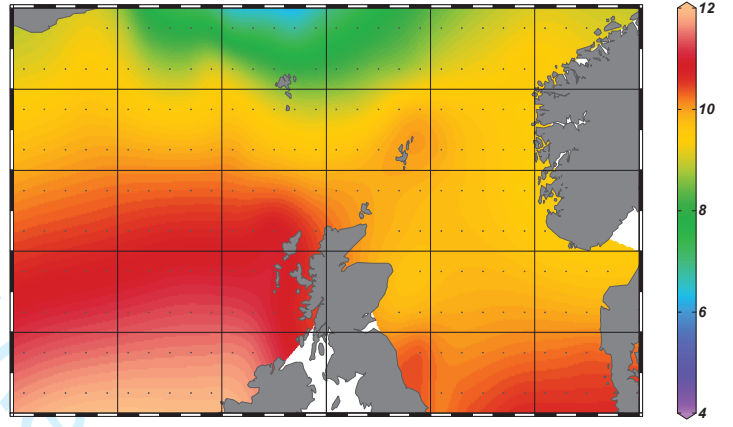
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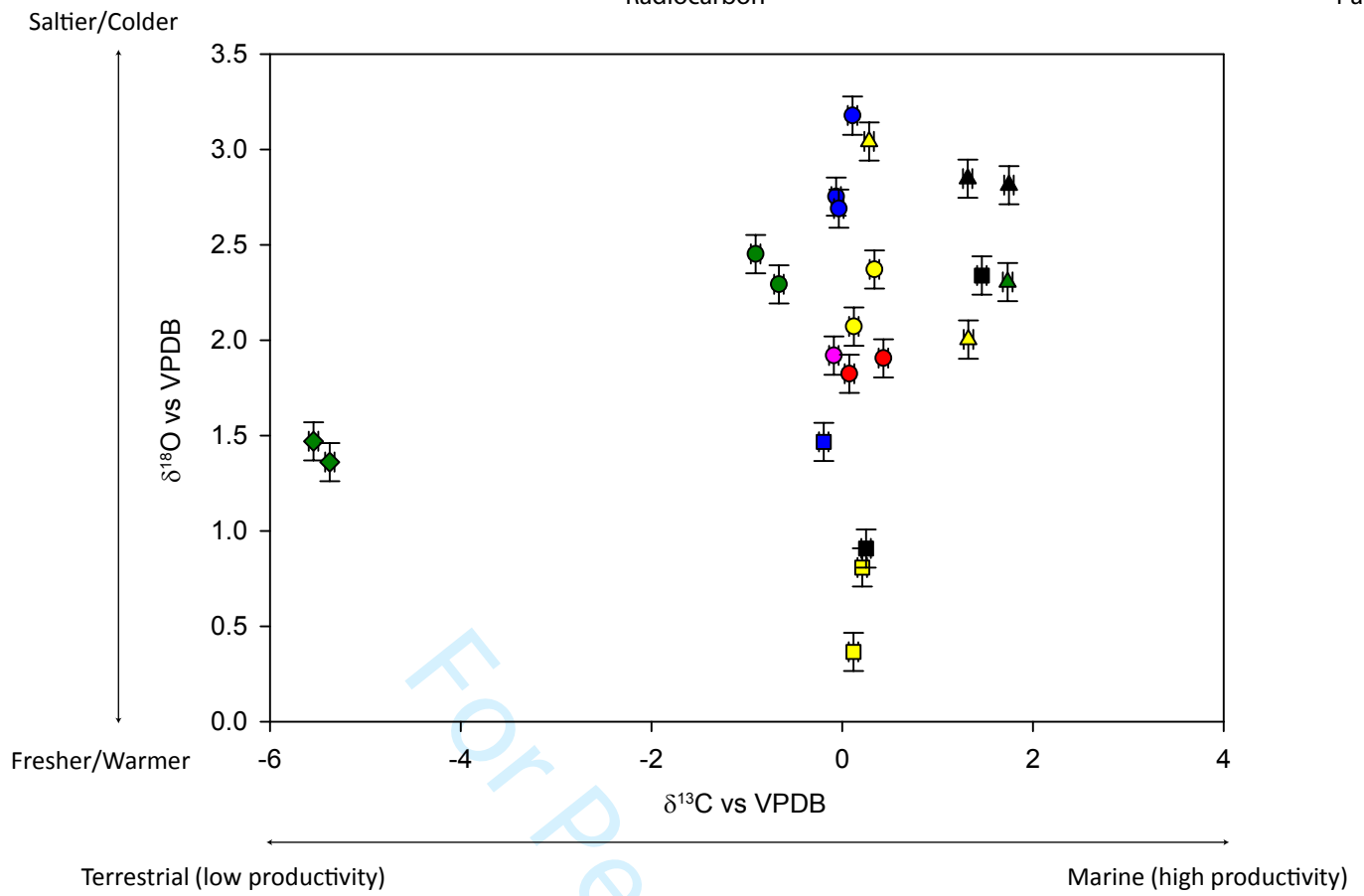
SSS (PSU)



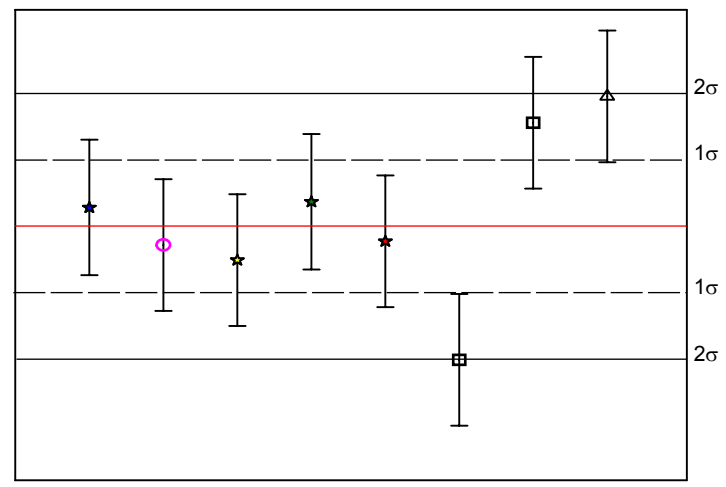
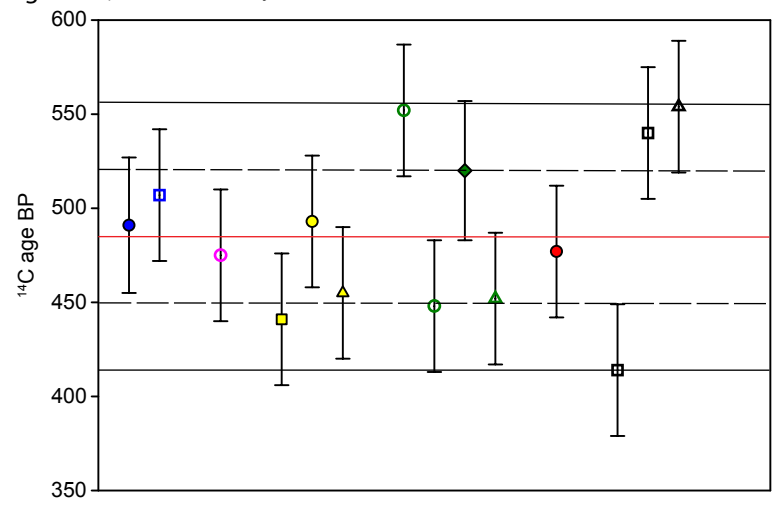
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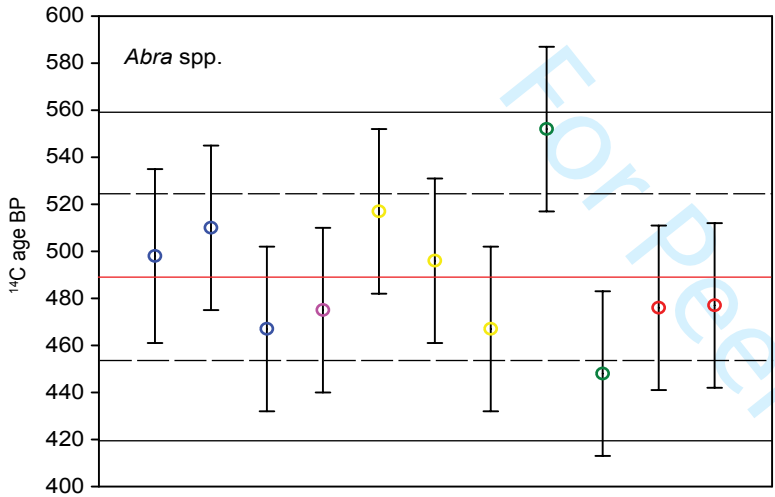
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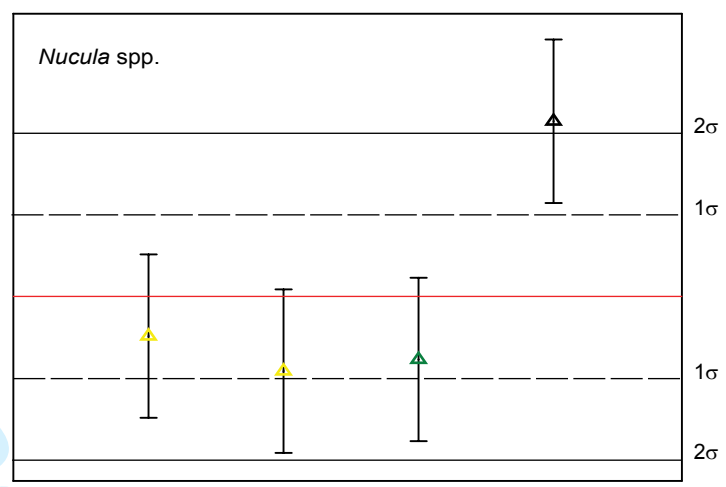
- Legend**
- Mixed feeders
 - Suspension feeders
 - ▲ Deposit feeders
 - ◆ Symbiont bearer
 - Shetland
 - Cromarty
 - Forth
 - Minch
 - Hebrides
 - Faroes



b) Intra species variability



c) Intra species variability



- Legend**
- Mixed feeders
 - Suspension feeders
 - ▲ Deposit feeders
 - ◆ Symbiont bearer
 - ★ Average ¹⁴C age
 - Shetland
 - Cromarty
 - Forth
 - Minch
 - Hebrides
 - Faroes