North Atlantic Ecosystem Sensitivity to Holocene Shifts in Meridional Overturning Circulation

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Key Points

- Holocene sea surface radiocarbon record was generated from NE Atlantic corals
- Sea surface hydrological changes occurred at 3.4, 2.7, 1.7 and 1.2 ky BP
- Collapses in coral ecosystems in response to sea surface hydrological changes.

Keywords

Marine radiocarbon, cold-water coral reef growth rate, Holocene, Atlantic meridional overturning circulation

1. Abstract

Rapid changes in North Atlantic climate over the last millennia were driven by coupled sea surface/atmospheric processes and rates of deep-water formation. Holocene climate changes, however, remain poorly documented due to a lack of high-resolution paleoclimate records, and their impacts on marine ecosystems remain unknown. We present a 4500 years absolute-dated sea surface radiocarbon record from northeast Atlantic cold-water corals. In contrast to the current view that surface ocean changes occurred on millennial-scale cycles, our record shows more abrupt changes in surface circulation. Changes were centered at 3.4, 2.7, 1.7 and 1.2 ky BP, and associated with atmospheric re-organization. Solar irradiance may have influenced these anomalies, but changes in North Atlantic deep-water convection are likely to have amplified these signals. Critically, we provide the first evidence that these perturbations in Atlantic Meridional Overturning Circulation led to the decline of cold-water coral ecosystems from 1.2 to ~ 0.1 ky BP.

2. Introduction

The Atlantic Meridional Overturning Circulation (AMOC) results in the ocean-scale transport of warm saline surface water masses northwards and deeper southward circulation of cooler, fresher waters [*Hansen and Østerhus*, 2000; *Read*, 2001]. The surface limb of the AMOC, the North Atlantic Current (NAC), loses much of its heat to the atmosphere on its way north, which helps regulate the climate over Europe [*Hall and Bryden*, 1982]. The NAC follows the boundary between the North Atlantic subpolar gyre (SPG) and the subtropical gyre (STG), and its density and flow are modulated by the SPG [*Hátún et al.*, 2005]. During periods when the SPG is enhanced (elongated E-W with strong outgrowth into the eastern Atlantic), the NAC transports fresher and cooler waters [*Hátún et al.*, 2005]. The strength of the SPG is assumed to be interconnected with the strength of the AMOC and production of cold dense Labrador Sea water, although the mechanisms connecting these remain unresolved [*Häkkinen*, 2001]. Since the density of the NAC is critical in the formation of deep waters [*Hansen and Østerhus*, 2000], which in turn affect climate through changes in heat flux, fluctuations in SPG dynamics are likely to be associated with changes in global climate.

Sediment cores from the subpolar North Atlantic record cyclic millennial-scale oscillations in the North Atlantic surface water composition associated with reduced deep-water convection during Holocene climatic deteriorations [*Bond et al.*, 2001; *Oppo et al.*, 2003; *Thornalley et al.*, 2009]. Consistent with modern mechanisms, these records showed that Holocene climatic anomalies are likely to be controlled by SPG dynamics [*Thornalley et al.*, 2009]. Centennial to millenial-time scale oscillations in sea surface hydrology during the Holocene thus seem primarily governed by changes in wind stress and/or freshwater input to the Labrador Sea, and appear to have affected SPG circulation [*Bond et al.*, 2001; *Thornalley et al.*, 2009]. The periodicity and triggers of these abrupt climatic events remain elusive, but likely involve changes in solar activity or internal oceanic forcing [*Bond et al.*, 2001; *Sorrel et al.*, 2012]. High-resolution and well-dated sea surface records of the Northeast Atlantic combined with ice-core data, for instance, are critical to strengthen our understanding of coupled ocean-atmosphere changes as well as defining any potential external driver such as solar activity.

Holocene climatic deteriorations were probably severe enough to impact populations and entire ecosystems [*Alley et al.*, 2003], but evidence for ecosystem responses in the marine biome are lacking. The skeletons of cold-water scleractinian corals are excellent archives of past climate changes. Many species build substantial reef frameworks that support rich biological communities and commercially valuable fisheries resources [*Roberts et al.*, 2006]. Recent studies have hypothesised that North Atlantic abrupt hydrological changes have affected cold-water coral occurrence and growth over the Holocene *[Frank et al.*, 2009*; Douarin et al.*, 2013]. Thus, combining cold-water coral growth history reconstructions and records of sea surface hydrology will be of great value to understand how marine ecosystems responded to changes in their environments and to evaluate the consequences for fisheries and the global economy that depends on them. It is also critical that policy-makers are equipped with accurate reconstructions of natural climate variability coupled with evidence for the sensitivity of marine ecosystems so that oceans can be managed in ways that enhance the resilience of these systems.

In this study, we used paired radiocarbon and U-series dates on cold-water corals to reconstruct atmosphere-ocean changes in the subpolar North Atlantic associated with abrupt Holocene climatic anomalies. Critically, we examined whether these anomalies impacted one of Earth’s most complex and biologically diverse marine ecosystems, cold-water coral reefs [*Roberts et al.*, 2006].

3. Material and Methods

3.1 *Lophelia pertusa* samples and study site

Seabed surface samples and downcore fragments of the coral *Lophelia pertusa* from the Mingulay Reef Complex were considered (56°50’N; 7°20’W; Supporting information Text S1 and Table S1). These coral reefs are located in relatively shallow (121 - 162 m) waters on the Western British continental shelf [*Roberts et al.*, 2005], and are ideally suited to document episodes of enhanced vertical mixing and surface AMOC changes (Figure 1).

Presently, the deepest waters (>100m) and the outer parts of the shelf of west Scotland are of Atlantic origin [*Inall et al., 2009*]. The coral ecosystem off Mingulay is thus primary bathed by the NAC [*Dodds et al.*, 2007]. The MRE of the NAC and derived branches averages about 400 years [*Stuiver et al.*, 1998]. However the East Greenland Current (EGC) and Labrador Current (LC), for example, are major pathways of sea-ice and freshwater input to the North Atlantic and are depleted in radiocarbon (MRE>450-500yrs) compared to the NAC [*Franke et al.*, 2008; *Eiríksson et al.*, 2011]. Enhanced SPG dynamics would favor the south/eastward advection of these older waters to the NAC, raising the MRE in Mingulay [*Hátún et al.*, 2005]. The Scottish Coastal Current (SCC, originating from Atlantic and Irish Sea waters) is considered to have a very minor influence at our site [*Inall et al.,* 2009]. However, the contribution of this surface current that is enriched in radiocarbon relative to the NAC would tend to lower the MRE in our study site [*Ascough et al.*, 2009].

3.2 Marine radiocarbon reconstructions

Radiocarbon was measured in U-series-dated coral fragments, previously used to generate a high-resolution record of reef growth [*Douarin et al.*, 2013, 2014]. The downcore U-series data published in *Douarin et al.* (2013) and new U-series data were recalculated using decay constants of *Cheng et al.* (2013) and uncertainties propagated using Monte Carlo techniques based on *McLean et al.* (2011) (Supporting information Text S2 and Table S2).

$\Delta^{14}C$ of the water in which the coral grew was calculated from the U-series and radiocarbon ages of the corals following *Adkins and Boyle*, (1997). Coral $\Delta^{14}C$ was compared to the atmospheric and modeled surface global ocean $\Delta^{14}C$ curves to examine any regional deviation associated with climatic and oceanic variables [*Reimer*, 2013] (Supporting information Text S3 and Table S3). The offset between the ^{14}C activity of the atmospheric and oceanic carbon reservoirs, was calculated using the ResAge package [*Soulet*, 2015]. Also known as the Marine Reservoir Effect (MRE), it deviates spatially and temporally in response to the rate of atmosphere-ocean gas exchange (e.g. caused by wind stress and sea-ice cover) and/or lateral advection [*Heier-Nielsen*, 1995; *Tisnérat-Laborde et al.*, 2010]. The reconstructed MRE is therefore inferred to represent past oceanic and atmospheric changes associated with Holocene climatic anomalies. This high-resolution MRE record was also compared to the growth history of Mingulay reefs [*Douarin et al.*, 2013] to determine if abrupt climate changes impacted this cold-water coral reef ecosystem.

4. Results

The reconstructed $\Delta^{14}C$ values for the Mingulay corals closely match the modeled surface global ocean $\Delta^{14}C$ curves between 4.3–3.5, 2.7–1.8 and at 0.055 ky BP (Figure 2A). The good agreement between the corresponding reconstructed MRE (290-410 yr; Figure 2B) and the age difference between the modeled surface global ocean (Marine13) curve and the atmospheric radiocarbon curve (IntCal13) for these three periods confirm the strong influence of Atlantic-origin waters (NAC) at Mingulay [*Dodds et al.*, 2007].

The first abrupt offset of the $\Delta^{14}C$ values for corals occurred between 3.5 and 3.4 ky BP. The corresponding MRE shifted from 414±36 to 592±41 yr in just 100 yrs. MRE values steadily decrease until 2.8 ky BP to 205±37 yr, followed by an abrupt increase over 100 yrs to 379±36 yr at 2.7 ky BP. The reconstructed $\Delta^{14}C$ values for corals exhibit two final deviations from IntCal13 and Marine13 at 1.7 and 1.2 ky BP, with MRE's of 513±46 yr and 561±37 yr, respectively (Figure 2B).

Atmospheric $\Delta^{14}C$ pulses (IntCal13), which are also seen in the modeled surface global ocean curve (Marine13), occurred synchronously with rather depleted $\Delta^{14}C$ for corals at 3.4, 1.7 and 1.2 ky BP [*Reimer*, 2013] (Figure 2A). The abrupt return to Marine13-like $\Delta^{14}C$ seen at 2.7 ky BP also matches a sharp atmospheric $\Delta^{14}C$ pulse (IntCal13). This inverse correlation between atmospheric and coral $\Delta^{14}C$ suggests that coral radiocarbon responded to oceanic and climate (sea-ice extent and atmospheric) variables rather than a lagged response to changing atmospheric ^{14}C concentrations.

5. Discussion

5. 1 Origin of Holocene sea surface radiocarbon variability

The low and/or declining ^{14}C events in the Mingulay corals at 3.4, 2.7, 1.7 and 1.2 ky BP are consistent with southward and eastward advection of ^{14}C-depleted Arctic-origin waters during periods of enhanced SPG circulation [*Ascough et al.*, 2009; *Eiríksson et al.*, 2011]. This is supported by the correlation between these events and peaks in hematite-stained grains in North Atlantic sediment cores (which are an independent proxy for the influx of cooler, ice-bearing surface waters from the Labrador and Nordic Seas; Figure 3A&B) [*Bond et al.*, 2001]. It is notable that while continuous sediment records have previously demonstrated that these SPG dynamics occurred over millennial timescales [*Bond et al.*, 2001; *Thornalley et al.*, 2009], our high-resolution $\Delta^{14}C$ reconstruction from Mingulay reveals for the first time that even shorter and more abrupt centennial-scale episodes of enhanced SPG water influence occurred during the late Holocene (Figure 3A). This highlights that sediment core records may be biased by factors such as bioturbation and low sedimentation rates that limit our ability to obtain records with less than millennial resolution. In addition, age models and the precise timing of the abrupt hydrological changes documented by such records relying on radiocarbon analyses can also be biased by variations in reservoir ages. Thus, the temporal weakness of the available marine record may well explain the temporal mismatch between available records. This, highlighting the need to provide more absolute dated and highly resolved sea-surface records. The abrupt changes in variations in SPG dynamics recorded in this study would potentially have modified the density of the northward flowing NAC and reduced the meridional heat flux thus affected climate over Europe (Figure 3A).

What caused the SPG circulation to increase remains uncertain, but one possibility is that enhanced westerlies over the North Atlantic increased wind-stress, driving enhanced gyre circulation [*Thornalley et al.*, 2009]. Low/declining ^{14}C events in the corals are preceded by periods of elevated Na^+ in GISP2 ice-core which are interpreted as sea-salt transported by strengthened westerly winds [*O'Brien et al.*, 1995; *Mayewski et al.*, 2004; *Jackson et al.*, 2005] (Figure 3A&C). Thus enhanced SPG circulation may have been caused by increased wind stress. We can only speculate as to the ultimate driver of these enhanced SPG events. Solar forcing is one possibility [*Stuiver and Braziunas*, 1993; *Bond et al.*, 2001; *Helama et al.*, 2010] as the low/declining ^{14}C events in the coral are synchronous with sharp centennial-scale troughs in total solar irradiance at 3.4, 2.8, 1.7 ka BP and 1.3 ky BP [*Steinhilber et al.*, 2009] (Figure 4A&B). The mechanism is not clear, but solar forcing appears to play a role in Holocene climatic anomalies, an effect that is amplified by ocean/atmosphere feedbacks, possibly through reduction in North Atlantic deep-water formation [*Stuiver and Braziunas*, 1993; *Bond et al.*, 2001; *Rind*, 2002; *Jongma et al.*, 2007]. Since the North Atlatnic deep water convection is a major component of the transport and sequestration of heat and atmospheric ^{14}C to the deep sea [*Clark et al.*, 2002], a reduction in deep-water formation could amplify climatic anomalies and would have also resulted in elevated atmospheric Δ^{14}C [*Stuiver and Braziunas*, 1993]. A correlation between the low/declining ^{14}C in the Mingulay coral and enhanced residual atmospheric Δ^{14}C values (Figure 4A&B) thus supports the prevailing concept that low solar irradiance plays a role in triggering enhanced SPG circulation.

The unusual enrichment in Δ^{14}C seen in the coral record at 2.8 ky BP (Figure 3A) could either be interpreted as enhanced advection of radiocarbon-enriched water masses, or enhanced gas exchange rates between the atmosphere and the surface mixing layers [*Ascough et al.*, 2009; *Tisnérat-Laborde et al.*, 2010; *Wanamaker et al.*, 2012]. We cannot at this stage easily reject either mechanism, although periods of climate change in the North Atlantic have been associated with strong connection between atmospheric and ocean circulation implying that enhanced rates of gas exchange are a plausible explaination [*O'Brien et al.*, 1995;

Thornalley et al., 2009; *Sorrel et al.*, 2012]. This episode is synchronous with strengthened westerly winds from Na^+ in GISP2 ice-cores record. Enanced wind stress could have contributed to homogenised the water column inducing enriched $\Delta^{14}C$ values from corals (Figure 3C). However, enhanced and stronger influence of STG water (enriched $\Delta^{14}C$) to the NAC could also be seen as a mechanism that stabilises AMOC [*Oppo et al., 2003 ; Thornalley et al.*, 2009]. Thus, the strengthened SPG circulation reported in our record 3.4 ka BP ago would have in turn reduced deep-water convection, such as that reported by Oppo et al., (2003). The subsequent convective shutdown would have reduced the SPG circulation and favoured the enhanced influence of STG waters to the North Atlantic, which would have been essential to restart deep convection and stabilise AMOC [*Thornalley et al.*, 2009]. Providing more absolute dated and highly resolved sea-surface records, that would be directly comparable with ice-core records would constitute a stepping stone toward understanding coupled ocean-atmosphere climatic system.

5.2 Sensitivity of marine ecosystems

Cold-water corals construct complex three-dimensional reef framework habitats for thousands of animal species including commercially exploited fish, and constitute a globally distributed but vulnerable ecosystem that needs to be conserved [*Roberts et al.*, 2006]. The sensitivities of these and other marine ‘ecosystem engineers’ to changes in their environments are poorly constrained. Shifts in the distribution of cold-water coral ecosystems over glacial/interglacial cycles and during the Holocene are typically attributed to changes in the physical and biological dynamics of their environments [*Frank et al.*, 2011; *Douarin et al.*, 2013; *Margolin et al.*, 2013; *Thiagarajan et al.*, 2013; *Henry et al.*, 2014] . Biogeochemical cycles driving productivity in the North Atlantic are sensitive to perturbation of the AMOC and potentially impact marine ecosystem [*Schmittner*, 2005]. For example, past changes in food supply have had significant control on coral occurrence and reef growth over thousands of years [*Eisele et al.*, 2011; *Frank et al.*, 2011; *Thiagarajan et al.*, 2013; *Hebbeln et al.*, 2014]. Other parameters affected by changes to the AMOC include larval supply, temperature, and dissolved oxygen and carbonate ion concentration, and these can also exert strong control in these ecosystems [*Dodds et al.*, 2007; *Davies et al.*, 2008; *Thiagarajan et al.*, 2013; *Douarin et al.*, 2014; *Henry et al.*, 2014]. Rapid changes in AMOC dynamics during the Holocene would therefore be expected to impact cold-water coral ecosystems, but to date proxy records of circulation changes have lacked the temporal resolution to study these effects.

In Figure 3A&D the growth history of Mingulay Reef Complex was compared with the reconstructed MRE. This reveals that the sharp increase in MRE between 3.3 and 3.4 ky BP was closely correlated with reduced reef growth, suggesting that the abrupt increase in SPG circulation initially destabilized the ecosystem. After 3.3 ky BP a progressive return of MRE values to close and even below that of the mean global ocean seems to have promoted reef growth and ecosystem recovery. The next sharp increase in the MRE from 2.8 ky BP to 2.7 ky BP marks another reduction in coral growth. The final hydrological shifts at 1.7 ky BP and 1.2 ky BP also appear to have been detrimental and triggered a severe decline in this already apparently weakened ecosystem. It is noteworthy that none of the 60 dated corals came from the interval 1.2 - 0.055 ky BP implying that this degraded ecosystem state persisted for a thousand years.

Numerous paleo-environmental records indicate an abrupt climatic anomaly during the Little Ice Age (LIA) at ~ 0.7 - 0.15 ky BP [*Wanner et al.*, 2008]. This period was characterised by an enhanced Arctic-water influence to the subpolar Atlantic [*Wanamaker et al.*, 2012] and is thus comparable to those we have documented at 3.4, 2.7, 1.7 and 1.2 ky BP. These conditions appear to have been unsuitable for coral reef growth in the NE Atlantic [*Douarin et al.*, 2013] and may explain the extended period of ecosystem decline at Mingulay. The reduced supply of NAC-derived Atlantic water to Mingulay during the LIA may also have limited inflow of coral larvae from deeper or more southerly coral sites [*Henry et al.*, 2014] preventing recolonization until the circulation of Arctic-water reduced at 0.055 ky BP [*Wanamaker et al.*, 2012].

This study reveals the sensitivity of marine ecosystems to sea surface hydrological changes associated with Holocene abrupt climatic anomalies. The known vulnerability of fragile cold-water coral reef ecosystems to impacts of commercial fishing combined [*Roberts et al.*, 2006] with this evidence of their sensitivity to abrupt climatic and oceanic change underscore the importance of implementing well-connected and internationally-managed networks of marine protected areas that can enhance ecosystem resilience in areas destabilized by human activities and exposed to the rapid progression of ocean warming and acidification [*Hennige et al.*, 2015].

6. Conclusion

This study presents a new high-resolution absolute dated Holocene sea surface radiocarbon record from scleractinian cold-water corals in the northeast Atlantic. Abrupt centennial scale episodes of coupled atmosphere-ocean re-organization were reported at 3.4

ka BP, 2.7-2.8 ka BP, 1.7 ka BP, and 1.2 ka BP. The unprecedented centennial resolution of this record demonstrate that sea surface hydrology changes associated with Holocene abrupt climatic anomalies happened much more abruptly than previously thought. The parallel with coral reef growth rate estimates shows that successive abrupt collapses in cold-water coral occurred in response to the coupled atmosphere-ocean re-organization and led to a pervasive thousand-year long demise of the ecosystem. The study highlights the sensitivity and speed with which deep-water marine ecosystems respond to sea surface hydrological changes associated with abrupt climatic change.

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two tables (Table S2 and Table S3) in an SI file; any additional data may be obtained from MD (melanie.douarin@univ-nantes.fr).

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9. Figure Legends

Figure 1: Location of the Mingulay Reef Complex (MRC; purple circle) and major surface circulation features of the North Atlantic showing how subpolar and subtropical (SPG and STG) waters meet, mix and feed into the North Atlantic Current (NAC). Black arrows

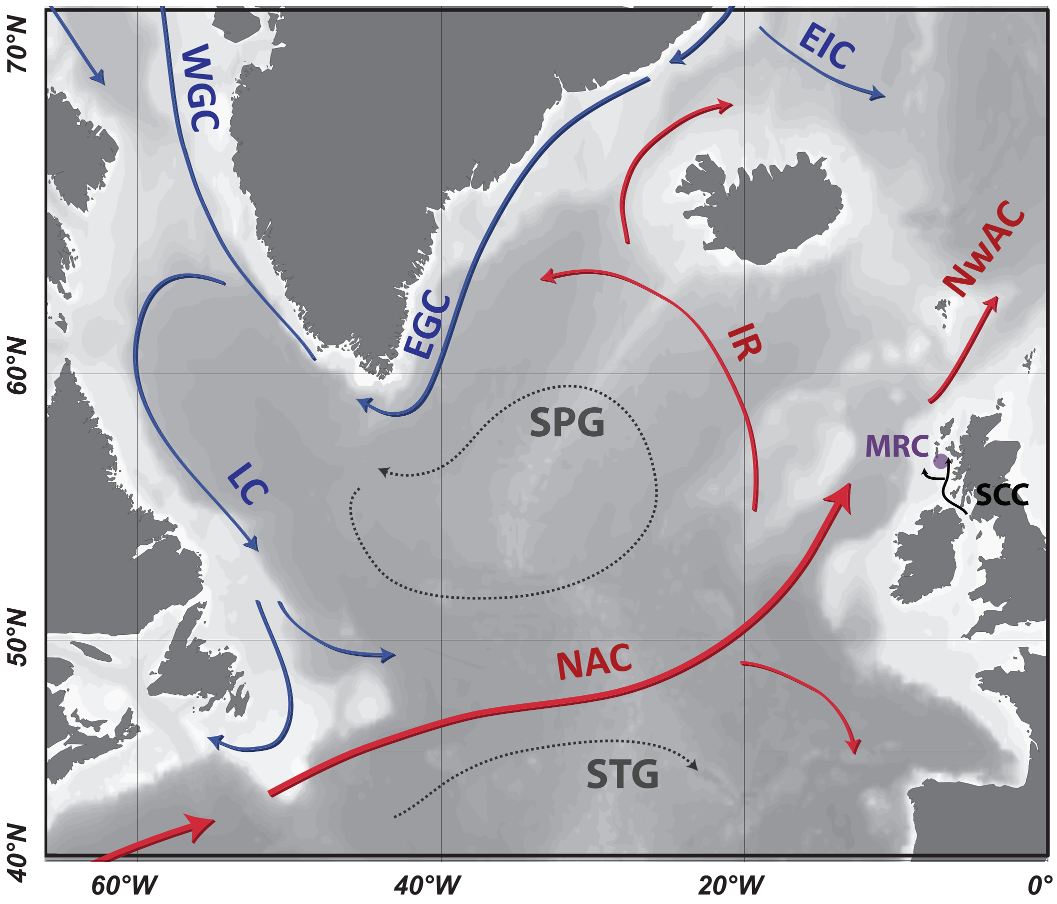
symbolized the Scottish Coastal Current (SCC). Red arrows show main branches of the warmer more saline North Atlantic Current (NAC), Norwegian Atlantic Current (NwAC) and Irminger Current (IR). Blue arrows show the main cooler fresher East Greenland Current (EGC), East Icelandic Current (EIC), West Greenland Current (WGC) and Labrador Current (LC). Note that an increase in the SPG will bring enhanced contribution of northern-sourced waters to the NAC.

Figure 2: A. Δ^{14}C reconstructed from Mingulay Reef Complex cold-water corals relative to the atmospheric (IntCal13) and modeled surface global ocean (Marine13) Δ^{14}C records [*Reimer*, 2013]. B. MRE reconstructed from the same corals against the difference of the Marine13 and IntCal13 radiocarbon ages. Graphed are seabed surface samples (diamonds surrounded in black), samples from core 930 (diamonds surrounded in red), and samples from core 929 (diamonds surrounded in yellow). Error bars for Δ^{14}C, MRE and the U-series chronology are presented with 1s uncertainties (note that the error bars may be smaller than the sample symbols used). The blue lines mark abrupt MRE increase.

Figure 3: A. MRE reconstructed from Mingulay Reef Complex cold-water corals against the difference of the Marine13 and IntCal13 radiocarbon ages [*Reimer*, 2013]. MRE symbols are as for Figure 2: seabed surface samples (diamonds surrounded in black), samples from core 930 (diamonds surrounded in red), and samples from core 929 (diamonds surrounded in yellow). B. Hematite-strained grains (%) from North Atlantic cores stack as a proxy of advections of cooler, ice-bearing surface waters eastward from the Labrador Sea and southward from the Nordic Seas [*Bond et al.*, 2001]. C. Greenland Ice Sheet Project 2 sea salt sodium as a proxy of westerly winds (2 pass low pass filter with a with a cutoff frequency at

1/200 Hz) [*O'Brien et al.*, 1995]. D. Reef growth rates estimated from downcore +56-08/930VE (pink) and downcore +56-08/929 VE (orange) U-series chonologies; grey dots indicate ages for seabed surface *Lophelia* dated by radiocarbon and/or U-series [*Douarin et al.*, 2013]. The blue lines indicate abrupt MRE increase. Error bars are presented with 1s uncertainties and may be smaller than the sample symbols.

Figure 4: MRE reconstructed from Mingulay Reef Complex cold-water corals relative to A. the Residual atmospheric Δ^{14}C curve [*Reimer et al.*, 2004] and B. the Δ Total Solar Irradiance (B. and C. 2 pass low pass filter with a with a cutoff frequency at 1/200 Hz) [*Steinhilber et al.*, 2009]. Uncertainties are presented by 1s error bars and may be smaller than the sample symbols. The blue lines symbolized abrupt MRE increase.


70°N
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SCC
SPG
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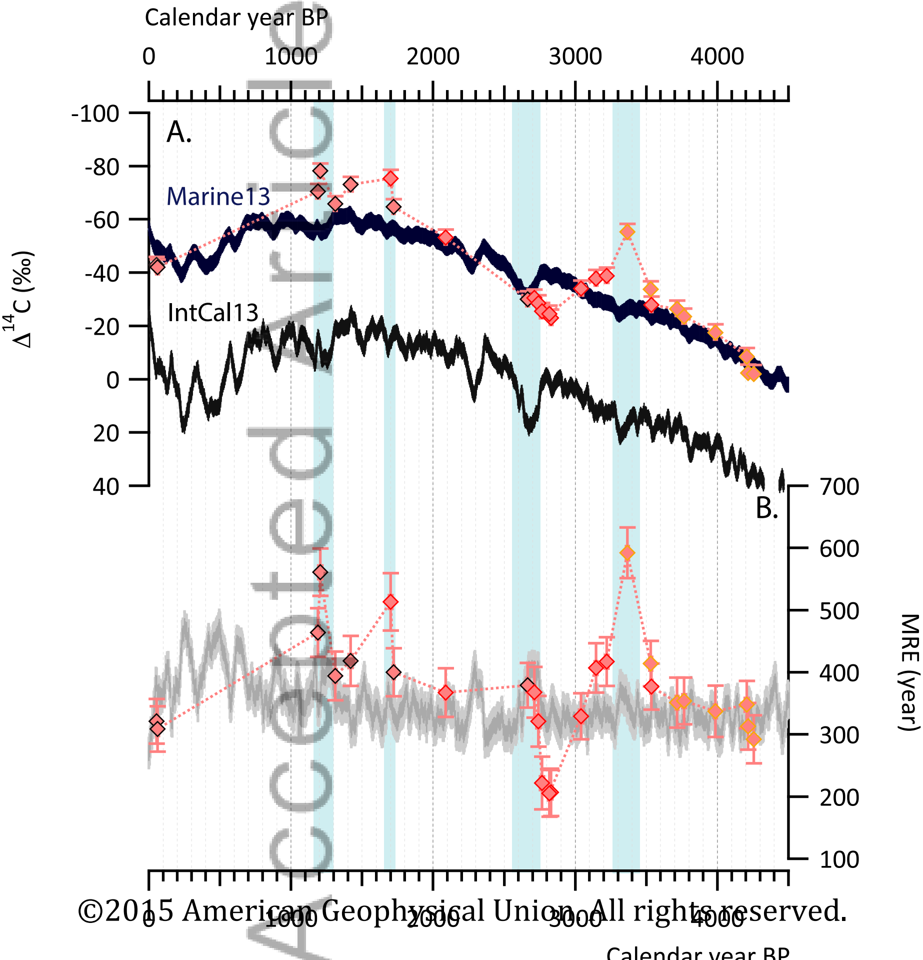
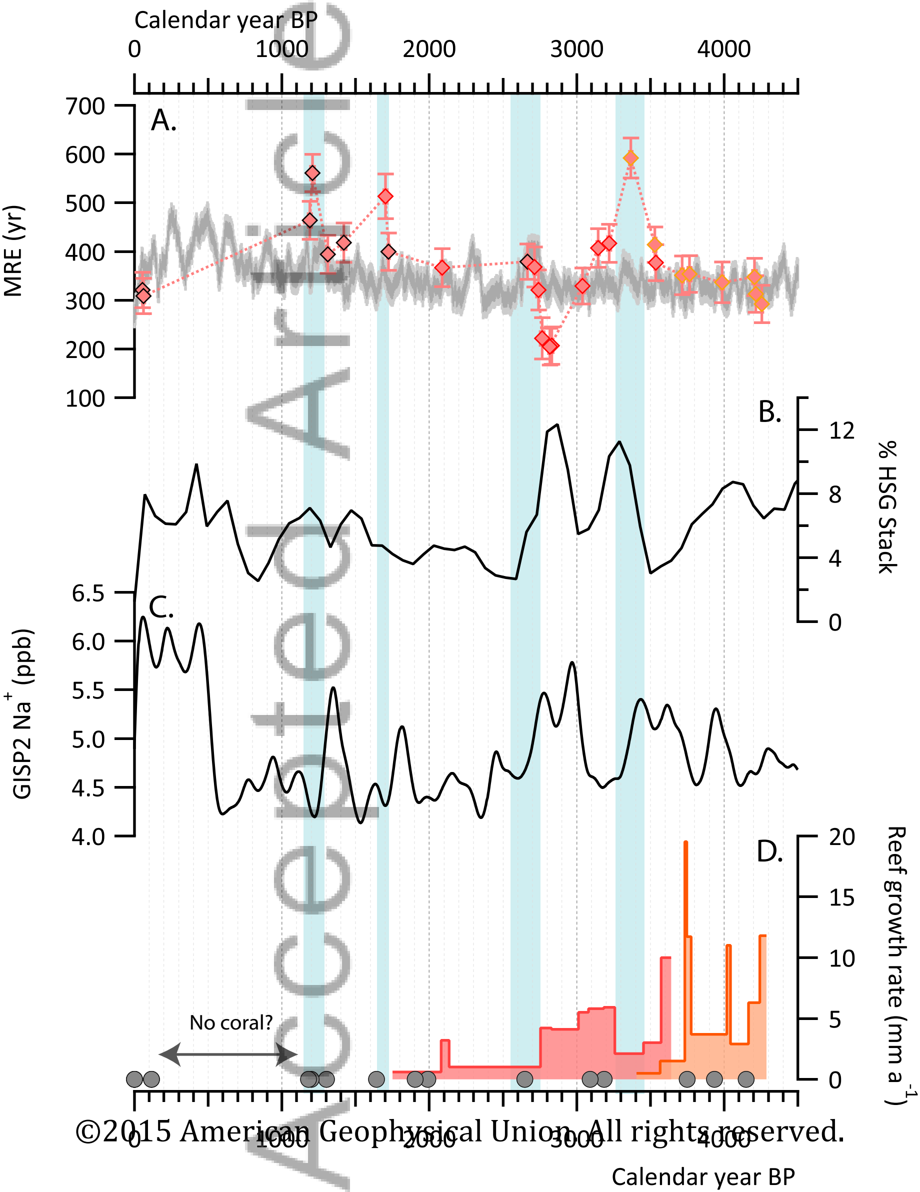
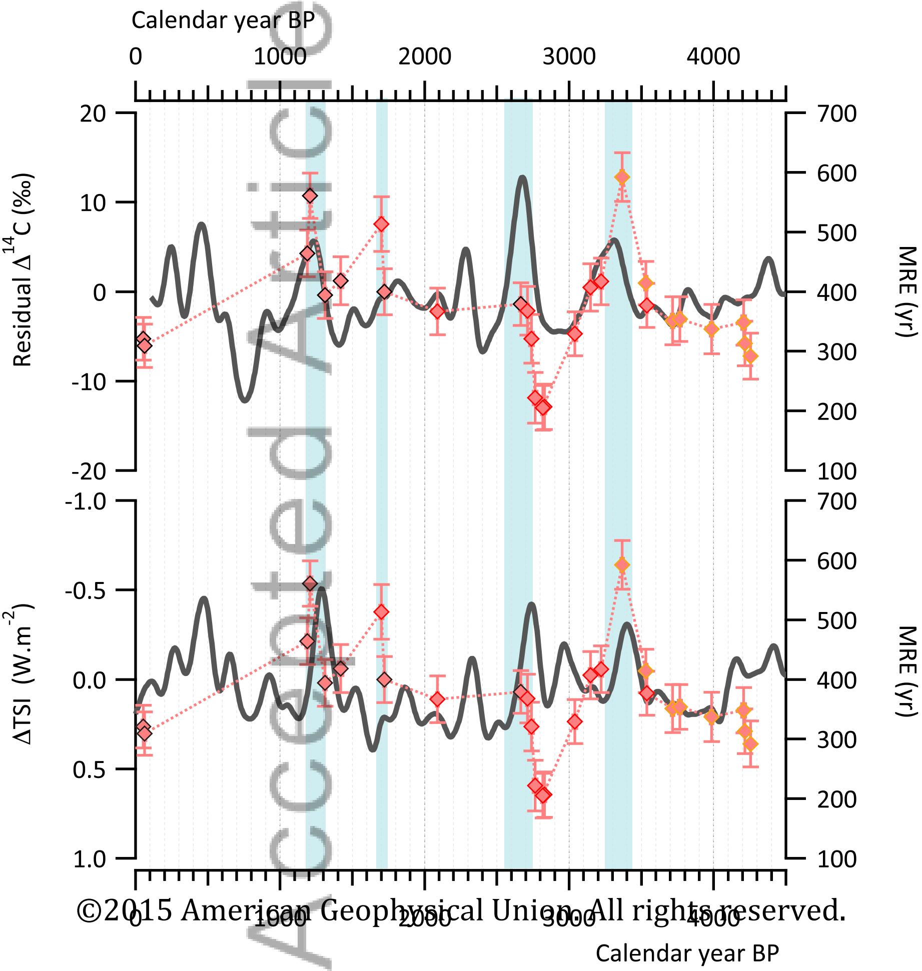

Calendar year BP
0
1000
2000
3000
4000
A.
-100
-80
-60
-40
-20
0
20
40
Δ^{14}C (‰)
Marine13
IntCal13
B.
700
600
500
400
300
200
100
MRE (year)
Calendar year BP


Calendar year BP
0
1000
2000
3000
4000
A.
MRE (yr)
700
600
500
400
300
200
100
B.
% HSG Stack
12
8
4
0
C.
GISP2 Na$^+$ (ppb)
6.5
6.0
5.5
5.0
4.5
4.0
D.
Reef growth rate (mm a^{-1})
20
15
10
5
0
No coral?
0
1000
2000
3000
4000
Calendar year BP


Calendar year BP
0
1000
2000
3000
4000
Residual Δ^{14}C (‰)
20
10
0
-10
-20
MRE (yr)
700
600
500
400
300
200
100
ΔTSI (W.m^{-2})
-1.0
-0.5
0.0
0.5
1.0
MRE (yr)
700
600
500
400
300
200
100
0
1000
2000
3000
4000
Calendar year BP