Movement of deep-sea coral populations on climatic timescales

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[1] During the past 40,000 years, global climate has moved into and out of a full glacial period, with the deglaciation marked by several millennial-scale rapid climate change events. Here we investigate the ecological response of deep-sea coral communities to both glaciation and these rapid climate change events. We find that the deep-sea coral populations of *Desmophyllum dianthus* in both the North Atlantic and the Tasmanian seamounts expand at times of rapid climate change. However, during the more stable Last Glacial Maximum, the coral population globally retreats to a more restricted depth range. Holocene populations show regional patterns that provide some insight into what causes these dramatic changes in population structure. The most important factors are likely responses to climatically driven changes in productivity, $[O_2]$ and $[CO_3^{2-}]$.

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1. Introduction

[2] Concern with future climate change has stimulated interest in how an increase in temperature and the continued release of CO_2 into the atmosphere might affect marine fauna, particularly corals. Since the Industrial Revolution, the oceans have taken up ~30% of the anthropogenic CO_2 emissions [*Keeling et al*., 1996]. An increase in the CO_2 content of the ocean lowers the saturation state of the water column for carbonate minerals that form the skeletons of marine calcifiers [*Feely et al*., 2004]. Observations and climate models have indicated that future global warming will also cause a decline in the $[O_2]$ of the ocean and a subsequent expansion of oxygen minimum zones (OMZ) [*Stramma et al*., 2008]. This expansion has dire consequences for marine fauna, as several marine macroorganisms become stressed under hypoxic conditions (60–120 μmol/kg of O_2) [*Vaquer-Sunyer and Duarte*, 2008].

[3] Deep-sea corals are a keystone species for benthic ecosystems with several other species relying on them for resources such as shelter, sites of reproduction, and nutrition [*Reed et al*., 2006]. With increasing ocean acidification and hypoxia, corals will have trouble maintaining their skeletons, negatively impacting other benthic organisms dependent on them, such as fish, sponges, urchins, and crustaceans [*Reed et al*., 2006]. Deep-sea corals are likely to be highly sensitive to environmental changes because they have evolved in a specialized and stable environment with cold, dark, and nutrient-rich conditions. Previously, it was thought that the deep-sea was a stable habitat buffered from short-term changes in the atmosphere or upper ocean, but recent work has shown that benthic ecosystems may respond quickly to seasonal and interannual shifts in upper ocean variables [*Ohga and Kitazato*, 1997; *Ruhl et al*., 2008].

[4] Several factors are thought to affect deep-sea coral growth, including temperature, $[O_2]$, the saturation state of the water column, and surface productivity [*Feely et al*., 2004; *André Freiwald et al*., 2004; *Guinotte et al*., 2006; *Cairns*, 2007]. Shallow water corals have a specific temperature range for optimal growth with recent temperature increases leading to coral bleaching events [*Harvell et al*., 1999]. However, temperature may play a less important role in setting optimal growth for azooxanthellate corals. The saturation state of the water column is likely important because deep marine calcifiers have lower rates of calcification with lower carbonate ion concentration [*Langdon et al*., 2000]. Deep-sea corals are sessile filter-feeding organisms that rely on organic matter falling from the surface; therefore, changes in surface ocean productivity can also be important to their growth. At intermediate depths in the ocean at least two of these key factors controlling coral growth, aragonite saturation state and dissolved $[O_2]$, are known to be decreasing now and are likely to continue in the future [*Stramma et al*., 2008; *Caldeira and Wickett*, 2003]. We do not understand these deep ecosystems well enough to accurately predict how deep-sea corals will respond to these changes.

All supporting information may be found in the online version of this article.

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[5] We can look to the paleoecological record to understand how coral populations have responded to global climate change on various timescales. The temperature, oxygen content, productivity and saturation state of the water column have all changed in the past on a variety of timescales from seasonal to glacial-interglacial cycles [*Zachos et al*., 2001; *Sachs and Anderson*, 2005; *Jaccard and Galbraith*, 2011; *Zeebe*, 2012]. We know that the distribution of deep-water masses at the Last Glacial Maximum (LGM) [*Curry and Oppo*, 2005] and the CO_2 content of the atmosphere [*Petit et al*., 1999] were both markedly different than they are today. We also know that the rapid climate changes documented in ice cores correspond to deep-ocean circulation changes [*Robinson et al*., 2005; *McManus et al*., 2004], surface ocean productivity shifts [*Sachs and Anderson*, 2005], and an intermediate depth [O_2] increase in the South Pacific [*Muratli et al*., 2010]. Here we look at how deep-sea corals have responded to past climate change concentrating on the last 40,000 years, which includes a glacial-interglacial transition and several millennial scale rapid climate change events. In particular, we look at the LGM (19–22 ka), Heinrich Stadial 1 (HS1) (18–14.7 ka), the Antarctic Cold Reversal (ACR) (14.8–12.9 ka), the Younger Dryas (YD) (12.7–11.7 ka), the Little Ice Age (~400 years ago), and the Holocene (10 ka to present). Using the paleo data, we can untangle the potential factors affecting deep-sea coral growth especially considering that very few experiments have been conducted to show how deep-sea corals react to changes in key environmental variables.

[6] Using species distributions in space and time to constrain aspects of the physical climate was epitomized in the CLIMAP program [*CLIMAP Project Members*, 1981]. As a successful effort to map surface assemblages of planktonic foraminifera during the LGM, CLIMAP attributed changing assemblages to variations in sea surface temperature. In this paper we are, in a sense, attempting the benthic version of CLIMAP. This effort is also similar to a data set from the deep North Atlantic that demonstrated the Quaternary ostracod species diversity responds to climate change on orbital to millennial timescales [*Cronin et al*., 1999]. However, instead of having to make age models for many sediment cores at several different depths, we use the new Reconnaissance Dating Method [*Burke et al*., 2010] to directly date more than 400 *Desmophyllum dianthus* samples. We present the largest record to date of changes in deep-sea coral distributions in the N. Atlantic and Tasmanian seamounts for the last 40,000 years. This paper's use of radiocarbon dating in an "age screening" mode also demonstrates how recent analytical advances can dramatically change the way radiocarbon dates are used in paleoclimatology and paleoecology.

2. Materials and Methods

2.1. Deep-Sea Coral Collection

[7] Since 2003 we have made a systematic effort to collect fossil deep-sea corals from two regions, each near a site of modern deep-water formation. We collected more than 5000 *D. dianthus* from the New England (34°N–40°N, 60°W–68°W) and Corner Rise seamounts (34°N–36°N, 47–53°W) in 2003–2005 using the deep submergence vehicles ALVIN and HERCULES. We also collected more than 10,000 *D. dianthus* from the Tasmanian Seamounts (43°S–47°S, 144°E–152°E) in 2008 and 2009 using the deep submergence vehicle JASON (Figure 1b). (These samples are available to the scientific community and have been cataloged and stored in the Caltech Deep-Sea Coral Storage facility (http://131.215.65.18/fmi/iwp/cgi?-db=coral&-loadframes)). Collection by Remotely Operated Vehicle and submarine ensured that the depth of each coral was precisely known and that corals were collected near growth position. During the dives we attempted to sample the entire available water column in each seamount region (below 920 m in the New England Seamounts and below 720 m in the Tasmanian seamounts). We spent considerable time searching below the maximum depth of *D. dianthus* in each region to ensure full coverage of this coral's habitat and worked to sample the bottom water depths evenly in the available time (Figure 2). Fossil coral distribution on the seafloor is patchy, but once in an area with abundant individuals, we systematically moved in either 50 or 100 m depth intervals to collect samples. Nets and scoops were used with the vehicles' manipulator arms to collect loose samples and scrape off attached individuals from the hard substrate. Mesh sizes (<1 mm) were small enough to catch whole individuals and skeletal fragments while still releasing sediment. At the time of collection we knew each specimen's latitude, longitude and depth but not its age.

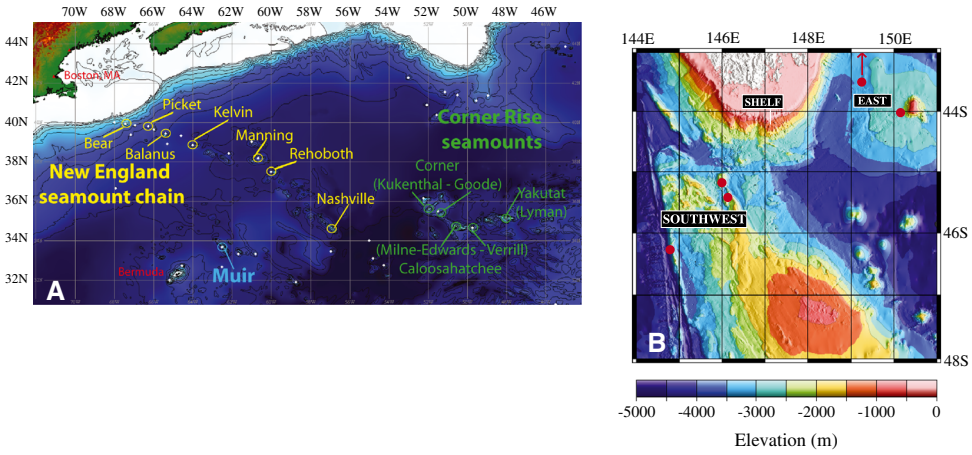

Figure 1. Sites of sample collection in the (A) North Atlantic and (B) Tasmanian Seamounts (red dots).

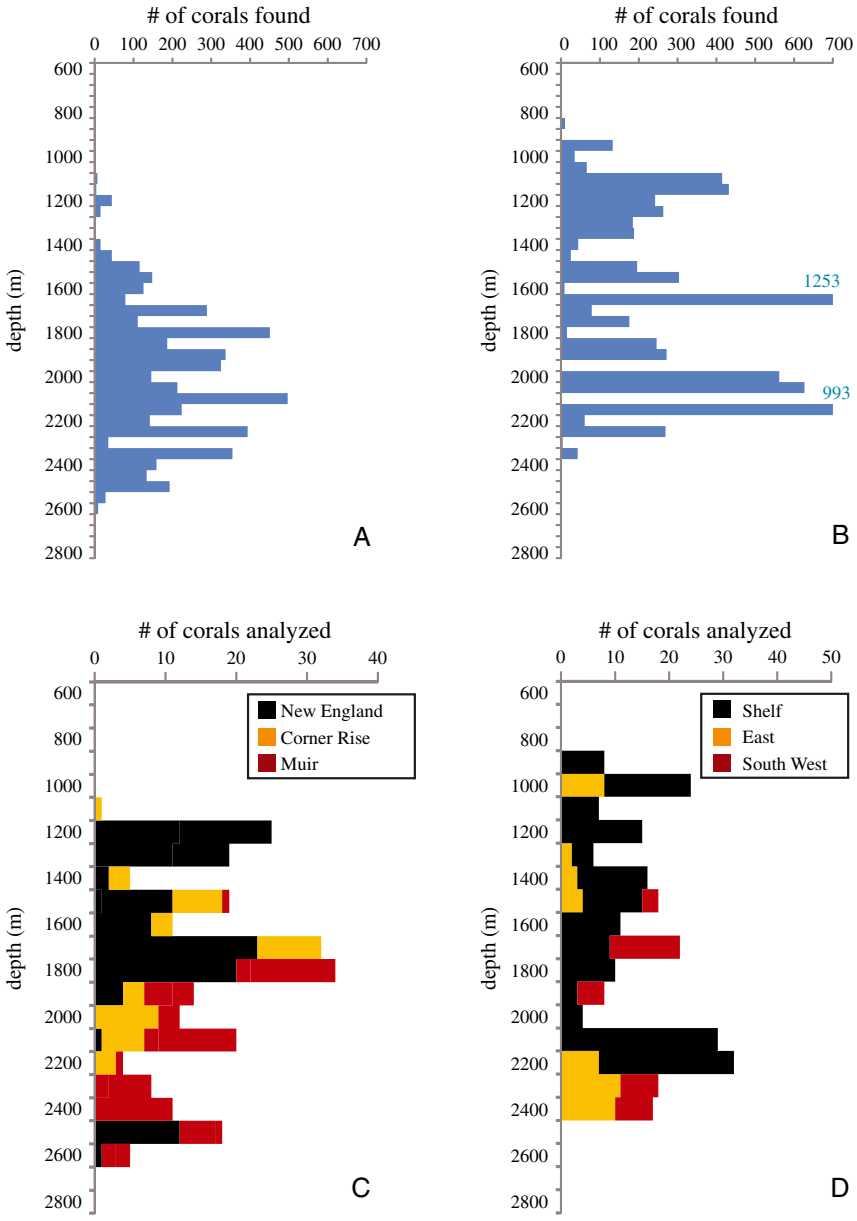

Figure 2. Depth distribution of the samples collected in the (A) North Atlantic and (B) Tasmanian Seamounts. Corals were collected from 1098–2740 m (while searching from 900–2800 m) in the North Atlantic and from 898–2395 m (while searching from 898–4000 m) in the Tasmanian seamounts. Depth distribution of samples from the (C) N. Atlantic and (D) Tasmanian seamounts analyzed for radiocarbon dates using the reconnaissance dating method and previously U-series dated corals from the New England Seamounts [*Robinson et al.*, 2007].

2.2. Cleaning Procedures

[8] Ninety-five corals from the New England and Corner Rise Seamounts and 249 corals from the Tasmanian seamounts were selected from our collection across several seamounts and all depths for radiocarbon analyses. The material analyzed was chosen from the collections while retaining an approximately equal representation across the coral's depth range at both sites. There is some possibility for a size bias in our record as whole corals with large septa were preferentially selected. However throughout the whole collection there is not a large difference in size between individuals and there is no difference in size range with age [*Thresher et al.*, 2011a]. Prior to radiocarbon analysis, the corals were cleaned to remove Fe-Mn crusts and organic contamination. For the corals cleaned in 2008, samples of 8–15 mg were taken from each coral and physically and chemically cleaned to remove the ferromanganese crust that was coating it [*Adkins et al.*, 2002a]. Corals analyzed in 2009 were physically cleaned using a dremel tool and a sandblaster. The samples were then chemically washed with methanol, which had been shown to be equivalent to the more labor-intensive cleaning carried out in 2008 [*Burke et al.*, 2010].

2.3. Radiocarbon Analysis-Reconnaissance Dating Method

[9] After cleaning, corals were radiocarbon dated following the method of *Burke et al.* [2010]. Corals were first combusted in an Elemental Analyzer and the resulting CO_2 from combustion was extracted cryogenically on a vacuum line attached to the Elemental Analyzer. The CO_2 was frozen into a reaction tube, which contained zinc, titanium hydride, and iron catalyst. The sample was then graphitized in a furnace for 3 h at 500°C and 4 h at 550°C, and then analyzed for $^{14}C/^{12}C$ at The National Ocean Sciences Accelerator Mass Spectrometry (NOSAMS) Facility at The Woods Hole Oceanographic Institute. Coral standards were run using the traditional hydrolysis method and the reconnaissance dating method to ensure that there was no bias to the reconnaissance dating method (Figure S1). Coral standards were also run at regular intervals during sample processing (Figure S2). Corals were blank corrected using the IAEA C-1 calcite standard. This method allowed for many more samples to be dated at a much lower cost than traditional hydrolysis techniques. Figure 3 shows the depth and age distribution of corals collected from the New England, Corner Rise, Muir, and Tasmanian seamounts.

2.4. Radiocarbon Analysis-Gas Ion Source

[10] After analyzing the 344 ^{14}C Reconnaissance measurements, 80 more corals were randomly selected from 1375–1575 m water depth from the Southern Ocean to improve the population statistics of intermediate water column coral distributions (Figure 4). These samples were run with another new development in radiocarbon dating, the Gas Ion Source (GIS) at NOSAMS [*McIntyre et al.*, 2011]. Rather than making graphite in off-line chemical reactions, the GIS-AMS method reacts corals with H_3PO_4 and takes the CO_2 evolved directly into the mass spectrometer. Trading precision for sample throughput, this new method can process dozens of coral samples per day and is readily adaptable to automated sample injection. This method does have a much higher background (Fraction Modern ~ 0.02) versus the Reconnaissance Dating Method (Fraction Modern ~ 0.007); however, this new NOSAMS facility represents an important next step in radiocarbon age screening techniques. Figure 4 shows the depth and age distribution of the 80 corals collected from the Tasmanian seamounts at intermediate water depths and analyzed with the GIS.

2.5. Radiocarbon to Calendar Age Conversion

[11] Radiocarbon ages are not equivalent to calendar ages for two reasons. First because the calculation of a conventional radiocarbon age assumes that the radiocarbon content of the atmosphere has been constant [*Stuiver and Polach*, 1977], an assumption that has not stood the test of time [*Reimer et al.*, 2011]. Second because radiocarbon ages of modern deep-sea corals are actually equivalent to the age of the water from which they grew [*Adkins et al.*, 2002a]. This deep-water radiocarbon age is a function of both the surface reservoir radiocarbon age from which it formed and the mean time the water parcel spent away from the atmosphere. Therefore, the radiocarbon age of a fossil deep-sea coral reflects a combination of its true calendar age and information about ocean circulation.

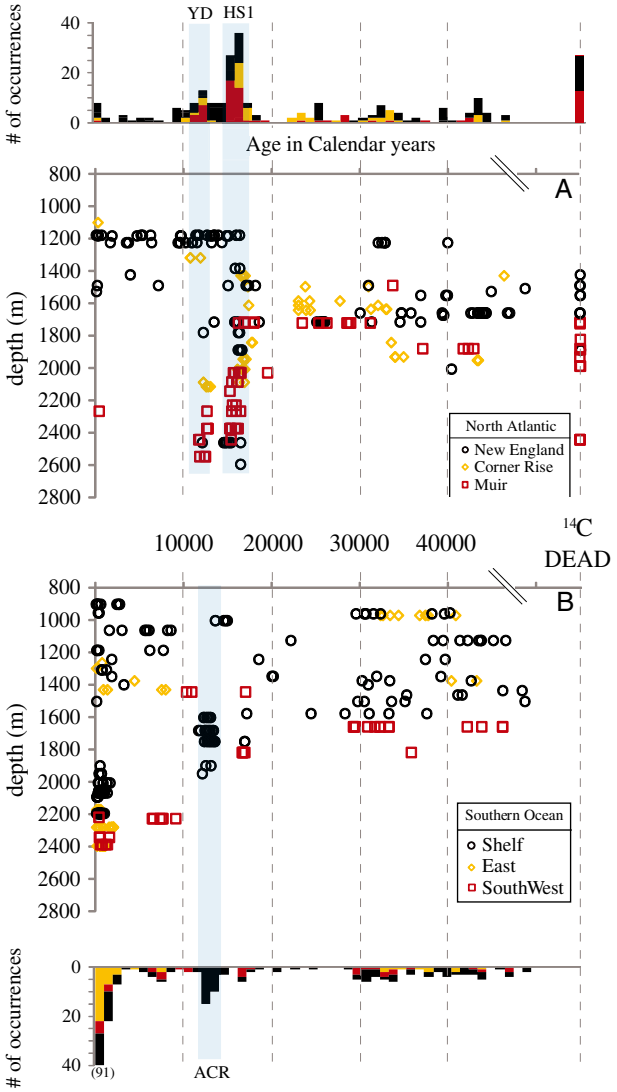

Figure 3. The Calendar age-depth distributions of deep-sea corals from the (A) North Atlantic and (B) Southern Ocean seamounts for the past 50,000 calendar years. These corals were dated using the reconnaissance dating method (and then converted to calendar age (see section 2.5 for details) and U/Th [*Robinson et al.*, 2007]. Each point represents a single age from a single *D. dianthus* coral. The histograms above and below the plots represent the number of corals for each 1000 year age bin. Radiocarbon dead corals dated simultaneously with the Tasmanian Seamount corals have an average age of 45,000 ± 2900 ^{14}C years. Therefore all Tasmanian Seamount corals older than 44,000 calendar years are likely to be radiocarbon dead as well.

[12] We converted all radiocarbon dates to calendar ages by applying four different constant offsets during four time periods. We used the modern age of the water column in the North Atlantic (600 years) and Southern Ocean (1250 years) to make a reservoir correction for all Holocene data. We used the ^{14}C age and U/Th age difference (1500 years) as measured in corals from the New England Seamounts during the YD to convert YD measurements [*Robinson et al.*, 2005]. For all other corals during the glacial time period in the North Atlantic we used the ^{14}C

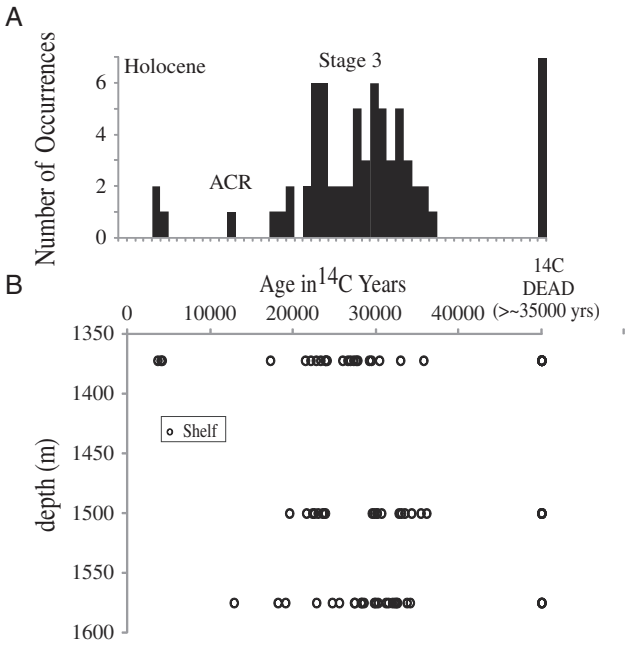

Figure 4. The ^{14}C age-depth distributions of deep-sea corals from 1350–1575 m water depth from the Tasmanian Seamounts. These corals were dated using the GIS-AMS method. We observe the minimum depth of the ACR to be 1575 m as corals do not appear in shallower depths and that the corals at intermediate depths prefer Marine Isotope Stage 3 (MIS3) relative to the Holocene. In the intermediate water column depths, there are two population modes in MIS3, possibly correlated with Heinrich 3 and Heinrich 4.

age and U/Th age difference (1000 years) measured in HS1 corals to make a reservoir correction [*Robinson et al.*, 2005]. For all glacial corals in the Tasmanian seamounts we used the average of the ^{14}C to U/Th age difference (1900 years) measured in the ACR (Table S4) to make a reservoir correction. We converted all ^{14}C dates to calendar ages using Intcal09 and the Calib 6.0 software.

2.6. Statistical Analysis

[13] We used the Wilcoxon Rank Sum and Brown-Forsythe Test to test for differences in coral distributions across depth. In particular, we try to determine whether the coral depth distributions at the YD, HS1, ACR, and LGM are unique compared to other time intervals. We looked at variability in the mean and the variance of the depth distribution of corals in 10,000 year intervals. We also compared coral population modes (YD (11.6–13 ka), HS1 (14.5–18 ka), LGM (20–30 ka), and ACR (13.5–12 ka) to each other and all 10,000 year intervals. The YD, HS1, and ACR age bins were chosen to include all the corals at each mode. The LGM bin of 20–30 ka was selected to include enough corals for the tests to be statistically meaningful.

3. Results

[14] Figures 2c and 2d show the depth distribution of all corals we analyzed for radiocarbon age using the reconnaissance dating method and previously U-series dated corals from the New England Seamounts [*Robinson et al.*, 2007]. Figure 3 shows the depth and age distribution of corals collected from the New England, Corner Rise, Muir and Tasmanian seamounts (Tables A1 and A2). Figure 3 also includes previously published U-series dated corals from the New England seamounts [*Robinson et al.*, 2007]. There are several prominent features in the distribution of corals. During the LGM, the coral populations in the North Atlantic shoaled to 1700 m, which roughly corresponds to the boundary between northern and southern source water as determined by δ^{13}C and Cd/Ca measurements [*Curry and Oppo*, 2005; *Marchitto and Broecker*, 2006]. Although the data are sparse, a similar boundary appears in the Southern Ocean. During the glacial time period in the North Atlantic, the bottom-most extent of the coral distribution remains constant at 2000 m. Similarly in the Southern Ocean there is a nearly constant depth limit of 1650 m until 18,500 ^{14}C years, after which the population bifurcates in depth with one branch deepening to 2400 m.

[15] The coral populations both in the North Atlantic and Southern Ocean respond to rapid climate changes [*Dansgaard et al.*, 1993; *Blunier and Brook*, 2001]. From sediment and ice core records we know that the YD and HS1 events were both times of large reorganization of the atmospheric and ocean system. These are also times when the size and the depth range of the coral population increased in the North Atlantic (Figure 3). The coral populations also expanded during the Little Ice Age in the North Atlantic (Figure 3), after a long period of coral growth at only the shallowest depths. In contrast to the New England seamount record, the Tasmanian Seamounts coral distribution has only one deglacial climate mode, the ACR. As radiocarbon dates in the deep ocean, and especially in the Southern Ocean, have a large "reservoir age", it is not possible to say with ^{14}C dates alone if the coral population modes in Figure 5 are truly separate from one another. To check these results

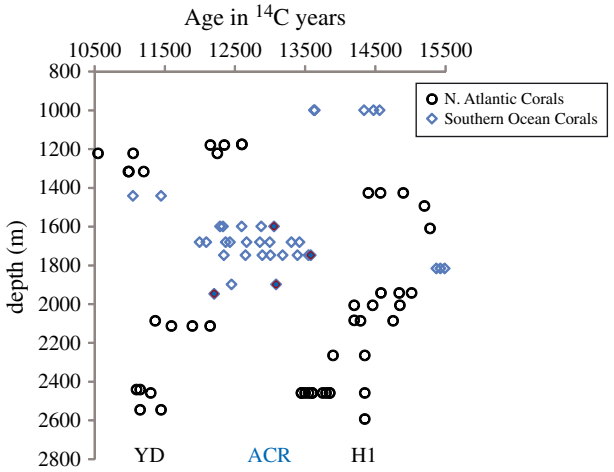

Figure 5. The ^{14}C age-depth distribution of deep-sea corals dated using the reconnaissance dating method during the last deglaciation. The coral depth distribution is sharply modal during the three rapid climate change events in the deglaciation: the Younger Dryas (YD), Antarctic Cold Reversal (ACR) and Heinrich 1 (HS1). ACR corals outlined in red have been dated for U-series dating (Table S4). Several North Atlantic HS1 and YD have been previously dated using U-series dating [*Robinson et al.*, 2007] and do not overlap with the bulk of the ACR corals.

we selected four samples from the ACR mode for U-series dating and plot an expanded view of all ACR dates in Figure 5 (Table A4). The ACR cluster of calendar ages is after the calendar age of corals in HS1 [*Robinson et al*., 2007] and before the start of the YD [*Eltgroth et al*., 2006]. Our data show that deep ocean populations respond dramatically to local rapid climate change events and that the populations in the North Atlantic and the Southern Ocean expanded at different times during the last deglaciation, a result that is consistent with many other oceanic tracers showing a "bipolar see-saw" [*Broecker*, 1998a] during the deglaciation.

[16] We use the Wilcoxon rank sum and Brown-Forsythe statistical tests to quantitatively assess the difference in medians and variances of the different coral population shifts in depth (Table A3). The population between 20,000 and 30,000 years in the North Atlantic is unique in its mean depth compared to all other North Atlantic 10,000 year time intervals and is unique in depth variance compared to other North Atlantic 10,000 year time intervals during the glacial time period. We interpret this as a unique depth distribution for the LGM population even though the age range we picked was widened to include enough corals to be statistically meaningful. In mean and variance tests, the population mode at HS1 is indistinguishable from the population mode at the YD. In the Tasmanian seamounts, the ACR distribution is unique compared to all other times and the YD and HS1 in the North Atlantic.

[17] Finally, to further quantify our results, a targeted selection of our Tasmanian seamount corals was analyzed by the new GIS-AMS technique at NOSAMS [*McIntyre et al*., 2011]. Individuals collected between 1350–1550 m were chosen to further test the robustness of our observations of coral distributions in time, based on the reconnaissance method. The GIS allows us to analyze even more samples in a short period of time and can therefore target specific questions related to gaps in the record. As the ACR does not appear in the corals sampled from 1372 to 1500 m in the GIS results (Figure 4), the minimum population depth of the ACR is 1575 m. This data set also confirms the scarcity of corals during the LGM in the Tasmanian seamounts as we did not find any more individuals of this age with this higher frequency sampling.

4. Discussion

4.1. Potential Sampling Bias

[18] Given these dramatic changes in coral populations in space and time, we can try to identify the factors that could

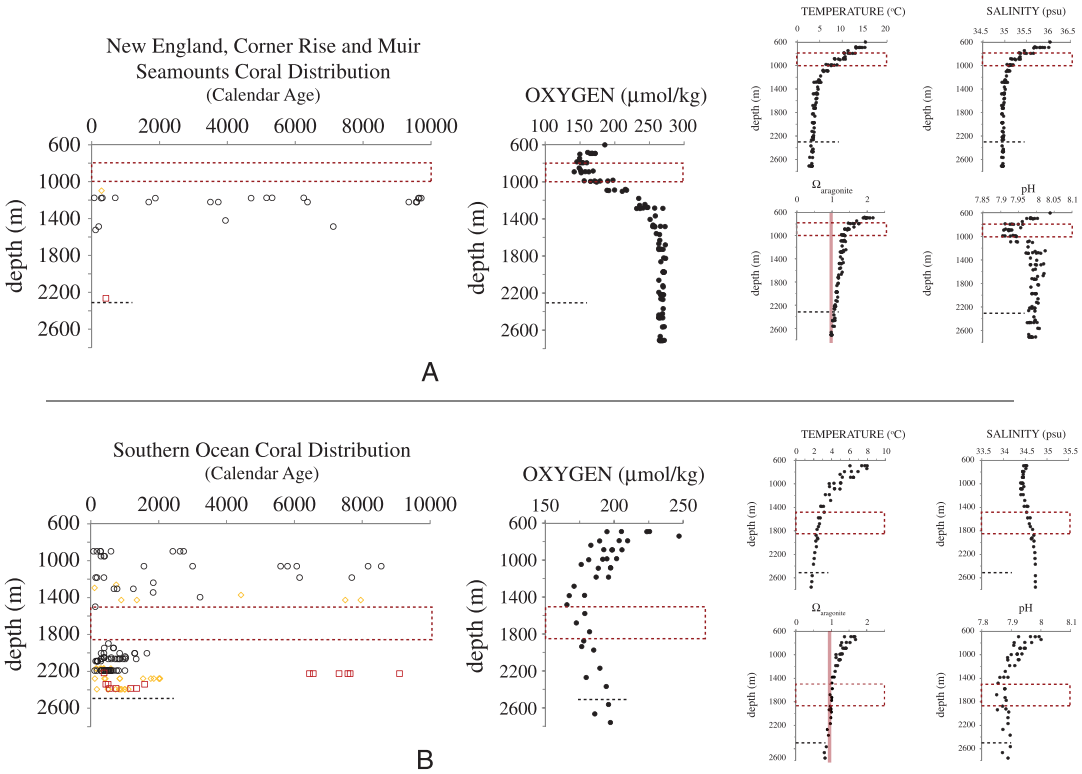

Figure 6. The Calendar age-depth distributions of Holocene deep-sea corals in the (A) North Atlantic and (B) Tasmanian Seamounts. These corals were dated using the reconnaissance dating method (and then converted to calendar ages) and the U/Th method [*Robinson et al*., 2007]. The dashed red boxes represent gaps in the coral distribution, which also correspond to the oxygen minimum zones. The black dashed line indicates the maximum depth of the Holocene coral distribution in each region. The red shaded box on the $\Omega_{aragonite}$ profile represents the region of $\Omega = 0.9–1$. The water column profiles of temperature, salinity, and oxygen are from World Ocean Atlas 2009 and from 34°N–40°N, 60°W–68°W in the North Atlantic and 43°S–46°S, 144°E–152°E in the Tasmanian Seamounts. pH and $\Omega_{aragonite}$ were calculated using CO2SYS (http://cdiac.ornl.gov/ftp/co2sys/).

affect the distributions. One possibility is that a sampling bias, either in the field or when choosing samples in the lab for radiocarbon dating, could have altered the population patterns seen in Figure 3. This is an unlikely explanation for both the North Atlantic and the Southern Ocean distributions. In the North Atlantic, coral abundance correlates poorly with the amount of time spent looking for corals at each depth [*Robinson et al*., 2007]. In all our field campaigns, sampling was depth-stratified to ensure representative material for the entire water column range of living and dead corals in the study area of 720–2400 m in the seamounts south of Tasmania, and 920–2600 m in the North Atlantic (see Methods). Subsamples for ^{14}C analyses were drawn from the field material as to provide approximately equal representation across the species' depth ranges. A sampling bias also cannot account for distributions that change over time unless material with age-related features are deliberately selected or avoided, which is impossible to know ahead of time. We used only whole corals rather than fragments for our analyses to avoid double counting, though this might mean we missed the oldest material at any one water column depth. Such selectivity, coupled with possible effects of low carbonate levels at depth, could produce a shoaling of apparent distributions with increasing specimen age. However, this is not consistent with the stable depth distributions we observe for material older than 20,000 years, nor would such a bias explain the rapid changes in distribution associated with climatic events. Skeletal dissolution also cannot explain the several cases where older corals survived multiple younger gaps in the population distribution at their depth.

4.2. Factors Controlling Coral Distribution

[19] With an understanding that sampling biases are unlikely to create the distributions seen in Figure 3, we seek other climate and ocean structure related reasons for coral population movement. Few investigations of the biological influence on deep-sea coral recruitment and growth have been conducted and these influences should not be overlooked in future studies. However, here we focus on climatic variables that affect deep-sea coral populations. Factors that are likely to influence coral growth are variations in food supply via surface ocean productivity or changes in lateral bottom currents, in situ temperature, water mass structure, deep water [O_2], and the aragonite saturation state of the water. The recent population distribution in the Tasmanian seamounts has a distinctive gap between 1575–1825 m and no corals below 2400 m, each of these features can help elucidate which of these hydrographic factors might be more important. The ~250 m thick region without a substantial population of *D. dianthus* cannot be ascribed to changes in surface ocean productivity because a large group of corals reappear below the gap. Unlike other benthic fauna whose abundances in the water column are tightly coupled to specific water masses [*Dingle and Lord*, 1990], a preference for Antarctic Intermediate Water or Pacific Deep Water is also not controlling the presence of the gap. Neither the salinity profile, the pH profile nor the monotonically decreasing temperature data show the peculiar characteristics of these waters at the correct depth (Figure 6). As there is a substantial modern population at temperatures lower than the temperature of the water at the gap, it is also unlikely that this variable alone is the main control on coral growth in this region.

[20] However, the gap in the coral distribution does correspond to the OMZ of 165 μmol/kg. Recent laboratory studies of another cosmopolitan deep-sea coral, *Lophelia pertusa*, have shown that the respiration rate of this species markedly declines at an oxygen concentration of approximately ~100–150 μmol/kg, depending on the growth temperature [*Dodds et al*., 2007]. These are similar in size to *D. dianthus* and are sessile filter feeders which need a relatively large concentration of O_2 to survive. The OMZ has long been recognized as a key oceanographic boundary for animals intolerant of hypoxia. There is lower macrofaunal diversity within OMZs and many taxa with calcified shells or exoskeletons, like copepods and benthic foraminifera, tend to be absent from the cores of OMZs [*Levin et al*., 2000; *Lutze and Coulbourn*, 1984]. While it does not have the distinctive gap of the Tasmanian seamounts, our North Atlantic population of corals is also absent at its local OMZ, which approaches the 150 μM threshold (Figure 6). We looked for corals with *Alvin* at shallow depths on Gregg Seamount in the North Atlantic and *D. dianthus* does not appear until ~1100 m. This correspondence between lab based metabolic limits and our field based population distributions in both the Southern Ocean and the North Atlantic suggests that the distinctive Holocene water column gap in Figure 3 is controlled by [O_2].

[21] The fossil population distributions also point toward oxygen as an important control on coral viability. During the last glacial period, AAIW may have increased both its [O_2] and its mass flux due to colder sea surface temperatures and higher wind speed [*Muratli et al*., 2010]. During the ACR in particular, it has been noted that there was an increase in oxygenation of AAIW [*Jaccard and Galbraith*, 2011]. This increase is seen in the coral distribution with the reappearance of deep-sea corals in the Southern Ocean at 1500 m. In the North Atlantic, a temporary extinction of cold-water corals due to anoxia has also been seen from 11.4–5.9 cal kyr BP in the Eastern Mediterranean [*Fink et al*., 2012].

[22] Below the modern Tasmanian seamounts population gap, [O_2] continues to increase and *D. dianthus* is abundant until 2400 m. This sharp cut off was apparent on all of our dives that crossed this depth threshold. From 1400–2400 m in the Tasmanian seamounts, the aragonite saturation state of the water column remains relatively constant at $\Omega \sim 0.9$–1.0, but at 2500 m, it begins to decrease much more rapidly (Figure 6). This suggests that the bottom-most extent of the coral distribution, similar to the observations of living *D. dianthus* [*Thresher et al*., 2011b], is a function of the aragonite saturation state of the water column. [CO_3^{2-}] control of calcification rates in corals is a well-known feature in both surface and deep-sea species [*Guinotte et al*., 2006; *Langdon et al*., 2000]. The apparent cut off in the North Atlantic population at ~2600 m, on the other hand, is an artifact of our sampling location. To access these depths we investigated a 'notch' in the long, linear feature named Muir seamount (Figure 1). This gap in the bathymetry is probably promoting coral growth as water circulating around the seamount moves through the opening and thus focuses the suspended matter food supply. Aragonite saturation state does not drop substantially below $\Omega \sim 0.9$–1.0 in this region until slightly deeper depths (Figure 6).

[23] Variations in the saturation state of the water column have also been determined over the past glacial cycle.

Broecker and Clark [2003] documented a decrease in $[CO_3^{2-}]$ during the LGM at the Ontong-Java Plateau relative to modern concentrations and *Yu et al*. [2010] showed a rising $[CO_3^{2-}]$ over the deglaciation and into the Holocene in a deep Pacific core. These observations are consistent with the bottom most extent of the Southern Ocean coral distribution gradually increasing in depth from the LGM to the Holocene as the whole ocean $[CO_3]$ responds to the deglaciation and CO_2 degassing from the deep ocean [*Broecker and Peng*, 1987]. However, this conclusion is at odds with previous studies of deep Pacific sediments which suggest that more extensive dissolution occurred during interglacials rather than glacials [*Farrell and Prell*, 1989; *Rickaby et al*., 2010]. Because the coral distributions is the combination is the $[O_2]$ and $[CO_3^{2-}]$ effects, we cannot definitively say what the saturation horizon history is at our site.

[24] Variations in surface ocean productivity have previously been documented to control benthic species diversity, community structure and distribution [*Ruhl et al*., 2008]. Recent work [*Eisele et al*., 2011] has shown a relationship between changes in deep-sea coral distributions and productivity that were attributed to changes in the location of the polar front. When all the deep-sea coral population studies published to date are considered along with our current data set, we see a consistent pattern. During the Holocene, there are abundant corals in the upper water column of the New England Seamounts bathed by the Gulf Stream, in the Rockall Trough and Porcupine Seabight regions near Iceland [*Frank et al*., 2005], and in the Sula Reef complex on the Norwegian Shelf (Figure 7) [*Freiwald et al*., 2002]. All of these regions are located in, or at the edge of, the subpolar gyre and are regions of relatively high productivity. On the other hand, there are few to rare occurrences of modern and Holocene deep-sea corals in the Corner Rise or the Gulf of Cadiz (Figure 7) [*Wienberg et al*., 2009] which are low productivity regions south of the Gulf Stream and in the subtropical gyre. In contrast, during the last glacial, atmospheric and oceanic circulation are thought to be more zonal (Figure 7) [*CLIMAP Project Members*, 1981]. At this time there were corals in the New England and Corner Rise seamounts, as well as the Gulf of Cadiz, but none in the Rockall Trough, Porcupine Seabight or the Sula Reef complex. These latter three locations were north of the ice rafted debris belt and likely under sea ice with less surface productivity to fuel coral growth, while the more southern locations were likely in more productive waters. During Heinrich stadials in the North Atlantic, surface ocean productivity increased as observed in Ba/Al profiles and C_{org} fractions in deep-sea sediments [*Hinrichs et al*., 2001]. This response of the surface ocean to rapid climate change corresponds to a distinct peak in coral growth. Over all the North Atlantic region compilation of coral population data sets from a number of authors shows that surface productivity is an important factor in setting coral growth patterns in the North Atlantic. However recent work on sedimentary alkenone concentrations in the Chatham Rise, near New Zealand has shown that the productivity in the Southern Ocean actually increased during Heinrich Events [*Sachs and Anderson*, 2005] but not the Holocene, unlike the coral population changes we see in the Tasmanian Seamounts where the ACR is a prominent time of population expansion. So while surface productivity is a factor influencing coral growth in general, it cannot be the only factor in the Tasmanian Seamounts.

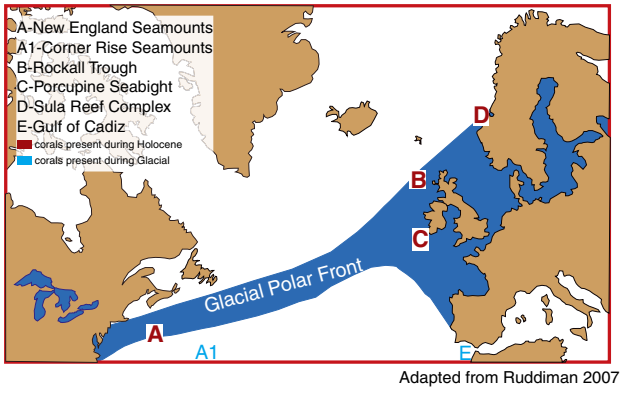

Figure 7. A map of modern and fossil occurrences in the North Atlantic. The New England Seamounts, Rockall Trough, Porcupine Seabight, and Sula Reef complex all have deep-sea corals during the Holocene while the Corner Rise Seamounts, Muir Seamount, and the Gulf of Cadiz have deep-sea corals during the glacial period. This pattern of deep-sea coral occurrences is consistent with subpolar front having a more zonal orientation during the glacial time period [*Ruddiman*, 2007] and therefore the Corner Rise Seamounts, Muir Seamount, and the Gulf of Cadiz being bathed by more productive waters.

4.3. Implications

[25] This ecological data set has implications for our interpretation of past ocean conditions. We believe that $[CO_3^{2-}]$, $[O_2]$ and surface ocean productivity are the most important controls for deep-sea coral distribution and that in a limited way, the population changes seen in Figure 3 can help constrain their history. Since the LGM, the Tasmanian Seamount corals have increased their maximum depth. This could be due to a deepening of the aragonite saturation horizon. If the bottom-most extent of the coral distribution during the LGM is controlled by $[CO_3^{2-}]$ under saturation (where $\Omega < 0.9$) and not $[O_2]$ (as there was more oxygen in the water column due to increased solubility with cooler temperatures), then the $[CO_3^{2-}]$ at the base of the distribution during the LGM should be similar to that of the base of the modern, except for temperature and pressure differences. Therefore, assuming that during the LGM, sea level is 125 m lower, the temperature is 2°C cooler [*Cutler et al*., 2003], and there is a salinity increase of 3.3% [*Adkins et al*., 2002b], we calculate that the $[CO_3^{2-}]$ at 1575 m during the LGM was ~85 µM. This estimate for $[CO_3^{2-}]$ during the LGM agrees with other estimates based on geochemical proxies [*Broecker*, 1998b; *Sanyal et al*., 1995].

4.4. Implications for Future Global Climate Change:

[26] Looking to the future effects of these variables on deep-sea coral populations with a changing climate, models of global warming have indicated that both the aragonite saturation state of the water column and the $[O_2]$ of the ocean will decline, increasing the areas of OMZs [*Stramma et al*., 2008; *Caldeira and Wickett*, 2003]. These two effects in conjunction will lead to deep-sea corals living in conditions that are not suitable for their growth. Genetic studies have

indicated an absence of vertical larval dispersal [*Miller et al.*, 2011], suggesting that as the aragonite saturation horizon rises, deep-sea corals will not be able to migrate to shallower depths. Therefore, it is likely that future increases in atmospheric CO_2 will lead to a decrease in the size of the deep-sea coral population and its associated habitat for a wide array of benthic organisms.

5. Conclusions

[27] In conclusion, we radiocarbon dated more than 400 *D. dianthus* samples from a range of depths in the N. Atlantic and Southern Ocean. We used two new radiocarbon dating techniques, the Reconnaissance Dating Method and the Gas Ion source at NOSAMS in WHOI to date many more corals more cheaply and quickly than previously possible. We find that deep-sea corals were affected by climatically driven changes in $[O_2]$, surface ocean productivity and the saturation state of the water column.

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