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Key Points:

- Ocean sediments suggest that the Iceland Basin warmed during the industrial era
- Basin-wide subpolar gyre circulation change contributed to warming during this period
- Late 20th century subpolar gyre state unprecedented in the last 10,000 years

Supporting Information:

- Supporting Information S1
- Data Set S1

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Exceptional 20th Century Ocean Circulation in the Northeast Atlantic

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Abstract The North Atlantic subpolar gyre (SPG) connects tropical and high-latitude waters, playing a leading role in deep-water formation, propagation of Atlantic water into the Arctic, and as habitat for many ecosystems. Instrumental records spanning recent decades document significant decadal variability in SPG circulation, with associated hydrographic and ecological changes. Emerging longer-term records provide circumstantial evidence that the North Atlantic also experienced centennial trends during the 20th century. Here, we use marine sediment records to show that there has been a long-term change in SPG circulation during the industrial era, largely during the 20th century. Moreover, we show that the shift and late 20th century SPG configuration were unprecedented in the last 10,000 years. Recent SPG dynamics resulted in an expansion of subtropical ecosystems into new habitats and likely also altered the transport of heat to high latitudes.

Plain Language Summary The Northeast Atlantic is of crucial importance for the global climate system and marine ecosystems. We can use sediment from the bottom of the ocean to reconstruct how the Northeast Atlantic has changed over thousands of years. In this study, we present the first evidence that 20th century Northeast Atlantic surface ocean circulation was unusual compared to the last 10,000 years. This change caused a replacement of cool, subpolar waters with warmer subtropical waters near Iceland and has impacted the distribution of marine organisms. The most striking aspect of our work is the exceptional nature of the shift in the 20th century (in contrast to thousands of years of relative stability), with implications for understanding future change.

1. Introduction

The North Atlantic is a critical region in the climate system. The subpolar gyre (SPG) provides the connection between the tropical Atlantic and the deep-water formation regions of the Iceland Basin, Nordic and Labrador Seas, and the Arctic Ocean (Lozier et al., 2019; Tiedje et al., 2012). It is characterized by cyclonic flow in the Iceland Basin and Irminger and Labrador Seas (Figure 1). On its southern edge, the North Atlantic Current (NAC) and subpolar front (SPF) separate the cold, fresh SPG waters from the warmer, saltier waters originating in the subtropical gyre. The NAC carries those warm waters into the northeast Atlantic. Changes in SPG dynamics influence the Atlantic Meridional Overturning Circulation (AMOC), Arctic ocean temperature, stratification and sea ice cover, and economically important ecosystems (Årthun et al., 2012; Hátún et al., 2009; Jansen et al., 2016; Østerhus et al., 2005; Rhein et al., 2011).

The short SPG observational record is dominated by decadal variability, including Arctic freshwater input, warming, salinification, redistribution of heat and salt, and faunal fluctuations (Haak et al., 2003; Hátún et al., 2009; Holliday et al., 2020; Robson et al., 2012). For example, from 1997 to 2005, the northeast Atlantic underwent warming, salinification, and nutrient decline (Bersch et al., 2007; Foukal & Lozier, 2017; Holliday et al., 2015; Johnson et al., 2013; Robson et al., 2012). Since 2012, this pattern has reversed, with the eastern SPG experiencing its greatest freshening in 120 years (Holliday et al., 2020). While still debated, the mechanisms to explain these trends include a retreat and subsequent advance of the eastward extent of the SPG/SPF and changes in northward heat transport associated with the AMOC

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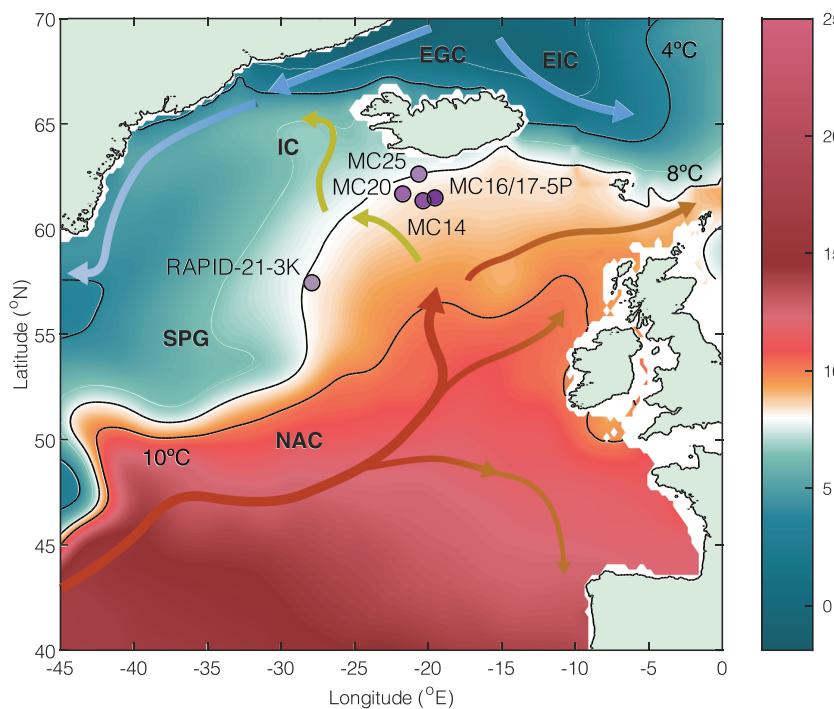


Figure 1. The eastern subpolar gyre (SPG), with locations of core sites used in this study. Schematic ocean currents are shown after Daniault et al. (2016): North Atlantic Current (NAC), Irminger Current (IC), East Greenland Current (EGC), and East Icelandic Current (EIC). Colors indicate the mean annual climatological sea-surface temperature (SST; °C) from the World Ocean Atlas (Locarnini et al., 2014).

(Bersch et al., 2007; Bryden et al., 2019; Hakkinen & Rhines, 2009; Hátún et al., 2005; Hátún & Chafik, 2018; Holliday et al., 2020; Koul et al., 2020).

Detailed observational data are limited to the last few decades, and, while there are a few reconstructions of the SPG that extend back to the preindustrial era with the resolution to capture the recent decadal variability, they are based on ice-core data or temperature reconstructions using continental records and are therefore indirect recorders of SPG variability (Osman et al., 2019; Rahmstorf et al., 2015). Nevertheless, these records hint that 20th century SPG decadal variability was superimposed on long-term trends. For example, analysis of Greenland ice-core dimethyl-sulfide products indirectly suggests a long-term decline in SPG productivity over the 20th century (Figure 2; Osman et al., 2019). Furthermore, reconstructions suggest an increasing intensity of the North Atlantic “warming hole” during the 20th century, a portion of the eastern SPG that has cooled relative to the northern hemisphere (Caesar et al., 2018; Rahmstorf et al., 2015; Thornalley et al., 2018). While this temperature fingerprint is associated with AMOC strength in coupled climate models, similar fingerprints are observed in simulations for changes in SPG strength (Jungclaus et al., 2014; Sgubin et al., 2017). Therefore, these reconstructions may also suggest changing SPG dynamics. Establishing the presence of any long-term trend in the SPG is important for developing our understanding of its future behavior.

Here, we develop a 10,000-year record of eastern SPG extent by applying established paleoceanographic techniques to a suite of rapidly accumulating sediment cores from the northern Iceland Basin (sedimentation rates of 30–140 cm/kyr). Their location near the eastern boundary of the SPG is ideal for evaluating changes in northward subtropical water penetration (Figure 1).

Our main findings derive from planktic foraminifera which, because of their habitat preferences (Be & Tolderlund, 1971), document changes in past ocean conditions (Jonkers et al., 2019). We also report the total abundances of planktic and benthic foraminifera which reflect surface export productivity (Eguchi et al., 2003; Herguera & Berger, 1991) and bulk sediment nitrogen isotope ratios ($\delta^{15}\text{N}$) which record the extent of nutrient utilization in surface waters (Altabet & Francois, 1994).

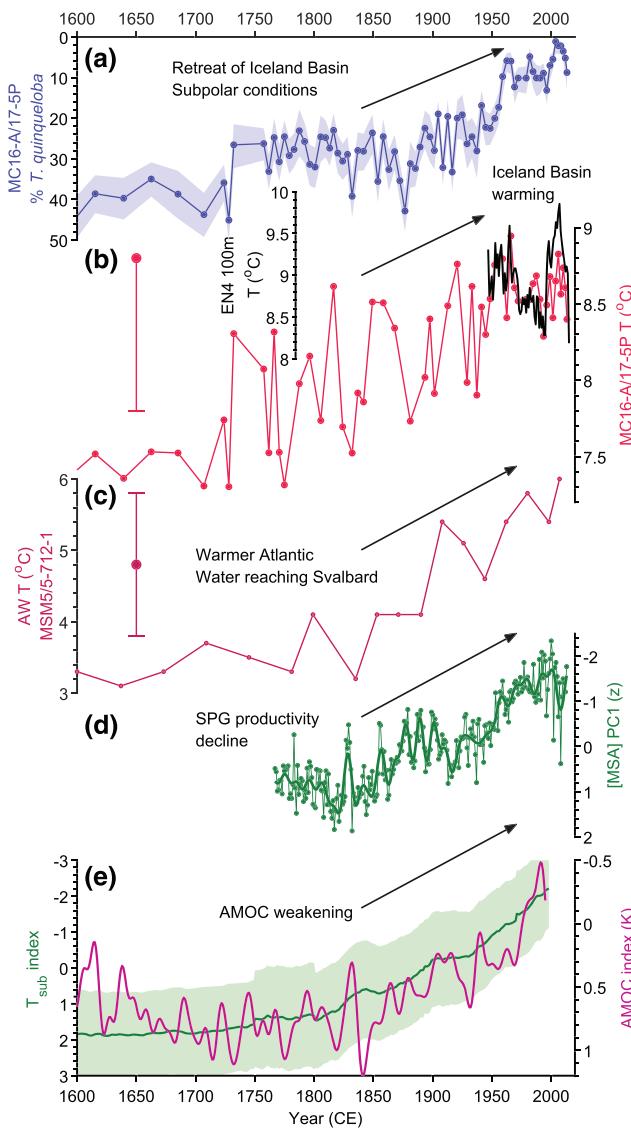


Figure 2. Records from the North Atlantic suggesting unusual industrial-era change. (a) MC16-A/17-5P *Turborotalita quinqueloba* % abundance ($\pm 2\sigma$); (b) Iceland Basin temperatures reconstructed using the SIMMAX method (red, Pflaumann et al., 1996), with mean ocean temperature at 100 m depth in the Iceland Basin box (black, Figure S4), from the EN4 reanalysis (Good et al., 2013); (c) temperature of “Atlantic Water” reaching Svalbard (Spielhagen et al., 2011); (d) subpolar gyre (SPG) productivity (Osman et al., 2019); (e) temperature fingerprint reconstructions of Atlantic Meridional Overturning Circulation (AMOC) strength from Rahmstorf et al. (2015) (pink) and Thornalley et al. (2018) (green).

We measured the $\delta^{15}\text{N}$ of bulk sediment after carbonate removal (Text S1).

2.5. Particle Tracking Experiments

Due to transport by the time-varying circulation over their lifetimes (up to 4 weeks), planktic foraminifera reflect the conditions over a wider area than directly above the core site. To determine possible provenance for our specimens, we ran particle tracking experiments using the VIKING20, 1/20th degree ocean model (Breckenfelder et al., 2017; Text S1).

2. Materials and Methods

Standard paleoceanographic methods were employed in this study, outlined below. Details are provided in the supplementary information (Blindheim & Østerhus, 2005; Döös, 1995; Eiríksson et al., 2004; Griffies et al., 2009; Kostianoy & Nihoul, 2009; Miettinen et al., 2011; Piechura & Walczowski, 1995; Ramsey, 2008; Reimer et al., 2013; Siccha & Kucera, 2017; Stuiver et al., 2020; Swift & Aagaard, 1981; Takahashi & Be, 1984).

2.1. Sediment Cores

A suite of multicores (MCs) was collected in Summer 2014 during cruise EN539 (Figure 1, Table S1), each preserving the sediment–water interface. Continuous sediment accumulation up to the date of coring was therefore assumed.

RAPID-17-5P is our only core to span the Holocene (to ~1,750 CE) and has been discussed previously (Moffa-Sánchez et al., 2014, 2015). Its collection location is within ~100 m of EN539-MC16 (Text S1). Records from these cores should therefore be comparable. We use the joint EN539-MC16-A and RAPID-17-5P cores (MC16-A/17-5P) as our primary data source. Comparisons with the other MCs and RAPID-21-3K (Sicre et al., 2011) are briefly discussed and shown in the supplementary figures.

2.2. Age Models

Age models for each core are based on a combination of ^{210}Pb and ^{14}C (Figure S7, Text S1). Sediment ages falling within the mid-20th century were verified by the presence of radiogenic ^{137}Cs (e.g., Perner et al., 2017) and spheroidal carbonaceous particles (SCPs; Rose, 2008, 2015).

2.3. Faunal Assemblages

Approximately 300 planktonic foraminifera per sample were identified in the $>150 \mu\text{m}$ size fraction (Text S1). Benthic foraminifera were counted in the same size fraction. Uncertainty on relative abundances was estimated using a binomial approach (Heslop et al., 2011). The possibility of preservation bias was assessed using a simple fragmentation index (Pfuhl & Shackleton, 2004).

To obtain a more robust estimate of the numbers of the subtropical foraminifera *Orbulina universa*, we also counted this species in the $>250 \mu\text{m}$ fraction of the whole sample. The conclusions were the same regardless of counting method.

Planktic faunal assemblages were used to reconstruct temperature at 100 m depth for RAPID-17-5P/EN539-MC-16-A, using the SIMMAX modern analogue technique equations outlined in Pflaumann et al. (1996) in MATLAB (Text S1).

2.4. $\delta^{15}\text{N}$ Measurements

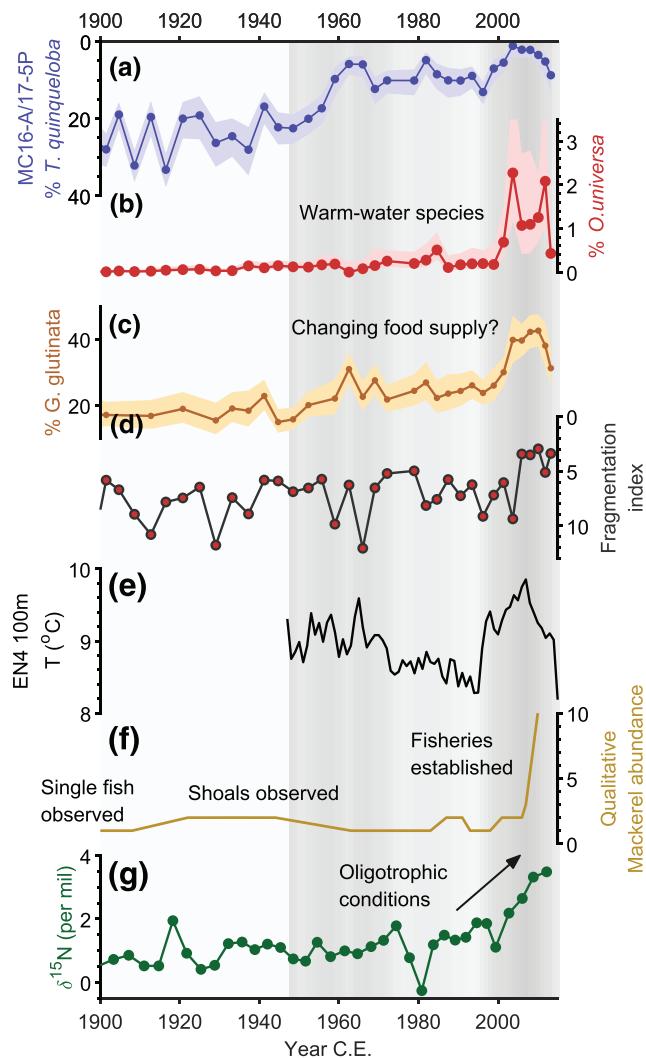


Figure 3. Centennial records of ocean change from the Iceland Basin. (a) MC16-A/17-5P *Turborotalita quinqueloba* % abundance ($\pm 2\sigma$); (b) MC16-A/17-5P *Orbulina universa* % abundance ($\pm 2\sigma$); (c) MC16-A/17-5P *Globigerinita glutinata* % abundance ($\pm 2\sigma$); (d) MC16-A/17-5P fragmentation index; (e) mean ocean temperature at 100 m depth in the Iceland Basin box (Figure S4), from the EN4 reanalysis (Good et al., 2013). Gray shading is colored according to this temperature curve. (f) qualitative, relative abundance of Atlantic mackerel reported near Iceland (Astthorsson et al., 2012); (g) MC16-a/17-5P nitrogen isotope ratios of bulk sediment.

late in the record, which is quite insensitive to temperature (Be & Tolderlund, 1971; Jonkers & Kučera, 2018), suggests a change in factors such as food-type availability (Figure 3).

Bulk sediment $\delta^{15}\text{N}$ increased by 3‰ during the 20th and 21st centuries in each of the cores analyzed for this proxy (MC16-B/17-5P, EN539-MC20-B, EN539-MC25-A; Figures 3, 4, and S5), indicating more complete nutrient utilization typical of subtropical oligotrophic waters. If we assume the $\delta^{15}\text{N}$ effect of nitrate consumption to be ~8‰ (Straub et al., 2013), then to first order, the 3‰ increase in $\delta^{15}\text{N}$ we observe towards the top of EN539-MC16-A suggests that nutrient utilization rose from ~80% to ~100% over the last 200 years, with most of the change occurring during the late 1990s/early 2000s.

The planktic foraminiferal species whose accumulation rate did not decrease during the industrial era are the subtropical species. *O. universa* appeared near the core tops of EN539-MC16-A/B, -MC14A/B, and

3. Results and Discussion

3.1. Industrial Era Changes in Proxy Data

Turborotalita quinqueloba, a species that prefers cool, productive waters and frontal systems (Be & Tolderlund, 1971; Husum & Hald, 2012) shows exceptional recent changes (Figures 2 to 4 and S5). For most of the Holocene, it made up ~40% of the planktic foraminiferal assemblage, suggesting subpolar (cold) conditions. Beginning at ~1750 C.E. (1675–1800, 95% confidence), the relative abundance of this species declined dramatically, with major declines occurring between 1675 and 1880, and between 1940 and 1970 (95% confidence). This species was replaced by a transitional (warmer) assemblage having a weaker association with ocean fronts (Figures 2 to 4), which the SIMMAX similarity index shows is similar to that found in the Rockall Bank/Trough area. Mean abundances of *T. quinqueloba* for the periods 1750–1950 (27%), 1950–2000 (15%), and 2000–2010 (4%) were more than two, five, and six standard deviations below the Holocene mean, respectively.

With respect to the timing of the initial decrease in *T. quinqueloba* abundance, it occurs between the two uppermost samples in RAPID-17-5P and may therefore be an artifact of the piston coring process. The radiocarbon dates are inconclusive as to whether RAPID-17-5P and EN539-MC16-A overlap in time. However, the very close spatial proximity of these cores means that their faunal assemblage should be comparable. The top of RAPID-17-5P must therefore be older than the base of EN539-MC16-A, and the drop in *T. quinqueloba* abundance occurs in the missing section, constrained by two radiocarbon dates to 1675–1800 C.E. (95% confidence).

The same general trends, although of smaller magnitude, are evident in EN539-MC14 and -MC20 after ~1850 C.E. (Figure S5). A downward step change also occurred in EN539-MC25 between 1750 and 1800 C.E. Prior to 1750 C.E., the highest relative abundances of *T. quinqueloba* occurred at the site of MC16-A/17-5P. Prior to ~1500 C.E., fluctuating relative abundances were found in the nearby EN539-MC14-A (3%–30%, Figure S5).

Since ~1750 C.E., the accumulation rates of planktonic foraminifera in MC16-A/17-5P also decreased (Figures 4 and S2), including decreasing fluxes of all major species (*T. quinqueloba*, *Neogloboquadrina incompta*, *Globigerinita glutinata*, and *Globigerina bulloides*). The total abundance of benthic foraminifera also collapsed during the 20th century (Figure 4), indicating declining export productivity (Herguera & Berger, 1991). A significant increase in *G. glutinata* relative abundance

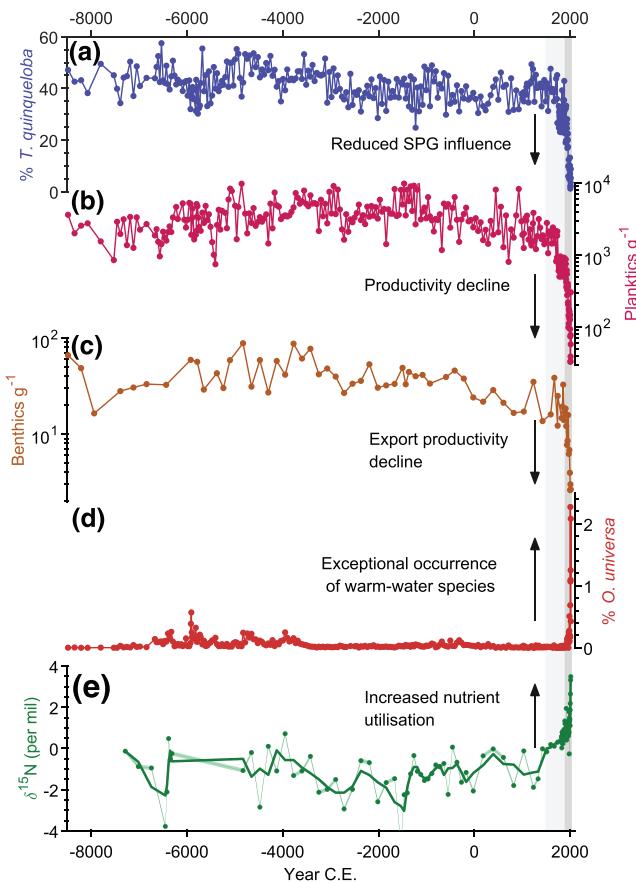


Figure 4. Ten thousand-year sediment records from MC16A/17-5P. (a) *Turborotalita quinqueloba* % abundance; (b) planktic foraminifera per gram of dry sediment; (c) benthic foraminifera per gram of dry sediment; (d) *Orbulina universa* % abundance; and (e) $\delta^{15}\text{N}$ of bulk sediment. Light and dark gray bars indicate the time intervals shown in Figures 2 and 3, respectively.

-MC20-B (Figures 3 and S5), along with the rare presence of specimens of *Globigerinoides ruber* (both pink and white forms) in MC16-A (Data Set S1). Around the mid-1990s, these species rapidly increased to a peak in relative abundance higher than anything found earlier in the Holocene, although the accumulation rate of *O. universa* was likely greater in the early-mid Holocene (Figures 3 and 4).

3.2. Inferred Industrial-Era Changes in Iceland Basin Hydrography

High relative abundances (>30%) of *T. quinqueloba* in the modern ocean are restricted to a narrow range of average annual sea-surface temperature (SST) between 4°C and 8°C, located on the southern side of the Arctic and Polar Fronts (Figure S3) (Blindheim & Østerhus, 2005; Döös, 1995; Eiriksson et al., 2004; Griffies et al., 2009; Kostianoy & Nihoul, 2009; Miettinen et al., 2011; Piechura & Walczowski, 1995; Ramsey, 2008; Reimer et al., 2013; Siccha & Kucera, 2017; Stuiver et al., 2020; Swift & Aagaard, 1981; Takahashi & Be, 1984). Annual average climatological SST in the likely source area of *T. quinqueloba* fossils in MC16-A/17-5P (Figure S4) is 8.5°C–10°C (Figure 1). Our data therefore suggest an increase of 0.5°C–2°C in the annual mean SST of the Iceland Basin during the industrial-era, mostly accomplished during the 20th century. The SIMMAX reconstruction of temperature at 100 m depth from MC16-A/17-5P also suggests a significant warming of ~1°C in the Iceland Basin since 1750, with variability that matches observed temperatures since 1948, although the magnitude of the reconstructed change is lower than observed (Figure 2).

In order to achieve the temperature increase outlined above, we suggest that there must also have been a change in the dominant water mass (from subpolar to warmer transitional Atlantic Water), which may also explain the other impacts. For example, very high Holocene *T. quinqueloba*, planktic, and benthic abundances are driven by higher productivity as well as lower temperature. In addition, widely differing preindustrial abundances of *T. quinqueloba* in closely located core sites suggests the presence of a strong barrier to particle transport in the upper ocean (Figures 3 and S5). This evidence suggests the presence of a frontal system close to MC16-A/17-5P that separated the northern and southern parts of the Iceland Basin, stimulating the very high productivity—absent in modern times. The late increase in nutrient utilization implied by the $\delta^{15}\text{N}$ data, in the presence of evidence for declining productivity, suggests a lower nutrient load in surface waters, which could also be explained by changes in frontal systems.

Hypothetically, the abrupt peak in (sub-) tropical species near the tops of EN539-MC16-A, -MC14-A, and -MC25-A may be an artifact of preservation bias (Zamelczyk et al., 2013). However, high fluxes of *O. universa* are also observed in the mid- and early-Holocene sections of 17-5P, showing that this species is not necessarily lost due to fragmentation/dissolution. In addition, other species such as *G. bulloides* may be more susceptible to dissolution than *O. universa* (Thunell & Honjo, 1981), and these and other fragile species (*T. quinqueloba*) show opposite trends in relative abundance and flux at the top of EN539-MC16-A when compared to *O. universa* (Figures S1 and S2). The sudden increase in *O. universa* therefore suggests a response to the gradual 20th century warming, amplified by sustained warmth during the 1990s–2000s. Additional evidence for a threshold response in northeast Atlantic ecology comes from the northward migration of Atlantic mackerel (*Scomber scombrus*), first observed in Icelandic waters in the late 1800s. During the 20th century, shoals were observed, and in the early 2000s, fisheries were established in both Iceland and Greenland (Figure 3; Astthorsson et al., 2012; Jansen et al., 2016).

In summary, our data suggest that during the Holocene prior to 1750 CE, the Iceland Basin was bathed by cool, productive, subpolar water and was separated from the warmer transitional water to the south by a

marked frontal system. After ~1750 CE, and mainly during the 20th century, warmer, less productive conditions expanded northwest to occupy the whole basin, affecting the distributions of plankton and animals from higher trophic levels.

3.3. Relationship of Iceland Basin Records to Changes Across the North Atlantic

The dramatic 20th century planktic foraminiferal faunal changes seen in our records are not found in other sites located either in the SPG interior (RAPID-21-3K and Perner et al., 2017, Figure S6) nor within the main body of the warm Atlantic water flowing into the Nordic Seas (Figure 3; Andersson et al., 2010; Mary et al., 2015; Staines-Urías et al., 2013). While these records tend to be of lower resolution than those presented here, the absence of similar trends in these regions highlights that the 20th century trends we observe were not predominantly caused by the mean effects of global warming, but instead reflect a northwestward expansion of the warm conditions in the Iceland Basin due to a change in ocean circulation.

Lateral expansion of warm Atlantic water also occurred in the Nordic Seas (Hald et al., 2011; Spielhagen et al., 2011), with the same timing as in the Iceland Basin (Figure 2). It is likely that areas close to water mass boundaries are particularly sensitive recorders of oceanographic variability because of the strong impact of changing water mass on the species assemblage, more so than relatively small changes in temperature within water masses. We note that the details of the timing of these changes in the Nordic Seas differ slightly amongst taxa (e.g., coccolithophores; Dylmer et al., 2013), likely due to differing habitat preferences such as depth.

Several other lines of evidence suggest that the changes we report are not limited to the Iceland Basin, but instead are symptomatic of larger scale reorganization of North Atlantic circulation. Long-term reconstructions of temperature, indicating warming in the western Atlantic and little change in the “warming hole,” have similar timing to the changes we observe (Figure 2; Thibodeau et al., 2010; Thornalley et al., 2018). The North Atlantic warming hole, while possibly a fingerprint of AMOC weakening, could also be a consequence of the inferred changes in the SPG (Jungclaus et al., 2014; Sgubin et al., 2017). In addition, our record of *T. quinqueloba* from MC16-A/17-5P closely parallels the Greenland ice core records of productivity decline over much of the SPG (Figure 2; Osman et al., 2019).

Thus, a suite of reconstructions now suggests that 20th century physical and ecological change in the North Atlantic were part of a unique basin-wide change in ocean dynamics. Moreover, our records show for the first time that subpolar North Atlantic 20th century levels of productivity and warmth were unprecedented during the Holocene.

3.4. Mechanisms for the Lateral Expansion of Warm Water in the Northeast Atlantic

Expansion of warm transitional water in the northeast Atlantic is related to an increase in the northward heat-flux to the region, for which the ocean is a primary driver (Asbjørnsen et al., 2019; Foukal & Lozier, 2018). Several mechanisms have been proposed that could explain such an increase, including SPG contraction (Hátún et al., 2005) and/or westward movement of the SPF (Holliday et al., 2020), wind-driven entrainment of subtropical water in the NAC (Hakkinen & Rhines, 2009; Marzocchi et al., 2015), and a delayed response to increased AMOC (Bryden et al., 2019; Robson et al., 2012).

While decadal warming/cooling in the Iceland Basin can be ascribed to propagation of anomalies across ~45°N or around the SPG (Bryden et al., 2019; Holliday et al., 2020), these anomalies tend to propagate throughout the SPG (e.g., Robson et al., 2012). The centennial trend of warming in the eastern subpolar North Atlantic as well as the relative lack of warming within the warming hole (Caesar et al., 2018) requires a more permanent redistribution of heat within the subpolar region, which may nevertheless be related to northward heat transport.

Modeling studies suggest that a spin-up of the eastern SPG can cause heat divergence within the SPG itself and heat convergence in the Iceland Basin, Nordic Seas, and eventually the Arctic (Jungclaus et al., 2014; Oldenburg et al., 2018). Mode shifts in SPG strength have also been modeled and can be achieved via freshwater addition to the North Atlantic, which also acts to weaken the AMOC (Sgubin et al., 2017). Freshening of the high latitudes due to greenhouse gas forcing is a common projection in coupled climate models (Held & Soden, 2006), and 20th century freshening trends have been documented for the SPG (Curry & Mauritzen, 2005; Friedman et al., 2017), mainly arising from a series of events known as great salinity

anomalies (e.g., Haak et al., 2003). Although the major assemblage changes occurred during the 20th century and may thus be attributable to this freshening trend, the earliest changes in the species assemblage (~1750 CE) seem too early to be influenced by anthropogenic greenhouse warming. Instead, they may have been a result of freshwater addition during the late Little Ice Age (Thornalley et al., 2018).

Alternatively, changes in wind forcing involving the North Atlantic Oscillation (NAO) can also alter the entrainment of water from the cold Labrador current into the NAC, the position of the SPF in the northeast, and being linked to North Atlantic freshening (Bersch et al., 2007; Holliday et al., 2020). Modeling and historical records have also suggested that the North Atlantic Ocean may be sensitive to volcanic forcing, via its impact on atmospheric circulation systems such as the NAO (Swingedouw et al., 2015). However, records of atmospheric circulation spanning the 20th century are contradictory, with reconstructions of the NAO index showing no long-term trend (but an increase in variability), and frequency of storms in the Northeast Atlantic either increasing, showing no change, or decreasing (Feser et al., 2015). In addition, volcanic eruptions of similar size to those thought to have caused changes during the 20th century have occurred at least four other times in the last 1,000 years (Swingedouw et al., 2015) and do not appear to have had a noticeable effect on our records.

Therefore, although there is some uncertainty regarding the cause of 20th century trends in the SPG region, we propose that freshwater input into the North Atlantic basin is the most likely candidate to explain the basin-wide change in SPG circulation. This hypothesis could be tested by further quantifying the sensitivity of the SPG to a range of freshwater fluxes and input locations.

4. Conclusions

We present new data from northeast Atlantic sediment cores. The foraminiferal faunal assemblages, abundances, and isotopic trends suggest warming and declining productivity in the Iceland Basin, likely beginning at ~1750 CE, but most prominent during the 20th century. Twentieth century trends exceed the range of variability observed in records from the same site spanning the last 10,000 years. The spatial structure of the changes and other reconstructions of the SPG indicate a basin-wide, 20th century shift in the ocean dynamics of the North Atlantic region. Although uncertainty remains, we suggest that increased freshwater input to the SPG was a likely cause for the circulation change. Given the important role that the SPG plays in modifying the impacts of climate change around the region, including in the climate-sensitive Arctic Ocean and for economically important ecology, it is imperative that future studies aim to constrain the underlying driver of this long-term shift in dynamics.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Sediment core data are available from the World Data Service for Paleoclimatology (<https://www.ncdc.noaa.gov/paleo/study/29030>) and supplementary information files. Particle tracking data are available from Zenodo (<https://zenodo.org/record/3727170>).

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