



Global ocean conveyor lowers extinction risk in the deep sea



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ABSTRACT

General paradigms of species extinction risk are urgently needed as global habitat loss and rapid climate change threaten Earth with what could be its sixth mass extinction. Using the stony coral *Lophelia pertusa* as a model organism with the potential for wide larval dispersal, we investigated how the global ocean conveyor drove an unprecedented post-glacial range expansion in Earth's largest biome, the deep sea. We compiled a unique ocean-scale dataset of published radiocarbon and uranium-series dates of fossil corals, the sedimentary protactinium–thorium record of Atlantic meridional overturning circulation (AMOC) strength, authigenic neodymium and lead isotopic ratios of circulation pathways, and coral biogeography, and integrated new Bayesian estimates of historic gene flow. Our compilation shows how the export of Southern Ocean and Mediterranean waters after the Younger Dryas 11.6 kyr ago simultaneously triggered two dispersal events in the western and eastern Atlantic respectively. Each pathway injected larvae from refugia into ocean currents powered by a re-invigorated AMOC that led to the fastest postglacial range expansion ever recorded, covering 7500 km in under 400 years. In addition to its role in modulating global climate, our study illuminates how the ocean conveyor creates broad geographic ranges that lower extinction risk in the deep sea.

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1. Introduction

1.1. Extinction risk in the deep sea

Global habitat loss and rapid climate change challenge the abilities of species to persist and threaten Earth with what could

be its sixth mass extinction event (Macleán and Wilson, 2011). Effective conservation urgently requires an understanding of extinction drivers and buffers and necessitates us to adopt management tools that increase resilience in species and habitats at imminent risk of extinction (Ricketts et al., 2005; Moritz and Agudo, 2013). At this time of global climate change when pressures from the trawl fishing and petroleum industries continue alongside emerging activities such as seabed mining, the need for an understanding of extinction risk in the deep sea has never been greater. Geographic range and wide habitat breadth are reliable predictors of species extinction risk in the palaeo-ocean (Payne and Finnegan, 2007; Harnik, 2011; Harnik et al., 2012; Nürnberg and Aberhan, 2013) and both have conferred resilience to many species during several global extinction crises over the last hundred million years (Thuy et al., 2012). However, geographic range itself is a product of multiple

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Fig. 1. High biological diversity of coral reefs principally constructed by *Lophelia*. Left: an alfonsino (*Beryx decadactylus*) passes a live coral reef on the Great Bahama Slope in the Straits of Florida (650 m water depth, ROV CHEROKEE Team, MARUM, University of Bremen). Right: a greater forkbeard (*Phycis blennoides*) swims above thriving reefs at the Logachev coral carbonate mound complex (684 m water depth, JC073 “Changing Oceans Expedition”, Heriot-Watt University).

biotic and external drivers: the outcome of extinction crises depends on a combination of drivers that in some cases can even lead to global species recovery and evolutionary diversification (Raup, 1994).

Paradigms of extinction risk in deep-sea fauna are largely developed from the fossilised remains of marine calcifiers such as bivalves, foraminifers, ostracods, echinoderms and corals (Thuy et al., 2012; Foster et al., 2013). However, it is the geological history of deep-sea ecosystem engineers such as reef framework-forming cold-water corals that uniquely place these taxa for advancing paradigms of extinction risk because these species also create biologically diverse habitats (Fig. 1; Roberts et al., 2006, 2009). These corals are threatened by human activities and climate change, with rising levels of carbon dioxide forecasted to cause up to a 70% global reduction in the distribution of the globally cosmopolitan cold-water coral *Lophelia pertusa* by 2099 (Guinotte et al., 2006). Uncertainty remains with regards to whether corals and other marine life can adapt or acclimate to these changes (Form and Riebesell, 2011; Wicks and Roberts, 2012), but distinct glacial–interglacial cycles of recovery have been documented for *Lophelia* (Dorschel et al., 2005; Frank et al., 2011). The nature of the last glacial for example meant that for much of its range in the northeast Atlantic, *Lophelia* was restricted to the temperate zone as ice sheet discharge and grounding increased while surface water productivity was reduced, and cooler sea surface temperatures characterised reef habitats off northern Europe (Frank et al., 2011). Even as the climate warmed during deglaciation, *Lophelia* was still absent from much of its range probably because of excessive ice-rafted debris and meltwater that would have altered water mass stratification and rates of terrigenous sedimentation to the continental shelf (Frank et al., 2011). The rapid Holocene return of this species across the northeast Atlantic suggests that even drastic geographic range retractions, such as those caused by glacial and deglacials, may be reversible in these corals.

Today, *Lophelia* is widespread across the Atlantic Ocean and typically inhabits a bathyal niche on continental shelves, slopes, seamounts and ridges across a range of temperatures (Roberts et al., 2009). Its aragonitic skeleton allows absolute and radiocarbon dating of well-preserved fossils, making it possible to study the distribution of this species across geological timescales. Using *Lophelia pertusa* as a model deep-sea organism with the capacity for wide larval dispersal, our aim was to identify the proximal causes for this successful recolonisation following the last glacial cycle in order to uncover key mechanisms that can buffer the risk of future extinction events in the deep sea.

1.2. An ecological role of the global ocean conveyor

Atlantic meridional overturning circulation (AMOC) is the Atlantic portion of the great ocean conveyor belt that globally re-distributes warm saline water masses northwards along shoaling density surfaces

accompanied by deeper southerly circulation of cooler fresher waters. Changes in the strength of the AMOC, such as those predicted over the next few decades, could have direct consequences for marine ecosystems, such as altered ocean productivity (Schmittner, 2005). We propose that AMOC variability also has other ecological consequences. Our quest to understand how extinction risk in the deep sea was buffered in the past targeted this feature of the global conveyor because AMOC could act as the mechanism for dispersing larvae across large distances and creating broad-scale ecological connectivity. Our ocean-scale approach reconciled a disparate and multi-disciplinary body of research that allowed us to uncover the key mechanisms underlying the resilience of a deep-sea species and the biologically rich habitats it forms.

We also examined the role that deglacial–Holocene changes in water mass circulation played in catalysing coral recovery by inferring potential pathways for coral dispersal out of deglacial refugia. Export of Mediterranean and Caribbean water masses into the Atlantic are thought to have helped re-establish a strong AMOC after the Younger Dryas (YD; Rogerson et al., 2006; Xie et al., 2012). Thus, central to our concept of the ocean conveyor belt dispersing corals across vast distances are Antarctic Intermediate Water (AAIW) flowing through the Caribbean into the warm near-surface Gulf Stream, and the northward export of Mediterranean Outflow Water (MOW) across the European shelf and slope.

The validity of each dispersal pathway was examined on a region-by-region basis relative to published coral biogeographic and genetic patterns and new estimates of historic gene flow. Consolidating recent community and population data along these pathways with palaeoceanographic patterns was vital to reconstructing coral history: understanding *Lophelia* biogeography and genetic patterns allowed us to infer migration pathways that were historically and are currently important to buffering extinction risk by promoting dispersal between habitats in the deep sea.

2. Materials and methods

2.1. Fossil coral chronology

We first investigated the relationship between the latitudinal range of fossil *Lophelia* occurrences and overturning strength. This was achieved by compiling 292 published and new uranium–thorium series ($U^{230}Th$) and radiocarbon (^{14}C) ages of fossil *Lophelia* < 25 ka from across the Atlantic Ocean and Mediterranean Sea (see Supplementary Table 1 and references therein). The new $U^{230}Th$ dates for Brazil were obtained from sediment coring expeditions on the Brazilian margin conducted with Petrobras (Petróleo Brasileiro S.A.), including core PC-ENG-111 (22° 24' 45.57"S, 40° 08' 40.96"W, 621 m water depth), core K-GLC-PPT-06 (23° 29' 27.04"S, 41° 06' 40.26" W, 626 m water depth), and core MXL-030 (24° 37' 33.96"S, 44° 01'

09.35°W, 808 m water depth) and dated following methods of Mangini et al. (2010).

2.2. Fossil history and AMOC strength

Coral occurrences in the Atlantic were ordered chronologically alongside a well-known and established kinematic proxy of AMOC strength history from deep-water records of sedimentary protactinium and thorium ($^{231}\text{Pa}/^{230}\text{Th}$; McManus et al., 2004; Lippold et al., 2009). This kinematic proxy was derived by combining data on uranium decay products collected from core sediments in OCE326-GGC5 (33.70°N, 57.58°W, 4550 m depth; McManus et al., 2004) on the Bermuda Rise and the Ocean Drilling Program Leg 172 Site 1063 (33.41°N, 57.37°W, 4584 m depth; Lippold et al., 2009). Thorium (Th) accumulates in sediments faster than protactinium (Pa), thus higher $^{231}\text{Pa}/^{230}\text{Th}$ ratios in sediments were used to infer slower overturning rates as less Pa is flushed through the ocean.

2.3. Dispersal pathways and palaeocirculation

Palaeocirculation proxies included authigenic neodymium (epsilon or ϵNd) and lead ($^{206}\text{Pb}/^{204}\text{Pb}$) isotopic compositions. Variability in isotopic neodymium from the Brazilian margin and Straits of Florida was derived using the sedimentary record in core KNR159-5-36GGC (27.51°S, 46.47°W, 1268 m water depth; Pahnke et al., 2008) and core KNR166-2-26JPC (24.33°N, 83.25°W, 546 m water depth; Xie et al., 2012), respectively. Variability in the flow path (reconstructed from $^{206}\text{Pb}/^{204}\text{Pb}$) of upper layer Mediterranean Outflow Water was derived from the sedimentary record in core M39008 (36.38°N, 7.07°W, 577 m; Stumpf et al., 2010).

2.4. Coral biogeography and genetics

New estimates of historic gene flow were inferred from maximum likelihood estimates of coral migration. Microsatellites were sequenced from *Lophelia* collected from Mauritania, the Santa Maria di Leuca cold-water coral bank province (eastern Mediterranean Sea), the Porcupine Seabight, Rockall Bank, and the Barents Sea (Norway). Tissue samples were extracted and genotyped as described in Dahl et al. (2012).

Coral migration rates among regions were estimated using MIGRATE version 3.2.19 (Beerli and Felsenstein, 2001). MIGRATE estimates historical migration rates and effective population sizes using coalescence theory and Markov chain Monte Carlo techniques. Parameter distributions were estimated using the Bayesian implementation of MIGRATE (Beerli, 2006) and microsatellite mutation was modelled as a continuous Brownian process. 100 short chains (5×10^5 iterations), two long chains (5×10^6 iterations) and the first 10^5 iterations were discarded as 'burn-in'. An adaptive heating scheme using four chains (start temperatures: 1.0, 1.5, 3.0, 10^6) was used to increase the efficiency of searches. A total of 5×10^5 and 5×10^6 genealogies were recorded at a sampling increment of 100 iterations for short and long chains, respectively. The program was run several times using different random number seeds and results were stable, suggesting that Markov chains had converged on the stationary distribution.

Extreme genet longevity due to clonality and low effective population sizes can reduce population differentiation (Dahl et al., 2012) because asexual reproduction affects genotype frequencies. Clonal uniformity depends on the number of individuals in the preceding generation and that from the contemporary population (Balloux et al., 2003; Bengtsson, 2003), with high retention of alleles and genotypes in founder populations mimicking a signal of gene flow. It is therefore difficult to estimate migration direction when only the frequency of alleles differ (Beerli and Palczewski, 2010), but we also considered the MIGRATE outputs in relative

terms and integrated these with other lines of evidence from the fossil record, coral biogeographical affinities and palaeocirculation.

3. Results and discussion

3.1. Coral recovery and AMOC spin-up

A moderate to strong AMOC probably persisted in the intermediate water mass layers that bathed *Lophelia* during the last glacial maximum (LGM) 19–21 kyr ago (Lynch-Stieglitz et al., 2007; Lippold et al., 2012; Ritz et al., 2013), but conditions would have been far from ideal for reef framework-forming cold-water corals as suggested by Frank et al. (2011), and this trend was reflected by the scarcity of LGM ages for *Lophelia* relative to the Holocene interglacial (Fig. 2, Supplementary Table 1). Scarcity of *Lophelia* in the North Atlantic continued into Heinrich Stadial 1 (HS-1) and the YD, when pulses of meltwater increased, as suggested by Frank et al. (2011), but also when AMOC slowed in both deep and intermediate water mass layers (McManus et al., 2004; Praetorius et al., 2008; Fig. 2). Thus regardless of AMOC strength, *Lophelia* disappeared from much of the North Atlantic because of a lack of suitable environmental conditions.

This chronology of coral history (Fig. 2) provided our first synoptic view of deep-sea ecosystem temporal dynamics at an ocean basin-scale. Few LGM occurrences were noted; available coral dates imply that *Lophelia* was restricted mostly to low latitudes off Brazil and in the Gulf of Cádiz. *Lophelia* remained rare throughout the deglacial 12–19 kyr ago alongside reduced AMOC. However, it is the large rebound in AMOC strength following the YD that is of particular interest in the context of species recovery. This rapid spin-up of overturning during the early Holocene coincided with a rapid and widespread return of *Lophelia* to northern Europe after a hiatus of over 65 ka (after Frank et al., 2011). Corals achieved an unprecedented re-expansion, colonising habitats over 7500 km away in <400 years. Although there were few fossil data from the western North Atlantic, our synthesis of available records suggests a range expansion from Brazil to the southeastern United States after a hiatus of up to about 10 ka. Thus, colonisation of *Lophelia* alongside AMOC renewal provides provocative new evidence for coupling between large-scale circulation phenomena and the capacity to buffer extinction events.

Coupling between coral history and what is widely known as the great ocean conveyor suggests that AMOC can achieve large-scale coral dispersal across ecological timescales. Building on the concept of AMOC-driven dispersal, we next examined how circulation features in the Atlantic and Mediterranean (Fig. 3) may have catalysed this process.

3.2. Pathways to recovery in the western Atlantic

Lophelia thrived off Brazil during the LGM, and persisted throughout most of HS-1 and the YD (Figs. 2 and 4) when records of authigenic neodymium isotope variability from Brazilian margin sediments detected negligible net changes in the presence of AAIW (Pahnke et al., 2008). A Brazilian deglacial refuge during periods of drastically slower overturning supports the concept that large-scale circulation of AAIW is capable of supplying larvae and homogenising coral assemblages on the Brazilian shelf and slope (Arantes et al., 2009), and triggering pulses of deep-sea coral recruitment (Thresher et al., 2011).

The capacity of AAIW to supply larvae may therefore precondition recovery of impoverished populations located downstream. Contemporary coral biogeography supports this idea; large-scale transport of AAIW maintains a high degree of cold-water coral

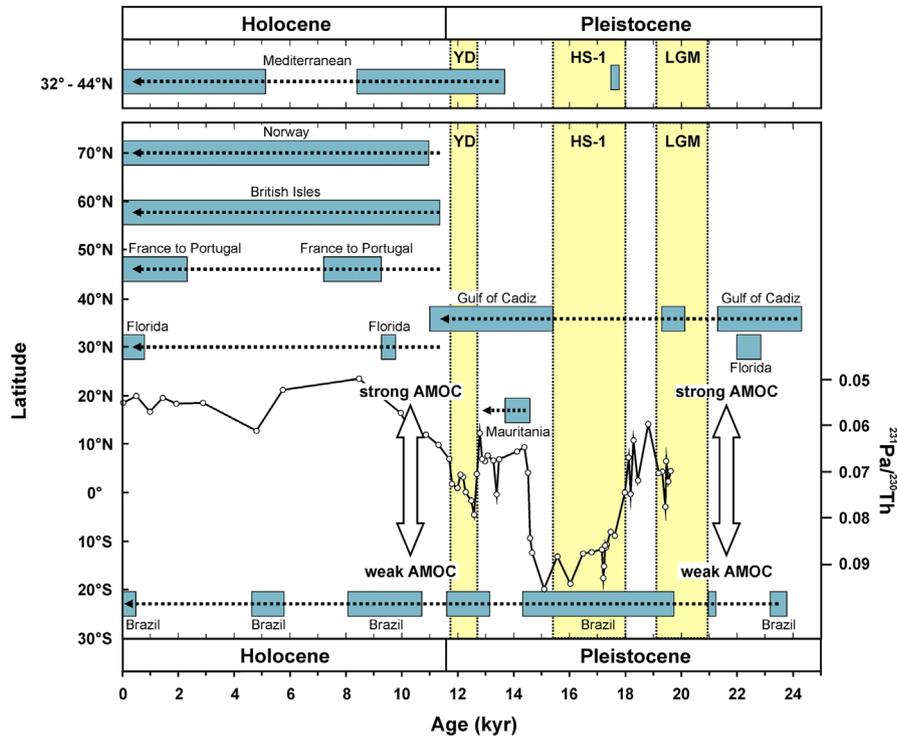


Fig. 2. Fossil chronology (blue bars) for Atlantic *Lophelia* over the last 25 ka in relation to latitude (left axis) and a three-point running mean of sedimentary $^{231}\text{Pa}/^{230}\text{Th}$ (right axis) as a proxy for AMOC strength. Most regions have < 10 specimens of *Lophelia* dated except for Norway, the British Isles, the Gulf of Cádiz and Brazil, which all have well constrained growth histories (> 10 corals dated; [Supplementary Table 1](#)). Yellow intervals show the LGM, HS-1 and the YD. Today, living *Lophelia* is widespread across most of the Atlantic from about 70°N–35°S. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

connectivity between Brazil, the Caribbean and Florida ([Kitahara, 2007](#)), with Brazil being a global centre of azooxanthellate scleractinian diversity ([Cairns, 2007](#)). The early Holocene shift to an oceanographic regime dominated by Southern Ocean water masses off Brazil and strong overturning ([Figs. 2 and 4](#)) carried AAIW into the Straits of Florida and Gulf Stream by about 11.3 ka ([Fig. 4](#); [Xie et al., 2012](#)). This re-established ecological connections between the Brazilian margin and Florida after a period of decreased AAIW during the YD ([Huang et al., 2014](#)).

The fossil history of *Lophelia* from the western North Atlantic is not yet well resolved ([Fig. 2, Supplementary Table 1](#)). One age from the Florida–Hatteras slope during the LGM ([Supplementary Table 1](#)) suggests either the occurrence of a glacial refugium for azooxanthellate reef framework-forming corals such as *Lophelia* or an impoverished relict population at a time when flow through the Straits of Florida and Gulf Stream strength was diminished ([Lynch-Stieglitz et al., 1999](#)). In this scenario, coral larvae could have been re-introduced into the Gulf Stream ([Fig. 3](#)) in the early Holocene. Variability in the ϵNd record from the Straits of Florida places modern AAIW pathways and entrainment into the Gulf Stream ([Fig. 3](#)) between 11.3 and 11.5 kyr ago ([Xie et al., 2012](#)). Thus in addition to renewing the upper limb of AMOC, modern AAIW pathways may have helped establish the flourishing *Lophelia* reefs present today in the Gulf Stream ([Figs. 1 and 4](#)).

To supplement fossil ages from the western North Atlantic region, we integrated biogeographic evidence with published estimates of genetic connectivity to derive a dispersal scenario driven by a renewed AMOC. Coral species connectivity between Brazil and Florida ([Kitahara, 2007](#)) indicates a possible historical link between renewed AAIW transport and the occurrence of *Lophelia* in the western subtropical North Atlantic. The pulse of AAIW (and likely coral larvae, [Fig. 3](#)) from Brazil into the Gulf Stream at about 11.3 ka preceded the next known coral age off Florida at about 9.5 ka ([Supplementary Table 1](#)). *Lophelia* genetic patterns mirror coral biogeography, with evidence for population

admixture between the Gulf of Mexico and southern Florida ([Morrison et al., 2011](#)) along the pathway of the AAIW-entrained Loop Current into the Gulf Stream ([Fig. 3](#)).

Genetic and biogeographical evidence suggests that northeasterly flow of the Gulf Stream does not impart ecological connectivity along its entirety. [Young et al. \(2012\)](#) found that the majority of bathyal invertebrate larvae exported out of the Caribbean and Gulf of Mexico are retained in natal geographic areas and not capable of trans-Atlantic dispersal. This is paralleled in deep-sea corals, wherein a faunal break occurs between subtropical and temperate regions of the western North Atlantic producing “northern” assemblages with affinities to the fauna from northern Europe ([Cairns and Chapman, 2001](#); [Morrison et al., 2011](#)). Insufficient coral samples from these northern populations preclude accurate estimates of gene flow directionality. Yet gene flow in coral-associated ophiuroids from the temperate western North Atlantic indicates dispersal in an east-to-west direction for species that exhibit broadcast spawning ([Cho and Shank, 2010](#)), a trait also exhibited by *Lophelia*. Instead of west-to-east dispersal that tracks Gulf Stream circulation, an east-to-west route would be powered by currents flowing counterclockwise from northern Europe to the east coast of North America as part of the subpolar gyre (SPG; [Fig. 3](#)). In this case SPG circulation in the North Atlantic could achieve trans-Atlantic connectivity in these deep-sea ecosystems.

3.3. Pathways to recovery in the northeastern Atlantic

North Atlantic gyres and their effects the North Atlantic Current (NAC), the eastward extension of the Gulf Stream, are also key to understanding how AMOC powered the rapid Holocene geographic range expansion in the northeast Atlantic. Notably, the return of *Lophelia* coincided with the spin-up in AMOC strength ([Fig. 2](#)) and the resumption of water-mass export flowing over vibrant deglacial cold-water coral communities in the Mediterranean ([Fig. 4](#)).

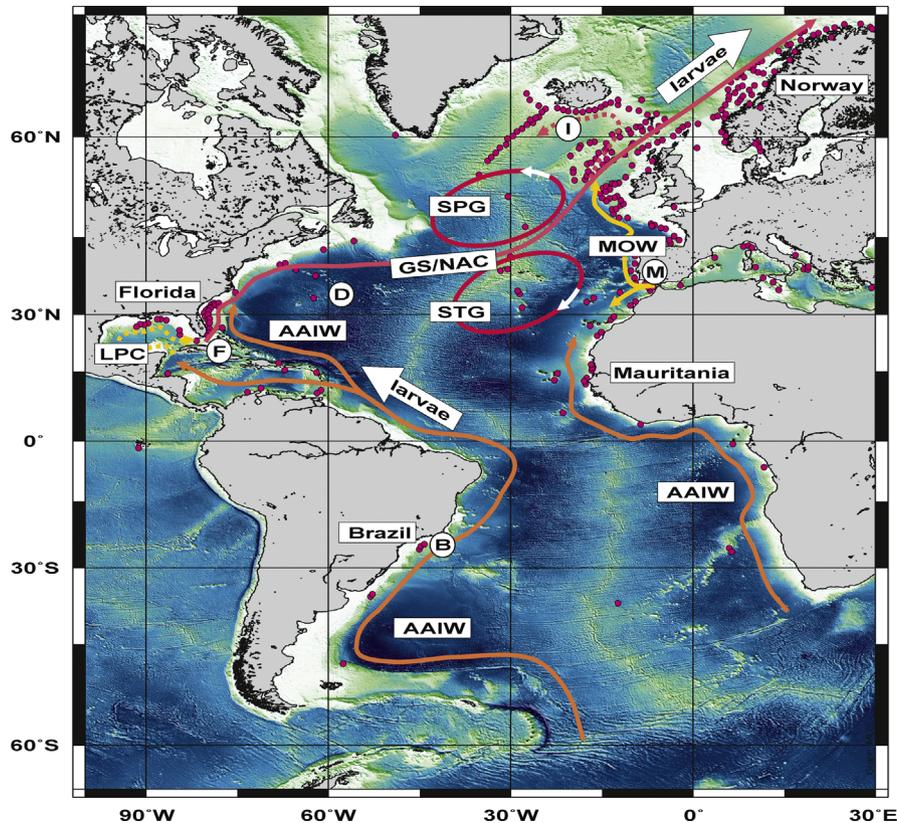


Fig. 3. Distribution of living *Lophelia* in the Atlantic Ocean today (red circles) in relation to simplified circulation features and proposed larval dispersal routes. LPC=Loop Current, GS/NAC=Gulf Stream/North Atlantic Current; SPG, STG=subpolar and subtropical gyres, respectively; MOW=Mediterranean Outflow Water; AAIW=Antarctic Intermediate Water. Deep and intermediate records of AMOC strength are indicated by circled letters D and I. Geochemical tracers of water mass history off Brazil, Florida and the Mediterranean are indicated by circles letters B, F and M, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

The position of the NAC between the two North Atlantic gyres (Fig. 3) results in a mixture of SPG and subtropical gyre (STG) waters being carried into the Rockall Trough (New et al., 2001; Fig. 3). However, the strength of the SPG in part controls the inflow, pathway and properties of the NAC by shifting the position of the eastern limb of the subpolar front (Hátún et al., 2005). In contrast to a weakened state that transports NAC along the western side of Rockall Bank up to Iceland, a stronger SPG shifts the subpolar front eastwards, splitting the NAC flow path such that a new branch is transported around the eastern side of Rockall Bank through the Rockall Trough up to Norway (Fig. 3; Hátún et al., 2005, 2009). Changes in the SPG state result in temporally variable contributions of SPG versus STG water masses off northern Europe (Lozier and Stewart, 2008). Paired ϵNd values and uranium–thorium ages from cold-water corals demonstrated that the early Holocene off northern Europe was characterised by a relatively stronger SPG at mid-depths (Colin et al., 2010; Montero-Serrano et al., 2011). Thus the NAC powered by a renewed AMOC would have been uniquely capable of rapidly transporting coral larvae across northern Europe's Atlantic margin because of SPG forcing on the NAC pathway.

In contrast to strong inter-regional genetic differentiation in the western Atlantic (Morrison et al., 2011), contemporary *Lophelia* populations in the northeast Atlantic have high connectivity (Le Goff-Vitry et al., 2004; Flot et al., 2013). Thus, we investigated a dispersal scenario whereby a strong SPG regime permitted the NAC to import coral larvae from southern Europe where deglacial corals occurred (Figs. 2 and 4, Supplementary Table 1), as opposed to from the western Atlantic. The latter scenario is unlikely because no deglacial *Lophelia* are yet known from the temperate western North Atlantic, and because northern European cold-water coral communities are dissimilar from those in the subtropical Atlantic or Brazil

(Cairns and Chapman, 2001; Morrison et al., 2011). Therefore we argue that corals originated from deglacial populations in the Gulf of Cádiz and/or the Mediterranean Sea (Figs. 2 and 4; Supplementary Table 1).

Although a subpolar front positioned closer to the European margin could block MOW incursion into the Rockall Trough (Lozier and Stewart, 2008), MOW converges and mixes with the NAC prior to this barrier at the Goban Spur off southwest Ireland (Fig. 3; Iorga and Lozier, 1999). Even a sporadic pulse of larval supply via this pathway or a temporarily dominant STG would be sufficient to prime the NAC for far-field coral dispersal, supporting a long-held view that coral mounds off northern Europe have Mediterranean origins (De Mol et al., 2005).

Geochronological data, water mass transport and current understanding of population genetics converge on this unified theory of range re-expansion. Export of saline MOW to the Atlantic greatly increased and culminated in its present-day hydrography and pathway 11.5 ka (Fig. 4; Stumpf et al., 2010). *Lophelia* persisted throughout the deglacial in the Gulf of Cádiz and Mediterranean, the latter characterised by thriving cold-water coral ecosystems by 14 ka and into the Holocene (Supplementary Table 1; Fig. 4). Thus enhanced Mediterranean thermohaline exchange with the Atlantic not only helped strengthen deglacial AMOC by increasing both deep-water convection and production in the Nordic Seas (Rogerson et al., 2006), but it also had ecological significance by exporting coral larvae out of a Mediterranean deglacial refuge and triggering renewed coral populations off northern Europe (Fig. 4).

New estimates of coral migration rates from Mauritania and the Mediterranean to the British Isles and Norway (Supplementary Tables 2 and 3) confirm the historical and on-going importance of Mediterranean *Lophelia* populations to those off northern Europe (Fig. 5). Gene flow was relatively much higher between the

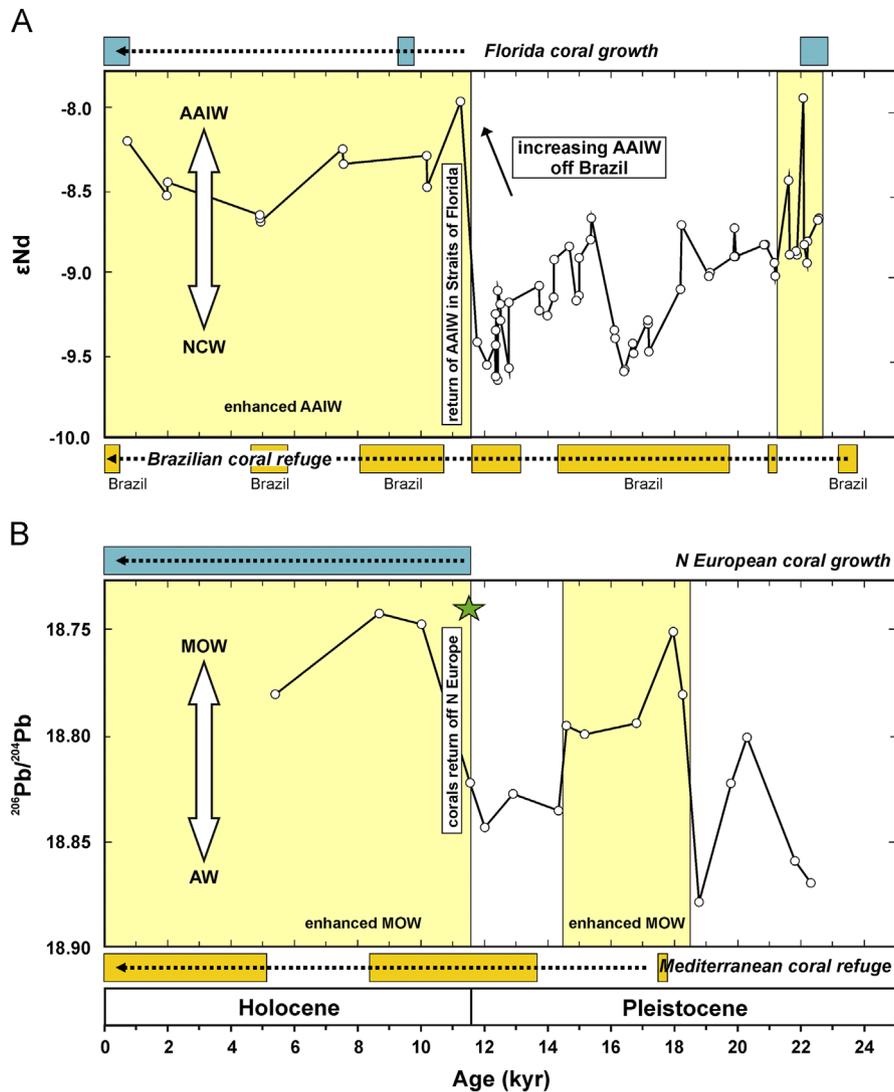


Fig. 4. Coral growth history (blue bars) off Florida and northern Europe in relation to enhanced AAIW and MOW transport. A: AAIW increased relative to northern component water (NCW) off Brazil at about 11.9 ka. AAIW reached Florida at about 11.3 ka, connecting corals from a Brazilian deglacial refuge (dark orange bar, x-axis) and Florida. B: corals from a Mediterranean deglacial refuge (dark orange bar, x-axis) were exported to northern Europe at about 11.3 ka (green star) via increased transport of upper layer MOW versus Atlantic water (AW) across the Iberian margin and Bay of Biscay. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Mediterranean and the British Isles, followed by migration from the British Isles to Norway. Relatively limited migration occurred directly from the Mediterranean to Norway or from Mauritania directly to northern Europe.

Coral migration rates imply a strong historical reliance on Mediterranean larvae for the coral diaspora off northern Europe (Fig. 5). Relatively lower migration directly between the Mediterranean and Norway also demonstrates for the first time that dispersal operated in a punctuated way, with populations off the British Isles acting as intermediate stepping stones that mediated dispersal to Norway. Relatively lower emigration from Mauritania to Europe supports evidence for strong biogeographic differentiation between equatorial African and European corals (Cairns and Chapman, 2001) and genetic differences in other deep-sea species such as the blackbelly rosefish *Helicolenus dactylopterus* (Aboim et al., 2005). Estimates of low to moderate gene flow out of Mauritania (Supplementary Table 3) likely reflect statistical artifacts due to the effects of asexual propagation and possibly unsampled populations, making it appear that corals from northern sites and

Mauritania are derived from common origins. Mauritanian *Lophelia* mounds are bathed by South Atlantic Central Water mixed with South Indian Ocean water, in which case Mauritanian coral dynamics may also be more closely related to the circulation of AAIW in the eastern Atlantic (Fig. 3).

4. Conclusions

Our study integrated new estimates of gene flow in the deep sea with a wide body of published cross-disciplinary data, an approach that uncovered a central role for the Atlantic limb of the global ocean conveyor. AMOC appears to lower extinction risk in the deep sea by facilitating larval dispersal, creating broad geographic ranges in the cold-water coral *Lophelia pertusa*. Export of corals from deglacial refugia in the deep sea was achieved by currents transporting larvae flowing along a re-invigorated AMOC, which produced an unprecedented range expansion across both sides of the Atlantic.

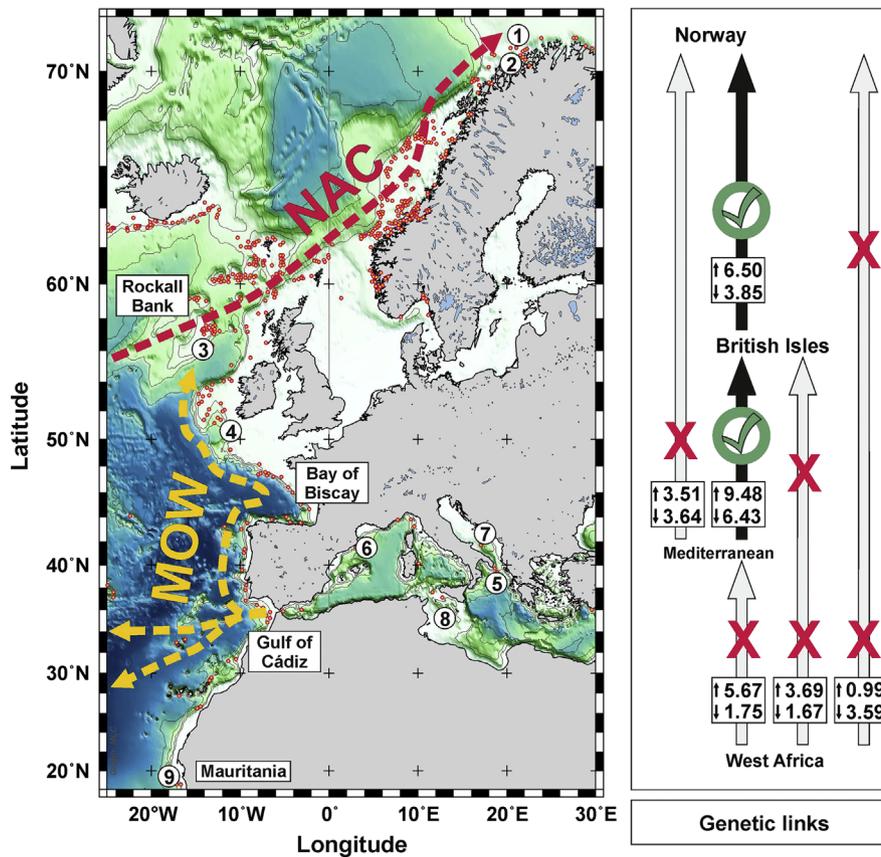


Fig. 5. Estimates of historic gene flow (Supplementary Tables 2 and 3). Left: dispersal to Norway (circled numbers 1 and 2) and the British Isles (circled numbers 3 and 4) from the Mediterranean (circled numbers 5–8) and Mauritania (circled number 9) in relation to MOW and the NAC. Right: northward (up arrows) and southward (down arrows) gene flow suggest likely (unlikely) dispersal scenarios that are indicated by green checks (red crosses). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4.1. Mitigating extinction risk for deep-sea conservation

We uncovered a close synergy between the capacity for wide larval dispersal potential and the strength of ocean currents. This highlights for the first time a new role for AMOC in the modern ocean wherein strong overturning maintains ecological connectivity across geo-political borders. Yet our discovery reveals two important caveats. First, variability in AMOC strength has implications for resilience and extinction risk in deep-sea species and habitats because slower overturning will reduce connectivity across large areas. The scientific evidence base for the fourth assessment round of the Intergovernmental Panel on Climate Change converged on the scenario that the AMOC will very likely slow over the next century (Soloman et al., 2007); our study shows how variability in AMOC strength has implications for deep-sea ecosystems that must be considered in management scenarios to restrict human activities in the next few decades. Second, source populations must be conserved. We identified candidate deep-sea refugia in the Mediterranean, off Brazil and possibly the Caribbean, and a high dependence of northern European habitats on those from lower latitudes. Critically, this second caveat underscores the imperative for the scientific community to study extinction risk, ecological connectivity and history across geo-political borders and ocean scales.

4.2. Recommendations

We show that AMOC created, and today maintains, ecological linkages across broad spatial scales in the deep sea. These linkages necessitate effective internationalisation and sharing of costly

deep-sea research infrastructure to monitor AMOC strength and help ensure the resilience of deep-sea species and the habitats they create.

Following United Nations Resolution 61/105 calling upon member states to protect vulnerable marine ecosystems such as those created by cold-water corals (UN, 2005) and the Conference of the Parties to the Convention on Biological Diversity's definition of Ecologically and Biologically Significant Areas (CBD, 2008), our study also adds to the awareness of the urgency for a ban on deep trawling (Watling, 2013) and the design of deep-water marine protected area networks that span international waters to prevent significant losses and extinctions in the future deep sea.

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Appendix A. Supplementary materials

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.dsr.2014.03.004>.

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