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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.

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 (Maclean 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; Harrnik 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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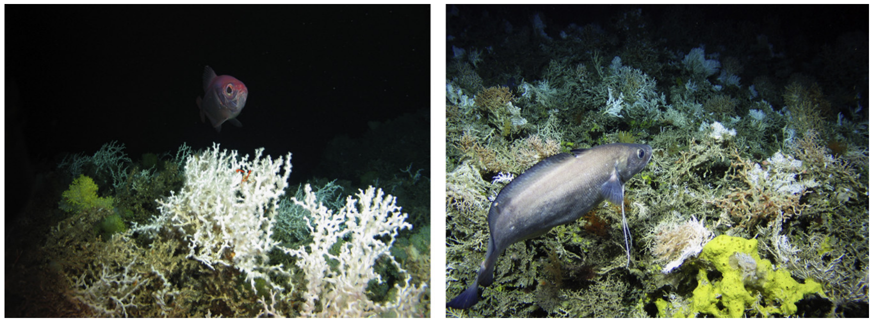

Fig. 1. High biological diversity of coral reefs principally constructed by *Lophelia*. Left: an alfonsino (*Beryx decadactylus*) passes a live coral reef on the Great Bahama Slope in the Straits of Florida (650 m water depth, ROV CHEROKEE Team, MARUM, University of Bremen). Right: a greater forkbeard (*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 glacials 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 multidisciplinary 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′