Cold-water corals from the deep-sea to the TV: development of shelf-edge mounds, assessment of anthropogenic stressors and geochemical parameters, and impacts of science communication

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by

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**DECLARATION**

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__________________________
Erica Terese Krueger
"I love deadlines. I love the whooshing noise they make as they go by."

- Douglas Adams
This thesis is dedicated to my aunt, Kathleen Cutchens.
ACKNOWLEDGEMENTS

If you had asked me 10 years ago what my life would look like in the future, I most definitely would have told you the complete opposite of what it is today. Even five years ago I never imagined I would have embarked on a journey towards achieving my PhD. I survived two years of 12+ credit hours each semester during my undergraduate degree while working as a research assistant in two labs, 40+ hour work weeks while taking the maximum number of credit hours and conducting my own research during my master’s degree, and moving to Ireland to pursue what I now know is a lifetime dream of being a PhD. These last four and a half years have seen an e(stears; they have survived a global pandemic, lockdowns that lasted almost two years (when it was only supposed to be 14 days), and multiple postponed and cancelled lab days. Despite all of this, I have come out on the other side alive and (semi) well.

I would like to acknowledge the many people that played a role in making this PhD possible. First, I must thank the Lord for putting me on this earth and equipping me with the means to become a research scientist. To my supervisor Quentin Crowley, I cannot thank you enough for taking the time to meet a then-master’s student in a Dublin coffee shop, give her a tour of the labs, and offer to be her supervisor a few hours later. You saw my potential as a researcher and took me on, invested time to teach me the skills needed to conduct research, and were by-far the best PhD mentor I ever could have imagined. It has been such an honour to learn from you over the past few years and I look forward to future collaborations. To Vincent Mouchi, thank you for paving the way for my research, inviting me to collaborate, and for being a tremendous co-supervisor, mentor, and friend. To Juan Diego Rodriguez-Blanco and Robin Edwards, thank you for serving on my advisory panel, being a sound board when I needed to talk through things, and providing valuable feedback and guidance.
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dissection flashcards in high school biology to evaluating the destruction of a cypress dome in the aftermath of a major hurricane in my MSc, you instilled a passion for science and research so deep in my soul that I had no other choice but to see how far I could go. Thank you to my previous research advisors Felix Jose and Michael Savarese, along with all the educators from my years at Florida Gulf Coast University; every single one of you taught me something that applies to my research today.

To Elspeth Sinclair, Fergus McAuliffe, Francesca Martini, and Stephen McHugh at iCRAG, your constant support throughout my PhD never went unnoticed and I thank you for helping me navigate funding applications and for introducing me to the world of science communication.

For the PORO-CLIM Expedition, I would like to thank Captain Denis, the officers and crew of the RV Celtic Explorer (especially Paddy and Maurice), and all of the RV operations staff at Eurofleets+, the Marine Institute and P&O Maritime for their hard work to ensure a successful cruise. A big thanks goes to Stacy Phillips for her guidance and expertise in the use of LEGO® figurines as an educational tool for science outreach. And to the one that kept me alive at sea - I owe you my life, Knife!

To Shane, Ian, Niall, Nieve, Shauna, Jess, Gill, David(s), Liam, Leo, Stefan, Daithi, and the kitchen crew at Lincoln’s Inn, thank you for treating me like family and keeping Table 21 open for me to write my thesis – whether it be rough days or celebrations, your pints of Guinness are always perfection and it feels like home every time I walk in the door.
On a more personal note, this accomplishment is not mine alone; I have been encouraged, inspired, sustained, and tolerated by the most tremendous cohort of individuals imaginable, and they deserve much praise. Thank you to all my family and friends – your support, both emotionally and financially, is what kept me going and I could not have finished this without each and every one of you. If I were to name everyone, this thesis would never end!

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Last but certainly not least, thank you to my absolute very best friend Carl O’Reilly. You’ll probably want to kill me for putting this in here, but you have been my rock, especially during the first few months of transitioning to life in Ireland…during a pandemic. From proofreading drafts and applications, taking care of Stevie and the rest of the plant family when I was away on holiday, providing comic relief and level-headed conversations when I was losing my mind or doubting my abilities, chatting over one too many pints on multiple occasions, and your never-ending friendship and support…a ‘thank you’ just doesn’t seem like it’s enough. And as they say in Hank and John’s hometown…
Cold-water corals (CWCs) are the hidden reef-builders of the deep ocean. They are out of sight, yet they perform important functions for marine ecosystems, play a role in stabilising climate change, and hold clues to study past climates. CWC reefs form biodiversity hotspots used as habitat and shelter for over 1,300 species of fishes and invertebrates; these biodiversity hotspots are especially important as nurseries for many juvenile fish species and macro-organisms. As CWCs form their skeleton, they passively record chemical information which reflects local environmental conditions, increasing their use as palaeoceanographic archives. The ocean is becoming warmer and increasingly acidic due to elevated concentrations of atmospheric and oceanic carbon dioxide, causing coral skeletons to become more fragile, and leaving CWC frameworks more at risk from breakage in strong deep ocean currents. It has been reported that dead coral frameworks are just as important as live corals, as they provide a base for coral reef formation in the deep sea. Destruction of CWCs would have a negative impact on marine biodiversity and deep-sea ecosystems as a whole; a reduction in biomass of these three-dimensional structures could result in a lessening of carbon cycling and a loss of these ecosystem engineers in the deep ocean. As important as CWCs are, they are still relatively poorly understood by the scientific community and undervalued by society.

This thesis aims to investigate the development of CWCs and environmental parameters (i.e. ocean acidification, rising seawater temperatures, geochemical proxies) associated with coral skeletons. Samples analysed in this study were obtained from three locations in the eastern boundary of the North Atlantic. For Chapter 2, two cores were collected from a previous research expedition in the Macnas Mounds, an area along the Irish shelf-edge margin at roughly 370 m water depth. Radiocarbon dating and particle size analysis from
these cores describe an environment that was once a thriving coral community. Previously thought to be sand dunes along the outer edge of the Porcupine Bank Canyon, radiocarbon dating constrains these coral mounds to 7.11 (±0.03) to 0.61 (±0.02) ky BP. Multibeam echosounder data and seafloor images from a more recent cruise assisted in confirming the past existence of these coral communities and provided novel data that assisted in the publication of this research.

Coral samples from the Nakken Reef (200-220 m water depth) were collected during a Norwegian research expedition to be analysed as part of the “FATE of cold-water corals—drivers of ecosystem change” project. Following the completion of this project, unused dead coral fragments were obtained for collaborative research for Chapter 3 of this thesis. This study invited an interdisciplinary aspect, partnering with researchers in the School of Engineering at Trinity College Dublin. Nanoindentation methodology normally used for human bone analysis was applied to dead coral skeletons exposed to various seawater temperature and increased carbon dioxide treatments to assess the effects on skeletal structure. This analysis determined that these stressors significantly impacted skeletal properties, resulting in possible breakage and decreased stability of coral mound development.

Chapter 4 provides preliminary data of CWC geochemical concentrations for Mg, Sr, and U and the potential for palaeoenvironmental proxies. As Sr and U are directly related in aragonite, a Sr-U thermometer has been successful as a seawater temperature proxy for tropical corals. However, more research is needed to determine the validity of the Sr-U thermometer in CWCs as other factors may influence the elemental concentrations. A comparison of Mg-U is analysed to support published literature that the two concentrations
are inversely related. Although this research is not new in terms of methodologies, preliminary results indicate further need to validate certain elemental pairings in CWCs as effective geochemical proxies due to impacts from environmental parameters. Future research objectives and possibilities are discussed in Chapter 6.

The desire to communicate science to the public is lacking, and there is an unprecedented need for scientists to be good communicators. It is imperative to demonstrate positive perspectives in research so that we can advance studies and continue learning. Throughout my PhD, I used science communication (Sci Comm) and public engagement to disseminate my CWC research and educate the public on the importance of these ecosystem engineers. Chapter 5 demonstrates how this involvement transformed the way I view science and have realised the critical need for understandable explanations of scientific research so the public feel engaged and involved. Participating in Sci Comm has enhanced my professional development skills in creative and non-scientific ways, such as the use of character-driven figurines. Through television, over 113,000 people tuned in to watch an episode of 10 Things to Know About where I discussed Ireland’s CWCs and my PhD research. From social media, a research collaboration was formed that resulted in critical data for the publication of Chapter 2. During a research expedition, the learner-led approach to Sci Comm resulted in over 100,000 engagements via Twitter/X, and greatly increased public knowledge of what a working research vessel is like. A culmination of these points above suggest that PhD programmes should require some form of Sci Comm or public engagement in their curricula through a combination of formal training and hands-on experience.
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<tr>
<th>Abbreviation</th>
<th>Description</th>
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<tbody>
<tr>
<td>ACC</td>
<td>Amorphous calcium carbonate</td>
</tr>
<tr>
<td>AERYN</td>
<td>Aspect enhancement by removing yielded noise</td>
</tr>
<tr>
<td>AMOC</td>
<td>Atlantic Meridional Overturning Circulation</td>
</tr>
<tr>
<td>AMS</td>
<td>Accelerator mass spectrometry</td>
</tr>
<tr>
<td>ANOVA</td>
<td>Analysis of variance</td>
</tr>
<tr>
<td>B/Ca</td>
<td>Boron-to-calcium</td>
</tr>
<tr>
<td>Ba/Ca</td>
<td>Barium-to-calcium</td>
</tr>
<tr>
<td>BMP</td>
<td>Belgica Mound Province</td>
</tr>
<tr>
<td>CaCO₃</td>
<td>Calcium carbonate</td>
</tr>
<tr>
<td>CH₂O₂</td>
<td>Formic acid</td>
</tr>
<tr>
<td>CMA</td>
<td>Centre for Microscopy and Analysis</td>
</tr>
<tr>
<td>CO₂</td>
<td>Carbon dioxide</td>
</tr>
<tr>
<td>COC</td>
<td>Center of calcification</td>
</tr>
<tr>
<td>CWC</td>
<td>Cold-water coral</td>
</tr>
<tr>
<td>DI</td>
<td>Deionised</td>
</tr>
<tr>
<td>E</td>
<td>Young’s Modulus</td>
</tr>
<tr>
<td>ECR</td>
<td>Early career researcher</td>
</tr>
<tr>
<td>ENAW</td>
<td>Eastern North Atlantic Water</td>
</tr>
<tr>
<td>ESC</td>
<td>European Slope Current</td>
</tr>
<tr>
<td>H</td>
<td>Vickers Hardness</td>
</tr>
<tr>
<td>HCl</td>
<td>Hydrochloric acid</td>
</tr>
<tr>
<td>H₂O₂</td>
<td>Hydrogen peroxide</td>
</tr>
<tr>
<td>HMP</td>
<td>Hovland Mound Province</td>
</tr>
<tr>
<td>HSD</td>
<td>Honestly-Significant Difference</td>
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**INFOMAR**  Integrated Mapping for the Sustainable Development of Ireland's Marine Resource

**LA-ICP-MS**  Laser ablation inductively coupled plasma mass spectrometry

**Li/Mg**  Lithium-to-magnesium

**MBES**  Multibeam echosounder

**Mg**  Magnesium

**Mg/Ca**  Magnesium-to-calcium

**MMP**  Magellan Mound Province

**MOW**  Mediterranean Outflow Water

**MPA**  Marine protected area

**MSCL**  Multi-sensor core logger

**OA**  Ocean acidification

**PORO-CLIM**  Porcupine and Rockall Climate Survey

**PSA**  Particle size analysis

**PSB**  Porcupine Seabight

**pCO₂**  Partial pressure of carbon dioxide

**Q&A**  Question and answer

**R**  Reservoir

**RAD**  Rapid accretion deposit

**ROV**  Remotely operated vehicle

**RV**  Research vessel

**SAC**  Special area of conservation

**Sci Comm**  Science communication

**SEM**  Scanning electron microscopy

**Sr**  Strontium

.xxx
<table>
<thead>
<tr>
<th>Abbreviation</th>
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<tbody>
<tr>
<td>Sr/Ca</td>
<td>Strontium-to-calcium</td>
</tr>
<tr>
<td>STEM</td>
<td>Science, technology, engineering, and mathematics</td>
</tr>
<tr>
<td>TCBE</td>
<td>Trinity Centre for Biomedical Engineering</td>
</tr>
<tr>
<td>TCD</td>
<td>Trinity College Dublin</td>
</tr>
<tr>
<td>TD</td>
<td>Thickening deposit</td>
</tr>
<tr>
<td>TTEC</td>
<td>Trinity Technology and Enterprise Campus</td>
</tr>
<tr>
<td>TV</td>
<td>Television</td>
</tr>
<tr>
<td>TZ</td>
<td>Transitional zone</td>
</tr>
<tr>
<td>U</td>
<td>Uranium</td>
</tr>
<tr>
<td>U/Ca</td>
<td>Uranium-to-calcium</td>
</tr>
<tr>
<td>VME</td>
<td>Vulnerable marine ecosystem</td>
</tr>
<tr>
<td>δ(^{18})O</td>
<td>Stable oxygen isotope</td>
</tr>
<tr>
<td>#</td>
<td>Hashtag</td>
</tr>
<tr>
<td>(^{14})C</td>
<td>Radiocarbon</td>
</tr>
<tr>
<td>W</td>
<td>Shapiro-Wilk</td>
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CHAPTER 1

Introduction
1.1 Thesis outline

- Chapter 1 introduces the thesis and sets out a general introduction to cold-water corals (CWCs) including hydrography in the eastern boundary of the North Atlantic, formation of carbonate mounds, and CWC species *Desmophyllum pertusum*.

- Chapter 2 focuses on the description and development of the Macnas Mounds using radiocarbon (\(^{14}\text{C}\)) dating and particle size analysis (PSA). The research in this chapter is the first to document and describe CWCs along the Irish shelf-edge margin in waters shallower than 500 m and provides support for how climate-driven influences can impact growth and distribution of CWCs. PSA was conducted at the Institut des Sciences de la Terre de Paris at Sorbonne Université and the Department of Geography at Trinity College Dublin (TCD). \(^{14}\text{C}\) dating of coral skeletons and foraminifera was performed by both Beta Analytic Inc. (Miami, FL, USA) and the \(^{14}\text{CHRONO}\) Centre at Queen's University Belfast (Belfast, Northern Ireland). A paper from this chapter has been accepted for publication (Krueger et al. 2024).

- Chapter 3 assesses impacts of anthropogenic stressors of ocean acidification (OA) and rising seawater temperatures) on dead coral skeletons. The research in this chapter is interdisciplinary and utilises technological advances through nanoindentation analysis to determine the structural changes in dead coral skeletons through strength testing and porosity. Nanoindentation analysis was carried out in the Trinity Centre for Biomedical Engineering (TCBE) laboratory at TCD; nanoindentation experiments are more conventionally applied to bone tissue (Arnold et al. 2017), so testing of CWC fibrous skeletal tissue in this way is extremely novel. Following nanoindentation testing, scanning electron microscopy (SEM) was conducted in the Centre for Microscopy and Analysis (CMA) laboratory in TCD and
analysed to determine structural changes (i.e. porosity) occurring in the coral skeletons. A paper from this chapter has been published (Krueger et al. 2023).

- Due to continued laboratory closures and rescheduling resulting from the COVID-19 pandemic, Chapter 4 provides preliminary geochemical analysis of coral samples for palaeoenvironmental reconstruction, focusing on the correlation between uranium (U) and strontium (Sr) concentrations, and the validity of U as a palaeothermometer. Further analysis on the correlation of magnesium (Mg) and U is presented to validate previously published research that the two are inversely related. Geochemical analysis through laser ablation inductively coupled plasma mass spectrometry (LA-ICP-MS) was conducted in the Trinity Technology and Enterprise Campus (TTEC) at TCD and reflected light microscopy was completed in the Fission Track Laboratory in TCD.

- Chapter 5 demonstrates the importance of science communication (Sci Comm) during a PhD. The research in this chapter is focused on the effectiveness of Sci Comm to disseminate my PhD research on CWCs (ultimately leading to a research collaboration that provided invaluable data for the publication of Chapter 2), educate the public on coral research, and the need to implement some form of public engagement into all PhD programmes. This chapter further provides a case study from a marine geophysical research expedition, demonstrating the impacts of educating the public through science communication. A manuscript from this chapter has been submitted to a peer-reviewed journal.

- Chapter 6 is a summary of the conclusions from the above chapters and future proposed work.
1.2 Overview of cold-water corals

1.2.1 Ecology and geography

CWCs are a key component of deep-sea (below 200 m water depth) ecosystems (Levin et al. 2019) and are considered ecosystem engineers (Dodds et al. 2009; Naumann et al. 2015). From an environmental reconstruction perspective, CWCs are useful as proxies for seawater temperature and for documenting environmental change (Chapron et al. 2018; Gaetani et al. 2011). These reef-builders create biodiversity hotspots, producing three-dimensional aragonite structures that are used as habitat and shelter for fishes and invertebrates, and represent deep-sea biogenic calcium carbonate (CaCO$_3$) sources that are useful in reconstructing past geochemical proxies and ocean circulation (Arnaud-Haond et al. 2017; Colin et al. 2010; Copard et al. 2010; Falini et al. 2013; Fanelli et al. 2017; Feehan et al. 2019; Mouchi et al. 2014; Mouchi et al. 2017).

CWCs form important reef structures that contribute to the biodiversity of deep-sea habitats for over 1,300 species (Fanelli et al. 2017; Freiwald et al. 2004; Roberts et al. 2006); less than 10 scleractinian CWC species are known to form these deep-sea reef frameworks (Davies and Guinotte 2011; Roberts et al. 2006). Likewise, their status has attracted researchers to further investigate the effects of man-made disturbances such as deep-sea trawling and overfishing, anthropogenic sources such as increased atmospheric carbon dioxide (CO$_2$) and OA, and natural disturbances such as sedimentation (Galand et al. 2020; Malhi et al. 2020). Losing branching corals has the potential to change the ecology of an entire ecosystem. As such, the comprehension of CWC biology, ecology, and physiology is of utmost importance since they play such an ecological role in these unique environments (Gómez et al. 2018).
1.2.2 Habitat

The distribution of CWCs expands to most of the world’s oceans where oceanic temperatures range from 4°C (Roberts et al. 2006) to 15°C (Puerta et al. 2020), apart from the Bering Sea and high latitude Arctic regions (Freiwald et al. 2004; Gori et al. 2016). CWCs are located from tropical to polar regions in shallow waters less than 40 m (Fanelli et al. 2017) to depths greater than 4000 m (Figure 1; Cairns 1994; Roberts et al. 2006), representing a significant biomass in the North Atlantic. The deepest record of a living scleractinian coral was discovered at a depth greater than 6,300 m in the Aleutian Trench (Keller 1976). It is important to note that this global distribution of CWCs is incomplete and new discoveries are being made as deep-sea research and seafloor mapping are continuously advancing.

![Global distribution of framework-forming CWC reefs](image)

**Figure 1.1.** Global distribution of framework-forming CWC reefs. From Roberts et al. 2006.

CWC ecosystems prefer areas with hard topographic highs (Roberts et al. 2006; Carlier et al. 2009) to facilitate colonisation, and strong bottom currents (White 2007). Unlike
temperate and tropical corals that are light and depth dependent as a factor of food supply and growth, CWCs rely heavily on water parameters such as temperature and salinity, as well as strong currents for nutrient and food supply and sediment input (White 2007; Foubert et al. 2008). Habitats range from continental shelves and slopes, straights and channels, fjords, landslides, oil rig legs, and mid-ocean ridges containing submarine canyons and seamounts (Freiwald et al. 2004; Fanelli et al. 2017).

More recently, CWCs were discovered colonising on a large, steep cliff face in the Porcupine Bank Canyon located in the Northeast Atlantic, confirming that many global locations may still be unknown (Wheeler et al. 2016). Cliff habitats in deep-sea submarine canyons such as the Porcupine Bank Canyon were found to be dominated by suspension feeders, having distinct and diverse benthic assemblages (Huvenne et al. 2011). Submarine canyons not only provide an environment for rapid sediment exchange, but act as a barrier for sediment and nutrient entrapment, creating a pathway from surface water to deep water, resulting in a very dynamic environment conducive to CWC colonisation (Canals et al. 2006; de Stiger et al. 2007).

1.2.3 Biology

The largest majority of CWCs in deep-sea habitats are azooxanthellate scleractinian corals, commonly referred to as stony corals (Roberts et al. 2003; Freiwald et al. 2004; Mouchi et al. 2014). Scleractinian corals obtain CaCO$_3$ in the form of aragonite from seawater to build a hard skeleton (Miller et al. 2011). This hard skeleton is accreted to form the structure in which the polyp resides (Figure 1.2). The cup that the polyp lives in is referred to as the corallite; the corallite wall is called the theca. The polyp is a double-walled sack consisting of two cellular layers, the endoderm (inner layer) and ectoderm (outer layer). The endoderm
houses zooxanthellae in tropical scleractinians, while cold-water scleractinians lack these photosynthetic algae symbionts. The ectoderm contains the calicoblastic layer, sitting in line with the skeletal surface and is proposed to have a role in skeletogenesis. These two layers are separated by the mesoglea, a jelly-like cell-less layer. The polyp is contained in the upper portion of the corallite known as the calyx and sits atop the dissepiment, a thin horizontal sheet separating the polyp from the skeleton below. As the corallite grows, the old dissepiment is left behind and a new one is formed (Cohen and McConnaughey 2003). Tabulae are formed when the dissepiments emerge past each septum and unite in the center, creating a corallite floor (Martin and Le Tissier 1988); the aragonite crystals/fibres are organised in sclerodermites, the basic unit of biomineralization for corals (Ogilvie 1896). These sclerodermites in the empty skeleton below will continue to grow (Druffel 1997; Pasquini et al. 2015). However, biomineralization will only occur in the calyx where living tissue is present. Trabeculae are vertical spines that develop from the upward growth of the sclerodermites (Pasquini et al. 2015). A group of trabeculae form the primary skeletal structure known as the septa; the septa radiate from the theca, extending upwards through the calyx, lengthening the coral skeleton, and ending with a dentation at the tip of each septum (Cohen and McConnaughey 2003). The tentacles are located at the top of the polyp and contain nematoceysts, specialised cells that inject an immobilising toxin into prey. A single gastrovascular cavity is located beneath the center of the tentacles, with an opening that serves as both the mouth and anus (Mouchi 2016). The basal plate is the floor of the corallite that attaches to the substrate.
CWCs can occur as solitary individuals, isolated colonies, dense aggregations, small patch reefs, or larger reefs that form carbonate mounds spanning several km in area and up to 300 m in height (Freiwald et al. 2004; Roberts et al. 2006). Colonial CWC species share genetically identical material, while each individual grows, reproduces, and dies on its own (Cohen and McConnaughey 2003).

Most coral species have two reproductive strategies: sexual reproduction and cloning. Research regarding CWC spawning is very limited, although it is thought that the process may be similar to the shallow-water scleractinian broadcast spawners (Roberts et al. 2009).
Additionally, it has been documented that the CWCs *D. pertusum* and *Madrepora oculata* are seasonal broadcast spawners (Waller and Tyler 2005). Waller and Tyler (2005) observed gametogenesis in a seasonal period from August to October, linking it to a July phytoplankton fall in the Northeast Atlantic Porcupine Seabight (PSB). A reduction in skeletal growth would be expected due to the costly energy consumption from gametogenesis during the spawning season; Mouchi et al. (2014) discovered decreased growth rates in *D. pertusum* during an autumn gametogenesis represented by low Sr concentrations.

### 1.2.4 Skeletal structure

Aragonite scleractinian coral skeletons are built through the process of biomineralization and contain two main components: (i) the centre of calcification (COC) – now more commonly referred to as the rapid accretion deposit (RAD) – which determines the spatial distribution of the overall skeletal architecture ([Figure 1.3](#)); and (ii) the fibres, aragonite structures that build and strengthen the coral from the COC (Meibom et al. 2006; Falini et al. 2013; Mouchi et al. 2014; Mouchi et al. 2017). The COCs are the zones of skeletal growth that provide a structural support for other skeletal features such as the thickening deposits (TD). Amorphous calcium carbonate (ACC) precursors that are reorganised are thought to produce RADs, while the aragonite crystals/fibres that form the theca result in TD regions. Opaque and translucent bands in the theca display these growth structures (Mouchi et al. 2014; Mouchi et al. 2017). Skeletal fusion aids in building colonies as their reef frameworks are mostly located below the photic zone (Hennige et al. 2014). It has been documented that local environmental conditions and seasonality both play a significant role in species-specific growth responses for certain CWC species (Lartaud et al. 2014; Lartaud et al. 2017).
Figure 1.3. Three-dimensional models of septal microstructures in fibrous skeletal tissue of corals. First model (A) shows perfect continuity between organo-mineral phases of deposits of rapid accretion and thickening deposit regions, whereas the second model (B) shows consistent discontinuity of these phases in longitudinal, perpendicular to septal plane section. From Stolarski 2003.

1.2.5 Biomineralization

Living organisms deposit a natural material based on biomolecules (e.g. proteins) formed from various metal ions (e.g. calcium, iron, magnesium, etc.) and anions (e.g. carbonate, phosphate, sulphate, etc.). CaCO₃-based minerals are widely found in organisms such as mollusc shells, tunicate spicules, bone and teeth of bony fishes and mammals, and coral skeletons (Crichton 2008; Falini et al. 2015). As previously mentioned, CWCs are biogenic CaCO₃ sources useful for palaeothermometry and water mass tracers, and as such, represent an under-explored potential as a high-resolution proxy for environmental change (Arnaud-Haond et al. 2017; Colin et al. 2010; Copard et al. 2010; Falini et al. 2013; Fanelli et al. 2017; Feehan et al. 2019; Mouchi et al. 2014; Mouchi et al. 2017). Biogenic carbonates are
formed from two main processes: (i) biologically-induced where crystallisation occurs due to an interaction in an organism’s physico-chemical state; and (ii) biologically-controlled where mineralization occurs within a chemically exclusive portion of an organism, usually caused by metabolic processes (Lowenstam 1981; Mann 1983). Biominerals have the potential to act as high-resolution proxies for environmental change, and biomineralization is the study of formation, structure, and properties of biominerals (Falini et al. 2015); corals can produce approximately $10^{12}$ kg/yr of CaCO$_3$, allowing for the formation of three-dimensional reef frameworks. For scleractinian corals, biomineralization can be biologically stimulated by precipitation from physico-chemical or environmental parameters, arrangements of biotic and abiotic processes, and precise biological control from a highly regulated organic matrix component (Weber 1973; DeCarlo et al. 2015; Falini et al. 2015).

1.2.6 *Geochemical proxies*

As CWCs are broadly distributed and have long lifespans, they have increasingly been recognised as palaeoceanographic archives (Gaetani et al. 2011). Similar to dendrochronology, sclerochronology analyses the growth patterns in the accreted hard tissue of organisms (Buddemeier et al. 1974; Oschmann 2009; Schöne and Gillikin 2013). Subsequently, sclerochemistry analyses the geochemical (i.e. elemental and/or isotopic) information stored in the accreted hard tissue (Gröcke and Gillikin 2008). Our knowledge of marine palaeoenvironmental and palaeoclimate records has significantly increased due to sclerochronological and sclerochemical records from preserved biomineral growth bands in mollusc shells, coral skeletons, and fish otoliths (Knutson et al. 1972; Schöne and Gillikin 2013). These growth bands record chemical signals capable of reconstructing nutrient and ocean temperatures, as well as seasonal growth patterns (Knutson et al. 1972; Montagna et al. 2006; Rüggeberg et al. 2008).
Relationships of skeletal element ratios provide insight into the mechanisms that produce these vital effects. Some of the well-studied and documented element ratio relationships include Sr-to-calcium (Sr/Ca) barium-to-calcium (Ba/Ca), magnesium-to-calcium (Mg/Ca), uranium-to-calcium (U/Ca), and boron-to-calcium (B/Ca) (Gaetani et al. 2011). The relationship between the precipitated aragonite and temperature is very strong for CWCs, producing noticeable variations in Sr/Ca environments where temperature variability is minimal, leading to strong vital effects (Gaetani et al. 2011). This observation suggests that the calcifying fluid had a strong Sr/Ca ratio close to seawater (~ 9.4 to 10.5 mmol/mol for *D. pertusum*). As U and Sr are directly related in aragonite, a Sr-U thermometer was proposed and has been successful as a seawater temperature proxy for tropical corals (Chen et al. 2021; DeCarlo et al. 2016; Gothmann and Gagnon 2021), yet lithium-to-magnesium (Li/Mg) is still the most widely used ratio (Montagna et al. 2014; Stewart et al. 2020).

### 1.3 Geography

#### 1.3.1 Hydrography

The Atlantic Meridional Overturning Circulation (AMOC) is the dominant current to the west of Ireland. This circulation pattern consists of a northward flowing warm, saline upper boundary that sits atop a cooler and less saline returning flow (Figure 1.4). The AMOC is crucial to Earth’s climate system, but its strength has varied over time. Following the last glacial maximum, the AMOC slowed down for a period of time (12-19 Kya). Fossil records indicate a rapid return of CWCs in northern Europe when the AMOC increased again (Frank et al. 2011).
The Northeast Atlantic waters surrounding Ireland are influenced by three main northward flowing water masses, namely the Eastern North Atlantic Water (ENAW; ~200-700 m water depth), the Mediterranean Outflow Water (MOW; ~700-1200 m water depth), and the Labrador Sea Water (below 1200 m water depth). The MOW is a highly saline water mass...
that originates from the Mediterranean Sea and flows counterclockwise through the PSB (Fentimen et al. 2020; Rice et al. 1991; Wienberg et al. 2020). Above that, the ENAW presents a relatively warm, less saline water mass that is partially transported toward the north by the Irish Shelf Edge Current (Pingree and Le Cann 1990; Rice et al. 1991; White 2007). Below the MOW lies the LSW, a colder water mass with relatively low salinity compared to the MOW above (Puerta et al. 2020, Wienberg et al. 2020).

The ENAW and the MOW heavily influence the PSB, where a pronounced transitional zone (TZ; 700-900 m water depth; Figure 1.5) water mass boundary formed by a nutrient-rich density layer (pycnocline) is established. The pycnocline has varied during the past 3 Myr, being shallower during peak glacial periods (e.g. Last Glacial Maximum, 21 ky BP) and deeper during peak interglacial periods (e.g. Holocene, 11.6 ky BP; Rüggeberg et al. 2016).

In the PSB, the ENAW-MOW-TZ boundary allows for nepheloid layers to develop which causes a longer persistence of particulate organics (Dickson and McCave 1986) beneficial for growth and distribution of deep-sea coral colonies (Dullo et al. 2008). The TZ further promotes significant along-slope sediment transport and provides large across-slope sediment movement and organic matter fluxes (Rice et al. 1991; White 2007, White and Dorschel 2010), as well as an association with a strong residual near-seabed current flow and enhanced energy induced by internal wave action and tides (Dickson and McCave 1986; White 2007). These high-energy, hydrodynamic environments with enhanced bottom current velocities are optimal for CWC prey capture during decreased current speeds (Orejas et al. 2016).
Figure 1.5. Schematic depth profile depicting the ENAW, MOW, TZ, and LSW across the Irish margin and shelf-edge slope in the PSB. Adapted from Rüggeberg et al. 2016 and Wienberg et al. 2020.

Brackish outflow from the Baltic Sea mixes with freshwater runoff from Norwegian rivers, creating the low-saline Norwegian coastal waters (Albretsen et al. 2012). These coastal waters combine with Atlantic water, forming the Norwegian Coastal Current (Figure 1.6). Bordering the North Atlantic Current, the Norwegian Coastal Current flows northward as a wedge-shaped low saline current along the coastline, split into a surface layer (up to 100 m water depth) and a deeper layer (100-200 m water depth; Albretsen et al. 2012). Like the ENAW-TZ-MOW, past records have indicated salinity and temperature fluctuations in the hydrographic conditions of the Norwegian Coastal Current, along with a change in volume flux (Albretsen et al. 2012).
Figure 1.6. A schematic map of Norwegian waters. The solid curved lines indicate the main position of the Norwegian Atlantic Current, typically found as slope currents 100–200 m deep as northward flow in the Norwegian Sea, the Atlantic flow entering the North Sea north of Shetland, and the return flow along the Norwegian coast. The dashed curved line denotes the position of the coastal currents (mainly the Jutland current and the NCC). The positions of the fixed coastal stations are indicated by names along the Norwegian coast. The positions of the Norway (Utsira)-Orkney transect and the Skagerrak (Torungen-Hirtshals) transect are drawn as solid, black lines. The isobaths for 200, 500, and 1000 m are denoted by different shading. From Albretsen et al. 2012.
1.3.2 Carbonate mounds

CWCs rely on food particle enrichment (Rüggeberg et al. 2007) and energy enhancements that contribute to sediment deposition for coral mound development (White and Dorschel 2010; Frank et al. 2011). Carbonate mounds can range from small mounds that are 10 m high and 20-35 m in diameter (e.g. Moira Mounds, Wheeler et al. 2011) to giant carbonate mounds 50-300 m above the seafloor and up to 5 km in diameter at the base (e.g. Rockall Trough, van Weering et al. 2003). Reef colonies are formed in a cyclical pattern, from larval settlement to coral growth and death. Bioerosion and breakage of dead coral will extend the reef area, which in time will trap sediment to continue this build-up process. Eventually, this will create a coral mound suitable for colonisation and growth (Figure 1.7). It is important to note that not all CWCs will form carbonate mounds.

![Figure 1.7](image)

**Figure 1.7.** Schematic illustration showing the following: (Outer circle) Cyclic stages of carbonate mound growth from initiation, development, retirement, and recolonisation. (Inner circle) Smaller scale cycle of reef microhabitats, succession, and faunal diversity. From Roberts et al. 2006.
1.4 Desmophyllum pertusum (formerly Lophelia pertusa)

Amongst azooxanthellate scleractinian CWCs that are widely distributed throughout the globe is *D. pertusum*, formerly named *Lophelia pertusa* (Addamo et al. 2016; Hoeksema and Cairns 2020). As previously mentioned, these ahermatypic stony corals are located where ocean temperatures are between 4 to 12°C, but display species-specific responses to temperatures above this range (Tsounis et al. 2010; Gori et al. 2016; Puerta et al. 2020). Food supply is important for growth and occurrence in CWCs (Naumann et al. 2015). CWCs ingest a wide range of food sources such as dissolved organic matter, bacteria, algae, zooplankton, and pelagic crustaceans (Tsounis et al. 2010; Mueller et al. 2014; Naumann et al. 2015). Although this scleractinian species thrives on a zooplankton diet (Carlier et al. 2009; Naumann et al. 2015), feeding habits have proven to be site-dependent and species-specific (Dodds et al. 2009); regional and/or seasonal variability in environmental conditions affects CWC food consumption and are different from their Atlantic conspecifics (Naumann et al. 2015).

*D. pertusum* is the most common and extensive CWC known thus far to create reef frameworks (Figure 1.8) and is the dominant CWC species in the Northeast Atlantic (Freiwald et al. 2004; Larsson et al. 2013; Addamo et al. 2016). It has been documented that the upper threshold for most CWCs is 14°C (Freiwald et al. 2004; Roberts et al. 2006), but *D. pertusum* can thrive at 15°C (Puerta et al. 2020) and withstand temperatures up to 20°C for a 24-hour period (Brooke et al. 2013). Although found at depths greater than 3,000 m (e.g. Northwest Atlantic seamount, Squires 1959), they are also located in shallower waters from 40 m deep where ocean temperatures are low enough (e.g. Tautra Reef, Norwegian Trondheimsfjord, Hovland and Risk 2003). These reef-building corals form colonies that can expand 1.3 m in length with polyp sizes that are approximately 10 mm in diameter and
5 to 15 mm high (Tsounis et al. 2010). *D. pertusum* is an opportunistic feeder, using suspension feeding to collect particles from the water column (Dodds et al. 2009; Mueller et al. 2014); they are known to display high capture rates of particles such as particulate organic carbon, phytoplankton, and zooplankton during low current velocities, from taking up dissolved organic matter to zooplankton up to 2 cm in size (Carlier et al. 2009; Tsounis et al. 2010; Larsson et al. 2013; Mueller et al. 2014; Orejas et al. 2016; van Oevelen et al. 2016).

**Figure 1.8.** (A) Scleractinian cold-water coral *D. pertusum* mound on Blake Plateau located 165 km off the east coast of Florida, at roughly 826 m water depth (image courtesy of the NOAA Office of Ocean Exploration and Research, Windows to the Deep 2019 [https://oceanexplorer.noaa.gov/oceanexplorer/explorations/ex1903/logs/july9/july9.html]), and (B) individual calicular and colony view respectively (adapted from Cairns and Kitahara 2012).
1.4.1 Marine conservation and management

CWC reefs have been noted as vulnerable marine ecosystems (VMEs), specialised centres of biodiversity in seafloor habitats that are highly sensitive to disturbances and have a slow recovery rate (Davies et al. 2008; Du Preez et al. 2020). These VMEs often lead to special areas of conservation (SAC) and marine protected area (MPA) designation (Henry et al. 2013). Unfortunately, many of these reef habitats fall under the Third United Nations Convention of the Law of the Sea, meaning there is no clear jurisdiction or regulation on fishing or over-exploitation (Davies et al. 2007).

One of the first deep-sea reef habitats to receive protection was the Oculina Habitat Area of Particular Concern in 1984, a section of the only known reef system to include the scleractinian ivy tree coral *Oculina varicose* (Harter et al. 2009; Fanelli et al. 2017). The Oculina Habitat Area of Particular Concern contains approximately 30% of the Oculina Bank, a deep-sea (60 to 120 m) reef system located roughly 37 km off the east coast of Florida that runs from Fort Pierce to Daytona. In 1994, a second section of the Oculina Bank came under protection; the Oculina Experimental Closed Area was designated due to grouper populations decreasing. The full extent of the Oculina Bank was not declared an MPA until 2000 (Harter et al. 2009). Following the protection of the Oculina Habitat Area of Particular Concern in 1984, reef protection for CWCs worldwide did not occur until 1999 when the Tasmanian Seamount Reserve in Australia and the Sula Reef in Norway came under protection (Davies et al. 2007; Fanelli et al. 2017). From 1999 to 2006, 14 more CWC protected areas were added to the list (Davies et al. 2007). Most recently, marine researchers have mapped the Blake Plateau, the largest known-to-date CWC reef, located off the southeastern coast of the United States (Sowers et al. 2024). The success of this nearly-complete mapping project provides insight into the extent of CWC ecosystems and
exemplifies the potential for conservation and best management practices. The PSB currently has a few offshore SACs, but stricter regulations need to be set in place to enhance protection of the vulnerable marine habitats (Appah et al. 2022).

The support to protect and conserve biodiversity hotspots such as CWCs is ongoing, as pressures increase from the continuation of fisheries and discovery of deep-sea resources (Armstrong et al. 2019). Anthropogenic factors (e.g. overfishing, chemical and plastic pollution, etc.) are having an increased effect on atmospheric CO$_2$ and greenhouse gases, triggering global climate warming, OA, weather alterations, and ice melt (Danovaro 2018). It is predicted that the geographic distribution of CWCs will decrease in the future if these anthropogenic stressors continue to progress (Gori et al. 2016).

1.5 Science communication
Scientists have been exploring new ways to communicate ocean literacy and research to those in scholarly communities and the public; identifying issues and communicating science in a positive way is one responsibility of researchers (Borja et al. 2022). One of the leading ways in which the scientific community engages public audiences is through science communication (Sci Comm). Sci Comm can be defined as simply as advancing public understanding of science (Treise and Weigold 2002) or more complexly as using appropriate activities, dialogue, media, and skills to produce awareness, enjoyment, interest, opinions, and understanding of science (Burns et al. 2003). Increasing Sci Comm for public engagement has been possible through television (TV) and print (Dudo et al. 2011). With technological advances, social media has been at the forefront as access is readily available and can be delivered globally and in real-time (Collins et al. 2016; Hicks 2019).
1.6 Research aims and objectives

CWCs from the Northeast Atlantic are used to assess various environmental parameters. Through PSA and $^{14}$C age dating, this research presents new evidence of shallow, shelf-edge coral mounds that were once a thriving coral community. With respect to modern-day processes, this research investigates the effects of anthropogenic stressors on CWC biomineralization and implications for geochemical proxies. Finally, this thesis looks at the effectiveness of Sci Comm to disseminate research, spark collaborations, and provide opportunities for professional development during the PhD process.

The objectives of this research are as follows:

- Describe and date the Macnas Mounds that developed along the Irish shelf-edge slope during the mid-Holocene in the North Atlantic.

- Assess the impacts of OA and rising seawater temperatures on dead CWC skeletal structural integrity for stiffness, hardness, and porosity.

- Investigate the use of U as a geochemical proxy to determine its effectiveness for palaeoenvironmental reconstruction and its correlation to Sr, and validate the inverse relationship between Mg and U.

- Assess the use of Sci Comm as an effective tool for research outputs, public engagement, and professional development during a PhD.
CHAPTER 2

Development and physical characteristics of the Irish shelf-edge Macnas Mounds, Porcupine Seabight, NE Atlantic
The research in this chapter has been published and can be found in Appendix A.


**Abstract**

Modern CWCs occur in a wide range of water depths, with *D. pertusum* being one of the most common species. Pleistocene, Holocene, and modern coral mound formation by living CWC reefs have previously been described in the PSB from water depths greater than 700 m in the vicinity of the TZ between the ENAW and MOW. The occurrence of fossil corals retrieved from two cores at 370 m depth in the Macnas Mounds, a relatively shallow occurrence for mounds on the Irish shelf-edge, is presented in this chapter. Both cores feature *D. pertusum* restricted to the upper two metres, immediately overlying an erosive surface and a coeval major down-core change in grain size from sand to mud. \(^{14}\)C dating of coral specimens indicates the CWC mounds initiated 7.11 (±0.03) ky BP. This study unequivocally documents the existence of Holocene shelf-edge coral mounds in the eastern PSB and highlights the possibility of other occurrences of CWCs in similar settings elsewhere in the Northeast Atlantic. Given that no living CWCs were encountered in the study area, it is suggested that the area previously experienced more favourable conditions for mound initiation and development along the shelf-edge margin, possibly due to differing conditions in the European Slope Current which flows northward along the continental slope from south of the Porcupine Bank to the Faroe-Shetland Channel.
2.1 Introduction

CWCs occur globally at all latitudes except the high Arctic regions (Davies et al. 2008; Roberts et al. 2009). CWCs are found in a range of seawater depths, from relatively shallow waters (e.g. 40 m water depth off the coast of Norway, Fosså et al. 2002) down to extremely deep waters (e.g. 4,000 m in the Mediterranean, Tsounis et al. 2010); this range suggests that their distribution is controlled by a combination of factors that include water temperature, food availability, aragonite saturation state, and a strong hydrodynamic regime (Davies and Guinotte 2011; Gómez et al. 2018; Naumann et al. 2015) more so than just depth (Keller 1976). Some species such as *D. pertusum* can construct aragonitic skeletons that form large coral reefs and mounds (De Mol et al. 2007; Foubert and Henriet 2009; Wheeler et al. 2005). These coral communities create biodiversity hotspots that serve as habitat structures for refuge and nurseries (Turley et al. 2007), as well as feeding grounds for fishes and other organisms (Biber et al. 2014; Costello et al. 2005; Dorschel et al. 2009; Henry and Roberts 2007; Henry and Roberts 2017; Söffker et al. 2011).

The PSB is a region west of Ireland that lies between the Porcupine Bank and the Irish Shelf margin (De Mol et al. 2002; Dorschel et al. 2007b; Pirlet et al. 2010; Wheeler et al. 2007). Some of the most well studied and described coral mound provinces in this region include the northern Magellan Mound Province (MMP, 450-700 m depth; De Mol et al. 2002; Huvenne et al. 2003; Huvenne et al. 2007), the central Hovland Mound Province (HMP, 725-900 m depth; De Mol et al. 2002; Rüggeberg et al. 2007), and the southeastern Belgica Mound Province (BMP, 600-900 m depth; De Mol et al. 2002; Dorschel et al. 2007b; Wienberg et al. 2020). Of these mound provinces, certain coral mounds have been described in detail including, but not limited to, the Mound Perseverance in the MMP (Pirlet et al. 2010); Propeller Mound in the HMP (Dorschel et al. 2007b); and the Challenger (Kano et
The formation of coral mounds is highly dependent upon environmental conditions (i.e. strong hydrodynamics, high nutrient availability, physico-chemical water mass properties) and satisfactory sediment supply that allow for steady growth and stabilisation of these framework-forming organisms (Matos et al. 2017; Wang et al. 2021; Wienberg and Titschack 2017). Lateral and vertical advection of phytoplankton and organic carbon along with near-bed currents that enhance food supply are important for the continued function and growth of coral communities (Davies et al. 2009; Maier et al. 2023). Furthermore, sediment input is important for mound development as deposition composes greater than 50% of coral mound material (Titschack et al. 2009). Sediments become baffled by the coral framework and are deposited between the skeletal remains, preventing bioerosion of coral skeletons and hence stabilising the biogenic construction (Huvenne et al. 2009; Titschack et al. 2009; Wienberg and Titschack 2017; Maier et al. 2023). The BMP was the first documented area in the PSB that displayed a co-occurrence of sediment drifts and CWC mounds (Van Rooij et al. 2003). Previous studies have concluded that coral mounds such as the BMP and MMP (Huvenne et al. 2003; Huvenne et al. 2007; Hebbeln et al. 2020a) and Pen Duick drift (Vandorpe et al., 2014) developed where strong bottom currents precluded sediment deposition around the mounds, creating moat features between established coral mounds (i.e. off-mound areas). As currents reduced, the parameters needed to sustain these mounds (i.e. nutrient and sediment input) were no longer available. Continuous
sedimentation buried some coral mounds and moats, eradicating any contouritic deposition indication (Hebbeln et al. 2020a).

Due to the nature of successive sediment deposition, coral mounds can be used as palaeoenvironmental archives as they preserve the history of coral growth and decline through the stratigraphic records (Wienberg and Titschack 2017). Along with the importance of CWCs as palaeoenvironmental archives and ecosystem engineers, the growing knowledge of shelf-edge corals in the Northeast Atlantic lends these areas to be considered VMEs; management approaches used to protect CWCs include SACs and MPAs.

The study area of the Macnas Mounds is located along the Irish shelf-edge margin on a west-facing slope between 300 and 500 m water depth, adjacent to the eastern border of the BMP (Wilson et al. 2007; Wienberg et al. 2010). Although the Macnas Mounds were previously surveyed using remotely operated vehicle (ROV) footage and gravity cores, they were described as small mound-like features of unknown origin composed of sand dunes with coral rubble that were thought to have been covered with live coral colonies at some point (Grehan et al. 2005; Wienberg et al. 2010; Wilson et al. 2007). The aim of this research is to present the first sedimentological description of the Macnas Mounds from two cores, and to temporally constrain coral occurrence within the area. A full description of two cores collected from the mound province is presented along with multibeam mapping and on- and off-mound imaging. Finally, a model of environmental conditions (i.e. shifts in water currents, anthropogenic impacts) that may have influenced the formation of the Macnas Mounds is proposed.
2.2 Methods

2.2.1 Cores

Two 11-cm diameter cores were recovered from 11-21 May 2011 using a 6 m barrel Geo-Vibro Corer 3000 + 6000 on board the RV *Celtic Explorer* during cruise CE11017, under the Integrated Mapping for the Sustainable Development of Ireland's Marine Resource (INFOMAR) programme (Monteys et al. 2011). Core C074 (51°26'05"N, 11°31'38"W; 556 cm core length) was recovered from 369 m water depth and core C075 (51°26'07"N, 11°31'45"W; 486 cm core length) was recovered from 372 m water depth (*Figure 2.1*). Cores were stored at a refrigerated temperature of 4°C during the cruise and in the laboratory. Cores were cut longitudinally with an electric saw into 1.5 m sections, split in two halves using a core splitter with a wire, and placed back in cold storage for analysis (Mouchi 2016).
Figure 2.1. (A) Overview map showing the locations of the Macnas Mounds area and the MMP, HMP, and BMP in the PSB off the southwest coast of Ireland (inset). (B) Detailed map of cores C074 and C075 described in this study, along with locations of previously studied coral mounds in the BMP and the eastern boundary of the Macnas Mounds. Map produced from INFOMAR Dynamic Bathymetric Viewer (https://www.infomar.ie/maps/interactive-maps/dynamic-bathymetric-viewer).

2.2.2 Particle size analysis

Sediment samples were collected from core C074 (n=14) and C075 (n=12) for PSA. Previous PSA for core C074 and sample C075_040 were provided by Mouchi (2016). The majority of sediment samples were collected from the upper core section containing abundant coral fragments, whereas additional sediment samples were collected from the lower section of the cores where there was a visual change in sediment matrix and a concomitant absence of coral fragments. Sediment samples were collected approximately every 15 cm, starting at a depth of 40 cm from the top of the core to avoid misinterpreting sediment mixing caused by core recovery. The sampling strategy is not intended to represent
an equal temporal spread through the core, rather the regular sampling intervals capture a
range of representative sediments over the selected time interval of deposition. Sediments
were wet sieved through a 2 mm mesh to remove larger shell or coral fragments using
standard processes, with a cover on top to prevent sample loss during agitation and a sieve
pan underneath to collect fine fraction. Only biogenic shell and skeletal fragments were
observed in > 2 mm fraction. Sieved sediments were subjected to PSA using a Malvern
Mastersizer 2000 at the Institut des Sciences de la Terre de Paris at Sorbonne Université
(Paris, France) and a Malvern Mastersizer 3000 at Trinity College Dublin (Dublin, Ireland).
Samples were chemically pre-treated with hydrochloric acid (HCl; 10%, 15°C overnight)
and hydrogen peroxide (H$_2$O$_2$; 30%, 15°C overnight) prior to analysis to remove CaCO$_3$
and organic matter (modified from Fentimen et al. 2020). This methodology of pre-treatment is
widely used with CWCs as it effectively removes any organic material from the coral
skeleton without compromising the integrity of the sample (Chapron et al. 2018; Mouchi et
al. 2019). Measured volume distributions were assigned to 100 logarithmically-spaced
classes ranging from 0.02 µm to 2 mm in diameter. The calculation of statistics was
processed using GRADISTAT for logarithmic method of moments from Blott and Pye

2.2.3 Radiocarbon dating of samples

Coral skeleton $^{14}$C dating from cores C074 (n=9) and C075 (n=9) was performed by both
Beta Analytic Radiocarbon Dating Laboratory (Miami, FL, USA) and the $^{14}$CHRONO
Centre at Queen's University Belfast (Belfast, Northern Ireland). Previous $^{14}$C dating for
samples C074_047, C074_080, C074_090, C074_127, C074_560, C075_150 were provided
by Xavier Monteys from Geological Survey Ireland, and samples C075_123, C075_215,
C075_220 were provided by Mouchi (2016). Acid etch pre-treatment protocols from both
laboratories were used for $^{14}$C dating. Benthic foraminifera were extracted for $^{14}$C age dating from the bottom sections of cores C074 and C075 where no coral fragments were present (Mouchi 2016). Foraminifera from core C074 (n=1) was extracted from around 5.5 m core depth, several metres below the first occurrence of *D. pertusum*, whereas those from core C075 (n=2) were extracted from 215 and 220 cm core depth, corresponding to an important change in particle size and immediately below the first occurrence of the CWC mound. Accelerator mass spectrometry (AMS) $^{14}$C age determination was performed, and mass fractionation was corrected by measurements of $\delta^{13}$C (relative to PDB standard) by isotope ratio mass spectrometry. All $^{14}$C dates were calibrated for the Reservoir (R) value using the marine20 database (http://calib.org/marine/; Heaton et al. 2020). The 10 nearest available modern data points from the sample location were used to obtain the $\Delta R$ and $\Delta R$ error; these were calculated by taking the mean of each respective column from the marine20 data results ($\Delta R = -185, \Delta R$ error = 45). To calculate the conventional $^{14}$C ages, the $^{14}$C age and standard deviation in age from laboratory analysis was put in the Data Input Menu in CALIB 8.20 (http://calib.org/calib/calib.html; Stuiver et al. 2021), selecting marine20 with the calculated $\Delta R$ and $\Delta R$ error for each sample.

2.2.4 *Multibeam echosounder data and seafloor imagery*

Multibeam echosounder (MBES) data and seafloor images were provided by Aaron Lim at University College Cork. MBES data were acquired using a Kongsberg EM302 mounted on the RV *Celtic Explorer* during cruise CE20011 (Lim et al. 2020a). The EM302 was operated at 30 kHz, surveying at a speed of 6 knots. Data acquisition was managed through SIS and was conducted with a gridded surveyed design, parallel to depth contours to ensure even distribution of soundings. The vessel was integrated with a sound velocity sensor to ensure quality control of the sound velocity profile, which were updated every 12 hours.
MBES data were stored as *.all files and imported to QPS Qimera where they were corrected for tide and anomalous soundings; data were exported as a 10 m geotiff. The cleaned bathymetric data were saved as *.gsf and processed using the geocoder algorithm in QPS FMGT. This removed all the gains used during acquisition and applied a series of radiometric and geometrical corrections to the original acoustic signals to obtain a correct value of backscatter strength. A series of images were retrieved from the Macnas Mounds and deeper Moira Mounds during ROV operations on cruise CE20011. During acquisition, the ROV maintained a height of approximately 2 m above the seabed to achieve a consistent field of view. A series of lights ranging from 250 to 400 watts were attached to the ROV at a fixed angle to maintain consistent illumination within the field of view. ROV positioning data were recorded using a Sonardyne Ranger 2 Ultra Short Baseline beacon with an accuracy of 0.2% of the slant range (Lim et al. 2020a).

2.3 Results

2.3.1 Core descriptions

In core C074, muddy sediments were observed from the bottom of the core up to 250 cm. Above this, there is a transition to sandy sediments and the presence of *D. pertusum* from 212 cm to the top of the core. Core C075 also documents a clear transition of muddy sediments from the bottom of the core up to roughly 220 cm, topped by sandy sediments and the presence of *D. pertusum*. In both cores (Figure 2.2), *D. pertusum* appears above the transition from muddy to sandy parts and prevails throughout the sandy sections of the cores. It should be noted that the transition from muddy to sandy sediments in core C075 is less pronounced when compared to core C074. Based on multiple visible characteristics (e.g. grain size, Munsell colour index, presence/absence of bioclasts, continuity of sediment layers), there was no evidence of reworking in either core from the vibrocoring process.
Figure 2.2. Description of cores C074 and C075 with measured $^{14}$C ages indicated for coral fragments (black text) and benthic foraminifera (italicised in grey text with an asterisk). Modified from Mouchi 2016.
2.3.2 Particle size analysis

Mean results from PSA for each sediment sample are presented in Table 2.1 and Figure 2.3 for cores C074 and C075. In core C074, two groups of samples are well defined as described above; these groups correspond to the lower muddy section below the coral rubble (mean particle size of 4.32 to 39.52 µm) and the upper sandy section which corresponds to the portion of the cores containing the abundance of coral rubble (mean particle size of 71.45 to 176.2 µm). Core C074 is composed of silt from the bottom of core to 310 cm, transitioning to a small section of very fine sand from 250 to 220 cm. Above that is fine sand from 201 cm to the top of the core, with one area of very fine sand at 110 cm. Core C075 is composed of silt from the bottom of the core up to 270 cm. The core transitions to very fine sand from 200 to 55 cm, with fine sand at 40 cm.
Table 2.1. PSA of sediment samples from cores C074 (n=14) and C075 (n=12). The grain size ($D_{50}$) is presented in both µm and logarithmic (f), with the mean grain size corresponding to the calculated mean fraction using logarithmic method of moments in GRADISTAT (Blott and Pye 2001). Samples in blue provided by Mouchi (2016).

<table>
<thead>
<tr>
<th>Sample</th>
<th>Sample core depth (cm)</th>
<th>$D_{50}$ (µm)</th>
<th>$D_{50}$ (f)</th>
<th>Mean grain size (f)</th>
<th>Wentworth size classification</th>
</tr>
</thead>
<tbody>
<tr>
<td>C074_040</td>
<td>40</td>
<td>139.8</td>
<td>2.839</td>
<td>3.175</td>
<td>Fine sand</td>
</tr>
<tr>
<td>C074_080</td>
<td>80</td>
<td>135.9</td>
<td>2.880</td>
<td>3.260</td>
<td>Fine sand</td>
</tr>
<tr>
<td>C074_110</td>
<td>110</td>
<td>109.4</td>
<td>3.193</td>
<td>3.916</td>
<td>Very fine sand</td>
</tr>
<tr>
<td>C074_140</td>
<td>140</td>
<td>176.2</td>
<td>2.505</td>
<td>2.572</td>
<td>Fine sand</td>
</tr>
<tr>
<td>C074_160</td>
<td>160</td>
<td>161.6</td>
<td>2.630</td>
<td>3.065</td>
<td>Fine sand</td>
</tr>
<tr>
<td>C074_190</td>
<td>190</td>
<td>139.3</td>
<td>2.844</td>
<td>3.170</td>
<td>Fine sand</td>
</tr>
<tr>
<td>C074_210</td>
<td>210</td>
<td>131.1</td>
<td>2.932</td>
<td>3.287</td>
<td>Fine sand</td>
</tr>
<tr>
<td>C074_220</td>
<td>220</td>
<td>125.5</td>
<td>2.994</td>
<td>3.576</td>
<td>Very fine sand</td>
</tr>
<tr>
<td>C074_250</td>
<td>250</td>
<td>71.45</td>
<td>3.807</td>
<td>4.570</td>
<td>Very fine sand</td>
</tr>
<tr>
<td>C074_310</td>
<td>310</td>
<td>18.73</td>
<td>5.739</td>
<td>6.231</td>
<td>Fine silt</td>
</tr>
<tr>
<td>C074_350</td>
<td>350</td>
<td>39.52</td>
<td>4.661</td>
<td>5.338</td>
<td>Coarse silt</td>
</tr>
<tr>
<td>C074_390</td>
<td>390</td>
<td>12.32</td>
<td>6.343</td>
<td>6.615</td>
<td>Fine silt</td>
</tr>
<tr>
<td>C074_460</td>
<td>460</td>
<td>4.32</td>
<td>7.857</td>
<td>7.867</td>
<td>Very fine silt</td>
</tr>
<tr>
<td>C074_520</td>
<td>520</td>
<td>8.55</td>
<td>6.869</td>
<td>7.151</td>
<td>Fine silt</td>
</tr>
<tr>
<td>C075_040</td>
<td>40</td>
<td>142.3</td>
<td>2.813</td>
<td>3.025</td>
<td>Fine sand</td>
</tr>
<tr>
<td>C075_055</td>
<td>55</td>
<td>88.93</td>
<td>3.491</td>
<td>4.076</td>
<td>Very fine sand</td>
</tr>
<tr>
<td>C075_090</td>
<td>90</td>
<td>95.56</td>
<td>3.387</td>
<td>4.069</td>
<td>Very fine sand</td>
</tr>
<tr>
<td>C075_115</td>
<td>115</td>
<td>104.1</td>
<td>3.264</td>
<td>3.869</td>
<td>Very fine sand</td>
</tr>
<tr>
<td>C075_140</td>
<td>140</td>
<td>114.0</td>
<td>3.133</td>
<td>3.696</td>
<td>Very fine sand</td>
</tr>
<tr>
<td>C075_175</td>
<td>175</td>
<td>88.15</td>
<td>3.504</td>
<td>4.169</td>
<td>Very fine sand</td>
</tr>
<tr>
<td>C075_200</td>
<td>200</td>
<td>94.65</td>
<td>3.401</td>
<td>3.814</td>
<td>Very fine sand</td>
</tr>
<tr>
<td>C075_270</td>
<td>270</td>
<td>6.013</td>
<td>7.378</td>
<td>7.122</td>
<td>Very fine silt</td>
</tr>
<tr>
<td>C075_320</td>
<td>320</td>
<td>7.638</td>
<td>7.033</td>
<td>6.689</td>
<td>Very fine silt</td>
</tr>
<tr>
<td>C075_350</td>
<td>350</td>
<td>14.72</td>
<td>6.086</td>
<td>6.110</td>
<td>Fine silt</td>
</tr>
<tr>
<td>C075_390</td>
<td>390</td>
<td>9.519</td>
<td>6.715</td>
<td>6.466</td>
<td>Fine silt</td>
</tr>
<tr>
<td>C075_480</td>
<td>480</td>
<td>24.95</td>
<td>5.325</td>
<td>5.665</td>
<td>Medium silt</td>
</tr>
</tbody>
</table>
Figure 2.3. Particle size distributions of sediment samples from cores (A) C074 (n = 14), and (B) C075 (n = 12) in the Macnas Mounds.

2.3.3 Radiocarbon dating

In total, $^{14}$C ages for 21 samples were performed on cores C074 (n=10) and C075 (n=11), presented in Table 2.2 and Figure 2.4. Coral ages range from 7.11 (± 0.03) to 0.61 (± 0.02)
ky BP for core C074 and 7.18 (± 0.03) to 0.67 (± 0.03) ky BP for core C075. Foraminifera ages range from 16.93 ± 0.07 ky at the base of core C074 to approximately 9.3 ky mid-core of C075 immediately above the shift in grain size from muddy to sandy sections.

Table 2.2. AMS $^{14}$C dates obtained from $D. pertusum$ samples extracted from cores C074 and C075 in the Macnas Mounds. Benthic foraminifera are italicised and denoted with an asterisk (*). R value was corrected using the 10 nearest available modern data points from the sample location ($\Delta R = -185$, error = 45) and applied to the marine20 calibration curve (Heaton et al. 2020). Conventional $^{14}$C ages were corrected for $^{13}$C and calibrated using the CALIB 8.20 (Stuiver et al. 2021). Samples in blue provided by Xavier Monteys and Mouchi (2016).

<table>
<thead>
<tr>
<th>Sample</th>
<th>Sample core depth (cm)</th>
<th>Conventional $^{14}$C age (ky BP)</th>
<th>$2\sigma$ (95%) Cal ky BP</th>
<th>Median probability age (cal ky BP)</th>
</tr>
</thead>
<tbody>
<tr>
<td>C074_027</td>
<td>27</td>
<td>0.61 (±0.02)</td>
<td>0.14-0.47</td>
<td>0.31</td>
</tr>
<tr>
<td>C074_047</td>
<td>47</td>
<td>1.25 (±0.03)</td>
<td>0.66-0.97</td>
<td>0.82</td>
</tr>
<tr>
<td>C074_067</td>
<td>67</td>
<td>2.36 (±0.02)</td>
<td>1.84-2.25</td>
<td>2.03</td>
</tr>
<tr>
<td>C074_080</td>
<td>80</td>
<td>6.64 (±0.04)</td>
<td>6.94-7.32</td>
<td>7.14</td>
</tr>
<tr>
<td>C074_090</td>
<td>90</td>
<td>4.45 (±0.03)</td>
<td>4.45-4.84</td>
<td>4.67</td>
</tr>
<tr>
<td>C074_117</td>
<td>117</td>
<td>7.11 (±0.03)</td>
<td>7.42-7.74</td>
<td>7.58</td>
</tr>
<tr>
<td>C074_127</td>
<td>127</td>
<td>7.10 (±0.04)</td>
<td>7.41-7.74</td>
<td>7.57</td>
</tr>
<tr>
<td>C074_151</td>
<td>151</td>
<td>4.50 (±0.03)</td>
<td>4.53-4.92</td>
<td>4.74</td>
</tr>
<tr>
<td>C074_174</td>
<td>174</td>
<td>6.70 (±0.03)</td>
<td>7.01-7.37</td>
<td>7.20</td>
</tr>
<tr>
<td>C074_560*</td>
<td>560</td>
<td>16.93 (±0.07)</td>
<td>19.46-20.07</td>
<td>19.75</td>
</tr>
<tr>
<td>C075_010</td>
<td>10</td>
<td>0.67 (±0.03)</td>
<td>0.15-0.47</td>
<td>0.33</td>
</tr>
<tr>
<td>C075_038</td>
<td>38</td>
<td>1.98 (±0.02)</td>
<td>1.40-1.74</td>
<td>1.57</td>
</tr>
<tr>
<td>C075_085</td>
<td>85</td>
<td>7.17 (±0.03)</td>
<td>7.48-7.81</td>
<td>7.64</td>
</tr>
<tr>
<td>C075_100</td>
<td>100</td>
<td>6.90 (±0.03)</td>
<td>7.24-7.55</td>
<td>7.39</td>
</tr>
<tr>
<td>C075_123</td>
<td>123</td>
<td>2.91 (±0.03)</td>
<td>2.51-2.89</td>
<td>2.72</td>
</tr>
<tr>
<td>C075_148</td>
<td>148</td>
<td>4.51 (±0.02)</td>
<td>4.53-4.93</td>
<td>4.74</td>
</tr>
<tr>
<td>C075_150</td>
<td>150</td>
<td>3.25 (±0.03)</td>
<td>2.94-3.34</td>
<td>3.13</td>
</tr>
<tr>
<td>C075_162</td>
<td>162</td>
<td>7.08 (±0.03)</td>
<td>7.40-7.71</td>
<td>7.55</td>
</tr>
<tr>
<td>C075_200</td>
<td>200</td>
<td>7.18 (±0.03)</td>
<td>7.49-7.82</td>
<td>7.65</td>
</tr>
<tr>
<td>C075_215*</td>
<td>215</td>
<td>9.28 (±0.04)</td>
<td>9.90-10.36</td>
<td>10.15</td>
</tr>
<tr>
<td>C075_220*</td>
<td>220</td>
<td>9.31 (±0.05)</td>
<td>9.93-10.40</td>
<td>10.17</td>
</tr>
</tbody>
</table>
Figure 2.4. The downcore records of calibrated $^{14}$C age against core depth for cores C074 and C075 in the Macnas Mounds.
2.3.4 Bathymetry and seafloor imaging

MBES data show that the furthest western extent of the Macnas Mounds is at the shelf edge, which is delineated by a northeast-to-southwest orientated blind channel. A total of 338 km$^2$ was mapped by MBES (Figure 2.5) from the eastern slope of the PSB. The continental shelf exists at 244 m water depth and slopes at approximately 3 degrees down the eastern slope of the PSB to a depth of 1160 m in the central PSB. To the west, the larger BMP exists, ranging in length from 850 to 2000 m along their long axis. Along the edge of the continental shelf, approximately 50 of the Macnas Mounds are imaged (Figure 2.5B). Although their diameter ranges from 50 to 200 m, they are typically 6 m in height. Likewise, their slope varies from 2 to 10 degrees which is reflected in their morphology where some of the mounds are elongate, while others are conical. Their spatial density is highest near the edge of the continental slope, progressively decreasing with distance towards the continental shelf. Conversely, the mounds with the largest diameter (200 m) occur along the shelf, while those with the smallest diameter (50 m) occur closest to the shelf edge.
Figure 2.5. MBES bathymetric map of the Macnas Mounds showing (A) the extent of mounds in the region and (B) a detailed image of the mound locations for cores C074 and C075 described in this study, where you can visualise the long axes of the mounds. Created from data collected during marine cruise CE20011 (Lim et al. 2020a).

2.3.5  Seafloor imaging

Seafloor images were retrieved on- and off-mound of the Macnas Mounds (Lim et al. 2020a;). The surface of the seafloor on a Macnas Mound (348 m depth – 51°28’22.774”N,
11°30’32.277”W) is displayed in **Figure 2.6A**; there was no live coral on top of the mound, mainly coral rubble. The adjacent area off-mound of a Macnas Mound (351 m depth – 51°28’20.749”N, 11°30’33.712”W) is displayed in **Figure 2.6B**; only a few scattered coral fragments were observed from this area. A lander image at the summit of a Macnas Mound (345 m depth – 51°28’22.684”N, 11°30’32.359”W; **Figure 2.6C**) with relatively sparse coral rubble present is contrasted to a lander image further downslope in the Moira Mounds (911 m depth – 51°26’51.792”N, 11°44’29.089”W; **Figure 2.6D**) on a coral-colonised sediment wave, where corals are presumed to be relatively the same age as the Macnas Mounds.

**Figure 2.6.** Seafloor images collected at the (A) summit of a Macnas Mound with scattered coral rubble on the seafloor surface and (B) off-mound from a Macnas Mound with very few coral rubble fragments (red arrows). Lander images capture the difference of (C) the summit of a Macnas Mound and (D) mid-slope of a coral-colonised sediment wave in the Moira Mounds (modified from Lim et al. 2020a).
2.4 Discussion

Most data on the Irish Shelf where coral mound provinces are located indicate a dominant current direction towards the north (Lim et al. 2018; Lim et al. 2020b; Summers et al. 2022; White 2007), including the lower MOW that flows counterclockwise in the PSB (i.e. along the same axis of the Macnas Mounds) and continues northward along the continental shelf (De Mol et al. 2005; Van Rooij et al. 2010; Wienberg et al. 2020). It is noteworthy that the majority of coral mounds off Ireland are located between 500 to 1000 m depth (e.g. White 2007; White and Dorschel 2010). Although CWCs along Ireland’s shelf-edge are relatively rare, there are documented occurrences in various locations within the eastern boundary of the Atlantic Ocean (Figure 2.7), i.e. Angolan and Namibian continental margins (Gori et al. 2023; Hebbeln et al. 2017; Hebbeln et al. 2020b; Tamborrino et al. 2019); Bay of Biscay (De Mol et al. 2011); Norwegian continental shelf (Mortensen and Lepland 2007; Titschack et al. 2015); and Mingulay Reef Complex off western Scotland (Douarin et al. 2013). Previous studies have concluded that coral mounds in the BMP and MMP (Huvenne et al. 2003; Huvenne et al. 2007; Hebbeln et al. 2020a) such as Pen Duick drift (Vandorpe et al. 2014) developed where strong bottom currents precluded sediment deposition around the mounds, creating moat features between established coral mounds (i.e. off-mound areas). It is possible that as current velocity reduced, the parameters needed to sustain these mounds (i.e. nutrient and sediment input) were no longer available.
Figure 2.7. Map of documented shelf-edge CWC occurrences along the eastern boundary of the Atlantic Ocean from the early to mid-Holocene in 500 m water depth or less. In the North Atlantic, shelf-edge CWCs have been documented off the (A) west coast of Norway, (B) southwest coast of Scotland, Ireland, and in the Bay of Biscay. (C) In the Southern Atlantic, shelf-edge CWCs have been documented along the Angolan-Namibian continental shelf.

Although the MOW is important for coral mound formation in the BMP (Wienberg et al. 2020), it is located from 700 m water depth, well below the area of the Macnas Mounds. It is unclear how the MOW may affect the initiation and development of the Macnas Mounds, and a more suitable current would be the European Slope Current (ESC), a northward flowing shelf current from the Bay of Biscay to the Faroe-Shetland Channel (McCarthy et al. 2023; Porter et al. 2018; Xu et al. 2015). Density distribution changes have an enhanced effect on the ESC and shelf-edge environment flowing through the Rockall Trough and being deflected onto the shelf (Marsh et al. 2017; Porter et al. 2018). Weakening and warming of the ESC has been documented in the last four decades (Clark et al. 2022). Over longer time periods, variability of the ESC and climatic changes following glacial periods
could be linked to basin-scale events that caused the demise of the Macnas Mounds, noting that warmer periods can decrease CWC populations (Frank et al. 2009).

Along with the Macnas Mounds presented in this study, these shelf-edge coral occurrences are all early to mid-Holocene in age and located at 500 m water depth or above (Table 2.3); *D. pertusum* started growing at the Manas Mounds around 7 ky BP. The age data presented here for corals from cores C074 and C075 are similar in Holocene age to a vibrant growth period documented in the Darwin Mounds (Victorero et al. 2016) that are dominated by the Continental Slope Current. A salinity maximum from 100 to 400 m water depth occurs across the eastern slope of the PSB (Wienberg et al. 2020) where the Macnas Mounds are located; a combination of salinity shifts combined with the ESC could have been favourable for CWC occurrence due to the possibility of enhanced density changes at the boundaries.
Table 2.3. Shelf-edge CWC occurrences along the eastern boundary of the Atlantic Ocean from the early to mid-Holocene as displayed in Figure 2.7.

<table>
<thead>
<tr>
<th>Mapped Coral Reefs</th>
<th>Area</th>
<th>Water Depth (m)</th>
<th>Coral Ages (ky)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Røst Reef (R)</td>
<td>Norway</td>
<td>327-344</td>
<td>0.68-2.62</td>
<td>Titschack et al. 2015</td>
</tr>
<tr>
<td>Mingulay Reef Complex (MR)</td>
<td>Scotland</td>
<td>72-254; 127-134</td>
<td>0.03-3.86; 1.75-4.29</td>
<td>Roberts et al. 2005; Douarin et al. 2013</td>
</tr>
<tr>
<td>Macnas Mounds (MM)</td>
<td>Ireland</td>
<td>369-372</td>
<td>0.61-7.18</td>
<td>This study</td>
</tr>
<tr>
<td>Bay of Biscay (BB)</td>
<td>France</td>
<td>260-350</td>
<td>1.41-9.07</td>
<td>De Mol et al. 2011</td>
</tr>
<tr>
<td>Angola Margin (A)</td>
<td>Angola</td>
<td>160-503</td>
<td>Early Holocene</td>
<td>Hebbeln et al. 2017; Hanz et al. 2019; Gori et al. 2023</td>
</tr>
<tr>
<td>Namibia Shelf (N)</td>
<td>Namibia</td>
<td>160-270</td>
<td>4.8-7.1</td>
<td>Hanz et al. 2019; Tamborrino et al. 2019</td>
</tr>
</tbody>
</table>

The corals presented here are age-constrained from 7.11 (±0.03) to 0.61 (±0.02) ky BP. Specifically for the two cores described in this study, age inversions could result from slumping, debris flows, or redistribution due to skeletal framework collapse; the smaller shelf-edge Macnas Mounds appear to be related to slumping on the continental slope, locally aligned to sediment slumps. It is noteworthy that neither process would show significant grain-size sorting effects, explaining why the reworking events are only evident from the $^{14}$C dates. Similar age inversions are observed in other Holocene mounds in the Northeast Atlantic (e.g. Rockall Bank, Frank et al. 2005; Rockall Trough, Victorero et al. 2016), suggesting skeletal framework collapse via bioerosion or redistribution of coral debris.
The influence of the vibrocoring process is excluded in relation to the presence of the age reversals, as there is no visible evidence of downcore tracking of coral rubble, marginal clasts, or sediment disruption. It is noted that the coarser siliciclastic grain-size distributions are within the mound, compared to the underlying hemipelagic sediments. Such a contrast in grain size distribution within the cores may suggest effective baffling on-mound from reduced near-bottom current velocity (Dorschel et al. 2007; Wang et al. 2021; Wheeler et al. 2011). There is a possibility that the grain-size distributions within the mound are comparable to the grain-size distributions off-mound before and after mound formation, which may indicate a shift in the bottom-water hydrodynamic regime. Strong currents coupled with a low baffling effect likely resulted in bypass of fine sediments during reef aggradation and the deposition of only coarse sediments. Although a change in sediment source is not excluded, there is an observed grain-size distribution within the cores and the elongated geometry of the Macnas Mounds (Wienberg et al. 2010). This is compatible with a combination of sediment waves and subsequent coral mound formation, potentially equivalent to the cigar-shaped reefs of the Træna Deep on the Norwegian shelf (Mortensen and Lepland 2007), and similarly shaped Darwin Mounds in Rockall Trough (Victorero et al. 2016). Using the $^{14}$C ages and core depths, an average mound aggradation rate was calculated to approximately 29 cm/ka. Although this aggradation rate is low for mound formation in general, it falls within aggradation rates observed in other shelf-edge coral provinces in the Northeast Atlantic such as 26 to 57 cm/ka on Røst Reef (Titschack et al. 2015) and 20 to 44 cm/ka on Cabliers Coral Mound Province (Corbera et al. 2021).

Previous multibeam data collected by the Irish National Seabed Survey revealed multiple mound features from the area of Macnas Mounds in the eastern PSB (GOTECH 2002). They
described the area of roughly 200 km² as a larger upper region that contained the majority of the mounds, separated from the lower region containing small mound patches by a definitive channel, similar to the findings in this study (Figure 2.5). GOTECH (2002) showed consistent coral rubble patterns in the upper region where the cores in this study were recovered from, suggesting that more than 8 km² of the Macnas Mounds were previously covered in live coral colonies. Between the mounds were rippled sediment and small dropstones. Although there were no visible live coral colonies, the area was observed to be scattered with small coral rubble on-mound with smooth sandy bottoms off-mound, the same as presented in this study in Figure 2.6.

2.5 Conclusion

This is the first study to provide ¹⁴C age determination and unequivocal evidence of past coral colonisation in the Macnas Mounds. The constrained ¹⁴C age of 7.11 (±0.03) to 0.61 (±0.02) ky BP is the first study to report a Holocene coral mound east of the BMP in an area shallower than 500 m water depth. Occurrence of CWCs from 370 m water depth in the Macnas Mounds is above the ENAW-MOW-TZ in this region (Van Rooij 2004; Wienberg et al. 2020), suggesting a change in the ESC over the course of its history. Both cores penetrated through the coral mounds to the base, where triggering controls can be inferred. Within both cores described, CWCs are absent from the lower muddy matrix, consistent with suboptimal conditions for coral growth (i.e. lack of a hard substrate, or insufficient bottom current velocities for organic nutrient delivery) at that stratigraphic level. An upward stratigraphic shift from mud to sand in the cores is indicative of a change in near-bottom hydrodynamics, with an increase in current velocities. It is suggested that the development of the Macnas Mounds is compatible with coral mound formation superimposed on pre-existing sediment waves similar to other Holocene coral provinces in the PSB. Whereas
previous authors (e.g. Frank et al. 2011) have documented climate-driven latitudinal oscillations of the biogeographic limit of coral development, this study highlights that temporally restricted local or regional changes in bathymetric extent of CWCs may occur, and may be linked to both broader interglacial periods (e.g. following the Little Ice Age) and regional or local climate-driven perturbations (e.g. dynamic shifts in the ESC). Finally, the demise of the investigated corals is likely attributed to a shift in hydrodynamics and diminished nutrient supply that was unfavourable for continued coral growth. Further analysis is needed to determine the extent of environmental drivers that impacted past mound growth in the Macnas Mounds and if present environmental conditions are still favourable for CWC growth and development, which would aid in sustainable management of the area as an SAC or MPA.
CHAPTER 3

Wanted dead or alive: Skeletal structure alteration of cold-water coral
Desmophyllum pertusum (Lophelia pertusa) from anthropogenic stressors
The research in this chapter has been published and can be found in Appendix B.


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**Abstract**

OA has provoked changes in the carbonate saturation state that may alter the formation and structural biomineralization of CaCO$_3$ exoskeletons for marine organisms. Biomineral production in organisms such as CWCs rely on available carbonate in the water column and the ability of the organism to sequester ions from seawater or nutrients for the formation and growth of a skeletal structure. As an important habitat structuring species, it is essential to examine the impact that anthropogenic stressors (i.e. OA and rising seawater temperatures) have on living corals and the structural properties of dead coral skeletons; these are important contributors to the entire reef structure and the stability of CWC mounds. In this study, dead coral skeletons in seawater were exposed to various levels of $p$CO$_2$ and different temperatures over a 12-month period. Nanoindentation was subsequently conducted to assess the structural properties of coral elasticity ($E$) and hardness ($H$), whereas the amount of dissolution was assessed through SEM. Overall, CWC samples exposed to elevated $p$CO$_2$ and temperature show changes in properties which leave them more susceptible to breakage and may in turn negatively impact the formation and stability of CWC mound development.
3.1 Introduction

CWCs are a key component of deep-sea ecosystems (Levin et al. 2019) and are known to occur in most of the world’s oceans except for the Bering Sea and high latitude Arctic regions (Freiwald et al. 2004; Gori et al. 2016). *D. pertusum* is a scleractinian CWC that requires CaCO$_3$ to construct an aragonite skeleton, is a well-distributed and dominant species in the Northeast Atlantic, and is found in most cold-water marine ecosystems globally (Freiwald et al. 2004). CWCs represent a deep-sea biogenic source useful in reconstructing past geochemical proxies and ocean circulation (Schleinkofer et al. 2019). Biomineral production in CWCs relies on the availability of CaCO$_3$ in the water column and the ability of the organism to sequester ions from seawater or nutrients for the formation and growth of a skeletal structure (Fitzer et al. 2015; Hennige et al. 2020). *D. pertusum* features thick epithecal and exothecal skeletal components with a clear lamellar growth pattern (Reitner 2005). OA has provoked changes in the carbonate saturation state (Cao et al. 2007; Jurikova et al. 2019) that may alter the formation and structural biomineralization of CaCO$_3$ exoskeletons for marine organisms (Fitzer et al. 2015) and is concerning for both tropical and CWCs (Wolfram et al. 2022). Little is known about how the microstructure of *D. pertusum* coral skeletons might be altered in such scenarios, but OA has been reported to decrease breaking strength, causing the coral skeleton to become more brittle and can lead to dissolution of both live and dead coral skeletons (Hennige et al. 2015; Hennige et al. 2020; Wolfram et al. 2022). If coral integrity is compromised due to OA and/or temperature intensification of both live and dead corals, there is a potential for framework collapse and loss of habitat complexity (Büscher et al. 2019; Hennige et al. 2020).

Framework-forming CWCs such as *D. pertusum* produce three-dimensional structures that are used by many organisms as habitat and nursery grounds, making them biodiversity
hotspots (Arnaud-Haond et al. 2017; Colin et al. 2010; Copard et al. 2010; Falini et al. 2013; Fanelli et al. 2017; Mouchi et al. 2014; Mouchi et al. 2017). CWC colonies are defined in zonations (i.e. macrohabitats) that are typically composed of a base of small coral fragments and sediments to large coral rubble, a matrix of sediment-entrained dead coral fragments and branches, followed by both live and dead coral framework (referred to as the coral degradation zone) and an upper layer of about 20 polyp generations of living corals at the top (Freiwald et al. 2004; Henry and Roberts 2016). In the dead coral framework where live corals are sparse, the highest density of associated organisms is found for the reef framework as a whole (Mortensen and Fosså 2006; Henry and Roberts 2016). For example, nearly 75% of the CWC colony at the Mingulay Reef Complex is composed of dead coral framework (Vad et al. 2017). In the BMP in the PSB, coral mounds were reported to yield 349 species; much of the live coral framework and dead coral rubble was densely colonised with macrobenthic biodiversity, including calcareous sponges (Henry and Roberts 2007). Megafauna such as bryozoans and macroboring fauna including bivalves, sponges, and polychaetes utilise the sediment-filled cavities of dead coral framework (Henry and Roberts 2016). Furthermore, reef fishes such as the blackbelly rosefish *Helicolenus dactylopterus*, lesser-spotted dogfish *Scyliorhinus canicula*, and blackmouth catshark *Galeus melastomus* rely on CWC frameworks for both hunting and spawning grounds, making these reef habitats more valuable as biodiverse ecosystems (Henry et al. 2013; Henry and Roberts 2016).

As an important habitat structuring species, it is essential to examine the impact that OA and rising seawater temperatures have not only on living corals, but on the structural properties of dead corals that contribute to the formation and stability of CWC carbonate mounds and reefs (Hennige et al. 2014; Hennige et al. 2020). Coupling of elevated CO$_2$ and global temperature increases have altered the Earth’s climate (Royer 2006); negative consequences
are predicted for CWCs if suboptimal ocean conditions persist. Climate change related environmental stressors such as increased seawater temperature and OA are hypothesised to act as contemporary environmental stressors for CWC communities (Gaetani et al. 2011; Gómez et al. 2018). Degradation of dead coral framework that is not supported by protective tissue like the live polyps can occur directly through chemical dissolution and indirectly due to increased bioerosion (Wisshak et al. 2012; Davidson et al. 2018; Büscher et al. 2022). If predictions are correct, increased OA will result in decreased calcification rates, and lower breaking strength along weak zones in the CWC skeleton, resulting in a lower defense against the strong hydrodynamic currents in which they thrive (Hennige et al. 2015; Büscher et al. 2017; Kurman et al. 2017; Gómez et al. 2018). The purpose of this study aims to determine if the structural integrity of dead coral framework will be affected or altered by increasing OA and seawater temperatures and the capacity that it can withstand these anthropogenic stressors.

3.2 Methods

3.2.1 Sampling collection

Coral samples were collected during a Norwegian research expedition aboard the RV Håkon Mosby from Nakken Reef at a depth of 200-220 m in Norway in 2016 (Figure 3.1; Carreiro-Silva et al. 2017). These samples were collected as part of the “FATE of cold-water corals – drivers of ecosystem change” project funded by the Research Council of Norway and provided by Janina Büscher. In a broader laboratory experiment, this project investigated the impacts of OA and seawater warming on the functioning of CWC ecosystems, including live and dead coral framework, key associated bivalve and sponge species, and changes in nutrient availability to the organisms.
Figure 3.1. Nakken reef off the coast of Norway (59°49'49.1"N, 5°33'22"E; red star), sampling site where *D. pertusum* were collected from a depth of 200-220 m in 2016.

The laboratory experiment took place at Austevoll Research Station, Institute of Marine Research in Bergen, Norway, where organisms were observed under various treatments of $p$CO$_2$ and temperature over a 12-month period (Figure 3.2). The general setup of the OA research facility was a flow-to-waste system consisting of circular fiberglass tanks with slightly conical bottoms as described in Andersen et al. (2013). Natural seawater with a salinity of ~35 ppt was pumped from 160 m water depth near the station and adjusted in temperature and $p$CO$_2$ in overhead tanks (see details of the temperature and $p$CO$_2$ control in Andersen et al. 2013) before being transferred to the experimental tanks. During the FATE project, the following treatments were applied to a total of 45 experimental tanks: control or “ambient” at 400 µatm $p$CO$_2$ and seawater temperature of 8°C, “high CO$_2$” at 1000 µatm
$pCO_2$ and seawater temperature of 8°C, and “high CO$_2$+T” at 1000 µatm $pCO_2$ and seawater temperature of 11°C (ambient seabed temperature plus 3°C increase). In all three temperature and $pCO_2$ combinations, three different feeding regimes were applied (low, ambient, and high food). For this study, only ambient food replicates (i.e. samples from unfiltered water tanks) were used.

![Figure 3.2](image)

**Figure 3.2.** Overview of the (A) laboratory experiment setup of the FATE project, (B) view of multiple tanks, and (C) an individual tank with organisms including dead *D. pertusum* branches circled in red. Photo credit: Janina Büscher.

### 3.2.2 Experimental conditions

Tests were performed on dead coral fragments (i.e. skeletons from which organic material had been removed prior to treatment exposure for the duration of the experiment) to assess the possible impacts of OA and seawater warming on skeletons without their protective soft tissue. For this, freshly dead coral skeletons free from bioerosion were sacrificed and the soft tissue was removed by a 10% diluted bleach solution before being transferred into the experimental tanks.
3.2.3 Sample preparation

Two samples were selected at random from each experimental tank (i.e. ambient, high CO₂, and high CO₂+T) for a total of six samples. Samples were cleaned and checked for integrity, taking note that no degradation due to biological factors was present. Samples were prepared by cutting coral branches at an aspect ratio as close to 1:1 as possible. As coral branches are not uniform and may be tapered, ideal geometry cannot be achieved. Following cleaning and preparation, coral samples were set in Struers EpoFix epoxy resin with 25 mm round puck mounts and cured in an oven at 38°C for 24 hours (Figure 3.3A). Once cured, samples were cut using a Buehler IsoMet 1000 Precision Saw at 225 reps per minute in the Museum Building Geology Laboratory at TCD. Samples were cut to expose the inside section of the coral for nanoindentation analysis and imaging (Figure 3.3B).

Figure 3.3. (A) Coral samples embedded in epoxy resin in yellow pucks and placed in a 38°C oven overnight to harden, and (B) a cured resin puck being cut with a low-speed saw to expose the coral surface.
The exposed surface of each mount was then polished in the Fission Track Laboratory using the Struers LaboPol-21 with LaboForce-3 polisher. A coarse disc with DiaPro diamond suspension was run for 10 minutes, followed by a 6 μm MD-Nap disc for 10 minutes, and finished with a 1 μm DP-Nap disc for 5 minutes. Samples were rinsed multiple times in an ultrasonic deionised (DI) water bath between polishing sets and at the end of polishing to remove any excess suspension. Mounts were examined under a microscope to ensure all saw marks were removed, and polishing was repeated if needed (Figure 3.4).

![Figure 3.4](image)

**Figure 3.4.** (A) Cut coral samples being polished on 6 μm MD-NAP polishing disc, and (B) a final polished coral sample ready for analysis.

### 3.2.4 Nanoindentation

Nanoindentation analysis was conducted in the Department of Mechanical and Manufacturing Engineering, School of Engineering, at TCD. An MTS® Nano Indenter XP fitted with a diamond tip (Figure 3.5) was used to assess coral properties to establish elasticity (i.e. stiffness) using Young’s modulus ($E$) and coral hardness using Vickers
hardness ($H$). Average $E$ and $H$ values were assessed at a nanoindentation depth range of 2000 nm along the solid white areas of the coral for a single coral fragment. In this study, stiffness is considered elasticity as the ability of the sample to resist deformation and return to its original state when a force being applied is removed, while hardness is the threshold to which the sample would become permanently deformed (Hennige et al. 2020). Six samples of $D. pertusum$ were analysed with a total of 142 indentations.

![Figure 3.5](image.png)

**Figure 3.5.** (A) Prepared $D. pertusum$ coral sample placed in the MTS® Nano Indenter XP holder (circled in red), and (B) a close-up image of sample being moved into position prior to beginning data collection.

### 3.2.5  Scanning electron microscopy

Following nanoindentation, SE and backscatter SE images were captured using the Tescan TIGER MIRA3 SEM in the CMA at TCD (Figure 3.6). Prior to imaging, coral samples were carbon coated to avoid excess charged particles. Images were taken at 5kV with a scanning speed of 6 and were used to detect visual changes in porosity.
3.2.6 Statistical analyses

A one-way analysis of variance (ANOVA) was run using JMP® Statistical Discovery Software (JMP®, version 16) to determine if there were statistically significant differences between the three experimental tank treatments (i.e. ambient, high CO$_2$, and high CO$_2$+T) for $E$ and $H$ (Fitzer et al. 2015). Due to small sample size, a post-hoc Tukey’s Honestly-Significant Difference (HSD) was run to determine how the treatments differed from one another by a pairwise comparison, and Shapiro-Wilk (W) was run to check for normality. Porosity was obtained by analysing SEM images along the outer coral wall using ImageJ software (Rasband, version 1.53t) and calculated from the percentage of the outer wall where visible porosity was located in the binary image (Sang et al. 2019) as shown in Figure 3.7.

**Figure 3.6.** (A) The Tescan TIGER MIRA3 SEM in the CMA at TCD and (B) capturing SEM images during laboratory analysis.
3.3 Results

Both nanoindentation analyses and SEM imaging indicated that changes in structural integrity of the coral skeleton are compromised in certain elevated CO$_2$ and temperature conditions (Table 3.1).

Table 3.1. Analysis of Young’s Modulus ($E$) and Vickers Hardness ($H$) mean and standard deviation of dead $D$. pertusum samples exposed to various experimental conditions.

<table>
<thead>
<tr>
<th>Condition</th>
<th>Indentation (n)</th>
<th>$E$ Mean (GPa)</th>
<th>$E$ Std. Dev.</th>
<th>$H$ Mean (GPa)</th>
<th>$H$ Std. Dev.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ambient</td>
<td>45</td>
<td>71.7</td>
<td>2.7</td>
<td>4.4</td>
<td>0.5</td>
</tr>
<tr>
<td>High CO$_2$</td>
<td>54</td>
<td>66.1</td>
<td>5.9</td>
<td>4.4</td>
<td>0.5</td>
</tr>
<tr>
<td>High CO$_2$+T</td>
<td>43</td>
<td>71.9</td>
<td>6.1</td>
<td>4.8</td>
<td>0.7</td>
</tr>
</tbody>
</table>

A one-way ANOVA showed a statistically significant difference for $E$ ($F=20.328$; $p<0.0001$); $E$ significantly decreased ($p<0.0001$) in high CO$_2$ samples, while there was no significant difference between ambient and high CO$_2$+T samples (Figure 3.8A). A significant difference was observed between ambient and high CO$_2$ samples ($p<0.0001$) and between high CO$_2$ and high CO$_2$+T samples ($p<0.0001$), suggesting that CO$_2$ influences...
coral elasticity to an extent that cause a structural change in the coral, such as increased porosity (W test for normality passed, P<W=0.45).

A statistically significant difference for was analysed for $H$ ($F=8.989; p<0.0002$), although it was less significant when compared to $E$. $H$ significantly increased ($p<0.0001$ for ambient; $p<0.0004$ for high CO$_2$) in high CO$_2$+T samples (Figure 3.8B). There was no significant difference between ambient and high CO$_2$ samples, but a statistical difference between ambient and high CO$_2$+T ($p<0.0001$) and between high CO$_2$ and high CO$_2$+T ($p<0.0008$) was observed, suggesting that combined high CO$_2$+T influences coral hardness to an extent (W test for normality passed, P<W=0.11).

Figure 3.8. A one-way ANOVA for $D. pertusum$ of (A) $E$ and (B) $H$ from ambient, high CO$_2$, and high CO$_2$+T conditions. High CO$_2$ was significantly different for $E$ and high CO$_2$+T was statistically different for $H$. The grey line across each figure is the mean of response.

SEM images were used to evaluate the microstructure and analyse relative changes in porosity of the dead coral samples. Visible degradation of the outer coral wall was observed in both coral samples exposed to high CO$_2$ alone (Figure 3.9). No degradation was observed in SEM images of the ambient samples. The presence of porosity changes along the outer coral wall can have a large effect that may lead to the coral bending and twisting as water
flows around it; surface defects have a strong effect in reducing the strength, especially in a brittle material such as CaCO$_3$.

**Figure 3.9.** SEM images for *D. pertusum* samples showing visible material alterations of the outer coral walls for (A) ambient, (B) high CO$_2$, and (C) high CO$_2$+T samples. Full coral sample images are on the left and the orange inset boxes display zoomed images on the right. Red arrows represent the area of the outer wall where changes in porosity were calculated.
3.4 Discussion
From this study, it is determined that structural integrity of the coral skeleton is compromised in certain elevated pCO$_2$ and seawater temperature conditions. $E$ significantly decreased in high CO$_2$ samples, so under increased CO$_2$ conditions this ability is reduced and the CaCO$_3$ becomes more brittle. $H$ significantly increased in high CO$_2$+T samples, as shown in Figure 4, leading to the postulation that deformation will come at a later stage. Since this is not observed in the high CO$_2$ variable, it is suspected that this is related to elevated temperature. It is observed that increasing pCO$_2$ and temperature caused partial dissolution of the biomineralized skeleton into the surrounding body of seawater. At higher temperatures, it is possible that some of the dissolved material reprecipitates back into the coral which could be one possible explanation as to $H$ increasing with a temperature increase (Plummer and Busenberg 1982; Burton and Walter 1987). Coral fragments from different colonies were placed in experimental tanks, but as no genome analysis was performed, the possibility of pseudoreplication (Colgrave and Ruxton 2017) cannot be excluded for the nanoindentation measurements. As such, it would been beneficial in the future to compare the nanoindentation measurements from each treated coral samples to determine possible statistical differences between the samples to determine if they are independent of one another.

Studies analysing the biomineralization of calcifying organisms are relatively novel, and few have been conducted on CWCs and bivalves. Hennige et al. (2015) conducted an experiment on $D. pertusum$ growth and respiration from the Mingulay Reef Complex to various increased CO$_2$ levels and temperature conditions over a 12-month period. They did not find significant impacts of OA and warming on respiration or growth, but postulated that to some extent $D. pertusum$ is able to acclimatise physiologically. However, there was a
negative correlation between increasing CO$_2$ levels and breaking strength of roughly 20-30% weakness in areas where coral tissue decreased and left the skeleton exposed. From this, they concluded that the exposed reef bases will become less effective ‘load-bearers’ and will be more susceptible to bioerosion and mechanical damage by the year 2100. In this study, even though $H$ is not changed in high CO$_2$, the decrease in $E$ would support the findings by Hennige et al. (2015) in regard to reduced structural integrity. Following the study from 2015, Hennige et al. (2020) again examined these same coral samples, focusing on the porosity of the coral skeleton. Live $D. pertusum$ displayed no loss in porosity except in areas where tissue loss occurred, yet dead corals had complete increased skeletal porosity of both the inner and outer walls when exposed to increased CO$_2$. “Coralporosis” as Hennige et al. (2020) refers to in their study as the loss of skeletal strength and/or density quite similar to osteoporosis in bones, could occur from decreased structural integrity, leading to framework foundation loss, and ultimately resulting in large-scale habitat loss or prevention of coral mound growth. The results in this study are similar to these findings of acidification-induced skeletal porosity along the outer walls of dead corals (Figure 5), and further validate the mathematical modelling presented by Hennige et al. (2020) for stress due to bending from water flow. Although similar in results, the significant differences reported in this study from increased $p$CO$_2$ and temperature could be explained by the difference in scenarios of the previous studies (i.e. experimental setup of our study for high CO2+T was at 1000 µatm at 11°C versus 750 µatm at 12°C from Hennige et al. 2015).

Wolfram et al. (2022) further analysed live coral samples from Hennige et al. (2020) with regard to the mechanisms of structural changes under increasing porosity and dissolution underpinning the laboratory experiments with mathematical and computational models. They revealed a compressive strength (462 MPa) and stiffness (45 to 67 GPa) of the skeletal
material that is 10 times stronger than concrete. Surprisingly, CWCs seem to retain their skeletal strength despite loss of stiffness under future ocean conditions. However, their models resulted in a significant increase of coral habitat crumbling from small porosity increases, concluding that OA affects dead coral skeletons through dissolution and porosity, leading to a decrease of thickness in the skeletal wall and ultimately a detriment to the fragility of exposed coral skeleton (Wolfram et al. 2022). This is supported by the study presented here showing decreased $E$ and increased porosity under future elevated CO$_2$ conditions. However, the increased level of $H$ in high CO$_2$+T contrasts the findings of Wolfram et al. (2022), which could be explained by different crystal arrangements used in this study.

Similar studies on the biomineralization and material properties of the common blue mussel *Mytilus edulis* were conducted by Fitzer et al. (2014; 2015). Fitzer et al. (2014) analysed mussel biomineralization to determine if there is a present OA threshold or tipping point. Their results showed that shell growth continued with increased $p$CO$_2$, yet the microstructure displayed crystallographic disorientation similar to findings in Hennige et al. (2015) for the CWC *D. pertusum*. Following that study, Fitzer et al. (2015) analysed $E$ and $H$ for *M. edulis* and found that under increased OA conditions, the outer calcite shell was more brittle and the inner aragonite shell was softer and less stiff. This shows that even though calcite is the more stable polymorph of CaCO$_3$ (Mucci 1983), similar results were found as in *D. pertusum* with its aragonitic skeleton. However, the significance of the $p$CO$_2$ impact was reduced in *M. edulis* when a seawater temperature variable was included, leading to the conclusion that there may be a threshold that mussels can withstand. The study presented here displayed similar results of significant increases in $E$ for increased $p$CO$_2$ compared with ambient conditions, as well as a reduced impact with the addition of
increased temperature. Thus, projected climate change will likely have an impact on shell structure and properties to some extent in both calcitic and aragonitic calcifying marine organisms.

In addition, bioerosion is found to be accelerated under OA both in tropical and in CWC reefs where simultaneous increase in temperature did not counteract the impact of acidification (Wisshak et al. 2012; Büscher et al. 2022). Accelerated bioerosion will further lead to a degradation and weakening of coral reef frameworks, which will have implications for the biodiversity of these ecosystems. From the results in this study and similar studies, we can therefore conclude that there is a concern for skeletal structure integrity, possible framework instability, a reduced load-bearing capacity, and a susceptibility to greater than normal bioerosion and mechanical damage for CWC reefs in the future if CO₂ and temperature levels continue to increase in our oceans.

3.5 Conclusion

The shift from a complex habitat comprised of live and dead corals to a less complex habitat comprised of live corals alone is a major threat to CWC ecosystem biodiversity (Hennige et al. 2020). As previously stated, dead corals provide a suitable framework for macrohabitats, leading to enhanced metabolic activity, high oxygen consumption, and mineralization of organic matter (van Oevelen et al. 2009; Maier et al. 2021) which is vital to reefs as a whole. A continued decrease in coral skeletal structure will ultimately result in a large-scale loss of habitat and prevention of future coral mound growth. Further long-term studies and microscopy imaging would provide useful insight to examine the change in porosity of dead coral framework. The results in this study suggest that increased OA and rising seawater temperatures will have an impact on the structural integrity of CWC reefs, especially to the
outer walls of dead corals. This study highlights the need to further validate CWC skeletal structure alterations on a larger scale with an expanded range of conditions, along with analyses of possible changes in mineralization and quantifiable reprecipitation from increased temperature through specific laboratory experiments. Modelling such changes may provide a better understanding of how and when these projected impacts will occur. Although the research presented here is a small-scale laboratory experiment, the results suggest that increased OA and rising seawater temperatures will be detrimental to the structural integrity of CWC reefs. Further work would be needed to validate this on a larger scale with an expanded range of conditions, and modelling such changes may provide a better understanding of how and when these projected impacts will occur. The next steps are to evaluate the microstructure of the dead coral samples using SEM imaging to calculate fracture toughness and analyse relative changes in porosity.
CHAPTER 4

Geochemical analysis for palaeoenvironmental reconstruction
Due to continued laboratory closures and rescheduling that resulted from the COVID-19 pandemic, this is an ongoing chapter that presents preliminary geochemical data for further analysis.

4.1 Introduction

Reconstructing geochemical properties into quantifiable environmental proxies whilst eliminating the influence of vital effects is a current major field of study surrounding CWCs (Schöne and Gillikin 2013). The most common temperature proxy used is that of stable oxygen isotopes ($\delta^{18}O$), although strongly affected by vital effects (Adkins et al. 2003). As a key component to global climate change models, the basis of palaeoclimate reconstruction is built from trace element abundance and isotope composition, particularly Sr/Ca and $\delta^{18}O$ compositions in coral skeletons (Meibom et al. 2006; Gaetani et al. 2011; Robinson et al. 2014). Sr has been used as a temperature proxy in both tropical and CWCs (Sun et al. 2004; Rüggeberg et al. 2008), and as a potential seasonal proxy in CWCs (Mouchi et al. 2014). However, biological effects have been determined to limit the precision of Sr as a temperature proxy in tropical corals (Meibom et al. 2003), and Li/Mg is most reliable as a seawater temperature proxy for both tropical and CWCs (Montagna et al. 2014; Stewart et al. 2020). Carbonate chemistry has documented that Sr and U are directly related in aragonite (Chen et al. 2021; Gothmann and Gagnon 2021), and the Sr-U thermometer has been successful as a seawater proxy for tropical corals (DeCarlo et al. 2016). As U concentrations are relatively high in biogenic aragonite, it is commonly used for $^{14}C$ dating and geochemical proxies, and has the potential to be used as a seawater proxy for CWCs (Chen et al. 2021). However, it is important to expand on the knowledge of CWCs as elemental proxies for seawater temperature and identify stressors that may impact the biomineralization of CWCs as they can be used to reconstruct ocean temperature variability (Meibom et al. 2006). This
study preliminarily analyses the relationship between Sr-U in *D. pertusum* to determine its possible use as a seawater temperature proxy, along with results for Mg-U correlations in scleractinian CWCs.

### 4.2 Methods

#### 4.2.1 Sample collection

Coral samples were collected during Leg 2 of the scientific research expedition M2005 (64PE237) aboard the RV *Pelagia* from 9-19 June 2005 (*Figure 4.1*). Samples were collected via boxcore from the southwest Rockall Trough margin (55°30.196’N, 15°47.149’W) at a depth of 664 m. This expedition was organised by the Royal Netherlands Institute for Sea Research and coral samples were provided by Furu Mienis (de Haas et al. 2005).

![Figure 4.1](image)  
*Figure 4.1. Study site for Leg 2 of Cruise M2005. Adapted from de Haas et al. (2005).*
4.2.2 Sample preparation

*D. pertusum* branches were repeatedly cleaned in an ultrasonic DI water bath to remove trapped sediment and visually inspect for bioerosion. Samples were cut from the main branches for longitudinal growth axes, soaked in 4.8% hydrogen peroxide (H$_2$O$_2$) for 5 hours to remove organic components (Figure 4.2) and rinsed multiple times with DI water.

![Figure 4.2](image)

**Figure 4.2.** Image of coral sample 64A_01 (A) before and (B) after H$_2$O$_2$ soak.

Samples were dried and set in Struers EpoFix epoxy resin with 25 mm round puck mounts and hardened in an oven at 38°C for 24 hours (Figure 4.3).

![Figure 4.3](image)

**Figure 4.3.** (A) Coral sample pucks hardening in oven and (B) “Puck-Off” device used to remove cured pucks from mount.
Once hardened, samples were cut using a Buehler IsoMet 1000 Precision Saw at 225 rpm in the Museum Building Geology Laboratory at TCD. Pucks were cut to 10 mm height to fit the geochemical analysis instruments (Figure 4.4). Cut pucks were then soaked in 4.8% H$_2$O$_2$ again for 5 hours to remove any residual organic components that might be inside coral polyps and rinsed multiple times with DI water.

**Figure 4.4.** (A) Sample cutting in the Museum Building Geology Laboratory with a low speed saw, and (B) sample 64A_04 in the process of being cut.

The exposed surface of each mount was then polished in the Fission Track Laboratory at TCD using a Struers LaboPol-30 with LaboForce-100 polisher. A coarse disc with DiaPro diamond suspension was run for 10 minutes, followed by a 6 μm DP-NAP-T disc for 15 minutes, and finished with a 1 μm MD-Nap disc for 10 minutes. Samples were rinsed multiple times in an ultrasonic DI water bath between polishings and at the end of polishing to remove any excess suspension. Pucks were examined under a microscope to ensure all saw marks were removed, and polishing was repeated if needed (Figure 4.5).
Figure 4.5. (A) Polishing coral samples in the Fission Track Laboratory, (B) coral sample before polishing, and (C) coral sample after polishing and ready for analysis.

4.2.3 Laser ablation inductively coupled plasma mass spectrometry

LA-ICP-MS was conducted in TTEC at TCD (Figure 4.6). The laboratory houses a Thermo Scientific™ iCAP™ Qs ICP-MS combined with an Analyte Excite 193 nm ArF Excimer LA system and installed with Thermo Scientific™ Qtegra™ Intelligent Scientific Data Solution™ software (version 2.2.1465.24). Six samples were selected for LA-ICP-MS analysis; various locations on each sample were chosen for geochemical mapping.
In total, 14 trace elements were selected for detection to include elements that are commonly used for palaeoenvironmental studies (i.e. Li, Mg, Sr; Montagna et al. 2014) and elements not as widely studied for concentrations in fossilised CWCs (i.e. Y, Ba, U). For each of the maps, a rectangular transect of parallel raster lines were selected and the spatial resolution parameters stayed the same for consistency and sound comparison. The laser repetition rate was set to 22 Hz with a 0.4 J/cm² laser fluence (modified from Mouchi 2016); a 24 μm spot size was selected using a speed of 34 μm/s. With these settings, maps took three to five hours each depending on the number of ablated lines. A NIST-612 external glass standard for carbonates was ablated on two lines before and after each area map. Laser dwell times for detection varied for each element (Table 4.1).
Table 4.1. Dwell times in seconds for each element.

<table>
<thead>
<tr>
<th>Element</th>
<th>Dwell time (s)</th>
</tr>
</thead>
<tbody>
<tr>
<td>$^7$Li</td>
<td>0.04</td>
</tr>
<tr>
<td>$^{24}$Mg</td>
<td>0.01</td>
</tr>
<tr>
<td>$^{25}$Mg</td>
<td>0.02</td>
</tr>
<tr>
<td>$^{27}$Al</td>
<td>0.03</td>
</tr>
<tr>
<td>$^{43}$Ca</td>
<td>0.01</td>
</tr>
<tr>
<td>$^{51}$V</td>
<td>0.04</td>
</tr>
<tr>
<td>$^{65}$Cu</td>
<td>0.04</td>
</tr>
<tr>
<td>$^{66}$Zn</td>
<td>0.03</td>
</tr>
<tr>
<td>$^{86}$Sr</td>
<td>0.01</td>
</tr>
<tr>
<td>$^{88}$Sr</td>
<td>0.005</td>
</tr>
<tr>
<td>$^{89}$Y</td>
<td>0.08</td>
</tr>
<tr>
<td>$^{133}$Cs</td>
<td>0.08</td>
</tr>
<tr>
<td>$^{137}$Ba</td>
<td>0.03</td>
</tr>
<tr>
<td>$^{139}$La</td>
<td>0.08</td>
</tr>
</tbody>
</table>

To conduct trace element output, collected ICP-MS isotope data were automatically converted using Iolite version 4 (Paton et al. 2011). When calculating the chemical composition of a coral, Ca is used as an internal standard for data processing in Iolite, and the weight percent of Ca in aragonite is 47.49 (Putranto et al. 2018).

4.2.4 Aspect enhancement by removing yielded noise

To clean up the decreasing trend in signal intensity from LA-ICP-MS maps, data was processed through the Matlab code Aspect Enhancement by Removing Yielded Noise (AERYN; Mouchi et al. 2016). The results of the code produce exported maps and delimited text files that enhance the accuracy of geochemical maps. Statistical analyses were run in Matlab to determine the significance of correlations between Sr-U and Mg-U.

4.2.5 Acid etching

Acid etching was conducted in the Museum Building Geology Laboratory at TCD. Coral pucks were dipped into 1% formic acid (CH$_2$O$_2$) for two seconds and thoroughly rinsed in DI water to reveal coral skeleton microstructures and crystals (Flöter et al. 2019) due to
differential etching of adjacent layers when viewed under the SEM (modified from Mouchi 2016; **Figure 4.7**).

![Image of coral samples](image)

**Figure 4.7.** Acid etching coral samples to better reveal growth bands and microstructures.

### 4.2.6 Reflected light microscopy

Reflected light microscopy was conducted in the Fission Track Laboratory at TCD using a Zeiss AXIO Imager.z1m Standing Microscope to expose growth bands and possible microstructures from acid etching to measure bands and compare with a pseudo-transect across the elemental map.

### 4.3 Results to date

#### 4.3.1 Geochemical mapping

Geochemical maps were produced for six coral samples on the LA-ICP-MS. Some elements displayed visible fluctuations in elemental concentrations, while other concentrations were too low to detect. A composite of all geochemical maps for 64A-05 is displayed in **Figure 4.8**.
Figure 4.8. Composite image of LA-ICP-MS geochemical output for 64A-05.
Following LA-ICP-MS, geochemical data was processed through AERYN to enhance the accuracy of the geochemical maps (Figure 4.9).

![Figure 4.9. A comparison of LA-ICP-MS and AERYN-processed geochemical maps.](image)

### 4.3.2 Reflected light microscopy

Opaque and translucent banding was observed under reflected light microscopy in the theca of *D. pertusum* samples (Figure 4.10). These bands alternate high and low concentrations for some geochemical elements such as Li, Mg, and U. Reflected light microscopy did not display viable microstructures needed to measure bands for most samples to compare with a pseudo-transect across elemental maps.
**Figure 4.10.** Reflected light microscopy image of exposed acid etched opaque (white) and translucent (grey) bands for coral sample 64A-02. Longitudinal growth is toward the top and radial growth is toward the right.
4.3.3 Elemental concentrations

Samples 64A-02 and 64A-05 yielded high quality geochemical maps and visible growth banding after methodologies were applied. An overlay of reflected light microscopy, LA-ICP-MS, and AERYN outputs are displayed in Figure 4.11 for methodological comparison.

**Figure 4.11.** Comparison of microscopy image against LA-ICP-MS and AERYN geochemical maps.
Transects across geochemical maps for samples 64A-02 and 64A-05 were analysed to determine the correlations between Sr-U and Mg-U concentrations. For 64A-02 (Figure 4.12), Mg concentrations ranged from 480-2,070 ppm, U concentrations ranged from 2.1-6.6 ppm, and Sr concentrations ranged from 7,000-13,900 ppm.

Figure 4.12. Comparison of Sr-U and Mg-U concentrations from sample 64A-02.
For 64A-05 (Figure 4.13), Mg concentrations ranged from 570-1,250 ppm, U concentrations ranged from 2.2-5.3 ppm, and Sr concentrations ranged from 6,500-12,300 ppm.

**Figure 4.13.** Comparison of Sr-U and Mg-U concentrations from sample 64A-05.
A correlation for both concentration pairings resulted in no significant correlation for either sample. Statistical analyses for 64A-02 resulted in $R = -0.1394$ and $p < 4.26 \times 10^{-4}$ for Sr-U, and $R = -0.6667$ and $p < 7.59 \times 10^{-83}$ for Mg-U (Figure 4.14A). Statistical analyses for 64A-05 resulted in $R = -0.1250$ and $p < 1.57 \times 10^{-4}$ for Sr-U, and $R = -0.5412$ and $p < 5.68 \times 10^{-59}$ for Mg-U (Figure 4.14B).

**Figure 4.14.** Correlation of Sr-U and Mg-U concentrations from samples (A) 64A-02 and (B) 64A-05.
4.4 Discussion

Concentrations between Sr-U are normally reported to be positively correlated, which is not the case in this study. The poor correlation of Sr-U in both samples could result from a response to the biomineralization process as similarly documented by Chen et al. (2021), stating possible disruptions from less saturated seawater, growth environment, and vital effects. Similar finding from Gothmann and Gagnon (2021) suggest U/Ca is better suited to understand impacts of OA and other environmental changes, and different approaches are necessary for establishing temperature proxies in CWCs (Stewart et al. 2020). Mg and U displayed a strong negative correlation in both samples, which is consistent with previously published research for scleractinian tropical and CWCs (Sinclair et al. 2006).

Coral aragonite can form in the COC via the precipitation of ACC (Schleinkofer et al. 2019). Environmental conditions such as OA could impact the biomineralization of the coral, resulting in reduced aragonite precipitation or crystallisation of nanograin particles (Tan et al. 2023). It is documented that Mg enrichment in aragonite fibres is attributed to ACC precipitation in the COC; however, this amorphous-to-crystalline CaCO₃ process could affect the trace element chemistry of the aragonite crystals in CWCs. As such, the variability of trace element records for some elements can be explained by a combination of Mg/Ca in ACC and carbonate chemistry of the surrounding seawater (Evans et al. 2020). These factors add a level of complexity to the understanding of chemical evolution in CWCs, which will need to be taken into consideration for further geochemical analyses of this chapter.

4.5 Conclusion

Correlated trace elements that are successful in tropical scleractinian corals may not be viable for scleractinian CWCs. For elements such as Mg and U, it is common to have an
inverse relationship in both tropical and CWCs. However, the preliminary data presented here provides implications of environmental parameters that affect the validity of geochemical proxies with regards to Sr and U for CWCs, making the Sr-U thermometer less valid. Further analysis of SEM imaging is necessary to determine the COC and microstructures of the coral samples to determine the possible seasonal calibration for Sr and U.
CHAPTER 5

What’s all the comm-ocean? Science communication for cold-water coral research and ocean literacy during a PhD
Abstract
Ocean education and public engagement are useful resources to improve public understanding of how their daily lives impact the health of the ocean. Sci Comm has become an integral way of disseminating ocean literacy and research to the scientific community and the public. Technological advances have allowed two-way global interactions between the public and scientists in real-time, leading to increased networks and collaborative research. Although social media can be used to spread scientific misinformation, it is more efficient in correcting this misinformation and building trust between scientists and the public. Along with social media, Sci Comm can be presented in various ways including traditional media such as TV and print, narratives through cartoons and characters, and direct public engagement. This chapter demonstrates the effectiveness of Sci Comm to engage various people in CWC research and foster scientific collaborations during a PhD through a culmination of activities. Furthermore, it addresses the importance of implementing some form of public engagement into the PhD curricula for professional development and inclusion of the public. A case study from a deep marine geophysical research expedition is included, demonstrating the success of interacting with and educating the public through Sci Comm for the project’s scientific goals and outcomes.

5.1 Introduction
The ocean provides sustainability, activity, economic resources, and ecosystem services for human health and well-being (Sandifer and Sutton-Grier 2014; Bindoff et al. 2019). Yet for the past millennia, human activity has impacted the ocean ecosystem (Bindoff et al. 2019; Knowlton 2021). Although many human-induced activities have resulted in negative impacts to the ocean (i.e. overfishing, OA, coral bleaching), researchers have implemented positive outcomes such as marine conservation and habitat restoration (Valentine and Heck
The health and conservation of the ocean is limited by many factors, some of which include general knowledge, experience, and lack of resources (McPherson et al. 2018; Santoro et al. 2017). To combat these limitations, ocean education and public engagement are helpful tools in which ocean-related information can be shared with the public (Santoro et al. 2017). Tools in these fields enhance public understanding of their impacts on the ocean and its impacts on them, more widely referred to as ocean literacy (Cava et al. 2005). Here I present the effectiveness and importance of Sci Comm for CWC research outputs and collaborations during my PhD through a culmination of traditional media outlets, social media, character-based narratives, and public engagement activities. Finally, a case study from a deep marine geophysical research expedition is also presented, with the aims of providing learner-led training for early career researchers (ECRs) during a working research expedition, along with designing and carrying out a public engagement programme that demonstrated the efficiency of the project’s scientific goals and outcomes.

5.2 Science communication in the media

5.2.1 Science through television

TV was the primary source of scientific information from the late 1970s to the early 2000s, with the popularity of the Internet taking its place by 2004 (Dudo et al. 2011). Although the Internet has now become the primary and advanced source of scientific information, TV is still seen as a popular source of informative media (Dudo et al. 2011). From educational shows such as *Bill Nye, the Science Guy* (Long and Steinke 1994), fictional series such as *The Big Bang Theory* (Li and Orthia 2015), and interview-style programmes such as *10 Things to Know About* (produced and broadcast in Ireland), TV offers a unique opportunity to effectively provide educational and informative scientific knowledge to a wide variety of
audiences (Hut et al. 2016). A high involvement of Sci Comm throughout my PhD led to a pitch submission to an open call for the 9th series of *10 Things to Know About*, an award-winning television series that showcases and celebrates the Irish science behind aspects of modern life. Each episode is themed around one core topic or research area and introduces researchers based in Ireland working on projects that affect viewers’ lives. The pitch was accepted by the production company New Decade in June 2023. Preparation included production work such as selecting filming locations and discussion points, practicing talking points for the public, and gathering CWC samples as props for the episode. I was interviewed for episode 5 of the series in September 2023 (Figure 5.1), which aired on 11 December 2023 on RTÉ One (a state broadcaster); the episode focuses on Ireland’s CWC community and the research conducted during my PhD.

![Image](image.png)

**Figure 5.1.** Screenshot from Series 9 Episode 5 of *10 Things to Know About*, filmed on Myrtleville Beach in Co. Cork, Ireland.
5.2.2 *Science through social media*

While traditional media outlets can disseminate information from one source to a targeted audience, technological advances in the form of social media allows for a two-way interaction with a global audience (Thaler et al. 2012; Darling et al. 2013; Stewart and Lewis 2017; Guenther and Joubert 2021). Social media can be described as electronic networking through personal web pages, blog posts, video uploads, social media networking sites (i.e. Facebook, Twitter/X, and LinkedIn), and more (Darling et al. 2013; Bik and Goldstein 2013; Tarantino et al. 2013). As social media has developed, it has altered the ways in which people can access and share information, interact with others, and has become an integral part of daily life for most people (Wilson et al. 2012; Collins et al. 2016). Furthermore, social media has become an accessible entity to familiarise the public with science literacy, awareness, and understanding (Burns et al. 2003). Academics and ECRs have previously used social media platforms (e.g. Twitter/X) to share scientific knowledge and communicate with other scholars (Priem and Costello 2010); yet more recently, they have shifted their use of these platforms to be a means of communicating and engaging public audiences with their scientific research (Bik and Goldstein 2013; Hicks 2019; Kahle et al. 2016; Priem and Costello 2010). For example, social media was used to promote *10 Things to Know About* prior to and following its original airing, which led to a larger viewer audience (*Figure 5.2*).
Social media has also been used to facilitate collaborations between researchers; the proper use of the hashtag (#) can lead people to social media posts that are of interest to both parties. Twitter/X campaigns can be useful tools to spread awareness and encouragement in science, such as the #OceanOptimism campaign that shared success stories of ocean conservation efforts, reaching over 76 million Twitter/X accounts (Knowlton 2017). One example of social media success from my PhD includes a published Twitter/X post with a caption containing #MacnasMounds (Figure 5.3). This post gained over 1,000 interactions and was seen by a coral researcher at a different university, leading them to reach out to discuss my PhD research in the Macnas Mounds. Due to this Sci Comm interaction, the researcher
became a collaborator on the project, providing invaluable MBES data that was integral to the project for publication in a peer-reviewed journal (Krueger et al. 2024).

![Twitter/X post](image)

**Figure 5.3.** Twitter/X post used to document a behind-the-scenes portion of my PhD through Sci Comm, featuring #MacnasMounds that led to collaborative efforts for the publication of Chapter 2 of this thesis (Krueger et al. 2024).

### 5.3 Science communication through public engagement

Public engagement is an umbrella term for activities that assist in bridging the gap between scientists and the public (Jensen and Buckley 2012; Weingart et al. 2021). In the UK and EU, more science policies have begun to include public engagement as an objective; these
activities have surpassed traditional settings, branching out into science and art festivals, public lectures and comedy nights, and science cafes and pubs (Jensen and Buckley 2012). Engaging the public with scientific research is an important aspect of Sci Comm, although formal training is not readily available for most scientists (Jensen and Buckley 2012; Varner 2014). Whether it be through dialogue or participation, public engagement is crucial for ocean literacy, dissemination of research, and professional development (Hetland 2014; Stofer et al. 2023).

Throughout my PhD, I participated in various public engagement activities with regards to my CWC research. Some of the activities were research based, while many others focused on bringing science to social settings and using creativity to enhance science (Roche et al. 2019). From a research-based perspective, I’ve had the privilege of participating in events such as Culture Night Dublin (https://culturenightdublin.ie) and European Researchers’ Night (Figure 5.4). Culture Night Dublin is a county-wide event that features cultural discovery through art, history, science, and more. European Researchers’ Night (https://www.start-ern.org) is a Europe-wide event that began in 2005, where the public can interact, learn, and celebrate research.
Figure 5.4. Displaying a poster from Chapter 3 of my PhD thesis along with various Irish cold-water corals at Start Talking About Research Today: European Researchers’ Night 2023.

One of the most rewarding public engagement opportunities was participating in Pint of Science (https://pintofscience.com), an annual science festival that began in 2013 and is organised by postgraduate and postdoctoral volunteers. Pint of Science aims to bring scientists and the public together in a relaxed atmospheres such as pubs and cafes to discuss their research (Garrard 2019; Richter and Thomas 2018). Since 2013, Pint of Science has grown into an international festival, occurring in over 400 cities with 150,000 attendees. Over the course of three evenings in May, scientists give presentations to the public about their research, sparking discussions, and allowing them to appreciate the human side of researchers. In May 2023, I participated in Pint of Science in Dublin, Ireland. The evening allowed for the opportunity to discuss my PhD research along with two other presenters to a pub filled with roughly 50 people (Figure 5.5). As people often go to the pub for
socialising, the event fostered opportunities to ask questions and learn about science in an upbeat and comfortable setting. Personally, the evening supported professional development through practicing public speaking outside of a scientific conference or lecture setting, and allowed me to bring my personality and humour into science. Pint of Science allowed me to think about my research in an unconventional way, incorporating creativity and comedy to present my research to a room full of multiple backgrounds.

![Figure 5.5](image_url)

**Figure 5.5.** (A) Pint of Science Instagram post featuring event details, and (B) discussing CWC research with roughly 50 audience members in a pub in Dublin, Ireland.

Not all public engagement activities occur in science-based settings. For example, two public engagement activities that I participated in during my PhD were the National
Ploughing Championships and Féile na Bealtaine. These events cater to target audiences outside the scope of ocean sciences. The National Ploughing Championships (https://www.npa.ie) is an annual outdoor agricultural event held in Ireland that incorporates a ploughing competition (Shortall 2002). I attended the National Ploughing Championships twice as an exhibitor during my PhD, joining over 1,700 exhibitors and 297,000 visitors (Figure 5.6). As the National Ploughing Championships is geared towards agriculture, this event has allowed me to discuss Ireland’s CWCs with a diverse audience of various backgrounds and ages. As most people do not realise that Ireland has coral reefs, the event fostered positive conversations around Ireland and its surrounding waters. The greatest joy I experienced during National Ploughing Championships was the excitement that people emanated when they learned of Ireland’s coral reef community.

Figure 5.6. (A) At the National Ploughing Championships holding an Irish cold-water coral used for public engagement, and (B) Lego Freddy with two different species of Irish CWCs to engage a younger audience.
In a much different setting from the National Ploughing Championships, Féile na Bealtaine (https://feilenabealtaine.ie) is a music and arts festival held annually in Dingle, Ireland. Although the festival is focused on various types of artistic expression (i.e. music, poetry, theatre), it lends itself as a public engagement opportunity to connect art with science (Stephenson 2018). One of the most popular activities of the festival over the past few years has been a beach fossil walk along Dingle’s coast. The beach fossil walk allowed the audience to peer into the geological history of Dingle, guided by researchers from iCRAG and Ireland’s Fossil Heritage (Figure 5.7). The event was curated by researchers to show that it was deliberate and focused on learning. The walk started with a welcome and brief history of the area, followed by a series of stations displaying various geological features. Instead of a lecture-style talk, enquiry-led learning was used, with participants encouraged to engage in the walk, describe what they recognise in the rock formations, and ask questions throughout the event.

Figure 5.7. (A) iCRAG and Ireland’s Fossil Heritage guides at Féile na Bealtaine, and (B) over 135 attendees at a fossil beach walk led by us during the festival in Dingle, Ireland.
Participants had an opportunity to explore the beach and chat with researchers, allowing for extended conversations about Ireland’s coral reefs and my PhD research. Many participants were impressed at the degree of international researchers that comprised the beach fossil walk leaders. At the end of the afternoon, the event was closed out with a spontaneous original poem about the geology of Dingle, written and performed in Irish by a local participant that also played traditional Irish flute music for everyone (Figure 5.8). This was an important interaction as it allowed the participants to contribute to the event, sharing the connection between art and science and reflecting the strong link between local people and music.

Figure 5.8. Local participant playing traditional Irish flute music for the group to end the beach fossil walk.
Following the beach fossil walk, an anonymous evaluation was given to participants. Feedback was positive and well received from everyone that filled out the evaluations. One of the organisers of Féile na Bealtaine sent an email to iCRAG that stated, “The geology event at Clogher was wonderful - to see geology changes over hundreds of millions of years in a 100 m stretch of beach was astounding. The students sharing their knowledge were outstanding - please pass on our congratulations and appreciation.”

5.4 Character-driven science communication

It is imperative for researchers to identify the proper target audience, especially with Sci Comm (Volkova et al. 2020). As a form of narratives and storytelling, cartoons and characters have been accepted as an important aspect of Sci Comm (Negrete and Lartigue 2004; Volkova et al. 2020; Yankelvich 2016). One form of character-driven narratives in Sci Com is through the use of LEGO®. The LEGO® brand is a globally recognised company that has been around for over 90 years (Zhou 2023). Although the main target audience for LEGO® is children from age 1 to 15 (Volkova et al. 2020), the company uses both traditional and modern marketing strategies to connect with a vast age range. Since the 1980s, LEGO® has established an educational component to involve children and adults in subjects such as science, technology, engineering, and mathematics (STEM), partnering with universities and governmental organisations (Zhou 2023). Stemming from experiential learning, LEGO® SERIOUS PLAY® was launched and workshops are available for businesses, educators, and researchers (Rueda et al. 2014). More recently, LEGO® has utilised social media outlets such as Twitter/X and YouTube to reach audiences of more than 50 million per month (Volkova et al. 2020). Through social networks, they have provided platforms for the public to show their use of LEGO® in individual and creative ways. As a
result of this public engagement, universities and researchers are using LEGO® to engage with people and present their findings in a way that is more relatable (Figure 5.9).

Figure 5.9. Various ways that universities and researchers use LEGO® to connect with a wider audience. (A) Image of LEGO® used for EGU General Assembly advertising in 2021 (with permission from Stacy Phillips), (B) use of LEGO® for advertising a Careers Fair at TCD, and (C) LEGO® mapping from ArcGIS (with permission from John Nelson).
To engage with the public from a scientific perspective, a personalised LEGO® figurine was created to disseminate information on CWC research during my PhD. Lego Freddy became the alter-ego of me as a PhD researcher in the form of character-driven Sci Comm (Figure 5.10).

Figure 5.10. Character-driven Sci Comm through the use of a personalised LEGO® figurine; (A) Lego Freddy conducting SEM analysis in the laboratory for her PhD research, (B) Lego Freddy with her CWC sample at a research conference with Sustainable Development Goal 14 in the background, and (C) holding Lego Freddy at Féile na Bealtaine public engagement beach walk in Dingle, Ireland.

Lego Freddy quickly gained a following through personal social media accounts; upon the request of multiple researchers and friends, an Instagram account was created for Lego Freddy (@LegoFreddyAdventures; Figure 5.11). The focus of this account is to utilise
character-based Sci Comm to share facts about CWCs, give insight as to what a PhD entails, and to connect audiences of various ages to coral research and ocean literacy in a fun and lighthearted manner. Lego Freddy’s Instagram account further provides a creative and unconventional outlet to share CWC information with the public in a way they can relate to.

Figure 5.11. Posts from Lego Freddy’s Instagram account featuring coral sample preparation, behind-the-scenes of 10 Things to Know About filming, and various samples of CWC Desmophyllum dianthus.
5.5 The PORO-CLIM Expedition: A case study

Cruise CE21008 was a 26-day marine geophysical data acquisition survey of the PORcupine and ROckall continental passive margins to investigate the cause of the Palaeocene/Eocene Thermal Maximum (Zachos et al. 2008; Zeebe et al. 2016), a natural CLIMate change event (hence project PORO-CLIM) that is the closest deep-time analogue of anthropogenic environmental change. The PORO-CLIM project was conceived to study interplay between the first-order geological processes of continental rifting and break-up (Jones et al. 2019), Large Igneous Province emplacement (White and McKenzie 1989; Eldholm 1994), and global climate change, providing ship-based training partnered with Sci Comm and public engagement experience for a cohort of international ECRs. Cruise CE21008 also includes a three-year post-cruise data work-up phase.

Cruise CE21008 went ahead with a science party of 13 (Figure 5.12), including approximately half the planned compliment of ECRs due to COVID-19 safety precautions. Beginning on 3 May 2021 after a 14-day pre-cruise isolation period, the science team travelled to the RV Celtic Explorer in Galway, Ireland. Cruise CE21008 ended on 31 May 2021, acquiring two deep seismic profiles and a dataset to further investigate physical oceanographic processes in the Northeast Atlantic Ocean.
Figure 5.12. Scientific research team of the PORO-CLIM Expedition. From left to right: Nicky White, Erica Terese Krueger (me), Niamh Faulkner, Benjamin Couvin, Stephen Jones, John Hopper, Per Trinhammer, Haleh Karbala Ali, Lars Rasmussen, Matthew Allison, Thomas Funck, María Pérez Tadeo, and Sigurd Bøgelund Andersen.

5.5.1 Developing the public engagement programme

The original PORO-CLIM proposal to Eurofleets+ placed significant emphasis on ECR training and involvement. The proposed training was based on a “floating university” model previously used by Eurofleets+ (e.g. Lebedev et al. 2019) and other research expeditions. However, due to a reduced science party to comply with COVID-19 restrictions, the floating university model was redirected as an outreach objective for education and public engagement.

Prior to the start of the PORO-CLIM Expedition, ECRs applied for and went through an interview process to join the scientific crew. The ECRs were selected based on scientific
skills and backgrounds, which were useful in designing the public engagement programme as well as executing necessary scientific tasks for collecting data. These skills ranged from higher education degrees (i.e. geology, marine science, physical oceanography) to prior technology experience (i.e. podcast recording, photography and videography). The ECRs held meetings before the expedition began to discuss expected outreach activities and possible audiences; planning consisted of training and certifications, outlining skill sets and usage of available equipment, expected social media and blog posts, connecting with elementary schools for live streaming from sea, and deciding which factors of the research project to share in real-time. Outreach aspects were planned with specific target audiences in mind (e.g. young adults, scientific community, etc.) and contingency plans were developed to combat the possibility of inclement weather or unstable network connection aboard the ship.

5.5.2 Social media posts

Prior to embarking on cruise CE21008, ECR Matt and I established online accounts in April 2021 for Sci Comm during the PORO-CLIM Expedition; this included a website with project background, science team information and blog entries, and social media accounts on Facebook, Instagram, Twitter/X, and YouTube. As I had the most social media experience at the time, I was tasked with being the social media liaison (Figure 5.13). Duties as the social media liaison included captions and images for all social media posts before, during, and after the cruise, along with proof-reading all blog posts for the website and keeping a log of all Sci Comm activities. Daily posts on Facebook, Instagram, and Twitter/X began during the two-week isolation period prior to disembarking on the RV Celtic Explorer to document COVID-19 isolation measures and familiarise online audiences with PORO-CLIM’s objectives. During the expedition, daily posts covered all aspects of life aboard a
research vessel which ranged from instrument mobilisation and safety drills, bad weather and contingency plan implementation, preliminary data and results, birthday celebrations at sea, and more. A series of blog entries corresponded with social media posts to give an in-depth look at life on board the RV *Celtic Explorer*. Blog entries allowed for an expanded explanation of activities on board such as data collection, deploying and retrieving instrumentation, and contingency plans.

![Figure 5.13. Preparing social media posts and updating the Sci Comm log in the Dry Lab on board the RV *Celtic Explorer*.

5.5.3 *Video Production*

Video production during the PORO-CLIM Expedition was a useful public engagement tool for disseminating background science of the project, instrumentation operation and deployment, life aboard a working research vessel, and a tour of the ship. Due to an unstable network connection whilst at sea, a plan for live streaming with primary school students was unattainable. However, the ECRs implemented a contingency plan to have questions sent in
from various primary schools prior to and during the cruise, answering them via a Question & Answer (Q&A) series (Figure 5.14).

Figure 5.14. Early career researchers Matthew (left) and Niamh (right) recording a Q&A session on safety aboard the RV Celtic Explorer for Bourneville Primary School (Birmingham, UK).

5.5.4 Use of cartoons and character-driven figurines

To better communicate the science behind the PORO-CLIM Expedition to a wider audience, a series of cartoons was illustrated by ECR Matthew (Figure 5.15). These cartoons included research aims, explanations of scientific instrumentation, and marine mammal observations from the Northeast Atlantic.
Figure 5.15. Cartoon illustration by ECR Matthew explaining the diversity of marine mammals and birds observed in the Northeast Atlantic during the PORO-CLIM Expedition.

To further engage with people across all age groups (particularly a younger audience), the ECRs obtained personalised LEGO® figurines for character-driven Sci Comm and public engagement. These “LEGO® Scientists” were used to document all aspects of the PORO-CLIM Expedition (Figure 5.16), from pre-cruise isolation protocols, the first day arriving at the Port of Galway, late night shifts collecting data, the effects of seasickness, enjoying downtime in Bantry Bay, Ireland, when a contingency plan had to be implemented due to inclement weather, and recording a podcast episode.
Figure 5.16. LEGO® Scientists (A) on the dock in the Port of Galway before departing for sea, (B) enjoying downtime in Bantry Bay whilst waiting for a storm to pass, and (C) recording an episode of the iCRAGorama Podcast at sea.

5.5.5 Outcomes of the PORO-CLIM Expedition

During the PORO-CLIM Expedition, the ECRs learned the fundamentals of various subjects by interviewing senior scientists and technicians, and summarising key points in a series of written and visual presentations. The communication-based model proved a more efficient and achievable way of providing ECR training than the originally proposed “floating university”. A considerable impact was achieved through Sci Comm and public engagement from the ECRs. Through 60 social media posts, eight videos, 16 blog entries, and two podcast episodes, the ECRs engaged international audiences including Europe and the United States. Twitter/X analytics displayed over 100,000 engagements during the month of May 2021 when the PORO-CLIM Expedition was at sea (Figure 5.17A). The LEGO®
Scientists series proved to be particularly popular and influenced a later expedition to document their forthcoming cruise with LEGO® figurines (Figure 5.17B).

Figure 5.17. (A) Twitter/X analytics displaying the most popular post featuring LEGO® Scientists during the PORO-CLIM Expedition, with the account reaching over 100,000 impressions and 8,000 profile visits in May 2021, and (B) a future research expedition sharing a LEGO® Scientist post and retweeting a LEGO® Scientist post from PORO-CLIM.

A Q&A series consisting of videos and blog entries allowed for direct engagement with schools in Detroit, Michigan (USA), Dublin (Ireland), and Birmingham (UK). Short videos documenting the expedition were posted to the University of Birmingham's pre-existing social media audience, reaching several thousand views. Due to the overwhelming success of the public engagement programme during PORO-CLIM, a baseline for attainable outreach during a research expedition was set. This has led to discussions with funding agencies (i.e. Eurofleets+) to incorporate a greater emphasis on Sci Comm during future research cruises. Furthermore, difficulties such as unstable network connections were noted, and plans to increase bandwidth aboard the research vessel have been discussed. As a result of this high level of engagement through Sci Comm, PORO-CLIM was anonymously
nominated and selected to be featured in the 2022 MadeAtUni Climate Action campaign (https://madeatuni.org.uk/). Furthermore, public engagement outputs from PORO-CLIM led to invitations for some of the ECRs to sit on Sci Comm panels and present at international research conferences (Figure 5.18). A complete list of all Sci Comm outputs are listed in Appendix C.

Figure 5.18. iCRAG flyer promoting an invited talk at Eurofleets+ Final Conference.

5.6 Discussion

There is an unprecedented need for scientists to be good communicators (Brownell et al. 2013), and the desire to communicate science is lacking (Pham 2016). As mentioned before, formal training for Sci Comm is limited, and many researchers are discouraged from engaging in activities that go beyond the laboratory (Pham 2016). Through Sci Comm and public engagement during my PhD, I have experienced a tremendous impact on the way in which my view of science has shifted. At the beginning of my PhD, I was very nervous to speak in front of an audience. Although I was required to participate in two public engagement events every year for my funding contract, I rapidly learned that this was a
positive challenge; the fear of public speaking has been greatly diminished. As I have developed and improved my Sci Comm skills, I’ve experienced the critical need for understandable explanations of scientific research so the public feel engaged and involved. Science in social media is frequently seen in a negative way, most commonly due to misinformation and misinterpretation of research (Anderson and Huntington 2017); it is imperative to demonstrate positive perspectives in research so that we can advance studies and continue learning. Although public engagement is difficult to measure, there are studies that show the correlations between effective Sci Comm and positive interactions with the public (Garnett 2001; Miller 1983; Schwan et al. 2014).

Technological advances are no longer just for the laboratory. With social media and TV being at the forefront of Sci Comm, disseminating important research has become easier than ever. During my PhD, I participated in multiple public engagement activities and engaged in Sci Comm through various outlets (Appendix D). Through TV, over 113,000 viewers tuned in to watch the 10 Things to Know About episode on CWCs on its original air date; utilising social media to promote the episode was successful, with over 6,000 interactions on just one Twitter/X post alone. The use social media and relevant hashtags on Twitter/X resulted in over 1,000 interactions that ultimately led to a research collaboration on one of my PhD chapters and a peer-reviewed publication (Krueger et al. 2024). Through character-driven Sci Comm, Lego Freddy has gained over 500 interactions on individual social media posts and has influenced other researchers to obtain their own LEGO® to use for Sci Comm. Public engagement interactions have sparked conversations with over 1,000 people through science-based and alternative festivals, aiding in professional development and a better understanding of CWCs in Ireland. The ECR-led Sci Comm for public engagement on the PORO-CLIM Expedition was highly successful; over 100,000 audience
engagements were recorded through social media for the month of May 2021 alone, having an international reach. Given the reduced science party, Sci Comm proved a more achievable and efficient aspect for the ECRs compared to the originally proposed “floating university” programme. Displaying the scientific journey of the PORO-CLIM Expedition through videos, blog posts, podcasts, and social media platforms allowed us to share their daily lives aboard a working research cruise, which gave the public access to behind-the-scenes moments of a research expedition and invited questions and comments from the public that increased learning and ocean literacy.

The culmination of Sci Comm involvement throughout my PhD led to an invitation to present a poster for the iCRAG 8 Year Review in 2023 (Appendix E); this opportunity allowed me to showcase the various aspects that I have been involved in over the past four years, but also how those experiences assisted in professional development and research collaborations. Furthermore, I have exponentially grown my professional development skills in creative ways outside of the general science forum. A culmination of these points above suggest that PhD programmes should require some form of Sci Comm or public engagement into their curricula, whether it be through formal training or hands-on courses and modules.

5.7 Conclusion
Sci Comm amplifies the reach of ocean literacy and research to potentially improve its acceptability and include the public in scientific and technological advances, especially when taking a creative approach through different types of content and addressing audiences of various ages and background. From a research perspective, Sci Comm and public engagement have fostered collaborations and interdisciplinary projects that resulted in publishable research and professional development, and are beneficial for PhD researchers.
From a public perspective, Sci Comm has proven to be an effective tool to educate people with regards to ocean literacy and CWC research, building a positive and trusting relationship between researchers and the public. Sci comm enhances the understanding of the importance of public participation in science; this results in better communication skills, active listening, empathy for the audience, and a different perspective for delivering science to the public. Sufficient involvement in Sci Comm or public engagement should be implemented into PhD curricula to encourage the continuation of positive scientific interactions with the public. There is a need for PhD programmes to implement a certain level of Sci Comm into their curricula, whether it be through training, modules, workshops, or hands-on participation.
CHAPTER 6

Future Work
6.1 Development and description of the Macnas Mounds

Chapter 2 provides an important contribution to our understanding of the spatiotemporal coral mound development off Ireland and complements our knowledge on shelf-edge coral mound provinces in general. This is the first publication to extensively describe and analyse the Macnas Mounds, an area previously considered to be sand dunes. It would be beneficial for future research in the Macnas Mounds to include computed tomography scanning technology and analysis of multiple cores on- and off-mound to add to the extent of what is known about Ireland’s shelf-edge corals and the Northeast Atlantic CWC community as a whole.

6.2 Structural integrity of cold-water coral skeletons

Chapter 3 combines novel methodologies with interdisciplinary collaborators to deliver relatively novel research on the importance of dead CWCs and the implications from climate impacts in the future. Future work includes validation of CWC skeletal structure alterations on a larger scale, possibly with an expanded range of conditions and anthropogenic contaminants (i.e. microplastics). Analyses of changes in quantifiable reprecipitation from increased temperature through specific laboratory experiments and modelling these changes may provide better understanding and a timeframe of how and when these projected impacts might occur.

6.3 Geochemical analysis for palaeoenvironmental reconstruction

Chapter 4 presents preliminary data for CWC geochemical analysis for palaeoenvironmental reconstruction of seawater temperature. Further analysis for this research includes SEM imaging to determine the COC and microstructures of the coral samples, analysing elemental concentrations across the entire geochemical map, and comparing previously collected in
situ seawater temperatures from the same location with the elemental concentrations. It would be beneficial to compare the concentrations of all elements analysed through LA-ICP-MS to determine any other possible couplings (i.e. Li/Mg) as a proxy for temperature and incorporate a machine learning aspect to obtain geochemical data across the entire map.

6.4 Science communication for public engagement and professional development

Chapter 5 highlights the importance of Sci Comm and how it not only connects the public to science, but how it lends itself to research collaborations and professional development. Through Sci Comm in the form of a Twitter/X post featuring #MacnasMounds in the caption, a new collaboration arose, highlighting the focus of my research to others working on the Macnas Mounds. Disseminating coral research through Sci Comm is an accessible entity for the public to learn about Ireland’s CWCs and the implications our actions as humans might have on these environments. Based on the success of published research and professional development from Sci Comm, baseline evidence is provided to propose implementing some form of Sci Comm and public engagement into the PhD curricula. Further analysis is warranted to investigate the addition of formal training and courses/modules as a requirement for postgraduate degrees moving forward.


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APPENDICES
Appendix A – Krueger et al. 2024

Development and physical characteristics of the Irish shelf-edge Macnas Mounds, Porcupine Seabight, NE Atlantic

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Abstract

Modern cold-water corals (CWCs) occur in a wide range of water depths, with Desmophyllum pertusum being one of the most common species. Pleistocene, Holocene, and modern coral mound formation by living CWC reefs have previously been described in the Porcupine Seabight from water depths greater than 700 m in the vicinity of the transitional zone between the Eastern North Atlantic Water and Mediterranean Outflow Water. Here we document occurrence of fossil corals retrieved from two cores at 370 m depth in the Macnas Mounds, a relatively shallow occurrence for mounds on the Irish shelf-edge. Both cores feature D. pertusum restricted to the upper two metres, immediately overlying an erosive surface and a coeval major down-core change in grain size from sand to mud. Radiocarbon dating of coral specimens indicates the CWC mounds initiated 7.82 Cal ky BP. Our study unequivocally documents the existence of Holocene shelf-edge coral mounds in the eastern Porcupine Seabight and highlights the possibility of other occurrences of CWCs in similar settings elsewhere in the northeast Atlantic. Given that no living CWCs were encountered in the study area, we suggest that the area previously experienced more favourable conditions for CWC mound initiation and development along the shelf-edge margin, possibly due to differing conditions in the European Slope Current which flows northward along the continental slope from south of the Porcupine Bank to the Faroe-Shetland Channel.

Keywords Cold-water coral · Desmophyllum pertusum · Radiocarbon dating · Porcupine Seabight · Macnas Mounds

Introduction

Cold-water corals (CWCs) occur globally at all latitudes except the high Arctic regions (Davies et al. 2008; Roberts et al. 2009). Cold-water corals are found in a range of seawater depths, from relatively shallow waters (e.g. 40 m water depth off the coast of Norway; Fosså et al. 2002) down to extremely deep waters (e.g. 4000 m in the Mediterranean; Tsoumis et al. 2010); this range suggests that their distribution is controlled by a combination of factors that include water temperature, food availability, aragonite saturation state, and a strong hydrodynamic regime (Davies and Guinotte 2011; Gómez et al. 2018; Naumann et al. 2015). Some species such as the scleractinian CWC Desmophyllum pertusum (recently synonymized from Lophelia pertusa; Addamo et al. 2016) are capable of constructing aragonitic skeletons that form large coral reefs and mounds (De Mol et al. 2007; Foubert and Henriet 2009; Wheeler et al. 2005), creating biodiversity hotspots that serve as habitat structures for refuge and
nurseries (Turley et al. 2007), as well as feeding grounds for fishes and other organisms (Biber et al. 2014; Costello et al. 2005; Dorschel et al. 2009; Henry and Roberts 2007, 2017; Stöffer et al. 2011). The formation of coral mounds is highly dependent upon environmental conditions and satisfactory sediment supply that allow for steady growth and stabilisation of these framework-forming organisms (Matos et al. 2017; Wang et al. 2021; Wienberg and Titschack 2017). Lateral and vertical advection of phytoplankton and organic carbon along with near-bed currents that enhance food supply are important for the continued function and growth of coral communities (Davies et al. 2009; Maier et al. 2023). Furthermore, sediment input is important for mound development as deposition composes greater than 50% of coral mound material (Titschack et al. 2009). Sediments become baffled by the coral framework and are deposited between the skeletal remains, preventing bioerosion of coral skeletons and hence stabilising the biogenic construction (Huvienne et al. 2009; Titschack et al. 2009; Wienberg and Titschack 2017; Maier et al. 2023). Due to the nature of successive sediment deposition, coral mounds can be used as paleoenviromental archives as they preserve the history of coral growth and decline through the stratigraphic record (Wienberg and Titschack 2017). Along with the importance of CWCs as paleoenviromental archives and ecosystem engineers, the growing knowledge of shelf-edge corals in the northeast Atlantic lends these areas to be considered vulnerable marine ecosystems; management approaches used to protect CWCs include special areas of conservation (SAC) and marine protected areas (MPAs). The Porcupine Seabight (PSB) currently has a few offshore SACs, but stricter regulations need to be set in place to enhance protection of these vulnerable marine habitats (Appah et al. 2022).

The study area of the Macnas Mounds is located along the Irish shelf-edge margin on a west-facing slope between 300 and 500 m water depth, adjacent to the eastern border of the Belgica Mound Province (BMP; Wilson et al. 2007; Wienberg et al. 2010). Although the Macnas Mounds were previous surveyed using remotely operated vehicle (ROV) footage and gravity cores, they were described as small mound-like features of unknown origin composed of sand dunes with coral rubble that were thought to have been covered with live coral colonies at some point (Grehan et al. 2003; Wienberg et al. 2010; Wilson et al. 2007). The aim of this research is to present the first sedimentological description of the Macnas Mounds from two cores, and to temporally constrain coral occurrence within the area. A full description of two cores collected from the mound province is presented along with multibeam mapping and on- and off-mound imaging. Finally, a model of environmental conditions (i.e. shifts in water currents, anthropogenic impacts) that may have influenced the formation of the Macnas Mounds is proposed.

Materials and methods

Cores

Two 11-cm diameter cores were recovered in May 2011 using a 6 m barrel Geo-Vibro Corer 3000+6000 on board the R.V. Celtic Explorer during cruise CE11017, under the Integrated Mapping for the Sustainable Development of Ireland's Marine Resource (INFOMAR) programme (Monneye et al. 2011). Core C074 (51°26'03" N, 11°31'38" W; 556 cm core length) was recovered from 369 m water depth and core C075 (51°26'07" N, 11°31'45" W; 486 cm core length) was recovered from 372 m water depth (Fig. 1). Cores were stored at a refrigerated temperature of 4 °C during the cruise and in the laboratory, cut longitudinally with an electric saw into 1.5 m sections, split in two halves using a core splitter with a wire, and placed back in cold storage for further analysis.

Particle size analysis

Sediment samples were collected from core C074 (n = 14) and C075 (n = 12) for particle size analysis (PSA). The majority of sediment samples were collected from the upper core section containing abundant coral fragments, whereas additional sediment samples were collected from the lower section of the cores where there was a visual change in sediment matrix and a concomitant absence of coral fragments. Sediment samples were collected approximately every 15 cm from the top of the core. The sampling strategy is not intended to represent an equal temporal spread through the core, rather the regular sampling intervals capture a range of representative sediments over the selected time interval of deposition. Sediments were wet sieved using a 2 mm mesh to remove larger shell or coral fragments using standard processes, with a cover on top to prevent sample loss during agitation and a sieve pan underneath to collect fine fraction. Only biogenic shell and skeletal fragments were observed in >2 mm fraction. Sieved sediments were subjected to PSA using a Malvern Mastersizer 2000 at the Institut des Sciences de la Terre de Paris (ISTeP) at Sorbonne Université (Paris, France) and a Malvern Mastersizer 3000 at Trinity College Dublin (Dublin, Ireland). Samples were chemically pretreated with HCl (10%, 15 °C overnight) and H2O2 (30%, 15 °C overnight) prior to analysis to remove calcium carbonate and organic matter (modified from Fentimen et al. 2020). Measured volume distributions were assigned to 100 logarithmically spaced classes ranging from 0.02 μm to 2 mm in diameter. The calculation of statistics was processed using GRADISTAT for logarithmic method of moments from Blott and Pye (2001).
Radiocarbon dating of samples

Radiocarbon ($^14$C) dating of coral skeleton samples from cores C074 ($n = 9$) and C075 ($n = 9$) was performed by both Beta Analytic Radiocarbon Dating Laboratory (Miami, FL, USA) and the $^14$CHRONO Centre at Queen’s University Belfast (Belfast, Northern Ireland). Acid etch pretreatment protocols from both laboratories were used for $^14$C dating (Beta Analytic: https://www.radiocarbon.com/preparation-carbon-dating.htm; $^14$CHRONO: http://14chrono.org/radiocarbon-dating/pre-treatment-analysis/; Burr et al. 1992). Benthic foraminifera were extracted for $^14$C dating from the bottom sections of cores C074 and C075 where no coral fragments were present. Foraminifera from core C074 ($n = 1$) was extracted from around 5.5 m core depth, several meters below the first occurrence of *D. pertusum*, whereas those from core C075 ($n = 2$) were extracted from 215 and 220 cm core depth, corresponding to an important change in particle size and immediately below the first occurrence of the CWC mound. Accelerator mass spectrometry (AMS) $^14$C age determination was performed, and mass fractionation was corrected by measurements of $\delta^{13}$C (relative to PDB standard) by isotope ratio mass spectrometry. All $^14$C dates were calibrated for the Reservoir (R) value using the marine20 dataset (Heaton et al. 2020) for the 10 nearest available modern data points from the sample location ($\Delta R = -185$, error = 45) and the CALIB 8.2 programme (http://calib.org/calib/calib.html; Stuiver et al. 2021). Scanning electron microscopy, X-ray diffraction, and cathodoluminescence results are presented in Mouchi et al. 2014 and Supplementary Information.

Multibeam Echosounder data

Multibeam Echosounder (MBES) data were acquired using a Kongsberg EM302 mounted on the R.V. Celtic Explorer during cruise CE20011 (Lim et al. 2020a). The EM302 was operated at 30 kHz, surveying at a speed of 6 knots. Multibeam Echosounder data were stored as *.gaf and processed using the geocoder algorithm in QPS FMGT to obtain a correct value of backscatter strength.
Seafloor imaging

A series of images were retrieved from the Macnas Mounds during ROV operations on cruise CE20011. During acquisition, the ROV maintained a height of approximately 2 m above the seafloor to achieve a consistent field of view. A series of lights ranging from 250 to 400 watts were attached to the ROV at a fixed angle in order to maintain consistent illumination within the field of view. Remotely operated vehicle positioning data were recorded using a Sonardyne Ranger 2 Ultra Short Baseline (USBL) beacon with an accuracy of 0.2% of the slant range (Lim et al. 2020a).

Results

Core descriptions

In core C074, muddy sediments were observed from the bottom of the core up to 250 cm. Above this, there is a transition to sandy sediments and the presence of *D. pertusum* from 212 cm to the top of the core. Core C075 also documents a clear transition of muddy sediments from the bottom of the core up to roughly 220 cm, topped by sandy sediments and the presence of *D. pertusum*. In both cores (Fig. 2), *D. pertusum* appears above the transition from muddy to sandy parts and prevails throughout the sandy sections of the cores. It should be noted that the transition from muddy to sandy sediments in core C075 is less pronounced when compared to core C074. Based on multiple visible characteristics (e.g., grain size, Munsell colour index, presence/absence of bioclasts, continuity of sediment layers), there was no evidence of reworking in either core from the vibrocoreing process. A full description of both cores, along with MSCL data and core images are available in Supplementary Information.

Particle size analysis

Mean results from PSA for each sediment sample are presented in Table 1 and Fig. 3 for cores C074 and C075. In core C074, two groups of samples are well defined as described above; these groups correspond to the lower muddy section below the coral rubble (mean particle size of 4.32 to 39.52 μm) and the upper sandy sections which correspond to the portion of the cores containing the abundance of coral rubble (mean particle size of 71.45 to 176.2 μm). Core C074 is composed of silt from bottom of core to 310 cm, transitioning to a small section of very fine sand from 250 to 220 cm. Above that is fine sand from 201 cm to the top of the core, with one area of very fine sand at 110 cm. Core C075 is composed of silt from the bottom of the core up to 270 cm. The core transitions to very fine sand from 200 to 55 cm, with fine sand at 40 cm.

Fig. 2 Core descriptions for C074 and C075. Measured radiocarbon ages are indicated for coral fragments (black text) and benthic foraminifera (italics in grey text)
Table 1  Particle size analysis of sediment samples from cores C074 (n=14) and C075 (n=12). The mean grain size (D₉₀) is presented in both μm and logarithmic, with the mean grain size corresponding to the calculated mean fraction using logarithmic method of moments in GRADISTAT (Blot and Pye 2001).

<table>
<thead>
<tr>
<th>Sample</th>
<th>Sample core depth (cm)</th>
<th>D₉₀ (μm)</th>
<th>D₉₀ (φ)</th>
<th>Mean grain size (φ)</th>
<th>Wentworth size classification</th>
</tr>
</thead>
<tbody>
<tr>
<td>C074_040</td>
<td>40</td>
<td>139.8</td>
<td>2.839</td>
<td>3.175</td>
<td>Fine sand</td>
</tr>
<tr>
<td>C074_080</td>
<td>80</td>
<td>135.9</td>
<td>2.880</td>
<td>3.260</td>
<td>Fine sand</td>
</tr>
<tr>
<td>C074_110</td>
<td>110</td>
<td>109.4</td>
<td>3.193</td>
<td>3.916</td>
<td>Very fine sand</td>
</tr>
<tr>
<td>C074_140</td>
<td>140</td>
<td>176.2</td>
<td>2.505</td>
<td>2.572</td>
<td>Fine sand</td>
</tr>
<tr>
<td>C074_160</td>
<td>160</td>
<td>161.6</td>
<td>2.630</td>
<td>3.065</td>
<td>Fine sand</td>
</tr>
<tr>
<td>C074_190</td>
<td>190</td>
<td>139.3</td>
<td>2.844</td>
<td>3.170</td>
<td>Fine sand</td>
</tr>
<tr>
<td>C074_210</td>
<td>210</td>
<td>131.1</td>
<td>2.932</td>
<td>3.287</td>
<td>Fine sand</td>
</tr>
<tr>
<td>C074_220</td>
<td>220</td>
<td>125.5</td>
<td>2.994</td>
<td>3.576</td>
<td>Very fine sand</td>
</tr>
<tr>
<td>C074_250</td>
<td>250</td>
<td>71.45</td>
<td>3.807</td>
<td>4.570</td>
<td>Very fine sand</td>
</tr>
<tr>
<td>C074_310</td>
<td>310</td>
<td>18.73</td>
<td>5.739</td>
<td>6.231</td>
<td>Fine silt</td>
</tr>
<tr>
<td>C074_350</td>
<td>350</td>
<td>39.52</td>
<td>4.661</td>
<td>5.338</td>
<td>Coarse silt</td>
</tr>
<tr>
<td>C074_390</td>
<td>390</td>
<td>12.32</td>
<td>6.343</td>
<td>6.615</td>
<td>Fine silt</td>
</tr>
<tr>
<td>C074_460</td>
<td>460</td>
<td>4.32</td>
<td>7.857</td>
<td>7.867</td>
<td>Very fine silt</td>
</tr>
<tr>
<td>C074_520</td>
<td>520</td>
<td>8.55</td>
<td>6.869</td>
<td>7.151</td>
<td>Fine silt</td>
</tr>
<tr>
<td>C075_040</td>
<td>40</td>
<td>142.3</td>
<td>2.813</td>
<td>3.025</td>
<td>Fine sand</td>
</tr>
<tr>
<td>C075_055</td>
<td>55</td>
<td>88.93</td>
<td>3.491</td>
<td>4.076</td>
<td>Very fine sand</td>
</tr>
<tr>
<td>C075_090</td>
<td>90</td>
<td>95.56</td>
<td>3.387</td>
<td>4.069</td>
<td>Very fine sand</td>
</tr>
<tr>
<td>C075_115</td>
<td>115</td>
<td>104.1</td>
<td>3.264</td>
<td>3.869</td>
<td>Very fine sand</td>
</tr>
<tr>
<td>C075_140</td>
<td>140</td>
<td>114.0</td>
<td>3.133</td>
<td>3.696</td>
<td>Very fine sand</td>
</tr>
<tr>
<td>C075_175</td>
<td>175</td>
<td>88.15</td>
<td>3.260</td>
<td>4.109</td>
<td>Very fine sand</td>
</tr>
<tr>
<td>C075_200</td>
<td>200</td>
<td>94.65</td>
<td>3.401</td>
<td>3.814</td>
<td>Very fine sand</td>
</tr>
<tr>
<td>C075_270</td>
<td>270</td>
<td>6.013</td>
<td>7.378</td>
<td>7.122</td>
<td>Very fine silt</td>
</tr>
<tr>
<td>C075_320</td>
<td>320</td>
<td>7.638</td>
<td>7.033</td>
<td>6.889</td>
<td>Very fine silt</td>
</tr>
<tr>
<td>C075_350</td>
<td>350</td>
<td>14.72</td>
<td>6.086</td>
<td>6.110</td>
<td>Fine silt</td>
</tr>
<tr>
<td>C075_480</td>
<td>480</td>
<td>24.95</td>
<td>5.325</td>
<td>5.665</td>
<td>Medium silt</td>
</tr>
</tbody>
</table>

Channel. A total of 338 km² was mapped by MBES (Fig. 5) from the eastern slope of the PSB. The continental shelf exists at 244 m water depth and slopes at approximately 3 degrees down the eastern slope of the PSB to a depth of 1160 m in the central PSB. To the west, the larger Belgica Mounds exist ranging in length from 850 to 2000 m along their long axis. Along the edge of the continental shelf, approximately 50 of the Macnas Mounds are imaged (Fig. 5B). Although their diameter ranges from 50 to 200 m, they are typically 6 m in height. Likewise, their slope varies from 2 to 10 degrees which is reflected in their morphology where some of the mounds are elongate, while others are conical. Their spatial density is highest near the edge of the continental slope, progressively decreasing with distance towards the continental shelf. Conversely, the mounds with the largest diameter (200 m) occur along the shelf while those with the smallest diameter (50 m) occur closest to the shelf edge.

Seafloor images were retrieved on- and off-mound of the Macnas Mounds (Fig. 6). The surface of the seafloor on a Macnas Mound (348 m depth—51°28’22.774” N, 11°30’32.277” W) is displayed in Fig. 6A; there was no live coral on top of the mound, mainly coral rubble. An image of the adjacent area off-mound of a Macnas Mound (351 m depth—51°28’20.749” N, 11°30’33.712” W) is displayed in Fig. 6B; only a few scattered coral fragments were observed from this area (Lim et al. 2020a).

Discussion

Although shelf-edge mounds in the eastern Atlantic are observed off Norway (Titschack et al. 2015), Scotland (Douarin et al. 2013), and Namibia (Tamborrino et al. 2019), the Macnas Mounds are less frequently observed on the Irish shelf-edge margin. The previous studies have concluded that coral mounds (i.e. BMP and MMP, Huvetten et al. 2003; Huvetten et al. 2007; Hebbeln et al. 2020a; Pen Duick drill, Vandorpe et al. 2014) developed where strong bottom currents precluded sediment deposition around the mounds, creating moat features between established coral mounds (i.e. off-mound areas). It is possible that as current velocity reduced, the parameters needed to sustain these mounds (i.e. nutrient and sediment input) were no longer available. Most data on the Irish Shelf where coral mound provinces are located indicate a dominant current direction towards the north (Lim et al. 2018, 2020b; Summers et al. 2022; White 2007), including the lower Mediterranean Outflow Water (MOW) that flows counterclockwise in the PSB, and continues northward along the continental shelf (De Mol et al. 2005; Van Rooij et al. 2010; Wienberg et al. 2020). It is also noteworthy that the majority of coral mounds off Ireland are located between 500 to 1000 m depth (e.g. White 2007;
Fig. 3  Particle size distributions of sediment samples from cores a C074 ($n = 14$) and b C075 ($n = 12$) in the Macnas Mounds.

White and Dorschel 2010). Although CWCs along Ireland’s shelf-edge are relatively rare, there are documented occurrences in various locations within the eastern boundary of the northeast Atlantic, i.e. Angolan and Namibian continental margins (Gori et al. 2023; Hebbeln et al. 2017, 2020b; Tamborrino et al. 2019); Bay of Biscay (De Mol et al. 2011); Norwegian continental shelf (Mortensen and Lepland 2007; Tischack et al. 2015); and Mingulay Reef Complex off western Scotland (Douarin et al. 2013). Although the MOW is important for coral mound formation in the BMP (Wienberg
<table>
<thead>
<tr>
<th>Sample</th>
<th>Sample core depth (cm)</th>
<th>Conventional $^1^C$ age (ky BP)</th>
<th>$2\sigma$ (95%) Cal ky BP</th>
<th>Median probability age (cal ky BP)</th>
</tr>
</thead>
<tbody>
<tr>
<td>C074_027</td>
<td>27</td>
<td>0.61 (±0.02)</td>
<td>0.14–0.47</td>
<td>0.31</td>
</tr>
<tr>
<td>C074_047</td>
<td>47</td>
<td>1.25 (±0.03)</td>
<td>0.66–0.97</td>
<td>0.82</td>
</tr>
<tr>
<td>C074_067</td>
<td>67</td>
<td>2.36 (±0.02)</td>
<td>1.84–2.25</td>
<td>2.03</td>
</tr>
<tr>
<td>C074_080</td>
<td>80</td>
<td>6.64 (±0.04)</td>
<td>6.94–7.32</td>
<td>7.14</td>
</tr>
<tr>
<td>C074_090</td>
<td>90</td>
<td>4.45 (±0.03)</td>
<td>4.45–4.84</td>
<td>4.67</td>
</tr>
<tr>
<td>C074_117</td>
<td>117</td>
<td>7.11 (±0.03)</td>
<td>7.42–7.74</td>
<td>7.58</td>
</tr>
<tr>
<td>C074_127</td>
<td>127</td>
<td>7.10 (±0.04)</td>
<td>7.41–7.74</td>
<td>7.57</td>
</tr>
<tr>
<td>C074_151</td>
<td>151</td>
<td>4.50 (±0.03)</td>
<td>4.53–4.92</td>
<td>4.74</td>
</tr>
<tr>
<td>C074_174</td>
<td>174</td>
<td>6.70 (±0.03)</td>
<td>7.01–7.37</td>
<td>7.20</td>
</tr>
<tr>
<td>C074_560*</td>
<td>560</td>
<td>16.93 (±0.07)</td>
<td>19.46–26.07</td>
<td>19.75</td>
</tr>
<tr>
<td>C075_010</td>
<td>10</td>
<td>0.67 (±0.03)</td>
<td>0.15–0.47</td>
<td>0.33</td>
</tr>
<tr>
<td>C075_038</td>
<td>38</td>
<td>1.98 (±0.02)</td>
<td>1.40–1.74</td>
<td>1.57</td>
</tr>
<tr>
<td>C075_085</td>
<td>85</td>
<td>7.17 (±0.03)</td>
<td>7.48–7.81</td>
<td>7.64</td>
</tr>
<tr>
<td>C075_100</td>
<td>100</td>
<td>6.90 (±0.03)</td>
<td>7.24–7.55</td>
<td>7.39</td>
</tr>
<tr>
<td>C075_123</td>
<td>123</td>
<td>2.91 (±0.03)</td>
<td>2.51–2.89</td>
<td>2.72</td>
</tr>
<tr>
<td>C075_148</td>
<td>148</td>
<td>4.51 (±0.02)</td>
<td>4.53–4.93</td>
<td>4.74</td>
</tr>
<tr>
<td>C075_150</td>
<td>150</td>
<td>3.25 (±0.03)</td>
<td>2.94–3.34</td>
<td>3.13</td>
</tr>
<tr>
<td>C075_162</td>
<td>162</td>
<td>7.08 (±0.05)</td>
<td>7.40–7.71</td>
<td>7.55</td>
</tr>
<tr>
<td>C075_200</td>
<td>200</td>
<td>7.18 (±0.03)</td>
<td>7.49–7.82</td>
<td>7.65</td>
</tr>
<tr>
<td>C075_215*</td>
<td>215</td>
<td>9.28 (±0.04)</td>
<td>9.90–10.36</td>
<td>10.15</td>
</tr>
<tr>
<td>C075_220*</td>
<td>220</td>
<td>9.31 (±0.05)</td>
<td>9.93–10.40</td>
<td>10.17</td>
</tr>
</tbody>
</table>

et al. 2020), it is located from 700 m water depth, well below the area of the Macnas Mounds. It is unclear how the MOW may affect the initiation and development of the Macnas Mounds, and a more suitable current would be the European Slope Current (ESC), a northward flowing shelf current from the Bay of Biscay to the Faroe-Shetland Channel (McCarthy et al. 2023; Porter et al. 2018; Xu et al. 2015). Density distribution changes have an enhanced effect on the ESC and shelf-edge environment flowing through the Rockall Trough and being deflected onto the shelf (Marsh et al. 2017; Porter et al. 2018). Weakening and warming of the ESC has been documented in the last four decades (Clark et al. 2022). Over longer time periods, variability of the ESC and climatic changes following glacial periods could be linked to basin-scale events that caused the demise of the Macnas Mounds, noting that warmer periods can decrease CWC populations (Frank et al. 2009).

Along with the Macnas Mounds presented in this study, shelf-edge coral occurrences in the northeast Atlantic are early to mid-Holocene in age and located at 500 m water depth or above; D. perutus started growing at the Manas Mounds around 7 ka BP. The age data presented here for corals from cores C074 and C075 are similar in Holocene age to a vibrant growth period documented in the Darwin Mounds (Victorero et al. 2016) that is dominated by the Continental Slope Current. A salinity maximum from 100 to 400 m water depth occurs across the eastern slope of the Porcupine Seabight (Wienberg et al. 2020) where the Macnas Mounds are located; a combination of salinity shifts combined with the ESC could have been favourable for CWC occurrence due to the possibility of enhanced density changes at the boundaries.

Specifically for the two cores described in this study, age inversions could result from slumping, debris flows, or redistribution due to skeletal framework collapse; the smaller-shelf edge Macnas Mounds appear to be related to slumping on the continental slope, locally aligned to sediment slumps. It is noteworthy that neither process would show significant grain-size sorting effects, explaining why the reworking events are only evident from the $^1^C$ dates. Similar age inversions are observed in other Holocene mounds in the northeast Atlantic (e.g. Rockall Bank, Frank et al. 2005; Rockall Trough, Victorero et al. 2016), suggesting skeletal framework collapse via biogenesis or redistribution of coral debris (Frank et al. 2005; Krueger et al. 2023; Victorero et al. 2016). We exclude the influence of the vibrocoring process in relation to the presence of the age reversals, as there is no visible evidence of downcore tracking of coral rubble, marginal clasts, or sediment disruption. We note the coarser silicielastic grain-size distributions within the mound, compared to the underlying hemipelagic sediments. Such a contrast in grain size distribution within the cores may suggest effective baffling on-mound from reduced near-bottom
current velocity (Dorschel et al. 2007; Wang et al. 2021; Wheeler et al. 2011). There is a possibility that the grain-size distributions within the mound are comparable to the grain-size distributions off-mound before and after mound formation, which may indicate a shift in the bottom-water hydrodynamic regime. Strong currents coupled with a low baffling effect likely resulted in bypass of fine sediments during reef aggradation, and the deposition of only coarse sediments. Although we cannot exclude a change in sediment source, we note the observed grain-size distribution within the cores and the elongated geometry of the Macnas Mounds (Wienberg et al. 2010). This is compatible with a combination of sediment waves and subsequent coral mound formation, potentially equivalent to the cigar-shaped reefs of the Trena Deep on the Norwegian shelf (Mortensen and Lepland 2007), and similarly shaped Darwin Mounds in Rockall Trough (Victorero et al. 2016). Using the $^{14}$C ages and core depths, an average mound aggradation rate was calculated to approximately 29 cm ka$^{-1}$. Although this aggradation rate is low for mound formation in general, it falls within aggradation rates observed in other shelf-edge coral provinces in the northeast Atlantic (e.g. 26 to 57 cm ka$^{-1}$ on Rast Reef, Titschack et al. 2015; 20 to 44 cm ka$^{-1}$ on Cabliers Coral Mound Province, Corbera et al. 2021).

Previous multibeam data collected by the Irish National Seabed Survey revealed multiple mound features from the area of Macnas Mounds in the eastern Porcupine Seabight (GOTECH 2002). GOTECH (2002) described the area of roughly 200 km$^2$ as a larger upper region that contained the majority of the mounds, separated from the lower region containing small mound patches by a definitive channel, similar to our findings (Fig. 5). GOTECH (2002) showed consistent coral rubble patterns in the upper region where the cores in this study were recovered from, suggesting that more than 8 km$^2$ of the Macnas Mounds were previously covered in live coral colonies. Between the mounds were rippled sediment and small dropstones. Although there were no visible live coral colonies, the area was observed to be scattered with small coral rubble on-mound with smooth sandy bottoms off-mound, the same as we present in this study in Fig. 6.
Fig. 5 Multibeam Echosounder bathymetric map of the Macnas Mounds showing a the extent of mounds in the region and b a detailed image of the mound locations for cores C074 and C075 described in this study, where you can visualise the long axes of the mounds.

Conclusions

This is the first study to provide $^{14}$C age determination and unequivocal evidence of past coral colonisation at the Macnas Mounds. The constrained radiocarbon age of 7.82 to 0.47 Cal ky BP is the first study to report a Holocene coral mound east of the BMP in an area shallower than 500 m water depth. Occurrence of CWCs from 370 m water depth in the Macnas Mounds is above the Mediterranean Outflow Water in this region (Wienberg et al. 2020), suggesting a change in the European Slope Current over the course of its history. Both cores penetrated through the coral mounds.
to the base, where triggering controls can be inferred. We suggest that the development of the Macnas Mounds is compatible with coral mound formation superimposed on pre-existing sediment waves similar to other Holocene coral provinces in the PSB. Although previous authors (e.g. Frank et al. 2011) have documented climate-driven latitudinal oscillations of the biogeographic limit of coral development, here we highlight that temporally restricted local or regional changes in bathymetric extent of CWGs may occur, and may be linked to both broader interglacial periods (e.g. following the Little Ice Age) and regional or local climate-driven perturbations (e.g. dynamic shifts in the European Slope Current). Finally, the demise of the investigated corals is likely attributed to a shift in hydrodynamics and diminished nutrient supply that was unfavourable for continued coral growth. Further analysis is needed to determine the extent of environmental drivers that impacted past mound growth in the Macnas Mounds and if present environmental conditions are still favourable for CWG growth and

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development, which would aid in sustainable management of the area as an SAC or MPA.

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Data availability The authors declare that the data supporting the findings of this study are available within the paper and its supplementary information files.

Declarations Conflict of interest The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work submitted in this publication.

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References


Core C074 description

Core C074 is 560 cm long (Figure S1.1). From 560 to 541 cm, numerous black spots were observed in a dark grey matrix comprised of clays. At 551 cm, a 1 cm-thick bryozoan-rich layer was noted. From 541 to 416 cm, the matrix is dark greyish brown, and its particulate size gradually coarsens to silt-grade. At 476 cm, a single small gastropod was found. At 465, 450 and 430 cm, other black spots were observed. From 416 to 388 cm, the silty matrix is very dark greyish brown with a small (< 1 cm) gastropod at 406 cm. From 388 to 212 cm, the matrix is dark greyish brown again with occasional black spots, gradually coarsening upwards. From 212 cm to the top, fragments of Desmophyllum pertusum occur within fine sand. The top 3 cm of the core have been reworked due to the entrance of the vibrocore in the sediment; apart from this, there are no obvious signs of reworking throughout the core. Over 80 coral fragments were observed throughout the section, as well as more occasional fossils (bivalves, echinoid spines and eunice tubes). An image from core C074 is provided (Figure S1.2) to visually display no corals migrated during the core cutting process. The top of the core corresponds to modern sediment surface.
Figure S1.1. Full core description for core C074.
Core C075 description

Core C075 is 486 cm long (Figure S1.3). From 486 to 444 cm, the sediment is comprised of dark greyish-brown medium silt with no other components. Occasional black bands of a few mm thickness are observed. From 442 to 366 cm, the mud is dark grey with additional black banding is occasionally observed, and grain size shifts from medium to fine silt. From 366 to 230 cm, the sediment is composed of dark greyish brown silt with no other components; the last occurrence of black banding occurs at 342 cm. From 230 to 210 cm, there is a gradual shift from very fine silt to very fine sand, with the first occurrence of *D. pertusum* occurring at 220 cm and continuing to the top of the core. From 230 to 215 cm, the sediment is dark greyish brown, transitioning to olive grey from 215 to 210 cm. From 210 to 167 cm, *D. pertusum* is very abundant in an olive-grey very fine sand. A calcareous worm tube was observed at 202 cm. A decrease in coral occurrence is noted, as well as occasional worm tubes and echinoid spines. From 167 to 88 cm, the matrix sediment between coral clasts is composed of olive coloured very fine sand with several occurrences of *D. pertusum*. 

Figure S1.2. Image of a section of core C074 to show no visible evidence of coral migration after core cutting.
Occasional worm tubes and other bioclasts are observed. From 88 to 42 cm, the olive grey very fine sand contains many bioclasts (echinoids, bivalves) in addition to *D. pertusum*. From 42 to 38 cm, a narrow band of light olive brown very fine sand is observed, within which *D. pertusum*, bivalves and echinoid spines are found. From 38 to 20 cm, light olive-grey fine sand is observed with *D. pertusum*, echinoid and bivalve clasts in addition to a single occurrence of the cold-water coral *Madrepora oculata*. Finally, the upper 20 cm of the core comprises a light coloured olive-brown fine sand containing *D. pertusum*, bivalve shells and echinoid spines. The top of the core corresponds to modern sediment surface.
Figure S1.3. Full core description for core C075.
Multi-Sensor Core Logger

The multi-sensor core logger (MSCL) for cores C074 (Figure S1.4) and C075 (Figure S1.5) are presented here. The logs represent two units, with the lower part exhibiting generally low values and the upper part showing high values and strong fluctuations in gamma density and P-wave velocity, while it is the opposite for magnetic susceptibility, with stable and high values in the lower part and stable and low values in the upper part of both logs.

The unit separation in core C074 is located around 280 cm. From the bottom of the core, there is a general density increase from 520 to 480 cm, which then decreases. Above that, the muddy section is distinguished in both gamma and P-wave velocity with some variations until it reaches 400 cm where the density and velocity stabilise. Gamma density in the top section of the core is separated at 103 cm, being slightly less dense. The P-wave velocity may show similar trends but is less clear. Magnetic susceptibility displays a gradual decrease from the bottom of the core to 280 cm, and then stabilizes to a very low measurement to the top of the core.
Figure S1.4. Full core description and downcore log of gamma density, P-wave velocity, and magnetic susceptibility for core C074.

The main unit separation in core C075 is located around 230 cm. There is a general stability for all logged parameters from 486 to 345 cm, slightly transitioning to a slow decrease in both gamma and P-waves from 345 to 230 cm. Magnetic susceptibility exhibits a gradual
decrease from 230 to 195 cm, while both gamma and P-waves show strong variations before an abrupt increase above 230 cm. The gamma density shows a slight decrease from 190 to 160 cm. This trend seems to correspond to the localized decrease in *D. pertusum* abundance as recorded in the core between 190 and 165 cm. This temporary decrease is less obviously recorded in the P-wave velocity log, but between 190 and 200 cm the velocity increases noticeably. A strong and brief positive anomaly is recorded in both gamma and P-waves at 108 cm, but no change is noted in the magnetic susceptibility.
Figure S1.5. Full core description and downcore log of gamma density, P-wave velocity, and magnetic susceptibility for core C075.

**Preservation status of coral samples**

Visibly unaltered *D. pertusum* samples were collected from core C075, cleaned with 5% H₂O₂ at room temperature for 12 hours, then rinsed thoroughly with deionized water. Corals
were subsequently cleaned with successive ultrasonic baths in deionized water. Specimens were dried, mounted in epoxy resin and cut longitudinally with a low-speed saw. Observations using scanning electron microscopy (Figure S1.6; Mouchi et al. 2014), cathodoluminescence, and X-ray diffraction (Figure S1.7, S1.8) analyses did not show any sign of recrystallization or alteration in the samples used in this study.

Figure S1.6. Scanning electron microscopy image of coral sample from core C075.

XRD analyses show aragonite and calcite content in a carbonate powder sampled inside the coral wall (Figure S1.7). Here, sample CE11075_125 (Figure S1.7) displays a small peak at the characteristic major calcite angle 29.4° (2θ), which is not the case for sample CE11075_123 (Figure S1.8). Samples presenting this calcite peak were not selected for dating analysis. There was no cathodoluminescence signal, indicating no recrystallization.
Figure S1.7. XRD graphs from coral rubble sample CE11075-125 from core C075.
Figure S1.8. XRD graphs from coral rubble sample CE11075-123 from core C075.
Wanted Dead or Alive: Skeletal Structure Alteration of Cold-Water Coral Desmophyllum pertusum (Lophelia pertusa) from Anthropogenic Stressors

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Abstract: Ocean acidification (OA) has provoked changes in the carbonate saturation state that may alter the formation and structural biomineralisation of calcium carbonate exoskeletons for marine organisms. Bimineral production in organisms such as cold-water corals (CWC) rely on available carbonate in the water column and the ability of the organism to sequester ions from seawater or nutrients for the formation and growth of a skeletal structure. As an important habitat structuring species, it is essential to examine the impact that anthropogenic stressors (i.e., OA and rising seawater temperatures) have on living corals and the structural properties of dead coral skeletons; these are important contributors to the entire reef structure and the stability of CWC mounds. In this study, dead coral skeletons in seawater were exposed to various levels of pCO2 and different temperatures over a 12-month period. Nanoindentation was subsequently conducted to assess the structural properties of coral samples’ elasticity (E) and hardness (H), whereas the amount of dissolution was assessed through scanning electron microscopy. Overall, CWC samples exposed to elevated pCO2 and temperature show changes in properties which leave them more susceptible to breakage and may in turn negatively impact the formation and stability of CWC mound development.

Keywords: biomechanics; biomaterialisation; climate change; cold-water coral; porosity; ocean acidification

1. Introduction

Cold-water corals (CWCs) are a key component of deep-sea ecosystems [1] and are known to occur in most of the world’s oceans except for the Bering Sea and high-latitude Arctic regions [2,3]. Lophelia pertusa, formally renamed to Desmophyllum pertusum [4], is a well-distributed scleractinian CWC found in most cold-water marine ecosystems globally, and is a dominant species in the northeast Atlantic Ocean [2]. Cold-water corals such as D. pertusum require calcium carbonate (CaCO3) to construct an aragonite skeleton. Such corals represent a deep-sea biogenic source useful for reconstructing past geochanical proxies [5] and ocean circulation, and have the potential to serve as important carbon sinks [6,7]. Bimineral production in CWCs relies on the availability of CaCO3 in the water column and the ability to sequester ions from seawater or nutrients to form and grow a skeletal structure [8,9]. Desmophyllum pertusum features thick epithelial and exothecal
skeletal components with a clear lamellar growth pattern [10]. Ocean acidification (OA) has provoked changes in the carbonate saturation state [11,12] that may alter the formation and structural mineralisation of CaCO₃ exoskeletons for marine organisms [8], and this is concerning for both tropical and CWCs [13]. Little is known about how the microstructure of D. pertusum coral skeletons might be altered in such scenarios, but OA has been reported to decrease breaking strength causing the coral skeleton to become more brittle, leading to the disintegration of both live and dead coral skeletons [9,13,14]. If structural integrity of both live and dead corals is compromised due to OA and/or temperature intensification, there is a potential for framework collapse and loss of habitat complexity [9,15].

Framework-forming CWCs such as D. pertusum produce three-dimensional structures that many organisms use as habitat and nursery grounds, making them biodiversity hotspots [16–22]. Cold-water coral colonies are defined in zones (i.e., macrohabitats) that are typically composed of a base of small coral fragments and sediments to large coral rubble, a matrix of sediment-entrained dead coral fragments and branches, followed by a degradation zone [23] of both live and dead coral framework, and an upper layer of about 20 polyp generations of living corals at the top [2,23]. In the dead coral framework, where live corals are sparse, the highest density of associated organisms is found in relation to the reef framework as a whole [23,24]. For example, with reference to North Atlantic CWC provinces, nearly 75% of the CWC colony at the Munglau Reef Complex off western Scotland is composed of dead coral framework [25]. In the Belgica mound province in the Porcupine Seabight off southwest Ireland, coral mounds were reported to yield 349 species; much of the live coral framework and dead coral rubble was densely colonised with macrobenthic biodiversity, including calcareous sponges [26]. Megafauna such as bryozoans and macrouric fauna including bivalves, sponges, and polychaetes utilise the sediment-filled cavities of dead coral framework [23]. Furthermore, reef fishes such as the blackbelly rosefish Helicolenus dactylopterus, lesser-spotted dogfish Sepiophis canicula, and blackmouth catshark Galeus melastomus rely on CWC frameworks for both hunting and spawning grounds, making these reef habitats more valuable as biodiverse ecosystems [23,27].

As an important habitat structuring species [28], it is essential to examine the impact that OA and rising seawater temperatures have not only on living corals but on the structural properties of dead corals that contribute to the formation and stability of CWC carbonate mounds and reefs [9]. Degradation of dead coral framework that is not supported by protective tissue can occur directly through chemical dissolution, or indirectly due to increased bioerosion [29–31]. Such degradation can result in increased skeletal porosity and the possibility of habitat complexity loss [9]. This study aims to determine if the structural integrity of the dead coral framework will be affected by increasing OA and seawater temperatures, and to assess the capacity of the dead coral framework to withstand these anthropogenic stressors.

2. Materials and Methods

Coral samples used here were collected during a Norwegian research expedition aboard the R.V. Helge Mosby from Nakken Reef at a depth of 200–220 m in Norway in 2016 (Figure 1) as part of the “FATE of cold-water corals—drivers of ecosystem change” project funded by the Research Council of Norway. As a follow-on laboratory experiment, this study investigated the impacts of OA and warming on the functioning of CWC ecosystems, including live and dead coral framework, key associated bivalve and sponge species, and changes in nutrient availability to the organisms. The laboratory experiment took place at Austevoll Research Station, Institute of Marine Research, Bergen, Norway, where organisms were observed under various treatments of partial pressure of carbon dioxide (pCO₂) and
temperature over a 12-month period. The general setup of the OA research facility is a flow-to-waste system consisting of circular fiberglass tanks with slightly conical bottom as described in Andersen et al. [32]. Natural seawater with a salinity of ~35 was pumped from 160 m water depth near the station and adjusted in temperature and pCO₂ in overhead tanks (see details of the temperature and pCO₂ control in [32]) before being transferred to the experimental tanks. During the FATE project, the following treatments were applied to 45 experimental tanks in total: control or "ambient" at 400 μatm pCO₂ and seawater temperature of 8 °C, “high CO₂” at 1000 μatm pCO₂ and seawater temperature of 8 °C, and “high CO₂+T” at 1000 μatm pCO₂ and seawater temperature of 11 °C (ambient seabed temperature plus 3 °C increase). In all three temperature and pCO₂ combinations, three different feeding regimes were applied (low, ambient, and high food). For this study, only ambient food replicates, i.e., samples from unfiltered water tanks, were used.

![Map of Norway showing the location of the Nakken reef](image)

**Figure 1.** Nakken reef off the coast of Norway (59°49'49.1" N, 5°33'22" E; red star), a study area where Desmophyllum pertusum samples were collected from a depth of 200–220 m in 2016.

Next, freshly dead coral skeletons free from bioerosion were selected and the soft tissue removed by a 10% diluted bleach solution. Following the 12-month experiment described here, two samples were selected at random from each experimental tank (i.e., ambient, high CO₂, and high CO₂+T) for a total of six samples. Samples were cleaned and checked for integrity, taking note that no degradation due to biological factors was present.
Samples were prepared by cutting coral branches at an aspect ratio as close to 1:1 as possible. As coral branches are not uniform and may be tapered, an ideal geometry cannot be achieved. Samples were individually mounted in epoxy resin (Struers EpoFix Kit) and cured in an oven at 30 °C for 24 h. Once cured, samples were cut using a Buehler IsoMet 1000 Precision Cutter (Lake Bluff, IL, USA) low-speed saw to expose a hollow section on the top surface of the mounts. The exposed surfaces of the mounts were further polished (Struers LaboPol-21 polisher with diamond suspension) to a 1 μm finish (Figure 2a). This process creates a planar and highly polished surface suitable for indentation across the section from the outside surface toward the inner surface. An MTS® Nano Indenter® XP (Eden Prairie, MN, USA) fitted with a diamond tip (Figure 2b) was used to assess coral properties to establish elasticity (i.e., stiffness) using Young’s modulus (E) and coral hardness using Vickers hardness (H). Average E and H values were assessed at a nanoindentation depth range of 2000 nm along the solid white areas of the coral for a single coral fragment (data file available in Supplementary Materials). In this study, we consider elasticity as the ability of the sample to resist deformation and return to its original state when a force being applied is removed, while hardness is the threshold to which the sample would become permanently deformed [9]. Six samples of D. pertusum were analysed with a total of 142 indentations.

![Image](a)

![Image](b)

**Figure 2.** Preparation of coral sample (a) Desmophyllum pertusum set in resin, cut and polished with exposed skeleton prior to nanoindentation, and (b) a prepared coral sample in the mount (red circle) of the MTS Nano Indenter® XP (Dublin, Ireland).

Following nanoindentation, backscatter scanning electron (BSE) images were captured using the Tescan TIGER MIRA3 (Brno-Kohoutovice, Czech Republic) scanning electron microscope (SEM) at the Centre for Microscopy and Analysis at Trinity College Dublin. Prior to imaging, coral samples were carbon coated to avoid excess charged particles. Images were taken at 5 kV with a scanning speed of 6 and were used to detect visual changes in porosity.
A one-way analysis of variance (ANOVA) was run using JMP® Statistical Discovery Software [33] to determine if there were statistically significant differences between samples taken from each of the three experimental tank treatments (i.e., ambient, high CO₂, and high CO₂+T) for E and H [8]. Due to the relatively small sample size, a post hoc Tukey’s honestly significant difference (HSD) was run to determine how the treatments differed from one another by a pairwise comparison and Shapiro–Wilk (W) was run to check for normality. Porosity was obtained by analysing SEM images along the outer coral wall using ImageJ software [34]. Porosity was calculated from the percentage of the outer wall where visible porosity was observed in the binary image as shown in Figure 3 [35].

![Figure 3. Examples of image transformation from (a) scanning electron microscope image to (b) binary image for porosity calculation using ImageJ [34].](image)

3. Results

Both nanoindentation analyses and SEM imaging indicate changes in the structural integrity of the coral skeleton at certain elevated CO₂ and temperature conditions (Table 1).

**Table 1.** Analysis of Young’s Modulus (E) and Vickers Hardness (H) mean and standard deviation of dead *Desmophyllum pertusum* samples exposed to various experimental conditions.

<table>
<thead>
<tr>
<th>Condition</th>
<th>Indentation (n)</th>
<th>E Mean (GPa)</th>
<th>E Std. Dev.</th>
<th>H Mean (GPa)</th>
<th>H Std. Dev.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ambient</td>
<td>45</td>
<td>71.7</td>
<td>2.7</td>
<td>4.4</td>
<td>0.5</td>
</tr>
<tr>
<td>High CO₂</td>
<td>54</td>
<td>66.1</td>
<td>5.9</td>
<td>4.4</td>
<td>0.5</td>
</tr>
<tr>
<td>High CO₂+T</td>
<td>43</td>
<td>71.9</td>
<td>6.1</td>
<td>4.8</td>
<td>0.7</td>
</tr>
</tbody>
</table>

A one-way ANOVA of indentation data showed a statistically significant difference for E (F = 20.328; p < 0.0001). Elasticity (E) significantly decreased (p < 0.0001) in high CO₂ samples, while there was no significant difference between ambient and high CO₂+T
samples (Figure 4a). A significant difference was observed between ambient and high 
CO₂ samples ($p < 0.0001$) and between high CO₂ and high CO₂+T samples ($p < 0.0001$), 
suggesting that CO₂ influences coral elasticity to an extent that caused a structural change in 
the coral, such as increased porosity (Shapiro–Wilk test for normality passed, $p < W = 0.45$).

![Figure 4. Statistical analyses (one-way analysis of variance) of indentation data for Desmophyllum per-
tusum (a) elasticity and (b) hardness from ambient, high CO₂ and high CO₂+T conditions. High 
CO₂ was significantly different for elasticity and high CO₂+T was statistically different for hardness. 
The grey line running across each figure is the mean of the response. Refer to Table 1 for number of 
indentations for each of the three experimental treatments.

A statistically significant difference was analysed for $H$ ($F = 8.988$, $p < 0.0002$); although it 
was less significant when compared to $E$. Hardness ($H$) significantly increased ($p < 0.0001$ 
for ambient; $p < 0.0004$ for high CO₂) in high CO₂+T samples (Figure 4b). There was no 
significant difference between ambient and high CO₂ samples, but a statistical difference 
between ambient and high CO₂+T ($p < 0.0001$) and between high CO₂ and high CO₂+T 
($p < 0.0008$) was observed, suggesting that combined high CO₂+T influences coral hardness 
to an extent (Shapiro–Wilk test for normality passed, $p < W = 0.11$).

The presence of porosity changes along the outer coral wall can have a large effect 
that may lead to the coral bending and twisting as water flows around it; surface defects 
have a strong effect in reducing the strength, especially in a brittle material such as CaCO₃. 
Scanning electron microscopy (SEM) images were used to evaluate the microstructure and 
analyse relative changes in the porosity of the dead coral samples. Visible degradation of 
the outer coral wall (Figure 5) was observed in both coral samples exposed to high CO₂ 
alone. No degradation was observed in SEM images of the ambient samples.
Figure 5. Scanning electron microscopy images for *Desmophyllum pertusum* samples showing visible material alterations of the outer coral walls for (a) ambient, (b) high CO$_2$, and (c) high CO$_2$+T samples. Full coral sample images are on the left and the orange inset boxes display zoomed images on the right. Red arrows represent the area of the outer wall where changes in porosity were calculated.
4. Discussion

Live CWCs are capable of producing calcifying extracellular mucus substances which are considered important in the formation of the thick epithelial skeletal tissue [10]. Once mineralised, the coral skeleton plays an important role in providing a framework for mound formation and stability. From this study, we determined that the structural integrity of the coral skeleton is compromised at certain elevated pCO₂ and seawater temperature conditions. Elasticity significantly decreased in samples exposed to the high CO₂ variable, meaning that with increased CO₂ conditions, the CaCO₂ coral skeleton becomes more brittle. Hardness significantly increased in samples exposed to high CO₂+T, as shown in Figure 4, leading us to postulate that skeletal deformation resulting from increased hardness may occur at a later stage with longer running experiments, or in natural systems. Since we do not see such changes in samples exposed to high CO₂ alone, we suspect that coral hardness is increased with elevated temperatures. Overall, we observe that increasing pCO₂ and temperature caused the partial dissolution of the biomineralised skeleton. At higher temperatures, some of the dissolved material may reprecipitate back into the coral which could explain H increasing with a temperature increase [36,37].

Studies analysing the structural properties of biomineralisation of calcifying organisms are relatively novel, and very few have been conducted on CWCs and bivalves. Hennige et al. [14] conducted an experiment on D. pertusum growth and respiration from the Mingulay Reef Complex to various increased CO₂ levels and temperature conditions over a 12-month period. They did not find significant impacts of OA and warming on respiration or growth but postulated that to some extent D. pertusum can acclimatise physiologically. However, there was a negative correlation between increasing CO₂ levels and breaking strength of roughly 20–30% weakness in areas where coral tissue decreased and left the skeleton exposed. From this, they concluded that the exposed reef bases will become less effective ‘load-bearers’ and will be more susceptible to bioerosion and mechanical damage by the year 2100. In our study, although H is not changed in high CO₂ samples, the decrease in E would support the findings by Hennige et al. [14] regarding reduced structural integrity. Hennige et al. [9] further examined the same coral samples as their earlier study, focusing on the porosity of the coral skeleton. Live D. pertusum displayed no loss in porosity except in areas where tissue loss occurred; yet, dead corals had completely increased skeletal porosity of both the inner and outer walls when exposed to increased CO₂. "Coralporosis", as Hennige et al. [9] refer to in their study, as the loss of skeletal strength and/or density quite similar to osteoporosis in bones could occur from decreased structural integrity, leading to framework foundation loss, and ultimately resulting in large-scale habitat loss or prevention of coral mound growth. Our results are similar to these findings of acidification-induced skeletal porosity along the outer walls of dead corals (Figure 5), and further, they validate the mathematical modelling presented by Hennige et al. [9] for stress due to bending from water flow. Although similar in results, the significant differences we present here from increased pCO₂ and temperature could be explained by the difference in scenarios of the previous studies (i.e., the experimental setup of our study for high CO₂+T was at 1000 μatm at 11 °C versus 750 μatm at 12 °C from Hennige et al. [14].

Wolfram et al. [13] further analysed live coral samples from Hennige et al. [9] with regard to the mechanisms of structural changes under increasing porosity and dissolution underpinning the laboratory experiments with mathematical and computational models. They revealed a compressive strength (462 MPa) and stiffness (45 to 67 GPa) of the skeletal material that is 10 times stronger than concrete. Surprisingly, CWCs seem to retain their skeletal strength despite the loss of stiffness under future ocean conditions. However, their models resulted in a significant increase in coral habitat crumbling from small porosity increases, concluding that OA affects dead coral skeletons through dissolution and porosity, leading to a decrease in thickness of the skeletal wall and ultimately a detriment to the fragility of the exposed coral skeleton [13]. This is further supported by our study showing decreased E (stiffness) and increased porosity under future elevated CO₂ conditions. How-
ever, again, the increased level of H in high CO2+T we present here contrasts the findings of Wolfram et al. [13], which could again be explained by different crystal arrangements in the corals used in our study.

Similar studies on the biomineralisation and material properties of the common blue mussel Mytilus edulis were conducted by Fitzet et al. [8,38]. Fitzet et al. [38] analyzed mussel biomineralisation to determine if there was a present OA threshold or tipping point. Their results showed that shell growth continued with increased pCO2; yet, the microstructure displayed crystallographic disorientation similar to findings in Hennige et al. [14] for the CWC D. pertusum. Following that study, Fitzet et al. [8] analyzed E and H for M. edulis and found that under increased OA conditions, the outer calcite shell was more brittle and the inner aragonite shell was softer and less stiff. This showed that even though calcite is the most stable polymorph of CaCO3 [39], similar results were found in D. pertusum with its aragonite skeleton. However, the significance of the pCO2 impact was reduced in M. edulis when a seawater temperature variable was introduced, leading to the conclusion that there may be a threshold that mussels can withstand. Our study presented here displayed similar results of significant increases in E for elevated pCO2 compared with ambient conditions, as well as a reduced impact with the addition of higher seawater temperature. Thus, projected climate change will likely have an impact on shell structure and properties to some extent, in both calcite and aragonite-calcifying marine organisms.

In addition, bioerosion is found to be accelerated under OA both in tropical and CWC reefs, where a simultaneous increase in temperature did not counteract the impact of acidification [29,31]. Accelerated bioerosion will further lead to the degradation and weakening of coral reef frameworks, which will have implications for the biodiversity of these ecosystems. From our results and similar studies, we can therefore conclude that there is concern regarding skeletal structure integrity, possible framework instability, a reduced load-bearing capacity, and susceptibility to greater than normal bioerosion and mechanical damage for CWC reefs in the future if acidification and seawater temperatures continue to increase in our oceans.

5. Conclusions

The shift from a complex habitat comprised of live and dead corals to a less complex habitat comprised of live corals alone is a major threat to CWC ecosystem biodiversity [9]. As previously stated, dead corals provide a suitable framework for macrohabitats, leading to enhanced metabolic activity, high oxygen consumption, and mineralisation of organic matter [40,41] which is vital to reefs as a whole. A continued decrease in coral skeletal structure will ultimately result in a large-scale habitat loss and prevention of future coral mound growth. Further long-term studies and microscopy imaging would provide useful insight to examine the change in the porosity of dead coral framework. Our results suggest that increased OA and rising seawater temperatures will have an impact on the structural integrity of CWC reefs, especially on the outer walls of dead corals. This study highlights the need to further validate CWC skeletal structure alterations on a larger scale with an expanded range of conditions, along with analyses of possible changes in mineralisation and quantifiable precipitation from increased temperature through specific laboratory experiments. Modelling such changes may provide a better understanding of how and when these projected impacts will occur.

Supplementary Materials: The following supporting information can be downloaded at https://www.mdpi.com/article/10.3390/oceans4010006/s1, Spreadsheet S1.

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Institutional Review Board Statement: Ethical review and approval were given for this study by the Trinity College Dublin School of Natural Sciences Research Ethics Committee on 18 November 2019.

Informed Consent Statement: Not applicable.

Data Availability Statement: The data presented in this study are available in Supplementary Materials.

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Conflicts of Interest: The authors declare no conflict of interest.

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Appendix C – PORO-CLIM Supplementary Information

Science team

The complete list of the PORO-CLIM science team can be found at https://www.poro-clim.org/science-party.

Video supplement

- Quarantine and mobilisation on an expedition (https://youtu.be/rxh5JHTLSuA)
- The science behind the PORO-CLIM expedition (https://youtu.be/T9E4WovRSNw)
- What is an ocean bottom seismometer? (https://youtu.be/0S9RnCXuo_I)
- PORO-CLIM expedition boat tour (https://youtu.be/gKEBZZGkM_w)
- PORO-CLIM geophysical survey (https://youtu.be/kMYaWD5KFwG)
- Highlights from the PORO-CLIM expedition (https://youtu.be/Zgz7ccxeYH4)
- Dry Lab music video (https://youtu.be/ulu5BXz25q8)

Social media accounts

- Blog: https://www.poro-clim.org/blog-1
- Facebook: https://www.facebook.com/PoroClim/
- Instagram: https://www.instagram.com/poroclim/
- Twitter: https://twitter.com/ClimPoro
- Website: https://www.poro-clim.org/

Podcast

iCRAGorama (https://www.icrag-centre.org/news-and-media/podcasts/)

- iCRAGorama at Sea Part 1: The PORO-CLIM Expedition
- iCRAGorama at Sea Part 2: Life Aboard the Celtic Explorer
- iCRAGorama All Stars: Reunited!

Articles

- Eurofleets+ News – “Expedition PORO-CLIM investigating how Earth’s deep interior has affected global climate in the geological past.”
(https://www.eurofleets.eu/2021/06/04/expedition-poro-clim-investigating-how-earths-deep-interior-has-affected-global-climate-in-the-geological-past/)

• MadeAtUni Climate Action campaign – “How UK universities are tackling the climate emergency.” (https://madeatuni.org.uk/)

Presentations

• Faulkner NFSF (2022) How to make Lego friends and influence people. Accepted flash talk: iGEO2022 Early Career Research Symposium.
• Faulkner NFSF (2022) Science communication: Thinking outside the box. Invited panel discussion: SCI:COM.
• Krueger ET (2023) Learner-led science communication from the open sea: The PORO-CLIM Expedition. Invited oral presentation: Eurofleets+ Final Conference.
Appendix D – Education and Public Engagement Activities

• Media appearance, “Oceans and Climate,” 10 Things to Know About Series 9, Episode 5. 11 December 2023. Read here, View here.
• Social media coordinator, Lego Freddy Adventures; 24 September 2023. View here.
• Public engagement, Fiery Forces of Ireland, Culture Night Dublin; Dublin, Ireland; 22 September 2023.
• Public engagement, National Ploughing Championships. 20 – 21 September 2023.
• Judge, iCRAG and SSPC National Crystal Growing Competition, Ireland; August 2023.
• Public engagement, UCD Festival; 10 June 2023.
• Public engagement, “Corals and climate: Even the ocean gets stressed,” Pint of Science Dublin; 24 May 2023.
• Public engagement, Féile na Bealtaine; 28 April – 1 May 2023.
• Vice President, Irish Geological Association; 2023.
• Student Representative, Irish Geological Association; 2023.
• Social media coordinator, Irish Geological Association; October 2022-2023; Facebook, Instagram, Twitter.
• Public engagement, National Ploughing Championships; 19-22 September 2022.
• Podcast guest, iCRAGorama All Stars: Reunited; 21 April 2022; Listen here.
• Feature, “Meet the Scientist,” STEM Matters Magazine Issue 2; October 2021; Read here.
• Writer, “Water Cycle in a Bag” experiment, STEM Matters Magazine Issue 2; October 2021; Read here.
• Podcast guest, iCRAGorama at Sea Part 2: Life Aboard the Celtic Explorer; 23 September 2021; Listen here.
• Podcast guest, iCRAGorama at Sea Part 1: The PORO-CLIM Expedition; 9 September 2021; Listen here.
• Judge, iCRAG and SSPC National Crystal Growing Competition, Ireland; June 2021.
• Social media coordinator and blog editor, The PORO-CLIM Expedition; April 2021 to current; Facebook, Instagram, Twitter, Website.
• Chief editor, The G(e)ossip, newsletter for the Department of Geology; Trinity College Dublin; Read here.
Appendix E – Invited poster presentation for iCRAG 2023 Site Review
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