



Trans-Atlantic Coral Ecosystem Study

SCIENCE PLAN

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i Preface

TRACES is an international initiative bringing Atlantic cold-water coral researchers together for both scientific and pragmatic purposes. There are more coral species in deep, cold waters than in tropical coral reefs. Of the many cold-water corals in the deep sea a few produce large, complex and long-lived habitats for other species. Recent work has shown that the oldest animal in the oceans is a 4000 year old cold-water coral. Corals like this record a uniquely detailed history of seawater conditions in the chemistry of their skeletons - an archive that we now know has captured past periods of rapid climate change. Recent seabed drilling has shown that large coral carbonate mounds in the northeast Atlantic trace their origins back two million years before the present day, making them exciting new storehouses of palaeoceanographic information. But studying cold-water corals is fraught with difficulties and our understanding of basic processes in cold-water coral habitats lags far behind that of shallow coral reefs. Living attached to the seafloor and occasionally releasing larvae into the water column, cold-water corals are intimately related to the geology of the seabed and the physical dynamics of the oceans. So understanding cold-water corals needs expertise across the marine sciences from geologists, hydrographers and biologists. And since cold-water corals are typically found along the continental margins, on offshore banks and seamounts they can only be reached with large sea-going research ships. This means that even the simplest questions about cold-water corals such as ‘What do they eat?’ and ‘When do they reproduce?’ need hugely expensive ships and sampling equipment.

As well as producing a coherent plan to study the cold-water corals of the Atlantic Ocean, TRACES will make the best use of expensive offshore infrastructure. Over the last ten years there have been many individual studies of cold-water corals both in Europe and North America, but these have all had different objectives and used different approaches. These studies also often showed that cold-water coral habitats had been damaged by bottom trawling, prompting marine scientists and conservation organisations to campaign for their protection by outlawing destructive fishing in areas of cold-water corals. But how can managers decide which areas should be protected when we don’t yet know how the coral habitats are related genetically or even how far coral larvae disperse? What stories of past ocean climate and circulation might be locked in the cold-water coral archives? The only way to tackle these issues is by working across the Atlantic; an ocean rich in coral records and where many cold-water coral habitats have already been mapped.

The TRACES project was launched at the American Association for the Advancement of Science’s Annual Conference in February 2008. The launch was quickly followed by meetings on both sides of the Atlantic to prioritise the TRACES research programme. This Science Plan represents the final product of these meetings. It is the collective effort of a large group of marine scientists interested in cold-water corals, the habitats they form and the palaeoceanographic archives they provide from an interdisciplinary, international perspective.

www.lophelia.org/traces

ii Acknowledgements

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i Executive summary

Concept

We are currently witnessing exponential growth in cold-water coral research. Recent discoveries have revealed cold-water corals as significant structural habitats in deep continental margin, seamount and mid-ocean ridge settings. They produce long-lasting reef and mound structures with individual skeletons



providing a uniquely effective palaeoceanographic archive. However, no programme of research has attempted to study connectivity, ecology, biodiversity and palaeoceanographic archives of cold-water corals at ocean basin scales. A programme of this size is only possible through interdisciplinary, international collaboration. The TRACES Science Plan sets

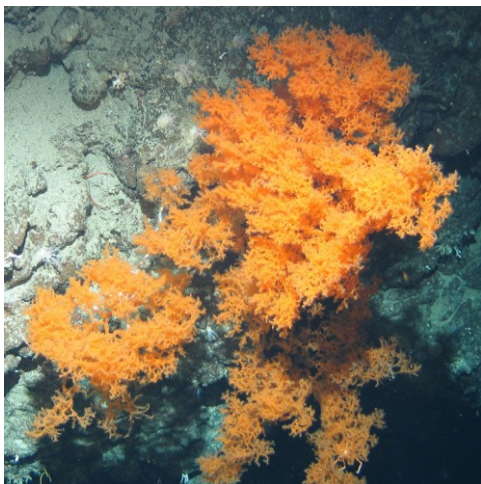
out topics and outlines a structure for an innovative and ambitious programme relevant to European and North American marine scientists and managers. TRACES is organised under four broad thematic areas: ecosystem, climate records, environment and policy. Projects relating to ecosystem research would encompass studies of linkage and connectivity of cold-water coral populations, particularly relevant as resource managers design marine protected areas for long-term habitat conservation. Other ecosystem studies would develop this research to include projects on the biology of the corals themselves and the biodiversity of the communities they support. Projects under the climate records theme would capitalise on cold-water coral carbonate as an intermediate water mass archive from which proxies are now available for several key oceanographic parameters. By understanding how cold-water coral habitats have waxed and waned during previous climate

change events we can better predict their response to ocean warming and acidification. Alongside these research priorities are topics relevant to all aspects of TRACES research including habitat mapping, the hydrographic environment and the policy regime in which cold-water coral habitats are conserved. Alongside these primary objectives, TRACES fosters a strong network of trans-Atlantic interdisciplinary marine science with training and mobility of researchers at its core.



Background

The last ten years have seen great advances in our understanding of cold-water corals as significant ecological engineers on the continental shelf, offshore banks, seamounts and canyons. Stony scleractinian cold-water corals can develop large deep-water reef frameworks providing complex three-



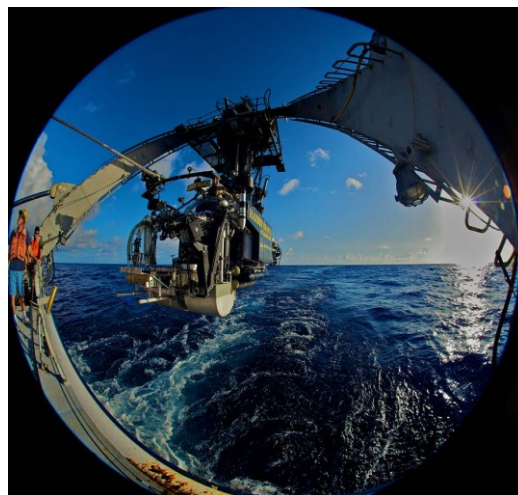
dimensional habitat for a spectacularly diverse associated fauna. Other groups of corals, such as gorgonians and black (antipatharian) corals also provide long-lasting habitat, notably on seamounts and mid-ocean ridges. Indeed, recent dating studies show that a cold-water antipatharian coral from the Hawaiian Seamounts is the oldest marine animal, and probably the oldest animal, on Earth. But cold-water corals are not only a biological or ecological curiosity. They develop deep-sea reefs and giant coral carbonate mounds that trace their origins back to the Pliocene

2.7 MYA. Their long-lasting skeletons give a new archive of intermediate water mass history providing records of the variability of important ocean properties during past periods of climate change.

Scientific studies of cold-water corals are increasing exponentially around the world. There is now a clear international agreement that to address 'big picture' questions of habitat connectivity, biodiversity, biogeography and palaeoceanography this work needs to expand to the scale of an ocean basin. As well as offering purely scientific benefits, international co-operation in deep-sea science dramatically drives down the costs associated with offshore research activities, offering substantial savings to individual funding agencies or national programmes.

Rationale

Until now, research into cold-water coral ecology and palaeoceanography has in large part been restricted to exclusive economic zones with funding from either national agencies or at the European level through the European Commission framework programmes. Research has also typically been driven by individual disciplines with ecological work focused on describing the diversity of life in these complex habitats and geochemical work focused on developing accurate dating techniques and novel environmental proxies from coral carbonate. There is now a clear scientific community consensus that to advance our understanding of coral ecology and realise the full potential of their palaeoceanographic archives we need



to work in a unified, interdisciplinary manner at the scale of an ocean basin. This consensus was thoroughly explored in 2008 through the development of TRACES, the Trans-Atlantic Coral Ecosystem Study. The TRACES initiative was launched in February 2008 and was followed by two scientific workshops in Wilmington NC (USA) and Faro (Portugal). These workshops attracted 85 participants from 14 countries who collectively discussed and prioritised the overall TRACES research agenda. Following these two workshops this TRACES Science Plan was prepared by a writing team where both European and North American researchers prepared each chapter. The writing team met at a Science Plan workshop (Woods Hole MA, USA) and both the TRACES Science Plan and reports from the earlier workshops are available online (www.lophelia.org/traces).

The ideas behind the TRACES basin-scale research programme will also attract the wider marine science community, including many who have not previously worked with cold-water corals. For example, in terms of ocean climate studies, records of palaeoproductivity and ocean circulation represent vital contributions to our basic understanding of the drivers of deep-sea biota at ecological timescales. Particularly exciting opportunities exist to use geochemical tracers occurring in both deep-sea sediments and coral habitats. These habitats are rich in associated species and dynamic in terms of local sedimentary regimes. Recent research shows that over the last 200,000 years, cold-water corals thrived in certain periods but were absent during others, often correlating with periods of past rapid climate change. As such they offer tremendous potential for broad, interdisciplinary deep-sea research and TRACES sets out the framework for a unique new collaboration between palaeoceanography and deep-sea ecology.



A TRACES programme is feasible now for a number of reasons: (1) baseline habitat mapping provides a database of target sites across the Atlantic basin, itself a global centre of cold-water coral records; (2) genetic markers (notably microsatellites) have recently been developed for a number of cold-water corals, allowing issues such as their genetic connectivity and clonality to be examined; (3) exciting geochemical advances have now produced coral skeletal proxies for several parameters including ocean ventilation history, seawater temperature, seawater provenance, nutrient status and even pollution history; (4) the seagoing infrastructure (e.g. remotely operated and autonomous underwater vehicles, coring and observation tools) and expertise available in European research groups have greatly expanded over the last decade. Understanding deep-water, suspension-feeding systems, such as those formed by cold-water corals, requires integrated interdisciplinary

research involving marine biologists, chemists, geologists and physicists. Developing appropriate tools for their long-term conservation not only requires understanding their ecological connectivity but also the policy context in which conservation strategies can further develop. Here social scientists and those working at the interface of science and policy are needed. TRACES is an ambitious programme designed to bring together European and American research groups to conduct internationally excellent deep-sea science.

TRACES

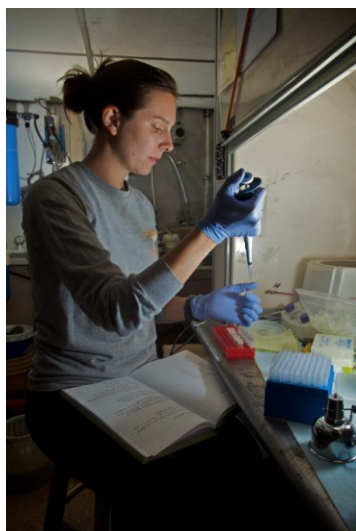
We envisage the TRACES programme as organised in a hierarchical scheme where research issues and overarching issues are grouped into four broad thematic areas. Overarching issues are those that will relate to several research projects. These are summarised briefly below with full detail provided in the individual sections of this Science Plan.

Ecosystem research: Linkages & connectivity

Cold-water coral habitats provide a fascinating natural laboratory to study genetic relationships between spatially separated marine populations. Sessile benthic marine species such as corals may be genetically connected (i.e. exchanging genetic material) by larval dispersal. Understanding how one coral habitat is (or is not) genetically related to others is vital to understand



ecosystem dynamics in space and time and to design ecologically coherent marine protected areas. If there is limited exchange between sites, one may predict that the populations present would evolve in isolation, lowering regional diversity and enhancing local endemism. Such populations would be vulnerable since the chances of recruitment from external populations are very low. The TRACES programme would expand upon the concept of the 'metapopulation' as it relates to cold-water coral habitats at a series of spatial scales across the Atlantic Ocean. This would allow investigations into which populations are sources or sinks of propagules and to examine how populations may recover from disturbance.



Priority research questions focus on identifying patterns of connectivity, and assessing the variety of linkages and factors influencing or controlling the connectivity of coral populations and their associated fauna over time. Hydrographic conditions may cause strong, steady or fluctuating ocean currents at various levels in the water column; these currents may promote or impede the dispersal of organisms from one place to another. Seafloor geological features may provide stepping stones for fauna to disperse, but actual

connectivity will depend on interactions with local hydrography and life history characteristics. Scales of larval dispersal remain unknown for most cold-water coral species and assemblages. Studies should be conducted both within patches (or habitats) and between patches (or habitats) across the Atlantic Basin. Finally, recent evidence from molecular phylogenetic studies has indicated that the evolution of some coral groups has involved exchanges between shallow-water and deep-sea ecosystems. Such processes are an essential context to understand patterns in cold-water coral community biodiversity and biogeography.

Ecosystem research: Biodiversity & biogeography

Cold-water corals are among the most three dimensionally complex structural habitats in the deep sea. As such they provide a great variety of physical niches and support many species (alpha diversity). In turn the variety and spatial patchiness associated with cold-water coral habitats creates significant variation in species between habitats, promoting high beta (or species turnover) diversity. Finally, regional lists of species reported from cold-water coral habitats show they also are associated with high gamma diversity. However, while they clearly form biodiversity ‘hotspots’, our understanding of spatial biodiversity and biogeographic patterns in cold-water coral habitats remains poorly developed. This is largely because studies to date cannot be compared because of variable sample collection protocols (e.g. trawl, submersible, box corer) and inconsistent taxonomic resolution (differing expertise between research groups leading to biases in the species subsequently identified).



TRACES sets out an ambitious study to examine biodiversity and biogeographic patterns. This should entail standardised field sampling both on and off scleractinian reef frameworks across the Atlantic from northern Norway to the US South Atlantic Bight. Carefully controlled sub-sampling for genetic and palaeoceanographic material can support other TRACES objectives. Standardised ROV and submersible visual surveys and selected sampling could be additional approaches to characterise wider habitat variability and to sample species associated with long-lived gorgonian and antipatharian coral colonies. Analytical consistency and co-ordinated use of international taxonomic experts organised through TRACES networking activities would

reveal new species and revisions to existing species descriptions. TRACES would complement and add to previous large-scale biodiversity initiatives, such as the Census of Marine Life, by targeting biodiverse cold-water coral habitats likely to contain many undescribed species.

Ecosystem research: Coral biology

Information on critical aspects of cold-water coral biology, such as respiratory physiology, trophic ecology, growth patterns and reproductive strategies,

have only begun to become available in recent years but remain restricted to very few species. This aspect of TRACES has clear relevance to the projects investigating linkages and connectivity since understanding reproductive and larval biology is central to understanding population connectivity. But in addition, a better appreciation of coral growth and calcification is needed to understand the ‘vital effects’ so clear in many attempts to derive proxies of past seawater temperature and other parameters from coral carbonate. Such vital effects manifest themselves in, for example, the strong correlation between stable carbon and oxygen isotopes in azooxanthellate scleractinian coral skeletons. While early studies struggled to derive palaeoceanographic information in the face of these vital effects, a large and growing body of work is showing greater success, see below. Furthermore, lack of physiological data limits our ability to understand cold-water coral responses to ocean warming and acidification, both causes of great current concern.



TRACES will support investigation of the reproduction, feeding ecology, growth and ecophysiology of major habitat-forming cold-water corals. It will capitalise on recent advances in maintaining cold-water corals under controlled laboratory conditions allowing studies of coral response to predicted scenarios of ocean warming and acidification. It aims to co-ordinate and control experimental studies so physiological and growth parameters will be normalised in a consistent manner allowing the results from separate studies to be compared and fed into broader models examining the flux of carbon and nitrogen under simulated field situations (informed by results being generated by studies related to the topic ‘Oceanography & food supply’). Studies of live coral maintained in flume conditions would allow the first detailed observations of feeding and response to controlled sediment exposure. Finally, repeatedly sampling field sites where year-round access is achievable can provide new insights regarding reproductive periodicity in a seasonal context.

Climate records research

The TRACES palaeoceanographic projects would set out to cover two main timescales with dual aims: (1) to understand the role of ocean circulation in a changing Earth climate system and (2) to examine these effects on cold-water coral habitats and biodiversity. Investigations of the recent past (millennia) coupled with instrumental records can provide a clearer picture of anthropogenic changes to ocean chemistry and circulation. Records of the past 25,000 years and beyond can provide unique information on ocean circulation in what is now known to be a strongly disturbed and dynamic climate system. It has now become well established that during glacial

periods the volume of southern source waters in the Atlantic increases while northern source waters shoal and are volumetrically less important. Instrument-based records have suggested that key Atlantic circulation patterns, such as the Meridional Overturning Circulation, may have slowed by 30% since 1992, but such interpretations are based on a few snapshots of available data since 1957. TRACES climate records research projects would contribute to the following major issues:

- Links between global climate and the rate of ocean circulation
- Links between past changes in ocean circulation and coral vitality
- Recent and long-term history of carbon cycle and ocean acidification
- Deep-ocean productivity, nutrient cycling and trophic changes

TRACES would exploit the significance of cold-water corals as recorders of intermediate water mass history: their ubiquity, high temporal resolution (unaffected by bioturbation), long-life spans and suitability for parallel U/Th and ^{14}C dating. Further studies would capitalise on the wide geographic sampling planned during TRACES to run proxy calibration exercises (e.g. to test temperature proxies across latitudinal transects, to calibrate nutrient proxies, and to refine proxies for past ocean ventilation, intrinsically linked to past atmospheric CO_2 levels).

Overarching issues: Mapping & habitats

High quality mapping and habitat characterisation should underpin all TRACES studies and take advantage of the survey and processing improvements made in recent years. Existing relevant regional data (e.g. sidescan sonar, multibeam bathymetry and backscatter) would be amassed using Geographic Information System software. Key areas currently unmapped would be surveyed at sea and ground-truthed using appropriate visual and sampling techniques. TRACES will produce one of the largest integrated deep-water habitat mapping efforts and will greatly assist standardisation and habitat categorisation by working closely with existing schemes and government agencies on both sides of the Atlantic. In addition to refining existing and developing new habitat maps, TRACES could also incorporate the emerging science of predictive habitat mapping using approaches such as Ecological Niche Factor Analysis and Maximum Entropy to predict geographical areas likely to support cold-water corals. Furthermore, dating fossil corals found during mapping surveys will enable researchers to produce ‘habitat maps’ of corals for the past, which in turn can be linked to ecological niches required for coral growth (i.e. for particular time periods or climatic and oceanographic conditions).



Overarching issues: Oceanography & food supply

Understanding the hydrographical context of cold-water coral habitats is vital to study food supply mechanisms, near-bed sediment flux, larval transport and the distribution of species across habitats. The importance of these issues places physical oceanography as a key overarching theme of TRACES. The programme aims to support studies addressing both local-scale physical characterisation of study sites, for instance by using benthic landers and moorings to deploy ADCP and single-point current meters alongside interpretation of larger-scale boundary currents, density horizons and internal wave dynamics. In addition, video-deployed lander systems can allow precise instrument positioning in complex coral habitats. Food sources could be examined using stable isotope and lipid biomarkers of collected coral fauna with parallel analysis of locally collected prey (e.g. net-collected zooplankton, sediment traps and seabed-pumped bottom water samples).

Overarching issues: Policy

The policy regime in which marine conservation measures are developed is complex and evolving. TRACES will contribute to the review and compilation of relevant information of maritime policy at national, European and international (High Seas) levels. The policy work should ensure clear two-way communication between the pure science projects and the policy-maker end users. Several social scientists are members of the TRACES community and their research could focus upon regional governance case studies to critically evaluate the process of conservation policy development for cold-water corals and deep-sea habitats in general.

Programme relevance, relation to on-going activities and other issues

Deep-sea science is a costly, interdisciplinary undertaking most effectively conducted by international collaboration. The trans-Atlantic vision of the TRACES programme relies upon collaborative research between American and European investigators. Several members of the TRACES community are already engaged in relevant research supported through European Science Foundation's EuroMARC scheme and the on-going development of TRACES forms a component of the European Commission's HERMIONE project. There are strong synergies to aspects of existing research in Canada, Europe and the USA but TRACES is carefully designed to complement and not duplicate these efforts. It is focused on distinct ecological and palaeoceanographic questions that can only be addressed at a trans-Atlantic scale.



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1 Introduction

Cold-water corals, also called ‘deep-sea corals’, have been known for hundreds if not thousands of years. Indeed, worldwide the majority of coral species are found in water >50 m deep (Cairns 2007; Roberts *et al.* 2009). The skeletons of long-lived precious octocorals such as *Corallium* have been used to make jewellery since Antiquity and the earliest trawl fishers often reported cold-water corals in their nets. However, it is only in the last ten years as improved seabed mapping technologies have been applied to wider areas that we have begun to appreciate the true extent and scale of cold-water coral habitats. This has led to a dramatic increase in research output (Fig. 1.1) showing that cold-water coral habitats are locally rich in biodiversity and an important new archive of past ocean climate history. But in many instances modern scientific surveys have not only revealed previously unknown coral habitats but that these habitats have been damaged by deep-water trawling. This has prompted significant conservation efforts both nationally and internationally through the United Nations to protect ‘vulnerable marine ecosystems’, including cold-water corals from further damage.

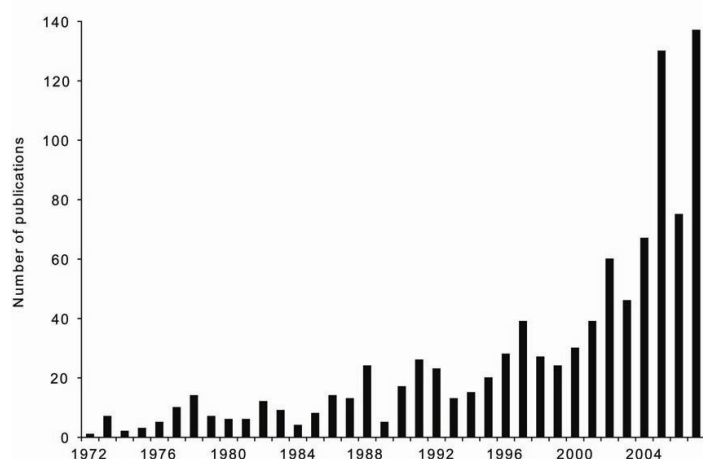


Figure 1.1 The number of research papers referring to ‘cold-water coral’ or ‘deep-sea coral’ between 1972 and 2007. This greatly increased research activity is a major reason why the TRACES programme is now both scientifically necessary and practically feasible. Figure from Roberts *et al.* (2009).

‘Corals’ are a varied group of animals from several taxa. While many species are single individuals (the solitary corals) others form complex, branching colonies supported by a common skeleton - these skeletons form some of the most structurally complex deep-sea habitats known. A few species of scleractinian stony corals form three-dimensional skeletal frameworks that, over hundreds to thousands of years, may accumulate to form deep-water biogenic reefs (Roberts *et al.* 2006).

This document presents a Science Plan for the Trans-Atlantic Coral Ecosystem Study ‘TRACES’ outlining priorities for cold-water coral research in the Atlantic Ocean from 2010 to 2020. The Atlantic is a natural focus for this first attempt to study cold-water corals at the scale of an ocean basin for several reasons:

- There are more cold-water coral records from the Atlantic than any ocean basin (Fig. 1.2). These scleractinian reef framework-forming

species themselves provide structural habitat for many other coral taxa and a very high regional biodiversity.

- Many coral sites have been mapped allowing sampling strategies comparing sites across to basin to be developed and standardised
- Atlantic cold-water corals have already provided palaeoceanographic information on past water temperature and ocean ventilation history, but no study has yet unified this work across the basin
- Several initiatives are currently being developed to conserve Atlantic coral habitats both in national waters and on the High Seas, leading to growing policy needs to understand how these habitats are connected genetically.

As sessile, habitat-forming species, reliant on water currents to supply food and disperse larvae corals fall at a natural confluence of biology, geology and oceanography. At its core, TRACES is a collaborative, interdisciplinary effort designed to span the Atlantic, crossing national and scientific boundaries so the scientific community can tackle major ecological and palaeoceanographic questions.

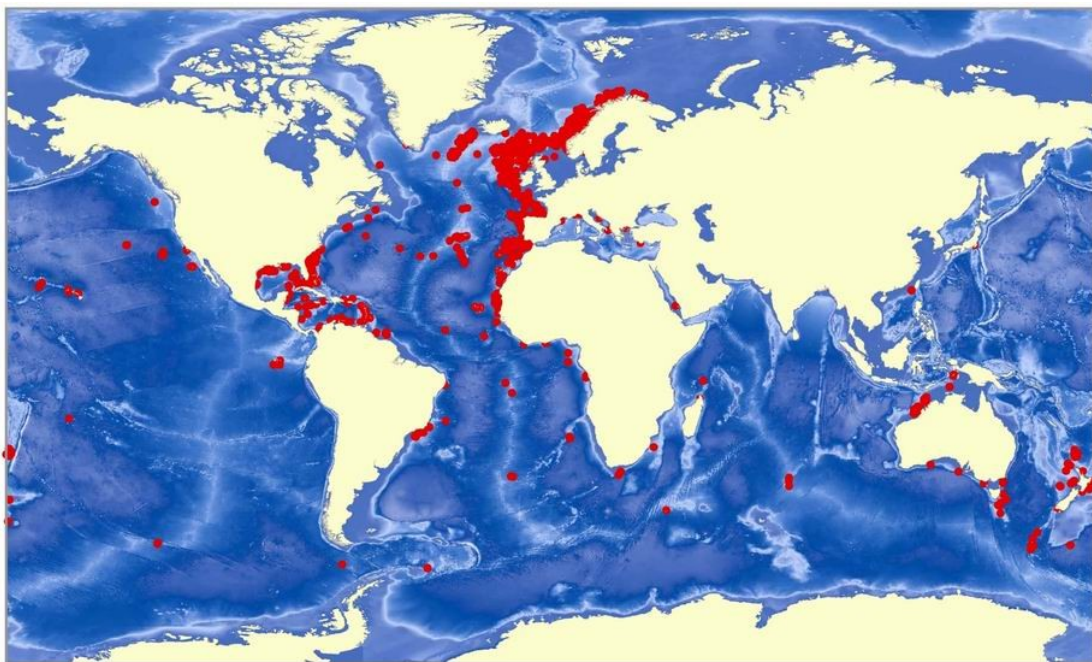


Figure 1.2 The global distribution of reef framework-forming cold-water corals showing concentration of records in the Atlantic Ocean. Figure from Roberts *et al.* (2006).

1.1 TRACES structure

The TRACES programme is organised into two research issues, ‘Ecosystem’ and ‘Climate records’, and several overarching themes that relate to both the research issues (Fig. 1.3). Our philosophy is to answer questions relating to the Ecosystem and Climate records themes in a co-ordinated, standardised manner using the best-available technologies and measurement approaches from deep-submergence vehicles at sea to advanced analytical equipment in the laboratory.

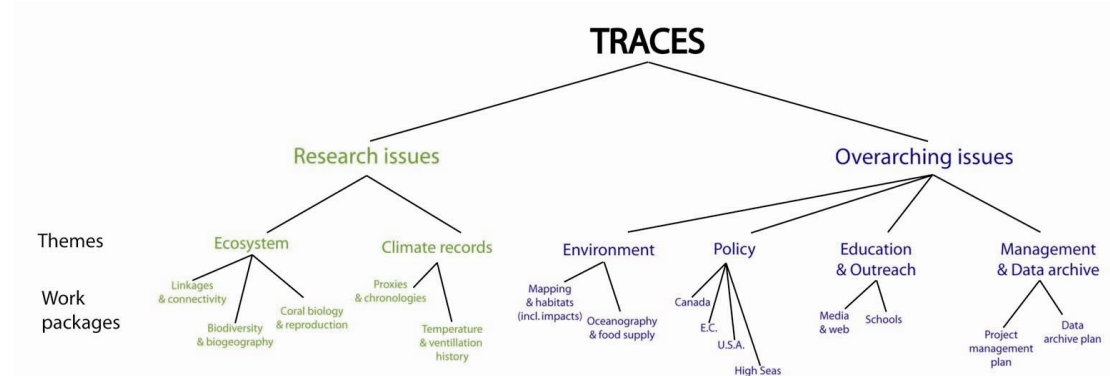


Figure 1.3 Organisational structure of the TRACES programme.

The issues described in the Science Plan were developed by consensus at two international workshops in early 2008. The North American workshop was held in Wilmington NC, USA (28-29 February) and the subsequent European workshop was held in Faro, Portugal (29-30 March). At each meeting delegates came up with a wide range of research questions organised by workpackage:

- A. Linkages & connectivity
- B. Biodiversity & biogeography
- C. Coral biology & reproduction
- D. Climate records (combining all palaeoceanographic aspects).

Each group was asked to identify three priority research questions listing for each: (1) Key geographic sites and (2) Methods & standardisation issues. Suggested criteria to help prioritise research questions were:

- Scientific merit
- Trans-Atlantic relevance
- Policy relevance
- Feasibility

Reports from these workshops can be downloaded from the project website (www.lophelia.org/traces). These reports list all the research topics suggested and summarise the discussion and prioritisation that followed. The following sections summarise these questions and outline plans to tackle them in a co-ordinated trans-Atlantic context. We also consider critical methodological and standardisation issues that must be addressed to allow trans-Atlantic comparisons. The TRACES programme will facilitate standardisation from the geochemical standards applied to palaeo-proxy analysis through to the sampling, processing and taxonomic identification of benthic biota.

2 Ecosystem Research

2.1 Linkages and connectivity

North American workshop priority questions

1. What are the spatial and temporal scales and patterns of connectivity?
 - Within populations (e.g. relatedness among individuals of a cold-water coral species at a site, such as a seamount, bioherm, bank, etc., including degree of sexual vs. asexual reproduction)
 - Between populations (e.g. what is the degree of differentiation between populations of cold-water coral species, larval source vs. sink dynamics, etc.)
 - Across regions (e.g. decreased connectivity across known oceanographic boundaries?)
2. What are the natural processes that control connectivity in Atlantic coral ecosystems?
3. How do anthropogenic influences affect connectivity?

European workshop priority questions

1. How does dispersal of cold-water corals and associated species influence deep water community structure at a range of geographic scales? Sub-questions:
 - Is genetic structure driven by large-scale biophysical coupling or by regional- to local-scale hydrodynamics?
 - What is the role of life history in structuring processes?
 - How does the genetic structure of populations influence resilience to human impact?
 - How will climate change affect larval dispersal?
2. What historical events have influenced the structure of coral communities?
 - On human timescales
 - For the last 1 million years
 - On longer timescales

2.1.1 Introduction

In ecology, connectivity refers to the exchange of genes among geographically-separated populations (Cowen *et al.* 2007). For benthic marine organisms, connectivity is achieved during the dispersive phase from reproduction to settlement. Connectivity is a primary factor in determining community structure, species cohesion and population persistence (Cowen *et al.* 2006). Understanding connectivity is therefore critical for the management of coral habitats, especially through the establishment of spatial conservation measures such as those recently proposed by regional management organisations in the North Atlantic (e.g. OSPAR and NEAFC).

Populations and communities are sustained by recruitment from locally-produced propagules or dispersal from more distant sites. The basic patterns of faunal dispersal among coral habitats are key unknowns to understanding the processes that structure both the diversity and biogeography of coral species and their assemblages. Demographic and genetic connectivity mediate the recovery of vulnerable ecosystems and resources. Knowledge of levels of connectivity among habitat patches is therefore critical to our understanding of how communities develop and are sustained. Without dispersal between sites, populations and communities evolve in isolation, which could lower regional diversity, enhance local endemism, and reduce their potential to recover from damage. Connectivity among cold-water coral populations results from both the passive transport of propagules and the active movement of older, motile species. These transport mechanisms are affected by biological and physical processes that operate at various spatial and temporal scales; biological interactions and linkages among coral hosts and their associates may further influence connectivity (Fig 2.1). For example, some coral and epifaunal species form apparently close associations with high specificity, such as the symbioses between gorgonians and ophiuroids on seamounts. On an ecological timescale, the successful recruitment of coral associates into a community may then depend on the prior establishment and growth of certain coral species. On an evolutionary timescale, these associations provide an untested ‘model’ system in which to address co-evolutionary processes in deep-water marine systems. We identify below priority research questions in the area of Linkage & Connectivity.

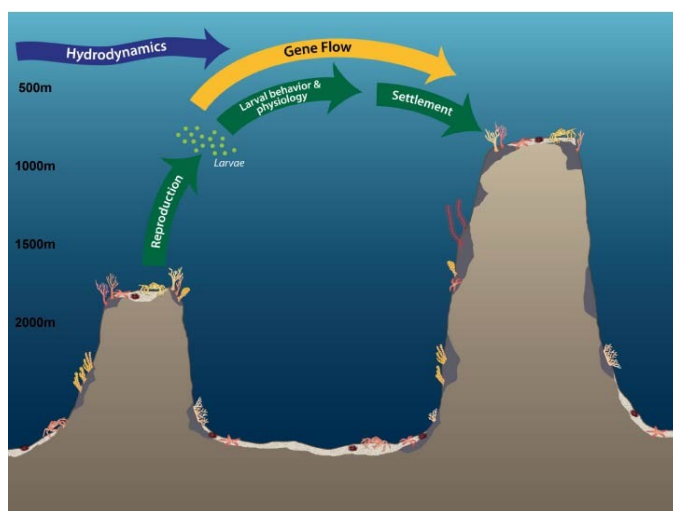


Figure 2.1 Schematic illustrating gene flow between seamounts showing significance of seafloor morphology, habitat availability (both biotic and abiotic), water depth, reproduction, settlement and hydrodynamics. Figure courtesy of T. Shank.

The concept of metapopulation dynamics is a useful theoretical framework for investigating how dispersal and population connectivity influence the dynamics of individual populations and their response to disturbance. Metapopulations are assemblages, discrete patches, or demes representing geographically separated populations or sub-populations linked by migration of individuals and exhibiting transient events of local extinction and (re)colonisation (Levins 1969; Hanski 1998). Corals and their associates are ideally suited to this concept because they inhabit seamounts and other patchy habitats in the deep sea, have the potential to disperse between habitats in their planktonic larval stage and have a very real possibility of local extinction. Metapopulation models integrate information about local

dynamics (e.g. reproductive output, trophic and other species interactions that affect population growth rates) with estimates of connectivity (e.g. current-mediated exchange of propagules, recruitment of immigrants and gene flow) to predict how processes in one patch may influence the dynamics in the others (Hanski *et al.* 1995; Hanski 1998). For instance, this approach can be used to investigate which populations may be sources or sinks of propagules, and to predict how individual populations may recover from disturbance.

Priority research questions are focused on identifying patterns of connectivity, and assessing the variety of linkages and factors influencing or controlling the connectivity of coral populations and their associated fauna over time. These objectives include, but are not limited to, the following questions:

1. How do the various factors (depth differences, habitat specificity, habitat availability, colonisation processes, reproductive and larval dispersal modes, physical and hydrographic settings) act as facilitators or barriers to the dispersal and exchange of corals and their associated fauna?
2. What are the patterns of dispersal, migration and connectivity of coral species and their associated fauna?
3. What are the dominant forces (e.g. co-evolution, isolation, etc.) structuring the distribution and dynamics of coral species and their populations?
4. How have climate change and the role of changing oceanic circulation shaped the evolution, diversity and biogeography of corals and their associated fauna throughout the Atlantic?
5. Do patterns of dispersal indicate that a given coral habitat (e.g. bank, seamount, knoll or canyon) may have served as a refuge or retained ancestral lineages for other coral habitats?
6. Is dispersal controlled by the influence of modern day current patterns? Is migration uni-directional, either toward or away from the Mid-Atlantic Ridge?
7. Can genetic connectivity studies identify key vulnerable coral habitats with a crucial role to be considered in the design and assessment of conservation and management strategies?

2.1.2 What are spatial scales of connectivity?

Depending on the geographic scales, different evolutionary forces may act to drive the spread of genes in space and time. Barriers to gene flow in ocean systems may not be obvious or easily identifiable (Vermeij 1987). While some studies have shown genetic homogeneity over regional or basin-wide spatial scales in some coral reef fishes (e.g. Shulman & Birmingham 1995), many recent studies of connectivity in marine organisms have found the spatial scale of connectivity to be smaller than larval dispersal potential (e.g. Taylor & Hellberg 2003; Baums *et al.* 2005; Cowen *et al.* 2006, 2007). The effects of geographic separation, depth difference and circulation patterns around isolated marine habitats on both the historical migration of marine fauna and their modern rates of gene flow are poorly known. There is growing awareness that the interaction of these factors with the life history of individual species is important to faunal dispersal in the oceans (e.g. Hedgecock & Edmands 2007; Treml *et al.* 2008). Hydrographic conditions may cause strong, steady or fluctuating ocean currents at various levels in the water column; these currents may promote or impede the dispersal of organisms from one place to another. Seafloor geologic features may provide critical stepping stones for fauna to disperse great distances, but realised connectivity will depend on interactions with local hydrography and life history characteristics of the species (see below). Dominant scales of larval dispersal or the extent of spatial connectivity are unknown for most cold-water coral species and assemblages.

We envisage conducting and encouraging projects that explore the interactions within, and connectivity between, spatially-isolated coral ecosystems. Cold-water coral communities have been identified in various deep-sea habitats of the North Atlantic, including seamounts, canyons, continental slopes etc., that are spatially isolated to varying degrees. Through these studies, we aim to identify areas or habitats that are likely to be sources of larvae for future generations, as well as corridors where habitats appear highly connected. This approach has recently been demonstrated using network theory to analyse genetic data from a clonal marine organism, the seagrass *Posidonia oceanica* (Rozenfeld *et al.* 2008).

Within patches (or habitats). Processes that structure and maintain cold-water coral communities begin at the local scale, e.g., seamount, canyon/fjord, bioherm, bank etc. Recent genetic studies of shallow-water coral species have demonstrated that complete mixing of genes often occurs only at small spatial scales, such as 100 m, during fertilisation (see Van Oppen & Gates 2006 for review; Underwood *et al.* 2007). For spawning corals, non-random mating may occur frequently due to restricted mixing of gametes. Successful fertilization may be more likely between individuals in close proximity and mating between relatives may occur often, resulting in a pattern called 'genetic patchiness', a phenomenon observed in several marine species from fishes to invertebrates (Johnson & Black 1982; Watts *et al.* 1990; Doherty *et al.* 1995; Arnaud-Haond *et al.* 2008). Such a scenario

would lead to small effective population sizes and locally adapted gene complexes, maintaining genetic subdivision (Whitaker 2004). We know little about the species-level relatedness between individuals within a cold-water coral population or their associates at these sites, including the relative contribution of sexual vs. asexual reproduction. Since coral samples may by chance come from genetically identical clones, this can quickly reduce the number of genotypes in any population genetic analysis, thereby biasing the results. This underscores the need to understand the level of clonality in cold-water coral populations - a particularly acute problem for colonial reef framework-forming species. For example, a recent study of an inshore *L. pertusa* reef in the NE Skagerrak found genetic clones extended for up to 100 metres (Dahl *et al.* unpublished data).

Between patches (or habitats). Habitat patches in the North Atlantic are spatially isolated at a range of geographic scales from:

- tens of kilometres (e.g. between seamount peaks, continental slope banks or reefs; along the mid-ocean ridge axis)
- hundreds of kilometres (regional scale, e.g. between seamounts and seamount chains; continental margins)
- thousands of kilometres (ocean basin scale, e.g., continental margins vs. offshore seamounts; eastern vs. western Atlantic; transoceanic scale, e.g. *Lophelia pertusa* in the Atlantic vs. Pacific Oceans).

Oceanographic and hydrographic conditions vary across these spatial scales. For example, cold-water coral communities in the southern North Atlantic may be influenced by Antarctic-derived water masses, whereas the more northern western Atlantic communities are bathed in North Atlantic Deep Water. Surface and deep-water boundary currents that promote connections among patches at one scale or depth range may act as isolating mechanisms at another scale. For example, studies of deep-sea fish (*Helicolenus dactylopterus*) populations in the North Atlantic have provided evidence for population connectivity on the continental slope off Europe, yet barriers to gene flow between the European continental slope, the Mid-Atlantic Ridge (Azores Islands) and the slope off the USA were also identified. There is also evidence for a major genetic discontinuity in *H. dactylopterus* populations north of the Cape Verde Archipelago (Aboim *et al.* 2005).

In cold-water corals, regional isolation among *Lophelia pertusa* populations along the eastern and western North Atlantic continental margins and the Gulf of Mexico has been identified using microsatellite markers (Morrison *et al.* unpublished data, see Figure 2.2). Sharp genetic breaks as well as obvious cases of gene flow in deep-sea sponge species along the continental slope off Europe support the predictions from the palaeoecological analyses (Frank *et al.* unpublished data; Schröder-Ritzrau *et al.* 2005) that recent glaciations had a strong influence on present day geographic distribution of genetic polymorphism. Glacial events may have forced some fauna towards more southern refugia such as the Mediterranean Sea, the region off NW Africa, providing opportunities for the evolution and diversification of taxa that subsequently colonised northern latitude reefs (Roberts *et al.* 2006). The upper bathyal coral ecosystems in Europe are therefore recognised as highly

dynamic environments, reinforcing the need to protect multiple lineages of these cold-water coral reefs.

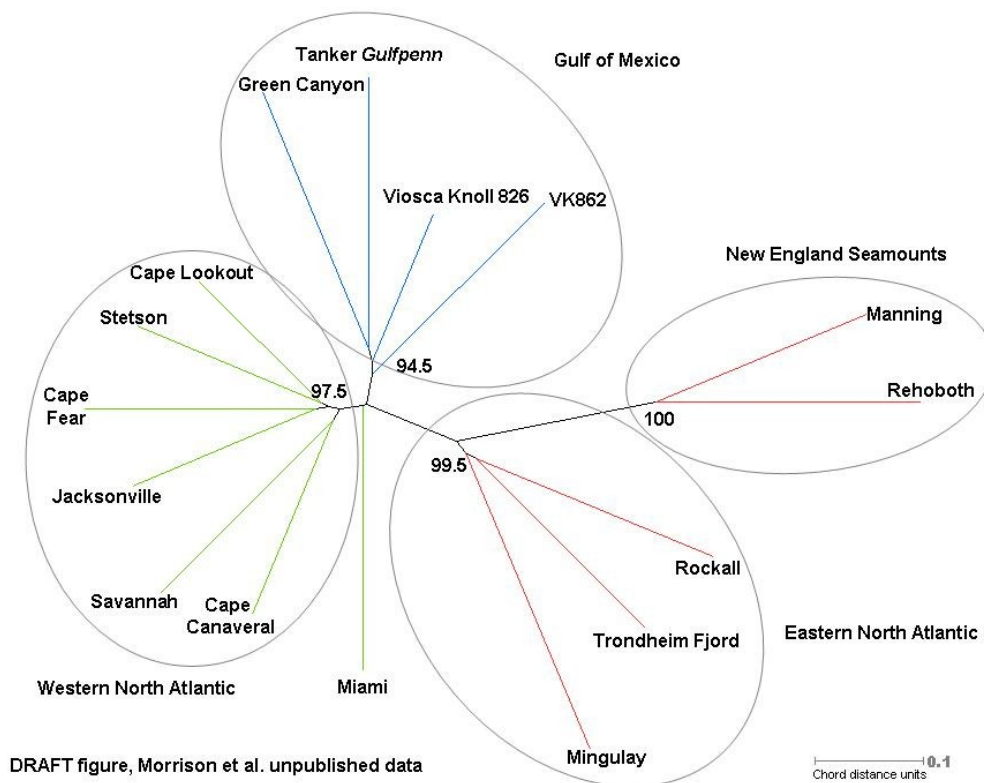


Figure 2.2 Unrooted neighbour-joining tree generated from pairwise genetic chord distances using microsatellite data from 341 unique *Lophelia pertusa* individuals and 16 sampling localities. Branch colours correspond to genetic clusters identified in a Bayesian clustering analysis (Structure). Ellipses include populations that formed a grouping supported by bootstrap analysis (bootstrap % at nodes). Figure courtesy of C. Morrison.

Evidence from non-coral associated deep-sea communities suggests that populations occurring at different depths can be genetically isolated or may be composed of closely-related cryptic species (e.g. France & Kocher 1996; Chase *et al.* 1998; Howell *et al.* 2004; Solis-Marin *et al.* 2004). Although genetic evidence is lacking, some coral species and their associates on seamounts of the eastern Atlantic, such as *Paramuricea* sp. and its associated ophiuroid *Asteroschema clavigera* are distributed across a broad depth range of >700 meters. Unexpected barriers to gene flow may exist with depth or depth-associated factors such as temperature, oxygen and pH. *Lophelia pertusa* reefs also occur at a broad range of depths in the Atlantic Ocean, from ~40 m in Norwegian fjords to 200-1000 m on the continental slope and 1500 m on New England Seamounts. Although too few samples from Norwegian fjords have been analysed to derive conclusive results, *L. pertusa* examined so far from fjord settings seemed different from continental slope populations (Le Goff-Vitry *et al.* 2004), a preliminary observation that deserves to be further explored. Likewise, *L. pertusa* from New England Seamounts (approx. 1,500 m) show substantial genetic differentiation compared with continental slope populations in the eastern and western North Atlantic Ocean (150-750 m; Morrison *et al.* unpublished data).

Understanding connectivity between cold-water coral populations depends upon studies encompassing distinct spatial scales: intra-population; local; regional and trans-oceanic scale. With better knowledge of the patterns of connectivity at various spatial scales, identification of the forces shaping population structuring, including abiotic factors will be feasible for the first time. This requires collaborative research efforts at the trans-Atlantic scale. Using several model organisms with wide distributional ranges, including the habitat-forming coral species, comparative phylogeographic studies of deep-sea coral ecosystems can begin and will allow common or overlapping phylogeographic breaks in the North Atlantic to be identified. Additionally, putative larval sources or pathways that play a critical role in the integrity of the metapopulation system may be identified. Taken as a whole, a better understanding of connectivity across the North Atlantic Ocean will allow for effective design of marine protected area networks.

2.1.3 What are temporal scales of connectivity?

Exchange of individuals on ecological timescales (weeks to decades) influences the dynamics of local populations and their potential to recover after catastrophic disturbance (resilience). When multiple species are considered in a metacommunity, their interactions (facilitative, competitive or trophic) affect the diversity of local ecosystems. If the metacommunity is highly connected then a local species extinction may be transient (if the local system is a sink), or alternatively it may extend regionally (if the local system is a source). Understanding the extent of connectivity is essential for predicting the consequences of local disturbance, such as might be caused by focused trawling or changes in the wider environment brought about by climate change. Over evolutionary timescales, limited connectivity may lead to genetic isolation of populations and eventually to speciation, influencing regional biogeographic patterns.

Observations of cold-water coral communities on seamounts in the western North Atlantic suggest highly patchy distributions of many coral species, both within and between seamounts. Video transects show species may be completely absent, in low or high densities at different locations along a single slope, on different slope faces, between seamount peaks, or between seamounts. Some observations of dead reefs also show that extinction may be recurrent on a local scale. One explanation for such distribution patterns is a rare recruitment event into an area followed by frequent local propagation, partly facilitated by the clonal nature of corals. Thus, connectivity may vary on temporal and spatial scales. This infrequent exchange with other populations, revealed by rather high genetic differentiation, may result in a local population that cannot recover quickly from a catastrophic disturbance that removes the adults; i.e., one with low resilience.

Recently, evidence from molecular phylogenetic studies have indicated that the evolution of some coral groups have involved exchanges between shallow-

water and deep-sea ecosystems in the course of evolution (e.g. Lindner *et al.* 2008). Timing of invasions of the deep sea from shallow-water ecosystems has been linked to past climatic change events (e.g. Little & Vrijenhoek 2003; Strugnall *et al.* 2008) and provide an important historical view on the possible impacts of global warming and cooling events on marine communities. Such historical events may explain many of the large-scale patterns in the distribution and diversity of deep-sea marine communities and are clearly relevant to the ‘Biodiversity’ objectives described in Section 2.2.

Finally, it is difficult to reconcile the age distribution of organisms like corals that can reproduce asexually, producing clones of potentially unlimited age, with the genetic structure of populations. Cold-water reef framework-forming scleractinian corals may live for >100 years but the reefs themselves can be >10,000 years old. The concept of gene flow is also very challenging in octocorals and antipatharians where individual colonies may be several thousand years old (Roark *et al.* 2006, 2009). This is also an issue with sponges associated with cold-water coral habitats, where ca. 200 Porifera species have been reported to dominate the reefs along the European margins (van Soest *et al.* 2007). Some groups, such as the hexactinellids (glass sponges) may also live for more than 100 years (Vacelet pers. comm.). Coupling genetic studies of population connectivity with studies of recruitment and reproduction in cold-water corals will be a significant feature of TRACES that will shed new light on the interpretation of genetic data from clonal and long-lived marine species. Those structures that have formed across centuries or millennia may indeed be particularly vulnerable and not resilient enough to recover from rapid, large-scale human disturbance.

2.1.4 What are the natural processes that control connectivity?

Connectivity is the result of biological traits (e.g. pelagic larval stage or adult movements) and factors (e.g. currents) favouring dispersal and those preventing it (e.g. physical barriers to gene flow or abiotic factors preventing the survival of migrants). Corals are sessile animals and are therefore largely dependent on the larval phase for the dispersal stage (gene flow or connectivity). Most cold-water coral species investigated to date have been found to be gonochoric (separate sexes) and most are broadcast spawners (see Section 2.3.1). However, there are major differences in the size of eggs produced by cold-water corals, the mode of larval development (planktotrophic vs. lecithotrophic) and in seasonality of reproduction. Some species show synchronous seasonal reproduction (e.g. *Lophelia pertusa*), others reproduce periodically but aseasonally (e.g. *Madrepora oculata*), whilst some show quasi-continuous reproduction (e.g. *Fungiacyathus marenzelleri*) (Waller *et al.* 2002; Waller 2005; Waller & Tyler 2005). Such differences in life history will affect the level and timing of recruitment to coral populations and the distances over which larvae may disperse. These factors will influence both the connectivity of coral populations and their resilience to human impacts such as the effects of fishing with bottom

contact gear (trawls and long lines). The role of intense or long-term fisheries activities on the structure and diversity of coral communities is now at the forefront of concern for ecosystem and fisheries managers interested in developing marine protected areas. Habitat-forming cold-water coral (and similarly sponge) assemblages are vulnerable to damage from bottom-tending fishing gears, especially bottom-trawling, as well as energy exploration and development, deployment of cables and pipelines, and other human activities that disturb the seafloor. Recovery from damage may require decades to centuries, as most cold-water corals and their associated communities grow slowly, and is directly dependent on levels of connectivity among sites allowing or preventing recolonisation of depleted areas. However, there is little or no direct information on the frequency or magnitude of recruitment to coral populations or on dispersal distances of the larvae of corals in the deep sea. Indeed, indirect assessment of dispersal by estimation of the genetic differentiation among coral populations remains the only practical way of assessing connectivity.

2.1.5 Methodology

An interdisciplinary approach combining genetic and oceanographic techniques will be needed to undertake the first basin-wide estimates of connectivity among various types of cold-water coral habitats. Much of the data necessary to estimate connectivity will overlap with other aspects of the ecosystem (sections 2.2 and 2.3) and environmental research (section 4) proposed in this Science Plan. Genetic studies are needed to compare regional samples and identify potential phylogeographic breaks in connectivity in many coral species and associated fauna. Finer-scale genetic studies will also be needed for select taxa to assess: (1) contributions of sexual versus asexual reproduction and relatedness among individuals at sites, (2) to assess population genetic structure and estimate gene flow among sites and (3) the potential for long term (i.e. evolutionary) impact of present day disturbance on mating system and migration patterns. Furthermore, better understanding of the reproductive cycles and larval life histories of key taxa, in combination with genetic estimates of gene flow, will allow for more accurate estimates of larval dispersal distances, or 'neighborhood sizes' (Palumbi 2004). Lastly, investigations into the physical oceanographic environment at both broad and local scales can be used to model expected connectivity. Model estimates can be compared with genetic estimates of connectivity to test model predictions using a 'seascape genetics' approach (e.g. Galindo *et al.* 2006). With such data in hand, accurate biophysical models of dispersal can be developed (e.g. Baums *et al.* 2006), which will allow estimates of resilience of reef areas and source-sink dynamics. Ultimately, biophysical models of multiple deep corals and associated fauna will be important tools for effective protection and management of deep coral habitats.

Bar coding and the Tree of Life. In all phyla, species delineation greatly depends upon the number of available diagnostic characters. Taxonomic and

systematic uncertainty may prevail, especially in species with a low number of informative characters (Klautau *et al.* 1999; Knowlton 2000). For instance, molecular analyses repeatedly revealed cryptic species and proved valuable in delineating species boundaries in Porifera (Klautau *et al.* 1994, 1999; Blanquer & Uriz 2007) and knowledge on speciation within cold-water coral-associated sponges might have potentially great consequences for the efficient conservation and economic use of this group (van Soest & Lavaleye 2005).

Phylogeography and historical connectivity. Broad-scale patterns of connectivity will be investigated for various corals and coral-associated fauna using DNA sequence data, systematic, phylogenetic and phylogeographic analyses such as statistical parsimony haplotype networks (Templeton *et al.* 1992; Clement *et al.* 2000). Researchers with expertise in certain taxonomic groups will lead phylogeographic investigations. Genetic samples (approximately 10 per site) will be preserved using a standardised protocol and will be transferred to the appropriate research team. Gene regions to be used for phylogeographic comparisons will vary according to taxon.

The marker of choice for phylogeography remains mitochondrial DNA, which allows the initial characterisation of population structure, to test population monophyly, or to infer maternal gene flow (Avice 1995, 2000). However, highly variable nuclear data are increasingly used to corroborate initial results based on cytoplasmic loci (Hare 2001).

Population genetics and connectivity. Fine-scale patterns of connectivity will also be investigated for select corals and associated fauna by using highly variable molecular markers, such as microsatellites. These markers have the advantage of distinguishing more readily between clonal individuals (with identical genetic makeup) versus those that are unique and therefore probably arose through sexual reproduction (Arnaud-Haond & Belkhir 2007; Arnaud-Haond *et al.* 2007). Clones can then be removed from subsequent analyses before genetic distances are calculated, which would otherwise artificially reduce estimates of gene flow. Taxa will be chosen depending upon geographic range, the availability of a large number of samples from various sites (>20 samples per site), and the availability of highly variable molecular markers. For the scleractinian reef-building coral *L. pertusa*, two sets of microsatellite markers have been published (Le Goff & Rogers 2002; Morrison *et al.* 2008). On-going studies of *L. pertusa* population genetic structure by Morrison (western Atlantic and Gulf of Mexico), Dahl (eastern Atlantic and Mediterranean) and those planned during the European CoralFish project will be expanded, standardised between research groups, and combined for a more complete assessment of trans-Atlantic gene flow. Additionally, a set of microsatellite markers have been developed for the scleractinian *Madrepora oculata* (Morrison unpubl. data). Markers are also now being developed for other species including an octocoral and black coral (E. Cordes pers. comm.).

Samples for genetic studies of this sort must be more numerous than the ones for phylogeographic studies (ideally between 25 and 50 samples per location)

and preserved in 95% ethanol or on FTA[®] Technology Classic cards, with careful recording of sample location information. Precise location information is particularly important for fine-scale connectivity investigations to allow estimates of relatedness and neighbourhood size within habitats and for input into either Bayesian clustering software, or spatial landscape genetic analysis software such as Geneland (Guillot *et al.* 2005), Alleles in Space (Miller 2005) or Tess (Chen *et al.* 2007). Additionally, analysis that does not require information regarding sampling sites can be used to cluster individuals into genetic clusters (e.g. Structure software, Pritchard *et al.* 2000). Collections made using manned submersibles or ROVs should provide high quality samples along transects which may reduce the chances of sampling clones produced by fragmentation and provide the material needed to assess relatedness among individuals. Samples from boxcores may be used, but are inferior for these purposes because frequently only one genetic individual is sampled per deployment, exact positioning is often not possible and corals often fragment.

Finally, settlement plates may be assayed in order to characterise recruits genetically and determine their putative source populations. With a defined population genetic dataset to compare with, genotypes of newly settled larvae can be analysed using software packages such as GeneClass (Piry *et al.* 2004) allowing possible parental populations to be identified.

2.2 Biodiversity and biogeography

North American workshop priority questions

1. How are cold-water coral communities structured and by what?
2. How do species utilise coral habitat?
3. What is the resiliency of deep coral communities?

European workshop priority questions

1. Do cold-water coral (communities) reflect established zoogeographic patterns?
2. Do different species fulfil key equivalent functional roles in cold-water coral ecosystems and in different biogeographic provinces?
3. Do cold-water coral habitats support (and maybe export) increased biodiversity compared with other habitats?

Integrated priority questions:

1. Are cold-water coral communities primarily defined by established biogeographic patterns, and what are the underlying factors (bathymetry, hydrography, biological interactions, etc. both contemporary and historical) that control their distribution?
2. Is cold-water coral community assembly explained primarily by random dispersal, migration, and local extinction processes (neutral theory) or by environmental gradients according to species' habitat requirements (niche theory)?
3. How does the biodiversity of cold-water coral habitats compare with other habitats?

2.2.1 Introduction and questions

Although cold-water corals have long been known, efforts to describe the biodiversity and biogeography of the corals and their associated fauna have only begun to be widely developed over the last decade or so. In the Atlantic basin, research has come predominantly from the north Atlantic, Mediterranean Sea and Gulf of Mexico regions; these include the large *Lophelia pertusa* reefs off Scandinavia (e.g. Mortensen *et al.* 1995, Mortensen & Fosså 2006), the coral mounds off the U.K. and Ireland (e.g. Henry & Roberts 2007; Roberts *et al.* 2008), the gorgonian forests off Nova Scotia (Henry 2001; Buhl-Mortensen & Mortensen 2005) and the New England Seamounts, and the *Lophelia* and *Oculina* banks off the southeastern U.S. (SEUS) (e.g. Reed *et al.* 2006; Ross & Quattrini 2007; Henry *et al.* 2008) and in the Gulf of Mexico (e.g. Schroeder *et al.* 2007; Cordes *et al.* 2008). There are very few studies from the south Atlantic and mid-Atlantic ridge (e.g. Mortensen *et al.* 2008) and off northwest Africa (e.g. Colman *et al.* 2005) despite the occurrence of *Lophelia pertusa* and other cold-water corals in these regions. Cold-water coral communities exhibit locally elevated biomass and diverse associated faunas (i.e. high alpha diversity - the number of species in a small area), by some estimates rivalling those of tropical coral

reefs (Jensen & Frederiksen 1992; Mortensen *et al.* 1995; Henry *et al.* 2008). In addition, the heterogeneous habitats associated with cold-water corals appear to support high beta diversity (species turnover across space) (Cordes *et al.* 2008; Roberts *et al.* 2008; Henry *et al.* in press).

However the mechanisms underlying cold-water coral community structure, diversity and distribution remain mostly unresolved, especially on an ocean basin scale. This is largely due to the lack of methodological and taxonomical standardisation needed to integrate of the available species datasets into an appropriate meta-analysis of Atlantic cold-water coral community biodiversity and biogeography. Consequently, we know very little about what controls biodiversity and biogeography in these habitats, or how to predict it.

Question 1:

Are cold-water coral communities primarily defined by established biogeographic patterns, and what are the underlying factors (bathymetry, hydrography, biological interactions, etc. both contemporary and historical) that control their distribution?

Coral associated communities are largely composed of species that also occur in adjacent habitats (Mortensen *et al.* 1995; Rogers 1999; Ross & Quattrini 2007; Cordes *et al.* 2008). Therefore, the coral associated fauna is generally expected to follow biogeographic patterns similar to those exhibited by the surrounding benthos (e.g. as in Watling 2009). Distinct biogeographic provinces are exhibited by many Atlantic deep-sea benthos including those that frequently inhabit cold-water coral communities including the corals themselves (Cairns & Chapman 2001), hydroids (Henry *et al.* 2008) and cumaceans (Watling 2009).

The biogeographical affinities of many species inhabiting cold-water coral communities largely correspond to depth. For example, shifts in scleractinian species composition occur at the shelf-slope transition, between the upper and lower slopes (1000-1500 m), and between the continental slope and abyssal plain. Similar patterns are found in the octocorals of the Atlantic (Watling *et al.* unpublished data). There is an assemblage of octocorals that occur principally on the continental slope of the western North Atlantic from north of Cape Hatteras to the Reykjanes Ridge and on the slopes of Europe extending northward from the British Isles. There is a deep (approximately 1500 m to 2500 m) fauna that extends along the Mid-Atlantic Ridge south of the Reykjanes Ridge and along the New England seamounts. There is also a shallow seamount octocoral fauna found only on the eastern North Atlantic and Corner Rise seamounts at depths <1000 m. If these trends in the scleractinians and octocorals are also found in the communities associated with cold-water corals, then sampling these communities across regions of the Atlantic or across predicted bathymetric boundaries should reveal them.

Concomitant with examinations of biogeographic patterns should be the collection of data to determine the underlying factors that best explain them. For *Lophelia pertusa*, aragonite saturation state, temperature, dissolved oxygen, nutrient levels, sedimentation and current speed appear to be among

the most significant factors (Davies *et al.* 2008). However, even for this relatively well-studied species, these variables need to be refined and their interactions need to be explored. For other species and taxa, far less is known although recent work shows habitat-forming gorgonian corals are associated with specific ranges of environmental factors that vary in a predictable manner between the families Paragorgiidae and Primnoidae (Bryan & Metaxas 2006, 2007). For the vast majority of the species commonly associated with cold-water corals, biogeographic boundaries remain poorly defined and there are little or no data on the environmental factors influencing their distribution. However recently Henry *et al.* (in press) used a spatially explicit model to measure the contribution of environmental and spatial factors predicted from multibeam bathymetry and ground-truthing to creating beta diversity in cold-water coral communities off the west coast of Scotland. Communities varied significantly with bathymetric variables, many of which themselves varied longitudinally on the reef complex, pointing to the potential importance of other unmeasured variables such as hydrography. Thus collecting a wide range of environmental data, along with quantitative species data at a variety of spatial scales, should be a priority for TRACES, as should the technological development of the best *in situ* platforms to integrate with remotely sensed and ground-truthed data.

Additional factors may influence the biodiversity and biogeography of coral species and their associated communities by affecting their evolutionary and ecological history on geologic time scales. The coral habitats of the Atlantic span a series of geological and glacial histories and oceanographic regimes. The *Lophelia pertusa* reefs of the North Atlantic show a periodicity of growth coinciding with the influence of glaciation (Roberts *et al.* 2006). It seems likely that post-glacial periods see the arrival of new species or the recolonisation of old ones from glacial refuges (e.g. Henry & Roberts 2007). The *L. pertusa* communities of the SEUS and Gulf of Mexico were not subjected to direct glacial activity, but an understanding of their long term growth on a geological timescale has not yet been established. The composition of octocoral communities may also have been affected, with more southerly or deeper sites providing refugia from glacial scouring. In the future, cold-water coral communities may also be subjected to pressures from ocean acidification, which may severely affect their global distribution and shift coral community structure from those that create aragonite skeletons to primarily calcitic skeleton fauna (Guinotte *et al.* 2006; Roberts *et al.* 2006). Co-ordination of this portion of the study with the palaeoenvironmental investigations is required to address these complicated questions and elucidate the effects of climactic history and future trends on coral biodiversity and biogeography.

Question 2:

Is cold-water coral community assembly explained primarily by random dispersal, migration, and local extinction processes (neutral theory) or by environmental gradients according to species' habitat requirements (niche theory)?

Niche theory (Tilman 1982) proposes that species specific traits govern their distributions over space, which therefore correspond to changes in the environment. These distributions are said to be environmentally deterministic, and as such, could be explained by changes in environmental variables.

It is currently thought that most of the organisms inhabiting scleractinian reef structures are also found in other habitats and are not endemic to reefs (e.g. Henry & Roberts 2007; Ross & Quattrini 2007; Cordes *et al.* 2008). However there may be specific niches provided by coral structure that are not always available in other habitats e.g. unoccupied space for settlement. Although species using coral structure in this way may be found in other habitats, they would proliferate in coral habitats with suitable niches. If this were the case, there should be species whose distributions reflect gradients in these habitats. For example in *L. pertusa* habitats, different taxa may associate with living coral, dead standing coral and coral rubble (Mortensen *et al.* 1995). Beta diversity in these areas is further promoted by the differences in species associated with coral framework, rubble and those found in off-reef habitats such as rock and sediment-dominated substrata (Henry & Roberts 2007; Roberts *et al.* 2008). The dominant components of coral communities, in terms of both composition and biomass, are suspension-feeding organisms, including the corals themselves, other cnidarians such as hydroids and anemones, polychaetes, echinoderms, sponges and bivalves. These organisms may use the coral structure or other hard substrata to provide elevation above the bottom into accelerated current regimes. In addition, large coral framework and rubble structures may provide additional resources, by trapping and concentrating food or providing substrata for biofilm growth. Small deposit feeders may take advantage of the coral framework for both shelter from larger predators as well as higher amounts of trapped phytodetritus. This trophic resource may remain unavailable to larger organisms such as non-selective detritivores or larger deposit feeders such as holothurians, due to the small interstices in the coral framework, although this remains to be demonstrated empirically.

Habitat usage may also have strong temporal components: diel, seasonal, or event driven. Coral structure can play a significant role in the life history of associated organisms, but may be limited to certain aspects of their ecology such as feeding, reproduction and shelter from predation or physical disturbance. Diurnally vertically migrating species may interact with the coral habitat only during the day. Reproduction of mid-slope species may be seasonal and may be tied to the coral habitat (Etnoyer & Warrenchuk 2007). Periodic physical disturbances may also cause some species to seek shelter in the coral structure. Although these species may have been observed or sampled with the corals, little information exists on their patterns of habitat usage. Addressing such questions will require sampling over a variety of habitats, including non-reef habitats, and over a long time series. Consistency in distributional patterns and behaviours will allow these questions to be resolved.

But while there are few documented obligate relationships between associated fauna and cold-water scleractinians, such relationships are more common within coral host taxa. Some of the most common obligate taxa include the Copepoda (Crustacea), Peracarida (Crustacea) and Ophiuroidea (Echinodermata) (Buhl-Mortensen & Mortensen 2005). The spectrum of symbiotic relationships (mutualism, commensalism and parasitism) is illustrated by octocorals and their associates. One example comes from the recent finding of the obligate *Gorgonophilus canadensis* (Copepoda: Lamippidae), which changes the shape of *Paragorgia arborea* polyps into galls off the coast of Nova Scotia (Buhl-Mortensen & Mortensen 2004). The prosobranch gastropod mollusc *Pedicularia* also forms a close associate with stylasterid corals (Zibrowius & Cairns 1992). Although their shells leave a characteristic trace on the coral's skeleton the nature of the relationship is not well understood. Observations of this sort suggest that niche theory is important in explaining some of the highly specialised obligate associations we observe within cold-water coral communities.

Neutral theory (Hubbell 2001) models biodiversity using dispersal and migration events along with local extinction dynamics. If one assumes the neutral model as a null hypothesis for species distribution, then demographically equal species would be spatially autocorrelated, due to the effects of random but spatially restricted dispersal and random migration/speciation/extinction from the overall metacommunity.

Various approaches can be used to elucidate the importance of niche versus neutral processes in controlling biodiversity in cold-water coral communities. Variance partitioning techniques can be used to detect spatial autocorrelation, for example, if a significant component of beta diversity was explained by geospatial location, which represents the distance between communities (Henry et al. in press). Observed species abundance distributions and decay with distance curves can also be compared to the expected null model assuming neutral dynamics.

Clearly data on species dispersal, migration and extinction are lacking from cold-water coral habitats, but the technological development of platforms through TRACES that could measure recruitment and dispersal offers a unique opportunity to fill these gaps and, importantly, combine biodiversity assessment with the temporal history of coral habitats derived from the large-scale dating studies outlined planned in the Climate Records theme (see Section 3).

Question 3.

How does the biodiversity of cold-water coral habitats compare with other habitats?

Cold-water corals may be considered ecosystem engineers (Jones *et al.* 1994) as they create biogenic habitat and modify the abiotic environment. They create complex three-dimensional structures that provide habitat for mobile fauna and direct physical settlement substrata for sessile organisms. Diverse communities of coral species, including scleractinians along with large

habitat-forming octocorals and antipatharians, create more heterogeneous structures that are likely to support even higher diversities of associates. These structures also alter current flow regimes and sedimentation rates and may locally enhance larval retention. However, these concepts, notably larval retention, have not yet been examined in detail across a range of cold-water coral habitat types.

As a consequence of ecosystem engineering, alpha, beta and gamma diversity (overall number of species in a large area) are expected to be higher in areas with cold-water corals than in adjacent areas and studies consistently show that coral habitats are more speciose than surrounding areas (e.g. Mortensen *et al.* 1995; Jonsson *et al.* 2004; Henry & Roberts 2007; Roberts *et al.* 2008) and that they generate beta diversity because community composition varies between areas with corals and without (Henry and Roberts 2007). Determination of the relative contribution of alpha and beta diversity to overall gamma diversity should also clarify the direct influence of coral structure versus the indirect consequence of increased habitat heterogeneity on regional diversity. Standardised sampling across coral and background habitats may detect a diversity halo - a region of elevated diversity in soft-bottom habitats adjacent to reef structures. Similar sampling in habitats surrounding non-biogenic structures (other hardgrounds devoid of corals) should reveal any direct effects that the corals have on their surrounding communities. Classical macroecological themes such as the latitudinal gradient in species diversity, species-area relationships and niche/neutral control of biodiversity can all be addressed under the large scale remit of TRACES, and will all be tractable following the development of simple, repeatable habitat classification schemes and standardised sampling methods.

2.2.2 Trans-Atlantic Relevance

These questions are best addressed in a collaborative effort investigating the cold-water coral communities of the Atlantic. Confirmation and delineation of the biogeographic and bathymetric boundaries to coral communities is a necessary step for answering these questions. Key target areas may be gleaned from investigations of the known boundaries of other communities. For example, questions related to the importance of glacial and water mass history on coral communities can only be addressed by consistent, standardised sampling using latitudinal transects that cross regions with an established glacial history. Therefore, in broad terms, sampling northeast Atlantic *Lophelia pertusa* reef communities that have likely developed since the Holocene and comparing these communities with those off West Africa and the Mediterranean that have potentially existed over longer timescales more remote from glacial influence offers a framework to examine these issues. Similarly designed sampling programmes in the western Atlantic, comparing the coral communities of Atlantic Canada to the Southeast U.S. and Gulf of Mexico, may reveal a different response to glaciation and inform our models of community assembly as well as population connectivity. This

analysis strategy, including focused sampling north and south of the terminal moraine of the last glaciation on both sides of the Atlantic would need quantitative data on the community composition of scleractinian as well as gorgonian and antipatharian biogenic habitats. In an Atlantic context, these issues can be tackled by applying an agreed, consistent, standardised sampling methodology across sites and we outline this approach in the following section.

2.2.3 Methods and standardisation

To answer these intriguing questions, we require a complete census of these communities from a wide variety of habitats, depths, and locations. Although a number of sampling methods have been used, traditional bottom trawls and dredges should be avoided due to their destructive nature. However, precisely controlled midwater trawls accompanied by detailed bathymetry can still provide valuable information on the benthopelagic fishes and invertebrates that may congregate near coral structures. Boxcores and grab samplers, though destructive on small scales, are among the best types of over-the-side gear for coral community sampling in large *L. pertusa* reef structures, because they provide discrete samples of the coral framework. However, the risk of sample washing on recovery due to an improperly sealed core frequently limits truly quantitative sampling. Video guidance of such gear permits habitat identification, selection and sampling. This is especially significant where corals are limited in abundance or patchily distributed.

The increasing use of manned and unmanned submersibles to investigate cold-water coral communities also requires the development of quantitative sampling gear for these platforms. Most submersible cold-water coral studies to this point, and the majority of studies of deep-water gorgonian and antipatharian communities, have used manipulator arm or suction samplers that are not quantitative and limited in their ability to collect mobile fauna. Customised quantitative sampling gear and submersible-deployed boxcores provide much higher-resolution and comprehensive samples, but have not yet been widely used. Such equipment combines the advantages of a quantitative camera-guided grab sampler with the precision and replication given by a submersible to provide comprehensive samples of specific habitat types while minimising impacts on coral structures. Furthermore, these devices allow one to avoid microhabitats not directly associated with corals themselves (e.g., underlying sediments) to ensure the precision of reported habitat associations.

Beyond physical sampling, it has long been recognised that direct observations provide additional data on deep-sea community composition and habitat associations. In order to rapidly and accurately quantify megafauna and habitat over a large area, state-of-the-art standardised photographic sampling methods using manned submersibles, ROVs and drop-frame cameras should be used. But even these tools can be improved. Low light videography should be developed in addition to normal high definition videography for faunal surveys. Quantifying video view area has always been problematic, and

current methods using scaling lasers may be inadequate on reef habitat. New methods for quantifying digital still and video data should be developed. Precise (to GPS standards) navigation of these vehicles will be required and is improving.

A combination of video footage and still photography with quantitative sampling can be used to investigate patterns in community structure at all size classes of organisms. Quantitative photographic sampling may also be used to scale up abundance and biomass data from physical sampling to entire reef structures or coral 'gardens' and even entire sites. For the meio- and macrofauna much can be learned from sampling approaches used at hydrothermal vents and cold seeps where qualitative sampling has largely been replaced by quantitative approaches. Both environments have biogenic substrates (i.e., corals versus tubeworm aggregations and mussel beds) in common. Specially designed grabs in combination with standardised photographic surveys allow the quantification of species richness and composition in different selected habitats associated with coral reefs.

The following summarises key sampling standardisation issues for faunal sampling for the major cold-water coral habitats of the Atlantic. To ensure comparability between studies, TRACES projects will all follow these guidelines.

At the site scale, a series of randomised transects should be obtained to describe the distribution of foundation (biogenic structure forming) species. Transects would be ideally chosen using a relatively fine scale multibeam map of the site. Both habitat mapping and photographic sampling would most effectively be accomplished using suitably equipped AUVs or ROVs. Alternatively, multibeam mapping from a surface ship along with photographic sampling from a towed camera platform could also be effective.

In order to investigate patterns in small macrofauna and meiofaunal communities, quantitative physical samples are needed. To complement these samples, detailed *in situ* photographic sampling of communities before collection provides critical information on the direct associations of organisms with habitat-forming species. Physical sampling of the communities would be determined by the type of foundation species in question.

1. Coral 'forest' habitats including gorgonian, antipatharian, alcyonacean, and stylasterid corals. Sample individual living coral colonies using ROV or submersible, ideally using mesh-bag sampling device to enclose colony and associated fauna. Sample individual dead colonies to examine attached epifaunal colonising community.

2. Scleractinian reef-frameworks. Where the habitats are large enough a heavy duty box corer (e.g. NIOZ pattern) ideally supplemented with video guidance should be used to recover both on and off-reef samples. The recently-developed UK video-grab sampler *HYBIS* shows great promise as a means of gathering quantitative bottom samples from scleractinian reef frameworks. On smaller habitats where coring or grab sampling would be

impractical or unduly destructive, smaller boxcores or customized sampling gear deployed from a submersible is the ideal method for obtaining quantitative samples. Samples should be then sub-sampled for meiofauna and sieved through 1 and 0.5 mm mesh before being preserved.

Faunal preservation methods depend upon both the faunal group and the ultimate destination of the samples. Taxonomic experts should be consulted for the best preservation method for vouchers and classical taxonomic work. Subsamples of key species should also be taken for genetic and stable isotope analyses. These should either be frozen, or for genetic samples, high-percentage ethanol solutions are appropriate.

2.3 Coral biology and reproduction

North American workshop priority questions

1. What are habitat-forming coral species' reproductive modes, fecundity and larval biology?
2. What controls the rate of coral skeleton growth and how does this affect palaeo-proxy record?
3. What is the flux of carbon through the coral animal and how could this change under altered temperature and $p\text{CO}_2$ conditions?

European workshop priority questions

Question 1: Biotic and abiotic factors that control biological processes in cold water coral species and communities:

- Effects of local sedimentation rates and hydrodynamics on coral health status?
- Which cues trigger spawning? Temperature, salinity, others?
- Is there any clear trend in reproduction patterns of deep corals

Question 2: Energy supply to and flow through cold water coral communities:

- Carbon flux through coral ecosystem. Energy budget of coral reefs, carbon fixing?
- Trophic interactions of cold water coral ecosystems and food web, supply and quality.
- Dynamic energy budget models.

Question 3: The processes of coral reproduction and recruitment:

- When do corals reproduce? Dispersal distances/larvae behaviour. Document embryo and larval development of cold water corals. (including life history, reproductive cycle, etc.)
- What are the conditions that favour or hinder larval settlement?
- What factors determine reproduction synchrony, cycles and fecundity?
- Link of coral biochemistry and reproduction.

2.3.1 Introduction

Although there have been many advances in cold-water coral research over the past decade, information on basic life history and biological processes is still absent or minimal for most coral taxa. There are some exceptions to this rule however, since some coral species or taxa are more readily available than others, and/or have characteristics that are appropriate for biological studies. The structure forming scleractinian *Lophelia pertusa* is regionally common and can be maintained successfully under laboratory conditions. This species has therefore been the focus of *ex situ* studies on reproduction, feeding behaviour, sediment and temperature tolerance, respiration and growth rates (Waller & Tyler 2005; Brooke *et al.* 2007, Dodds *et al.* 2007; Orejas *et al.* 2007b). Some gorgonians and antipatharians have regular patterns of growth that can be measured and aged reliably, and the skeletal

chemistry of older specimens of these taxa has also been used to gain insight into historical ocean conditions (e.g. Sherwood *et al.* 2005a,b,c).

Information on reproductive cycles has been limited by sample availability. Description of a full gametogenic cycle requires frequent sampling, preferably over multiple years; however the reproductive strategy has been inferred from less rigorous sampling regime for several species of cold-water corals. The reef framework-forming scleractinians appear to be universally broadcast spawners, releasing eggs and sperm into the water column for larval development (Brooke & Young 2003; Burgess & Babcock 2005; Waller 2005; Waller & Tyler 2005). Seasonality is unknown for most species but *Lophelia pertusa* has been studied in both the eastern and western Atlantic. This species has an annual spawning season, which occurs in late February in the eastern Atlantic, and appears to be around October in the western Atlantic (Brooke *et al.* 2007). This temporal offset raises interesting questions regarding environmental influences on reproductive cycles including the effects of physical disturbance which has been shown to induce premature larval shedding in the cold-water octocoral *Gersemia rubiformis* (Henry *et al.* 2003). The reproductive biology has been studied for a few species of octocorals (Cordes *et al.* 2001; Orejas *et al.* 2007a) but reproductive strategy (broadcast spawning vs. brooding, seasonal vs. continuous) appears to be taxon-specific, and there are too few data to assess any overarching trend. Cold-water hydrocorals studied to date are gonochoristic brooders, releasing planula larvae. Reproduction in the shallow water *Allopora californica* is seasonal, but whether the deep water species studied reproduce seasonally or continuously is not clear (Ostarello 1973; Brooke & Stone 2007).

Very little is also known of the larval ecology of cold-water corals in general, but there is some information on larvae of the structure forming scleractinian *Oculina varicosa* (Brooke & Young 2003, 2005), three species of Antarctic cup corals in the genus *Flabellum* (Waller *et al.* 2008), and the Pacific hydrocoral *Allopora californica* (Ostarello 1973). The former has relatively long-lived planktonic larvae, and the others are short-lived 'crawl-away' forms. Information on larval lifespan and behaviour can be incorporated into hydrodynamic models to predict potential dispersal and recruitment patterns, which is particularly important for understanding controls of connectivity at different spatial scales, and assessing recovery potential after large scale mortality events.

Studies on the trophic ecology of cold-water corals are scarce, and again have focused on few selected species. Studies using stable isotopes have shown that *Lophelia pertusa* in relatively deep northeast Atlantic coral carbonate mound settings occupies a similar trophic level as tunicates and bivalves, feeding on small particulates from the water column (Duineveld *et al.* 2007). More recent studies analysing fatty acids from *L. pertusa* not only revealed diagnostic copepod lipid biomarkers but that the likely prey varied from herbivorous calanoid species in shallow reefs to carnivorous or omnivorous non-calanoid copepods at deeper sites (Dodds *et al.* in press). Several *in situ* observations have recorded zooplankton capture by *L. pertusa* and other deep coral species, and aquaria experiments have shown that *L. pertusa* can

capture, and survive on planktonic crustaceans such as brine shrimp (Tsounis *et al.* in prep). Other planktonic food sources, such as nano and microplankton also constitute an important element of the diet of some deep Antarctic octocorals (Orejas *et al.* 2003). In order to establish the energetic requirements of keystone species, more qualitative and quantitative knowledge on feeding preferences and patterns is needed. Food quantity and quality may play a critical role in driving the distribution and abundance of these corals both spatially and temporally. Laboratory studies on feeding should be augmented with *in situ* research on food flux and quality, temporal and spatial variation in food distribution and coral condition to place *ex situ* studies in context.

The growth rates of most cold-water corals have yet to be determined or even estimated, but recent research has provided some information. The focus again, to a large extent, has been on *Lophelia pertusa*. Linear branch extension rates have been estimated at 5-26 mm yr⁻¹ from *in situ* and aquarium studies, and from growth ring analyses (e.g. Duncan 1877; Freiwald *et al.* 1997; Mortensen & Rapp 1998; Gass & Roberts 2006, Orejas *et al.* 2007b). The wide range in growth rates observed in these studies may be a reflection of the irregular growth form of this species, as well as differences in experimental or environmental conditions. However, even at the fastest growth rate it would take decades to form a colony one metre high, and thousands of years to form the extensive reefs that have been discovered in the north Atlantic.

For other cold-water coral taxa, such as the gorgonians and antipatharians, growth rates have been evaluated in a number of ways. Some skeletal structures develop growth zones that are quantifiable (Risk *et al.* 2002; Sherwood *et al.* 2005c); however, many do not provide reliable growth zones and radiometric methods (e.g. Lead-210 and bomb radiocarbon dating) have been used to provide age and growth estimates (Druffel *et al.* 1990; Adkins *et al.* 2004; Andrews *et al.* 2005; Roark *et al.* 2006). In addition, some applications have validated the annual formation of growth zones and provided an independent estimate of age and longevity (e.g. Andrews *et al.* 2002). Data thus far has provided evidence that the large gorgonians, antipatharians and scleractinians commonly found in cold-water coral ecosystems can be decades to hundreds, or maybe even thousands, of years old (Andrews *et al.* 2002; Thresher *et al.* 2004; Noé & Dullo 2006; Roark *et al.* 2006; Love *et al.* 2007; Noé *et al.* 2008). It is important, however, that standardised nomenclatures and methodologies are used when comparing results from different researchers.

2.3.2 Methods and sites

A combination of approaches can be used to address the above questions. These can be divided into two main categories: (1) laboratory or *ex situ* studies, using samples that are maintained for manipulative experimentation or preserved in the field then further processed in the laboratory; (2) *in situ*

observations and long term monitoring. Each of these approaches is described in further detail below:

1. Laboratory studies

Lophelia pertusa has been maintained in laboratory aquaria to measure growth rates and conduct initial studies examining the effects of sediment, food availability, temperature and oxygen levels. This species has been kept in different locations around the world, and there is potential for similar experimental approaches for other cold-water coral taxa, indeed aquarium maintenance of *Madrepora oculata*, *Dendrophyllia cornigera*, *Desmophyllum cristagalli* as well as *Javania* sp. has also been conducted successfully (Olariaga *et al.* 2009). Live specimens are particularly valuable for: (1) assessing behavioural and physiological responses to environmental variables; (2) feeding experiments (food source selectivity, capture rates); (3) reproductive manipulations (spawning induction, fertilisation and larval ecology); (4) photographic documentation of behaviour under controlled conditions; (5) measurement of calcification rates and changes in skeletal density under different ocean acidification scenarios; (6) use of genetic techniques and cellular diagnostics to assess stress response under either natural or manipulated conditions. The addition of elemental and isotopic supplements can also be used to track the movement of different compounds through the tissue and skeleton. Samples of *L. pertusa* collected from Scandinavian fjords during the peak of the gametogenic cycle have been spawned in the laboratory, but with low developmental success (J. Järnegren & S. Brooke pers. comm.). Larvae obtained from laboratory spawning can be used to determine ecologically relevant information such as larval lifespan and behaviour as well as the effects of environmental factors on larval survival. It is encouraging to note that in early 2009 laboratory spawned *L. pertusa* resulted in successful planula larvae development (A. Larsson & T. Lundälv pers. comm.). Laboratory spawning is needed for other species of cold-water corals, including antipatharians, octocorals and stylasterids. Aquarium culture also allows trophic ecology studies based upon feeding trials examining food types and concentrations with experimentally manipulated current patterns. These then form a natural complement to trophic studies of field-collected specimens based, for example, upon stable isotopes and lipid biomarkers.

Age and growth studies need samples of coral skeletons from various species and locations to investigate evidence for any growth zones and their periodicity. It is often important that the entire animal or colony be collected, taking care to preserve the oldest part of the colony basal structure - typically the basal attachment point. Analysis of the specimen would involve a combination of microstructural and radiochemical investigations on whole or sectioned skeletal portions. Examining microstructural characteristics is usually performed using microscopic observations with either transmitted or reflected light. For finer growth structure, scanning electron microscopy (SEM) may be used to look for daily or sub-annual growth increments. To determine the periodicity of growth zone formation (or in cases where no growth zone structure is quantifiable), radiochemical techniques can be applied to provide a temporal context to

growth. In radiochemical investigations, micro-milling is commonly used to produce a sample series along the growth axis. Whether extracted with a micro-mill or simply cut from the skeleton, radiochemical analyses involve a considerable amount of preparation and analysis. This focus of investigation ties into the Climate Records Research objectives of TRACES (Section 3) since time series observations of skeletal chemical composition have to be calibrated against known age/growth structure.

Preserved coral samples may be used for histological assessment of reproductive status, ultra-structural observations and larval dispersal and population connectivity studies using genetic techniques. Studies of coral diet also need preserved samples, as well as the samples of the potential food sources. Each of these applications requires a specific preservative or fixative, but any one sample may be used for multiple purposes if sub-sampled and preserved using different methods. In an effort to encourage sample optimisation, Etnoyer *et al.* (2006) created a handbook with standard protocols for cold-water coral sample collection and preservation. There are many other uses for preserved samples, and since this material is so difficult and expensive to collect, scientists in all regions would benefit from a sample sharing infrastructure, such as proposed by the TRACES programme. All sampling techniques and experimental methodology should be standardised across TRACES researchers and locations for comparative purposes.

2. In situ observations and long term monitoring

Researchers are only able to visit cold-water coral habitats infrequently and for short periods of time, therefore it is difficult to obtain long-term information during research cruises. To overcome this limitation, the collection of long-term *in-situ* environmental measurements can be made using a variety of benthic data loggers, either deployed directly on the bottom using benthic landers or suspended in the water column on moorings. This infrastructure can support a variety of sensors to measure physical parameters (current speed and direction, temperature, turbidity etc.) and collecting devices to estimate biological variables (plankton flux, larval settlement). Long-term environmental data are crucial to place information from other studies (e.g. biodiversity) into an ecological context. Data collection stations may also have time-lapse cameras to document vagrant fauna and their responses to changes in environmental conditions. Long-term stations should also be established in critical areas for *in situ* studies; for example, growth and recruitment rates, changes in skeletal density over time and behavioural studies.

2.3.3 Criteria for study sites

Repeated access to study sites is essential to conduct many hypothesis-driven biological studies, but this is a logistical limitation with deep-water ecosystems. There are areas where deep-sea biota are much more accessible, such as fjords, where deep-water species can be found at relatively shallow depths (<100 m). Several fjord sites also have available survey and sampling

resources through near-by research stations. However, because local environmental conditions influence certain biological parameters (fecundity, density of calcified skeleton, trophic ecology, energy content, growth etc.), both inshore and offshore sites should ideally be included in biological studies. If monthly data can be collected from areas with easy access, it helps to place information that is collected sporadically from deeper areas into both a temporal and regional context.

Collecting baseline data on biological parameters from a variety of regions is critical for a proper assessment of the effects of global climate change. Suggested sites for monitoring stations include areas that are under threat from direct (e.g. mechanical) or indirect (e.g. changes in ocean chemistry) human impact. Protected areas and other sites where direct human impact is minimised need to be included for comparison (control areas). Known cold-water coral areas with ongoing research programs include the New England Seamounts, Corner Rise Seamounts, the Mid Atlantic Ridge spanning the NW Atlantic, Le Danois Bank in the Cantabrian Sea, the Mingulay Reef Complex, Norwegian continental margin and several locations in the Mediterranean Sea (especially the Cap de Creus canyon and Santa Maria de Leuca, as well as several more canyons from the Gulf of Lions). Because there is a great deal of variability in biological factors, spatial data cannot be used to identify subtle responses to environmental changes, particularly since anthropogenic effects will be region-specific; therefore, temporal data should be collected to document effects of environmental change. The southwest Atlantic *Lophelia* bioherms and lithoherms are the most extensive and (to our knowledge) unimpacted deepwater scleractinian assemblages off the USA. This large area has been proposed for protected status by the South Atlantic Fishery Management Council and would make an ideal study area for the north western Atlantic. A similar site in the north eastern Atlantic would be the reef and coral carbonate mound tracts known off Ireland, Scotland and Norway. Study sites should include representatives of each coral habitat type (e.g. scleractinian, gorgonian, hydrocoral dominated) in both the western and eastern Atlantic, with linked studies in the adjoining Gulf of Mexico and Mediterranean Sea basins. They should also include impacted and unimpacted sites for comparison.

2.3.4 Trans-Atlantic relevance

This section of the TRACES programme represents the first attempt at standardised basin scale research on cold-water coral biology. Understanding biological processes provides an essential context for the other TRACES sections; biogeography and biodiversity, linkages and connectivity, and climate records. With respect to biogeography and biodiversity, this includes growth and structure of corals, feeding ecology, coral reproduction and recruitment patterns and environmental tolerances. For linkages and connectivity, information on reproductive parameters such as larval ecology enhances the accuracy of larval dispersal models and understanding environmental tolerances helps explain larval distribution. The age and

growth information also feeds into the climate record aspect of TRACES; chemical records of climate change stored in the skeletal structure of corals must have a temporal context to provide a timeline for any recorded perturbations.

Data on biological similarities and differences between regions provides the foundation for investigation into the drivers of biological processes. The cosmopolitan distribution of some cold-water coral species offers the possibility of studying the responses of the same species in different environments. For example, *Lophelia pertusa* in the north Atlantic spawns during late February/early March, but in the northern Gulf of Mexico and South Atlantic Bight, current evidence suggests that spawning occurs around October. Such seasonal variation in reproduction is also seen in many solitary cold-water scleractinians, and is probably driven by one or more environmental parameters (e.g. temperature, food, current speed). There are other trans-Atlantic coral species (e.g. *Paragorgia* spp.) that can be studied in a similar comparative manner, which would increase the sparse knowledge of basic biological processes on these species.

Trans-Atlantic studies using standardised techniques will also allow us to compare processes between areas at a range of spatial scales. Previous comparisons between regions have been hampered by a lack of comparable techniques, for example: (1) recruitment studies have used different experimental designs and substrata; (2) feeding experiments applied different tank shapes and flow conditions; (3) age and growth studies have been conducted using a variety of methods, some of which have not been validated with independent chronologies. A successful approach to ocean scale deep-water research will involve multiple research organisations that work together with common objectives within a rigorous research framework. One of the most important aspects of TRACES is the use of standardised methodologies to generate comparable information.

Experts in the Coral Biology section of TRACES will work together in proposing a research transect across the Atlantic that will address the priority questions outlined in this section. The TRACES programme forms multiple sections with different research objectives; specific transect locations will be chosen to optimise data collection efficiency and integrate objectives wherever possible. Because these ecosystems are vulnerable and valuable, research will be carefully co-ordinated to minimise impact.

3 Climate Records Research

3.1 Introduction

Many species of corals form hard parts made from carbonate that may endure for hundreds of thousands of years on the seafloor and within marine sediments. We have geochemical techniques that allow us to date individual corals, determine growth rates and extract information on their growth environment. Due to their rapid growth and widespread distribution, coral skeletons provide high-resolution archives of changing oceanic conditions. Extracting such information from coral carbonate using geochemical techniques can yield quantitative *in situ* records of local environmental conditions over the lifetime of that coral. We envisage a strong geochemical component of TRACES directed towards improving, developing and using cutting edge technologies that will allow us to take full advantage of the unique records left behind as corals calcify. These geochemical techniques will be central to all aspects of TRACES, adding unique insights into many issues including past climates, preferred coral habitats, stressors, ecosystems, coral responses to climate and anthropogenic forcing, population dynamics and recruitment events.

We will address the following questions, identified at the European and North American TRACES workshops:

1. How reliable are chemical proxies for determining age and ocean environment?
2. What is the history of cold-water coral ecosystem development? For example, we know that coral growth has been sporadic over tens of thousands of years and differs between the NW and NE Atlantic, but the reasons for this remain unclear.
3. How can we improve our understanding of past ocean circulation (including heat transport and the carbon cycle on decadal and glacial time scales) through basin-wide studies of cold-water coral ecosystems?
4. What are controlling factors on cold-water coral ecosystem development?
5. What is the sensitivity of cold-water coral ecosystems to global change and ocean acidification?

3.1.1 Why study circulation in the deep and intermediate ocean?

With increasing emissions of greenhouse gases to the atmosphere humanity is conducting a climate experiment of unprecedented scale. The outcome of this global experiment is unknown. Computer models of the ocean-atmosphere system forced with rising CO₂ predict various degrees of warming, a weakening of the thermohaline circulation in the North Atlantic (Vellinga & Wood 2002), and alterations in the amount and distribution of precipitation

(Held & Soden 2000) among other global effects. However, key components of these numerical models are only a crude representation of the true climate physics. To improve this situation, examining the history of climate change has become an important part of future climate prediction (IPCC chapter 6). Of course, it is better to use direct observations, but they are not always available. Our instrumental record of climate in the pre-satellite era is sporadic and short-lived. Therefore, we must turn to archives of past climate to obtain records that allow investigation of climate variability in the past few thousand years and even across glacial interglacial transitions.

Over the last three million years deep-sea cores show dozens of transitions between cold times with large ice sheets over northern latitudes and warm times of higher sea level. These cycles are paced by variations in Earth's orbit around the sun on 20, 40 and 100,000 year timescales, the so-called Milankovitch cycles (Hays *et al.* 1976). In the mid-1980s the first ice core records of past CO₂ levels showed that this important greenhouse gas also varies with the glacial cycles. It is clear from these data that CO₂ is an important amplifier of climate change, but how this works is one of the largest unsolved problems in palaeoclimate.

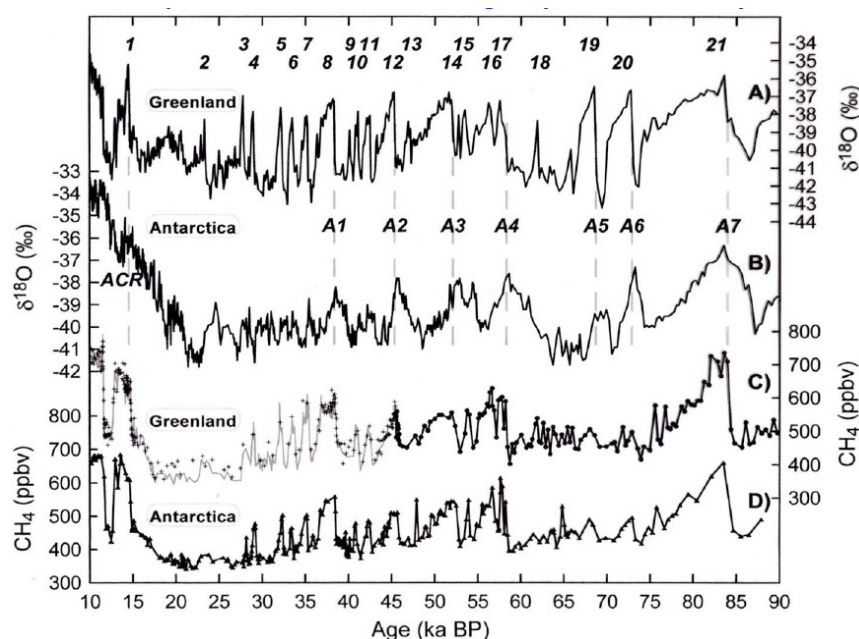


Figure 3.1 Rapid climate change throughout the past 90 thousand years as recorded from ice cores (Blunier & Brook 2001).

Over the last decade, studies of past climate have undergone a profound change from understanding glacial-interglacial climate change. We now recognise the global prevalence of large amplitude climate shifts on very short time scales (Dansgaard *et al.* 1993; Greenland Ice-core Project Members 1993; Grootes *et al.* 1993). What was formerly considered 'noise' in the Greenland archives is now well established to be real climate signal (Alley *et al.* 1995). Twenty-two separate interstadial events (brief returns to warmer climate) have been recognised in the Summit ice core records (Figure 3.1). Huge volumes of ice-rafted debris are recognised roughly every 7,000 years in

North Atlantic sediments as armadas of icebergs were shed from continental ice sheets (Ruddiman *et al.* 1980; Heinrich 1988; Hemming 2004). Antarctica warms several thousand years before Greenland, a signal that is most likely the result of changes in the deep ocean structure and circulation. Collectively these observations represent a new challenge for palaeoclimate studies. One of the largest outstanding questions in our field is: what mechanisms cause these large and rapid shifts, Heinrich, deglacial and interstadial, and specifically what is the role of ocean circulation in their realisation?

The role of the deep ocean in climate change has been a central theme of palaeoceanography from the early days of the field. As the locus of nearly all the mass, thermal inertia and carbon in the ocean-atmosphere system, the deep ocean's overturning rate is a crucial parameter in understanding past climates, both in their steady state and in their propensity for rapid shifts. Today the work of transporting equatorial heat to the high latitudes is roughly evenly divided between the ocean and the atmosphere. The portion of this heat transport that can be attributed to the overturning circulation seems to be variable on both glacial-interglacial timescales and possibly on centennial-millennial timescales.

One of the most robust results of paleoceanography is that during glacial periods the volume of southern source waters in the Atlantic increases while northern source waters shoal and are volumetrically less important (Boyle & Keigwin 1982; Curry & Lohmann 1983; Boyle & Keigwin 1985; Oppo & Fairbanks 1987; Raymo *et al.* 1990; Labeyrie *et al.* 1992; Oppo & Lehman 1993; Oppo & Horowitz 2000). Nutrient based tracers also leave clear signatures of reconfiguration of deep and intermediate depth ocean circulation during times of abrupt climate change (Boyle & Keigwin 1987; Marchitto *et al.* 1998). These deep-water circulation changes are central to understanding the glacial-interglacial CO₂ changes (Sigman & Boyle 2000). However, nutrient-based reconstructions cannot tell us about rates or other physico-chemical water mass properties. Several proxies that contain dynamic information have been used to look at past ventilation rates including mean sortable silt grain size (Bianchi & McCave 1999), ²³¹Pa/²³⁰Th activity ratios (McManus *et al.* 2004; Fig. 3.2), density reconstructions (Lynch-Stieglitz *et al.* 1999) and radiocarbon (Broecker *et al.* 1988; Shackleton *et al.* 1988; Duplessy *et al.* 1989; Keigwin 2004). However, we are still far from being able to quantify ocean circulation rates even in the recent past.

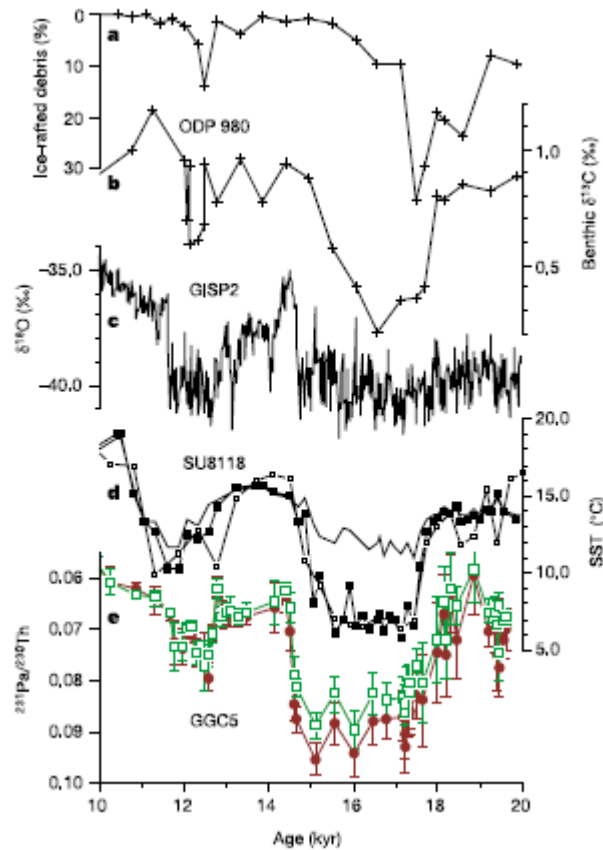


Figure 3.2 Deglacial records (20 to 10 thousand years ago) of ocean circulation and climate in the North Atlantic region (McManus *et al.* 2004). a. Ice-rafted debris record from ODP Site 98025. b. Benthic foraminifera $\delta^{13}\text{C}$ from ODP Site 98025. c. $\delta^{18}\text{O}$ in Greenland ice. d. Sea surface temperature estimates from the subpolar North Atlantic. e. Sedimentary $^{231}\text{Pa}/^{230}\text{Th}$ from GGC5.

Recently, Bryden *et al.* (2005) published a high profile but contentious article suggesting that the Atlantic Meridional Overturning Circulation (MOC - the Atlantic ‘limb’ of the THC) might have already slowed by 30% since 1992, with southward deep-water flow being replaced by an increased recirculation of surface waters in the eastern Atlantic. Critics of this work point out that just five discrete ‘snapshots’ of the ocean state since 1957 are set against the naturally variable background of the ocean system. Decades of data would be necessary to conclusively reveal any anomalous changes to the THC (Kerr 2006). The Bryden study illustrates one of the major difficulties with studying anthropogenic change; ideally their results, and those of others, would be interpreted against long time-series of ocean circulation, but these records simply do not exist. While a few instrumental time-series go back to the mid 20th century, (Østerhus & Gammelsrod 1999; Hansen *et al.* 2001), these are rare and restricted to a few locations.

In addition to climate-driven changes in ocean dynamics, about one third of the CO_2 released in the atmosphere by anthropogenic activities has been absorbed by the world’s oceans. The uptake of carbon dioxide increases the acidity of the ocean and reduces the carbonate saturation state, which affects marine organisms that form calcareous skeletons or shells. In order to

understand ocean acidification and its possible impacts, it is important to understand the history of carbon in the marine realm. Once dissolved in seawater, CO_2 can either be used by photosynthesis or other biological processes, or remain free in its different dissolved forms in the water. As CO_2 dissolves in the ocean it reacts with water molecules (H_2O) and forms carbonic acid. Most of this acid dissociates into hydrogen ions (H^+) and bicarbonate ions (HCO_3^-). The increase in H^+ ions reduces pH and the oceans acidify. The average pH of today's surface waters is 8.1, which is approximately 0.1 pH units less than the estimated pre-industrial value 200 years ago. Coral ecosystems may well be affected by ocean acidification, but future predictions of acidification are limited as the complex carbon cycle is poorly constrained.

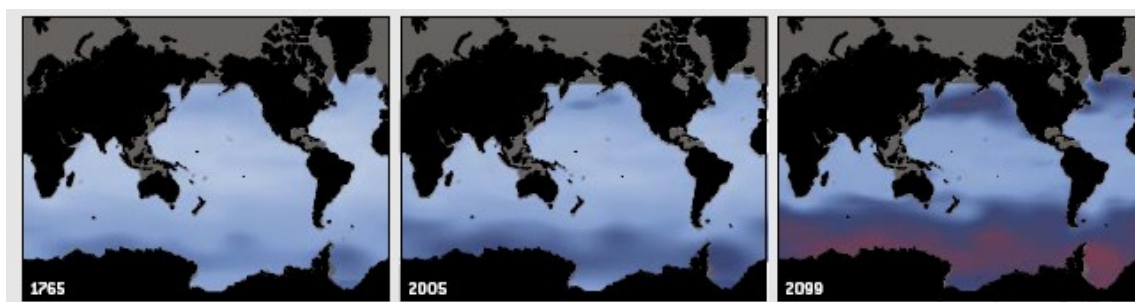


Figure 3.3 Before the Industrial Revolution (*left*), most surface waters were substantially 'oversaturated' with respect to aragonite (*light blue*), allowing marine organisms to form this mineral readily. But now (*centre*), polar surface waters are only marginally oversaturated (*dark blue*). At the end of this century (*right*), areas such as those surrounding Antarctica, are expected to become undersaturated (*purple*), making it difficult for organisms to make aragonite and causing aragonite already formed to dissolve. (Doney 2006)

Timescales and themes of the TRACES climate studies:

Two main timescales are identified for the TRACES programme with dual aims: (1) to understand the role of ocean circulation in a changing earth climate system and (2) to examine these effects on cold-water coral habitats and biodiversity. Investigations of the recent past (millennia) coupled with instrumental records will provide a clearer picture of anthropogenic changes to ocean chemistry and circulation. Records of the past 25,000 years and beyond will provide unique information on ocean circulation in a strongly disturbed and dynamic climate, i.e. the abrupt transitions described above.

During TRACES we intend to address climate questions in the following areas:

- Links between global climate and the rate of ocean circulation
- Recent and long term history of carbon cycle and ocean acidification
- Deep ocean productivity and nutrient cycling and trophic changes

3.1.2 Why use corals for paleoclimate?

The deep and intermediate ocean play a crucial role in modulating global climate during times of rapid climate changes, but sedimentary archives of climate often lack the temporal resolution to constrain rapid events (Figure 3.2 shows some of the highest resolution sedimentary data available in the north Atlantic). Of course marine sediments have given valuable information on long term variations but, with rare exceptions, these archives are of most use over timescales of thousands to hundreds of thousands of years, and factors such as bioturbation, slow sedimentation rates, and diagenetic alteration often limit our ability to interpret records over short timescales (10s to 100s of years). Though the collection of high sedimentation rate cores has accelerated in the last 10 years, the extent to which the deep ocean participates in abrupt change is still under-constrained. In addition, most absolute age models in sedimentary cores depend on radiocarbon dating which can be strongly biased during times of rapid change. Cold-water corals show great promise as deep ocean archives: they are long-lived (Druffel *et al.* 1990; Druffel *et al.* 1995), are found in a broad depth and geographic range (Freiwald *et al.* 2004; Roberts *et al.* 2006), and their skeletons are ideal for U-series and ¹⁴C dating (Adkins *et al.* 1998; Risk *et al.* 2002; Smith *et al.* 1997). Many species deposit calcium carbonate skeletons continuously which record environmental information through the incorporation of trace elements and isotopes in amounts that reflect, in part, the physical and chemical conditions of the coral's growth environment (Chave 1954; Weinbauer & Velimirov 1995; Heikoop *et al.* 2002; Williams 2005).

Over the last few years the skeletons of fossil cold-water corals have been used more and more to answer key climate and palaeo-biogeographic questions. The chemical composition of a cold-water coral skeleton records information about the water mass in which it lived. By sampling along the growth axis in modern or fossil corals we can produce records comparable in resolution to ice cores. For example, the solitary coral *Desmophyllum dianthus* (Fig. 3.4) has been shown to live for ~100 years (Adkins *et al.* 2004) and has been used to create decadal scale records of ocean chemistry (Adkins *et al.* 1998; Eltgroth *et al.* 2006; Robinson *et al.* 2007). By analysing multiple individuals, for example from piles of fossil corals, longer records can be generated (Frank *et al.* submitted). Colonies of other coral groups, notably antipatharian corals, can live for several thousand years (Roark *et al.* 2005, 2009).

In summary cold-water corals are excellent climate archives because:

- 1) They form skeletons that can be sampled for geochemical analyses
- 2) Chemical signatures of growth environment are recorded in the skeletons
- 3) They have a global distribution (geographic and bathymetric)
- 4) Their longevity leads to long records
- 5) Sub-sampling can yield high resolution records
- 6) Fossil skeletons can be dated using radioactive decay methods

In addition, in some settings cold-water corals trap sediments efficiently, providing a direct link to more traditional palaeoceanographic studies (e.g. stable isotopes in Foraminifera). Those can provide additional stratigraphic information for the coral containing sediments and reef evolution through time and may help to identify diagenetic processes that influence coral records.

3.2 Growth rates and dating of ancient corals

3.2.1 Growth rates

For climate studies on any timescale it is important that we know the growth rate of coral species. There are a variety of methods for estimating growth rate, depending on the growth morphology and skeletal architecture. The radioactive decay of ^{210}Pb (half life of ~ 22.3 years) allows longevity studies of up to ~ 150 years (Adkins *et al.* 2004).

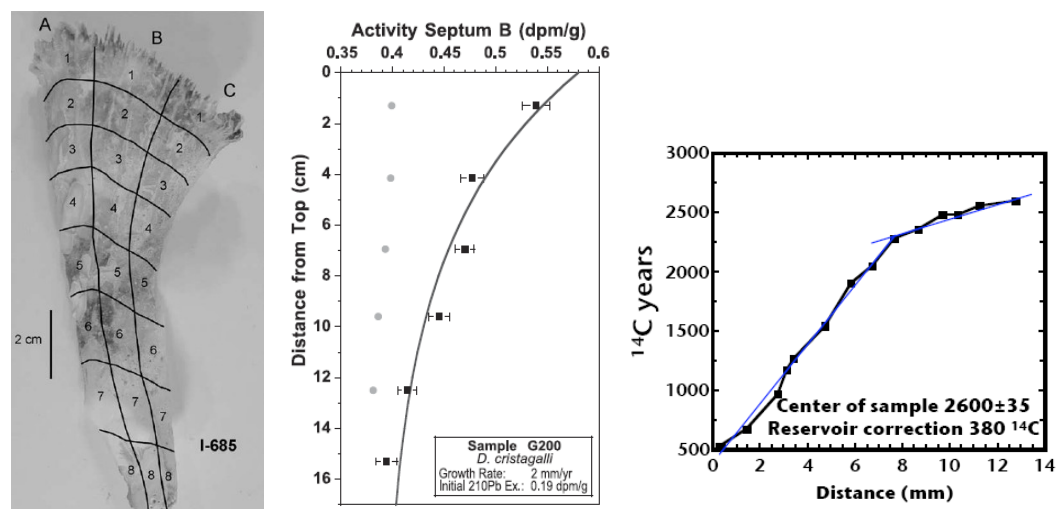


Figure 3.4 Left panel: Image of sub-sampling scheme for *Desmophyllum dianthus* coral. Centre panel: ^{210}Pb data along growth axis of *D. dianthus* used to generate age model (Adkins *et al.* 2004). Right panel: Radiocarbon transect across a specimen of *Leiopathes glaberrima* with an age of ~ 2377 years (Roark *et al.* 2006).

Radiocarbon analyses produced using Accelerator Mass Spectrometry (AMS) can be used to reconstruct the life-spans and growth rates of calcium carbonate and proteinaceous cold-water corals in two ways. First, radiocarbon ages can be calculated using the radioactive decay equation and accounting for the changing $^{14}\text{C}/^{12}\text{C}$ ratio of the atmosphere to estimate when a coral started growing, when it died and its radial growth rate (e.g. Druffel *et al.* 1995; Adkins *et al.* 2002; Roark *et al.* 2005, 2006). The precision decreases with increasing age, but this method can be applied to samples up to $\sim 50,000$ years old. The second method is based on ‘bomb radiocarbon’. In the late 1950s through early 1960s nuclear weapon tests produced an excess

of ^{14}C in the atmosphere that has subsequently invaded the surface and mid-depth ocean. Since we know the timing and shape of this curve relatively well, we can compare it to that measured in corals to produce a stratigraphy. This method works best with proteinaceous corals as they incorporate recently exported particulate organic carbon (POM) from surface waters (e.g. Roark *et al.* 2005, 2006, 2009; Sherwood *et al.* 2005c) but can also be used in species with carbonate skeletons living in waters shallow enough that the bomb carbon has penetrated to the those depths (e.g. Roark *et al.* 2005).

3.2.2 Dating fossil specimens

Corals that are collected dead (fossil) can be precisely dated to find out when they were alive so palaeoclimate records can be placed in a chronological context with respect to other climate studies. Again, methods for this type of dating rely on radioactive isotopes.

As described above, radiocarbon analyses can be used to date corals up to about 50,000 years old. Scleractinian corals make their skeletons from aragonite and incorporate sufficient uranium to be dated using the decay of uranium to thorium (e.g. Mangini *et al.* 1998; Cheng *et al.* 2000). Making the assumption of an initial $^{230}\text{Th}/^{238}\text{U}$ ratio of zero and a seawater $^{234}\text{U}/^{238}\text{U}$ ratio we can use the ingrowth of ^{230}Th (analysed by mass spectrometry) as a chronometer (Fig. 3.5a). Each coral has to be cleaned rigorously to remove contamination that may bias the final age (Fig. 3.5b). Once clean, the uranium and thorium are separated from the rest of the skeletal material. Advances in mass spectrometry now allow precisions that can be better than a few hundred years even for corals of up to 400,000 years age (Adkins *et al.* 1998; Mangini *et al.* 1998; Cheng *et al.* 2000; Schröder-Ritzrau *et al.* 2003; Robinson *et al.* 2005). High precision U-series dating can also be used on samples as young as a few decades (Frank *et al.* 2004; Pons Branchu *et al.* 2006).

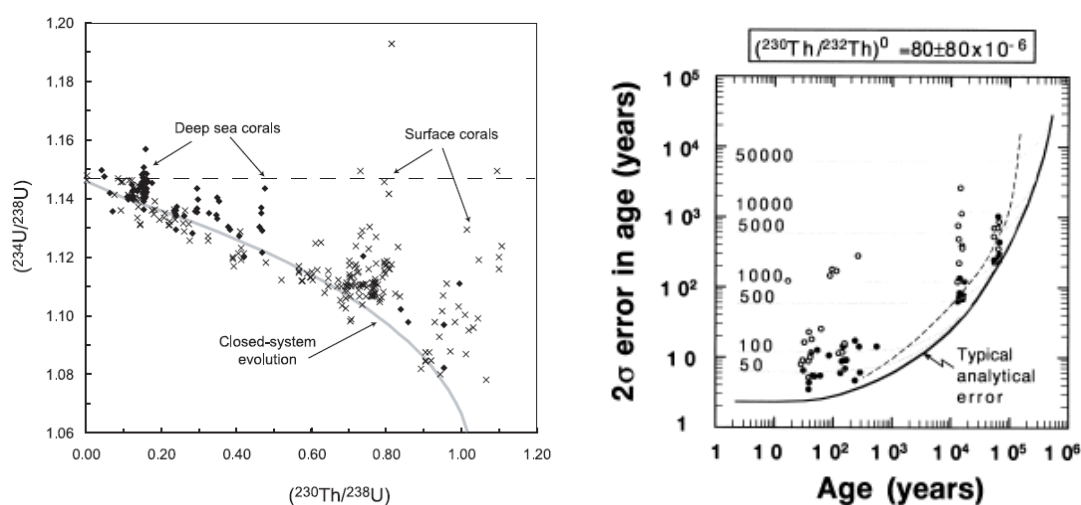


Figure 3.5 Left: Comparison of measured deep-sea (diamonds) and shallow-water coral (crosses) $(^{234}\text{U}/^{238}\text{U})$ and $(^{230}\text{Th}/^{238}\text{U})$ values (after Robinson *et al.* 2007). The solid gray line shows the isotopic evolution of a closed system starting with a $(^{234}\text{U}/^{238}\text{U})$ of 1.1465 and a

($^{230}\text{Th}/^{238}\text{U}$) of zero. Deviations from this line are symptomatic of diagenetic alteration from a closed system. The dashed line is at the modern seawater ($^{234}\text{U}/^{238}\text{U}$) activity ratio. Right: Age plotted versus $2s$ error. Solid points are the uncorrected deep-sea coral data and are close to the typical analytical uncertainty (solid black line). After correction (open circles) points are shifted to younger ages and larger errors. Higher ^{232}Th results in a larger absolute age uncertainty. For young ages, the error is dominated by uncertainty in the initial Th correction. The older the age and the smaller the measured [^{232}Th] the lower the relative age error.

3.3 Coral archives over long time periods

In order to address the outstanding climate questions discussed previously, dated deep-sea coral skeletons will be analysed geochemically. But how do we convert geochemical parameters into climate records? The cold-water coral proxy field is in its infancy, many years behind the study of other proxies in Foraminifera. We have several notable successes, including the study of radiocarbon in the past. However, we are not yet in a position to exploit coral skeletons to their full potential. Ongoing studies and research that will happen as a part of TRACES will improve our knowledge, capabilities and collections allowing us to address the questions raised in this chapter of the Science Plan. Some of the successes and approaches with promise for future studies are laid out below both for scleractinian and gorgonian corals. TRACES will promote further innovative approaches as they develop.

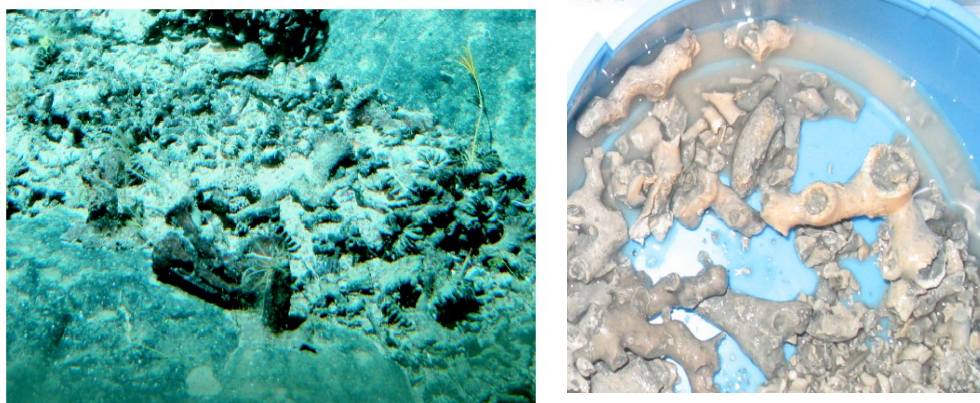


Figure 3.6 Left: Image of fossil *D. dianthus* on seafloor viewed from the *Alvin* submersible. Right: Fossil corals collected from mound sediments using *RV Marion Dufresne*.

3.3.1 Reconstructing seawater $\Delta^{14}\text{C}$ using cold-water corals

Radiocarbon is a versatile tracer of past climate; its radioactive decay provides an internal clock with which to assess the rates of processes, and it can be used to trace the movement of carbon through the Earth's system (e.g. Stuiver *et al.* 1983; Duplessy *et al.* 1989; Broecker *et al.* 1995; Beck *et al.* 2001; Hughen *et al.* 2004). In the modern ocean the distribution of $\Delta^{14}\text{C}$ is one of our most powerful constraints on the overturning rate of the deep-sea and atmosphere-ocean carbon exchange. Thus far the most successful palaeoclimate studies from cold-water coral skeletons have been reconstructions of the radiocarbon content of seawater. Radiocarbon is produced in the upper atmosphere, and enters the ocean through exchange with surface waters. The difference between the radiocarbon content of a

deep-water mass at its site of formation and in the deep ocean can act as a clock, providing a measure of how long the deep water has been isolated from the atmosphere. The radiocarbon content of deep-sea corals has been extremely useful in putting constraints on ocean circulation both in the last few decades (Sherwood *et al.* 2008a) and further back in time (e.g. Adkins *et al.* 1998; Mangini *et al.* 1998; Goldstein *et al.* 2001; Schröder-Ritzrau *et al.* 2003; Frank *et al.* 2004; Robinson *et al.* 2005; Eltgroth *et al.* 2006).

From a modern calibration (Adkins *et al.* 2002) we know that this initial radiocarbon value is the value of the dissolved inorganic carbon in which the coral grew (Fig 3.7). In all species that have been tested, the aragonite skeletons of cold-water corals reflect the radiocarbon content of the dissolved inorganic carbon of the water column.

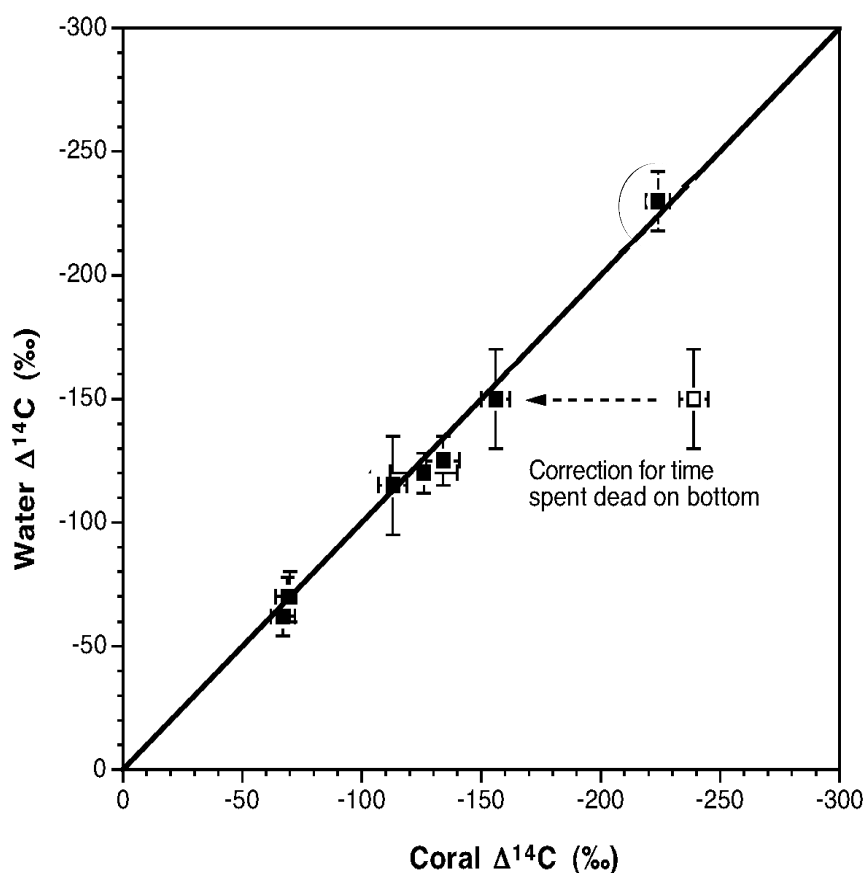
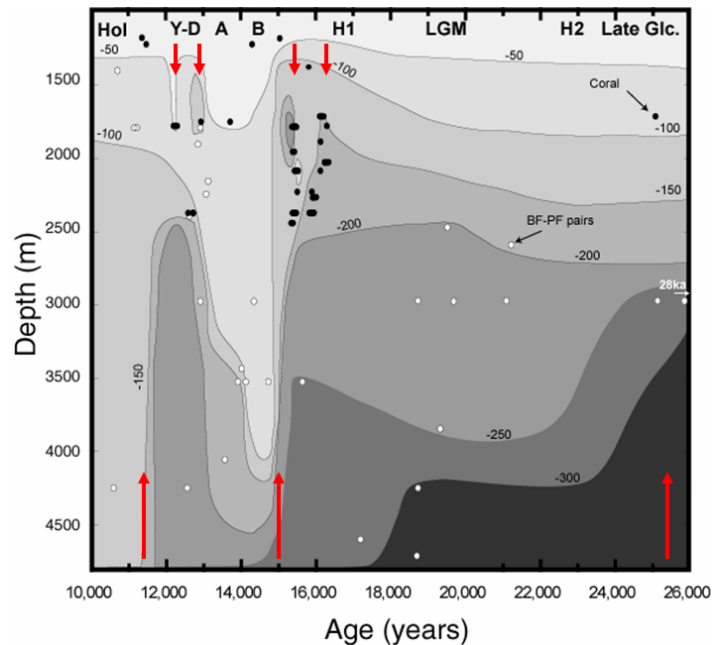


Figure 3.7 Modern calibration of $\Delta^{14}\text{C}$ in scleractinian deep-sea corals (after Adkins *et al.* 2002). This one to one relationship has been tested for 8 different scleractinian coral species (*Caryophyllia* sp., *Enallopsammia rostrata*, *Flabellum impensum*, *F. marenzelleri*, *Solenosmilia variabilis*, *Stephanocyathus campaniformis*, *S. nobilis*, *Desmophyllum dianthus*) by Adkins *et al.* (2002). The samples range in age from 30 to 850 calendar years. The open black square shows how a ^{14}C date is transformed into the $\Delta^{14}\text{C}$ at the time of death by correction with a ^{230}Th age. After correcting these for ^{14}C decay since death of the coral, all data fall on a 1:1 correlation line. Two modern *Lophelia pertusa* samples also reflect nearby water column measurements (Frank *et al.* 2004).

By measuring age using U-series and $^{14}\text{C}/^{12}\text{C}$ by AMS (see above) we can use deep-sea corals to directly constrain the initial seawater $\Delta^{14}\text{C}$:

$$\Delta^{14}\text{C}_{\text{deep-water}} = \left(\frac{e^{-14\text{CAge}/8033}}{-\text{CalendarAge}/8266} \right) \times 1,000$$

Figure 3.8 Radiocarbon in the North Atlantic from cold-water corals (black dots) and Foraminifera (white dots) from 26,000 to 10,000 years ago. Dark colours have less radiocarbon than pale colours, and deep water is typically more depleted (Robinson *et al.* 2005). Red arrows highlight times of large radiocarbon shifts in the intermediate (top) or deep (bottom) of the North Atlantic.



The $\Delta^{14}\text{C}$ of cold-water corals has been used in a number of studies to investigate radiocarbon in the past ocean. By combining cold-water coral with benthic and planktonic foraminiferal data from the North Atlantic, Robinson *et al.* (2005) showed that the last deglaciation was marked by switches between radiocarbon-enriched and -depleted waters (Fig. 3.8). Multiple measurements from within a single coral show radiocarbon shifts of more than 100‰, far greater than the full range in the modern North Atlantic water column. Similar results have been obtained from *L. pertusa* corals of the Gulf of Cadiz, which demonstrate a dramatic decrease of seawater radiocarbon even at shallow depths of less than 1000 m during the last glacial maximum and also corals off the slopes of Brazil shown strongly variable radiocarbon seawater level dependent on rapid climate change during the past 20000 years. Over the course of the past 10,000 years seawater radiocarbon of the mid-depth Northeast Atlantic has been variable on millennial and centennial time scales, most likely reflecting changes in Labrador deep convection and export through the east Atlantic (Frank *et al.* in prep.).

3.3.2 New Proxies showing great potential in scleractinian corals

Water Mass mixing: Traditional nutrient-based water mass mixing tracers such Cd/Ca and $\delta^{13}\text{C}$ are strongly affected by vital effects in cold-water corals. There are two new tracers which may circumvent this problem, and these are being developed for use in scleractinian corals. The neodymium isotopic composition of seawater is captured by cold-water corals and is preserved over long time periods (van de Flierdt *et al.* 2006; Robinson & van de Flierdt 2009; van de Flierdt unpublished data; Colin *et al.* in prep.; see

Fig. 3.9a). Different water masses in the ocean display distinct Nd isotopic compositions, whose values are ultimately derived from the continents and delivered to the ocean through weathering, erosion, and particle-seawater interaction and so it can act as a quasi-conservative water mass mixing tracer.

A second potential mixing tracer relies directly on nutrient distributions. Phosphorus is a primary nutrient in the ocean, and has much higher concentrations in nutrient enriched southern source water. A number of studies have shown a correlation between P/Ca in seawater and P/Ca in coralline aragonite (Montagna *et al.* 2006; Anagnostou *et al.* 2007, 2008; LaVigne *et al.* 2008; see Fig. 9b). Phosphorous to calcium variations may also reveal changes in the inventory of the ultimate limiting nutrient of the ocean, a primary control on ocean productivity.

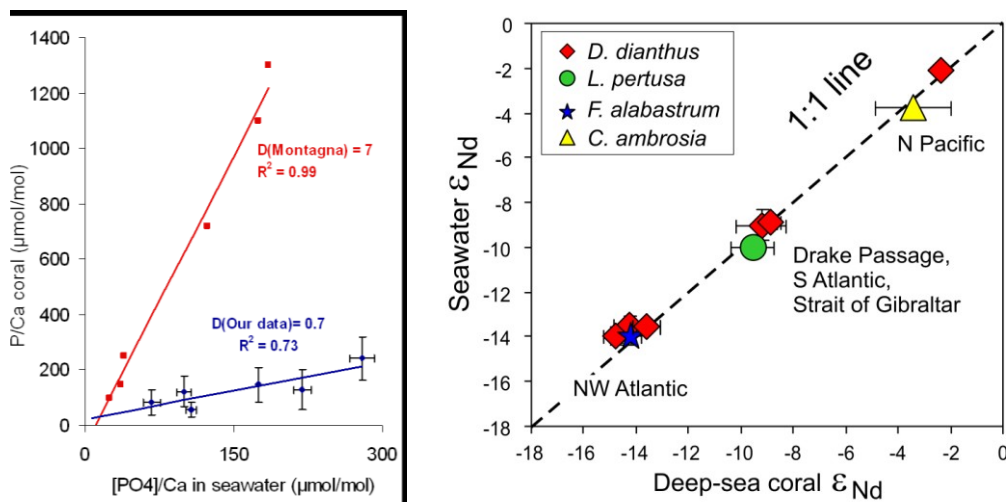


Figure 3.9 Left: Modern calibration of the neodymium isotopic composition in four different species of cold-water corals. All coral points fall on a 1:1 line, allowing us to use the Nd isotopic composition of carefully cleaned cold-water coral aragonite as a proxy for the water column (unpublished data from T. van de Flierdt). Right: Phosphorous/calcium global calibrations against seawater data from nearby hydrographic stations (unpublished data from Montagna *et al.* (2006) and Sherrell). Both calibrations, while defined by few points at present, show good linearity and negligible intercepts. However the slopes differ. TRACES will help resolve the reasons behind this discrepancy allowing P/Ca to be used as a nutrient tracer.

Temperature: Several tracers show promise for reconstructing temperature based on stable isotope and element fractionation (Fig. 3.10a). The first is the $\delta^{88/86}\text{Sr}$ ratio shown in Rüggeberg *et al.* (2008). The second is based on the doubly substituted isotopes of carbon and oxygen (C-13-O-18 bonds) in carbonate minerals which are sensitive to growth temperatures, independent of bulk isotopic composition (Eiler 2007). A third technique is under exploration but recently first evidence has been presented on the use of the Li/Mg ratio as strongly dependent on coral growth temperatures (Marchitto *et al.* 2008; Montagna *et al.* in prep.).

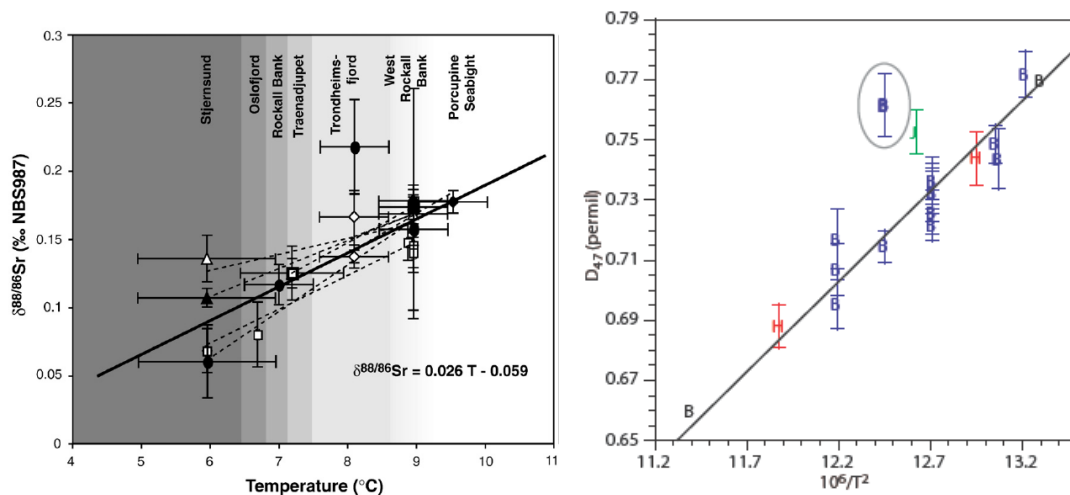


Figure 3.10 Left: Stable strontium isotope ratios ($\delta^{88/86}\text{Sr}$) of *Lophelia pertusa* samples from the north east Atlantic against ambient temperature. All regression lines (dashed lines) show similar positive slopes around 0.025‰ per °C indicating temperature dependent strontium isotope fractionation. The weighted mean regression line (thick solid line) expresses the mean $\delta^{88/86}\text{Sr}$ -temperature relationship ($0.026 \pm 0.003\text{‰}/^\circ\text{C}$) of *L. pertusa* (Rüggeberg *et al.* 2008). Right: ‘Clumped’ ^{18}O - ^{13}C bonds in modern cold-water coral skeletons versus their growth temperature (here T is in °K, blue points are *Desmophyllum dianthus*, red points are *Caryophyllia* sp. and the one green point is *Enallopsammia rostrata*). D_{47} is a measure of the number of carbonate groups with both ^{13}C and ^{18}O atoms relative to their random distribution. Positive numbers are enrichments, or clumps, of the rare isotopes. The solid line is the temperature relationship for inorganic carbonates made in the lab, not a curve fit to the coral data. Overall this new thermometer is good to $\pm 1^\circ\text{C}$ and shows great promise for past temperature reconstructions of the deep ocean.

3.4 Coral archives over the last few thousand years

Bamboo and black corals have been shown to be extremely long-lived, with great potential for reconstructing high resolution records of the last millennia, particularly given their relatively straightforward concentric growth bands that appear much like tree rings. The most successful applications have been made using the stable isotopes of N and C in the organic skeletons of gorgonian and antipatharian corals which reflect the composition of their food sources, and thus find application as tracers for productivity and nutrient cycling in the surface ocean (Heikoop *et al.* 2002; Sherwood *et al.* 2005a). Coupling isotopic studies in the organic and carbonate components of Primnoidae and Isididae corals allows simultaneous determination of the deep and surface signatures of $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and $\Delta^{14}\text{C}$ (Sherwood *et al.* 2008b). Corals in the Gulf of Mexico have a depleted $\delta^{15}\text{N}$ signature relative to specimens off the south east USA due to the large input of low $\delta^{15}\text{N}$ fertilizers via the Mississippi River (Williams *et al.* 2006). Repeated depletions of $\delta^{15}\text{N}$ are thought to reflect changes to the plankton community composition, specifically a shift in the ratio of phytoplankton to zooplankton (Williams *et al.* 2007). Some studies have also shown a potential for trace metals to record temperature (Bond *et al.* 2005). Using these and developing approaches offers an exciting new direction for determining past climate conditions at an unprecedented temporal resolution.

3.5 What factors limit our ability to use corals?

There are two crucial limitations to our current ability to make use of the full potential of coral skeletons as palaeoceanographic archives: development of proxies and collection of key samples. Both of these limitations will be overcome during the TRACES programme.

3.5.1 Vital effects

Like many other calcifying organisms, cold-water corals can exert a strong control over the chemical composition of the elements that are incorporated into their skeletons, phenomena known collectively as ‘vital effects’. The stable isotopes of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ show strongly coupled micron-scale variations in cold-water corals, and are ubiquitous in the records from many coral genera (McConnaughey 1989; Smith *et al.* 2000). We now understand in greater detail how physiology affects stable isotope records (Grottoli 1999; Grottoli 2002; Adkins *et al.* 2003; McConnaughey 2003; Blamart *et al.* 2005; Blamart *et al.* 2008). Similarly, trace element distributions show strong gradients across skeletal features in *Desmophyllum* and *Lophelia* (Figs. 3.11 and 3.12) (Meibom *et al.* 2004; Cohen *et al.* 2006; Sinclair *et al.* 2006; Gagnon *et al.* 2007). The coupled variations appear to originate in the initial rapidly-deposited skeleton (centres of calcification) which have a distinct trace element (and stable isotope) composition to the rest of the skeleton. Mathematical models suggest that these variations could arise from chemical changes as the coral modifies its calcifying environment (Adkins *et al.* 2003; Sinclair 2005; Gaetani & Cohen 2006; Sinclair & Risk 2006; Gagnon *et al.* 2007).

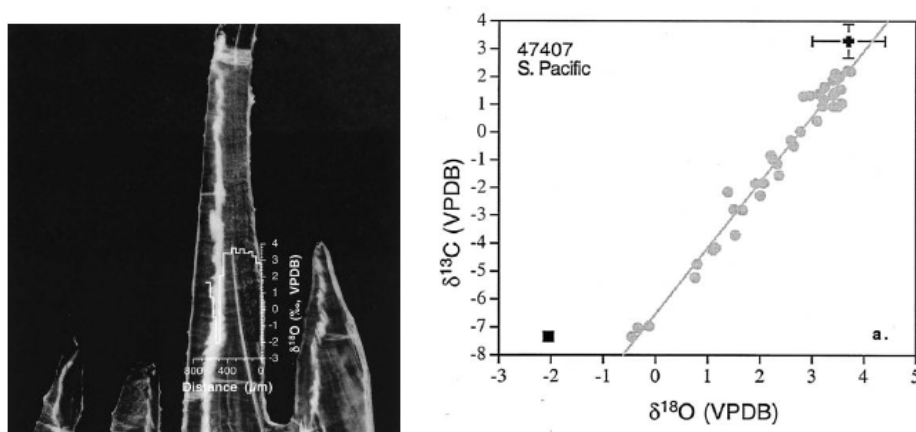


Figure 3.11 Left: A transect of $\delta^{18}\text{O}$ across a single septum of *D. dianthus* shows a large deviation in the centre of calcification. Right: Both $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ from the same corals show the wide fractionation present as a result of biomineralisation. From Adkins *et al.* (2003).

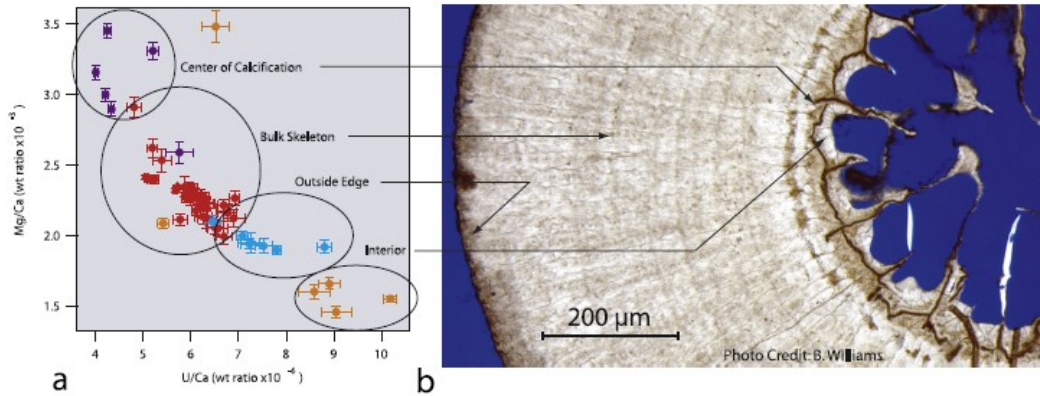


Figure 3.12 Laser analyses across a section of *Lophelia pertusa*. There are systematic variations in Mg/Ca and U/Ca that coincide with different section of the coral. From Sinclair *et al.* (2006).

In order to use corals for climatic reconstruction it is important that we document and understand these processes. A second valuable outcome of this work will be to better understand the strategies that corals use to adapt to their environment e.g. growth rates (see above).

3.5.2 Proxy calibration

One of the most significant barriers to reconstructing climate from cold-water corals is a lack of systematic calibration studies. There are two major reasons for this. Firstly, coral samples are often from deep ocean environments where there are no long-term *in situ* observations against which to compare coral records. Secondly, the expense and difficulty in obtaining good coral samples has typically limited our ability to collect multiple specimens from across environmental gradients, so calibration studies thus far have by necessity been of an opportunistic *ad hoc* nature.

3.5.3 Sample collections

The lack of focused cold-water coral collections in key climate locations is the second major limitation in our ability to use them as palaeoceanographic proxies. So far sampling has mainly been opportunistic, piggy-backing on other research cruises, or has been single-PI driven. Beyond the deep-sea coral community, collecting cold-water corals for palaeoclimate research has been viewed in the context of a ‘fishing trip’ where reviewers are not convinced that suitable coral material can be found or collected. Through the interdisciplinary collaborations of TRACES we will be able to overcome these barriers for the first time by pulling together cross-cutting expertise that enables us to locate and collect the samples that are needed to answer key climate questions.

3.6 Using geochemistry to help understand deep-sea coral biology and biogeography

The geochemical techniques outlined in this chapter have been heavily focused towards climate-driven questions. The data that are collected as part of this effort will have important implications for our understanding of how and why corals are distributed over time. In addition, we will be able to use our records of environmental variability to support our knowledge of the tolerances of cold-water corals to environmental change.

An excellent example of this interaction comes from the long term distributions of coral growth over time (Fig. 3.13). The growth of cold-water coral species in the North Atlantic may be related to a number of environmental conditions, such as food supply, current activity, and sedimentation - all of which have changed through time. Constructional cold-water corals grew plentifully in the north east North Atlantic (above 50°N) during the past interglacial periods, but during glacial times they are much less common (Frank *et al.* 2005). In contrast, similar species appear to be sustained in the temperate North Atlantic during glacial times. A similar story emerges on the slopes of Mauritania and within the Gulf of Cadiz. The solitary coral *Desmophyllum dianthus* has also experienced significant population changes through time, with few individuals alive today, or during the last 10,000 year Holocene period, but with thriving populations during the last glacial, particularly during times of abrupt climate change (Robinson *et al.* 2007).

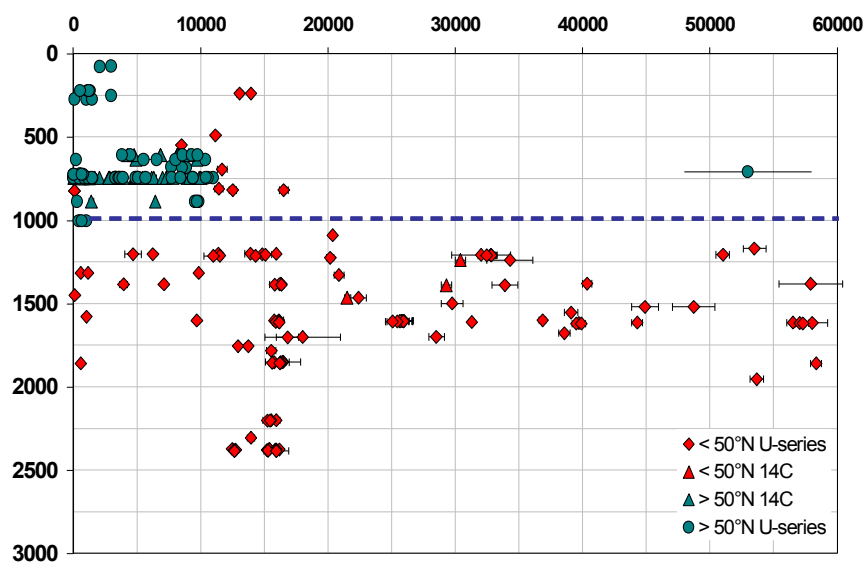


Figure 3.13 Ages of cold-water corals determined by using either U-series dating or ^{14}C dating. Green symbols represent corals from the northern North Atlantic between 50° and 70°N, while red symbols reflect corals from the temperate east and west Atlantic between 30°N and 50°N. Note that red symbols mostly represent solitary *Desmophyllum dianthus* corals while green symbols mostly reflect reef framework-forming *Lophelia pertusa* corals. Recent dating of *L. pertusa* from the Mauritanian slope has shown a relationship between coral appearance in this region and cold northern Hemisphere climate conditions (Eisele *et al.* unpublished data) implying that such southern areas become refuges for cold-water corals in glacial periods.

Overall, only relatively few corals (hundreds of specimens) have so far been dated, and further work is needed to make these initial patterns more robust and detailed. TRACES aims to better understand the linkages of coral habitats throughout the Atlantic and this temporal dimension will form a crucial piece of supporting evidence in understanding coral habitat connectivity and biogeography.

3.7 How will TRACES realise the palaeoceanographic potential of cold-water corals?

To address the outstanding questions on past and recent ocean climate changes requires a dedicated effort to collect depth and zonal basin scale sections of corals from across the Atlantic. The corals then need to be dated to determine growth rates and ages using accurate dating techniques. Innovative technologies need to be explored to measure new tracers and proxies for ocean climate reconstruction. There is also a clear need to further calibrate proxies through comparison of the geochemical composition of modern coral specimens with seawater bathing them. A concerted effort to combine geochemical techniques, a dedication to cutting edge technologies, and close collaboration through different disciplines of TRACES will allow us to overcome the barriers identified above.

3.7.1 Task 1: Establish focused collections of corals for geochemical proxy calibrations and in places of key climate importance

Our initial goal will be to make focused collections that provide samples suited to calibration of tracers and proxies. Second, to achieve a well constrained picture of modern and past ocean circulation from corals at least three trans-Atlantic sections are needed. These sections are well suited to the connectivity and biodiversity aims of TRACES:

- 1) A North Atlantic transect along the sills of deep water injection to the Atlantic Basin will allow investigation of modern and past exchange and ventilation along the source regions of deep and northern intermediate water formation.
- 2) A trans-Atlantic section close to 30° N will constrain the southward flow of deep and intermediate water in the West Atlantic and resolve the re-circulation in the east Atlantic.
- 3) A crossing of the South Atlantic at ~30° S to investigate temporal and cross Atlantic changes of water mass properties and flow of South Atlantic intermediate and deep waters towards the North.

We emphasise here that both sampling corals at various depth and sampling key species is crucial to the success of TRACES as we need to identify the depth and spatial structure of the thermohaline circulation in the Atlantic.

Key species are aragonite forming *D. dianthus*, *L. pertusa* and *M. oculata* corals because they occur at a variety of depths and because they are sufficiently long-living to provide measures of decadal changes in ocean climate. However, other coral taxa such as gorgonians and antipatharians will be of great interest to construct high resolution time series from individual skeletons or to make use of the particular recording of surface and deep water properties as outlined above.

Given the two identified timescales we need to establish complementary sample collections along those transects consisting of both modern and ancient (fossil) material. Modern cold-water corals are needed at various depths that cross orthogonal geochemical space allowing us to decouple the influences of various parameters such as temperature, alkalinity and productivity. Coral sampling will be accompanied whenever possible by seawater sampling to investigate the transfer of tracers and proxies into the coralline aragonite or calcite. Ancient coral specimens are needed to resolve changes in intermediate and deep-water circulation in the past.

Many samples have already been collected, particularly over the past 10 years along the west and east Atlantic. However, as a programme TRACES is designed to provide trans-Atlantic sampling of similar species and at variable water depths. This task will be achieved through participation of all partners of the TRACES project and is crucial to further research on ocean climate and coral biology.

3.7.2 Task 2: Dating of corals

Once in possession of large sets of fossil corals a major emphasis will be placed on dating. This aspect of TRACES is of crucial importance for ocean climate research and other aspects of TRACES such as understanding coral habitat development through time and space. We anticipate that thousands of coral specimens will be dated to provide statistically meaningful information on the timing of coral growth episodes. Moreover, they will provide new insights on the life span and growth rates of corals needed to understand calcification and growth processes and to assess their potential to recover from damage. With respect to the two identified timescales for ocean climate research a number of different dating techniques are needed as outlined above.

Within TRACES we plan to extend the database of coral ages by at least a factor of ten. This will improve our understanding of the temporal framework of coral development across the Atlantic. The need for rapid and precise dating of corals will steer new developments in mass spectrometry and should further promote inter-calibration exercises. Rapid continuous flow ^{14}C dating and ICP-QMS U-series dating will be explored to provide cost-effective age screening procedures to identify the most valuable samples for ocean climate research.

3.7.3 Task 3: Tracer and proxy calibration and application

To measure ocean climate change on well-dated coral collections a number of geochemical techniques have been identified that we intend to apply and further develop. In addition, TRACES will encourage the development of new proxies for climate and ocean circulation.

Several of the proposed tracers are well established and have been tested during the past decade and TRACES will make full use of them in the trans-Atlantic context. Most promising are radiocarbon, neodymium isotopes and clumpy isotopes (Δ^{47}). For well established tracers we intend to develop and improve the analytical techniques defining quality control standards in as many as possible participating laboratories to produce a large number of measurements over the course of TRACES.

Other proxies, including, but not limited to P/Ca, Mg/Ca, B/Ca, B-isotopes, Cd/Ca, rare earth elements/Ca, Li/Mg need further analytical developments and calibration efforts prior to their systematic exploitation on coral collections. Consequently the strategy is twofold. For recently developed tracers and new geochemical proxies we intend to better calibrate those by comparing modern corals and seawater and by carrying out research on the relationship of coral calcification and tracer/proxy incorporation and preservation.

Measuring a suite of geochemical tracers that allow reconstruction of water mass distribution, movement, and temperature along defined ocean transects will provide unprecedented insights for understanding past climate change. So far many efforts to retrieve a quantitative and mechanistic understanding of the ocean's role in climate change are hampered by having single-site, single depth information only. TRACES will overcome this hurdle, bringing our understanding of past ocean dynamics to a new level.

3.7.4 Task 4: Explore vital effects to learn about coral biomineralisation and biological processes

The skeletons of cold-water corals develop in a nearly perfect natural 'laboratory', in which variation in physical (e.g., temperature) or chemical (e.g., salinity or seawater composition) parameters of the ambient environment tend to be small compared to surface ocean processes. In addition, they do not have algal symbionts that can complicate the interpretation of coral-controlled biomineralisation processes. In certain cases, therefore, substantial variation in chemistry and isotopic composition of the skeleton on micrometer to millimetre length scales, particularly across layers of contemporaneous growth, can thus be ascribed to the effects of processes involved in biomineralisation. Techniques that measure trace elements and isotopes at very fine spatial scales will be applied to test models of coral growth. The TRACES programme will provide the opportunity to investigate cold-water corals over a wide range of physico-chemical

environments in the Atlantic Ocean and thus provide the possibility to investigate 'vital effects' systematically. In addition, TRACES will investigate the geochemistry of corals in laboratory environments.

Efforts towards understanding biological processes that result in 'vital effects' on trace elements and isotopes will improve our understanding of coral biology as fractionation occurs during the transport of trace elements within cellular processes. Thus fractionation may provide hints on these transport pathways and internal cellular control processes. Such information is crucial to better constrain internal pH adjustments of these species, their capacity to store nutrients and the role of feeding and cellular seawater circulation as well as oxygen consumption and CO₂ transformation. By understanding biological growth mechanisms we hope to learn about corals' dependence on environmental factors, their sensitivity to changes in temperature and ultimately their resilience to environmental change.

4 Environmental Context

4.1 Mapping & habitats

Maps form the backdrop to all TRACES studies - connectivity, distributions and biogeographic relationships are best depicted in a geographic environment. In addition, benthic maps are an essential tool for seabed management and assessing human impacts on cold-water coral habitats. As conservation efforts develop, repeated habitat mapping will become increasingly necessary in order to monitor any habitat change following protection measures such as fishery closures.

The term ‘habitat’ has been defined by the International Council for the Exploration of the Sea (ICES) as “*a particular environment which can be distinguished by its abiotic characteristics and associated biological assemblage, operating at particular but dynamic spatial and temporal scales in a recognizable geographic area*” (ICES 2006). Habitat mapping, in a broad sense, deals with mapping of the abiotic and biotic components, or parts thereof. *Sensu stricto* it has been defined as “*the activity of plotting the distribution and extent of habitats to create a complete coverage map of the seabed with distinct boundaries separating adjacent habitats*” (MESH project; Foster-Smith *et al.* 2007). A wide range of techniques can be used at a variety of spatial scales, depending on the aims of the survey and budgets available (see for example Coggan *et al.* 2007; Reynolds & Greene 2008). Fosså *et al.* (2005) give an overview of coral mapping strategies used in Norwegian waters to map cold-water coral reef habitat. Traditionally, habitat maps are based on a combination of coverage-type data sets (e.g. multibeam bathymetry, side-scan sonar data), mainly illustrating the abiotic environment, and point- or line-based information (e.g. video data, grab samples) providing ‘ground-truthing’ and biological information.

4.1.1 Mapping methods

The most common methods used for cold-water coral (habitat) mapping are the following (Fig. 4.1):

A. *Multibeam Echosounder (MBES)*

Multibeam echosounders are acoustic systems that can obtain full bottom coverage of the seabed morphology (depth) using a fan-shaped set of acoustic beams oriented in a strip across the platform’s track. The depth grid is acquired through the accurate measurement of the two-way travel time and angles of emission and reception of the sound energy for each of the repeated pulses sent from the transducer. Typically, MBES systems can achieve a swath width of four to seven times the water depth. This illustrates an important characteristic of MBES surveys: a trade-off exists between water depth (and hence seabed coverage) and spatial resolution. In addition, due to absorption effects and spreading losses in the water column, increasing water

depths require lower frequency systems, resulting in lower vertical resolution as well. An overview of typical frequencies, depths, swath widths and resolutions is given in Coggan *et al.* (2007).

Longer-range, lower resolution multibeam echosounders are most often mounted on the hull of a ship. Higher resolution systems are often mounted on other platforms, such as ROVs (Remotely Operated Vehicles, e.g. Foubert *et al.* 2005; see Fig. 4.2b) or AUVs (Autonomous Underwater Vehicles, e.g. Grasmueck *et al.* 2006; see Fig. 4.2d), that can be deployed closer to the seafloor to record greater detail. Towed or autonomous systems, however, may present additional challenges in terms of correct positioning of the vehicle and data. For cold-water coral research, each of these configurations has its uses: the large-scale surveys map the geomorphological setting, and are ideal tools for the identification of large reefs and mounds (Beyer *et al.* 2003). More detailed surveys are used to map the morphology of individual reefs (e.g. by ROV, Huvenne *et al.* 2005) or reef clusters, including the associated current-induced bedforms (e.g. by AUV, Grasmueck *et al.* 2006; see also Fig. 4.3).

In addition to the depth measurements, MBES systems also record the seabed backscatter strength or relative intensity of returned acoustic energy for each of the beams. These data give information about the seabed type, and have the potential to distinguish various benthic habitats, e.g. the occurrence of live/dead coral or different background sediments (e.g. Roberts *et al.* 2005).

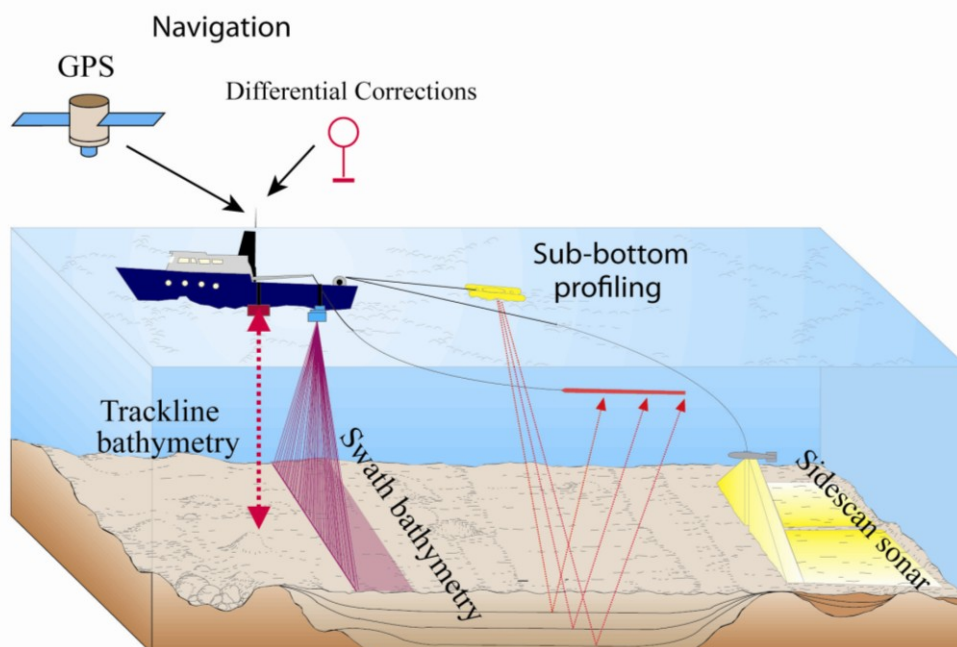


Figure 4.1 Schematic illustration of various tools used for cold-water coral (habitat) mapping (USGS 2008).

B. Side-scan sonar

Side-scan sonars are also acoustic systems using across-track sound pulses. However, the returning energy is recorded at port and starboard side as seabed backscatter as a function of time, not as bathymetry (water depth)

(Blondel & Murton 1997). The systems are commonly mounted on towed platforms, and so can be operated closer to the seabed than MBES and therefore often provide higher-resolution maps. In addition, they have a wider swath angle, which means they can cover a larger surface area for each single line (although they sometimes need to be towed at slower speeds than during an MBES survey). This, together with a lower cost, make side-scan an economical alternative to MBES, although it is important to note that side-scan does not provide bathymetric data. The main drawback, however, especially with towed systems, is positional uncertainty. Ultra Short Base Line (USBL) systems may provide a solution, but add to the survey cost (Coggan *et al.* 2007).

Seabed backscatter from side-scan sonars is determined by: (1) the slope angle towards the acoustic system, (2) the micro-roughness (i.e. grain size) and (3) the physical properties of the seabed (e.g. compaction, water content) (Blondel & Murton 1997). This makes side-scan sonars useful tools for the mapping of cold-water coral habitats. For example in surveys of reef habitats they may be able to distinguish live coral reef and open coral framework from sediment-clogged framework and different types of background sediments, often at a higher resolution than MBES backscatter records. However, non-structural cold-water coral habitats, (biostromes, as opposed to structural bioherms), such as the gorgonian and soft coral habitats of Atlantic Canada (Wareham & Edinger 2007), may be more difficult to characterise as their acoustic signature is likely to be determined largely by the abiotic components, especially coarse glacial and glaciomarine deposits. Mapping these habitats may require using acoustic remote sensing combined with additional tools (such as bottom photography) or the most advanced numerical interpretation techniques, in order to distinguish similar physical environments supporting cold-water corals from those that do not.

As with MBES systems, side-scan sonars are available in different frequencies and resolutions, each with their application for cold-water coral mapping and research. Regional surveys have been carried out over the coral mounds in Irish waters using the 30 kHz TOBI system (Towed Ocean Bottom Instrument, Fig. 4.2a. e.g. Mienis *et al.* 2006; Dorschel *et al.* submitted). Higher resolution surveys of smaller areas use higher frequency sonars (>100 kHz) capable of imaging individual coral colonies such as the large single *Lophelia pertusa* colonies found on the Sula Ridge Reef Complex offshore Norway (Freiwald *et al.* 2002).

In terms of data analysis, the traditional visual interpretation of side-scan sonar and MBES backscatter records can be enhanced by using computer-assisted image analysis techniques, which may make interpretation less subjective (e.g. Huvenne *et al.* 2002; Hühnerbach *et al.* 2007). However, any type of acoustic/remote sensing data always has to be accompanied by adequate groundtruthing, because backscatter levels and patterns may not be unique and therefore may need to be identified separately for each study area.

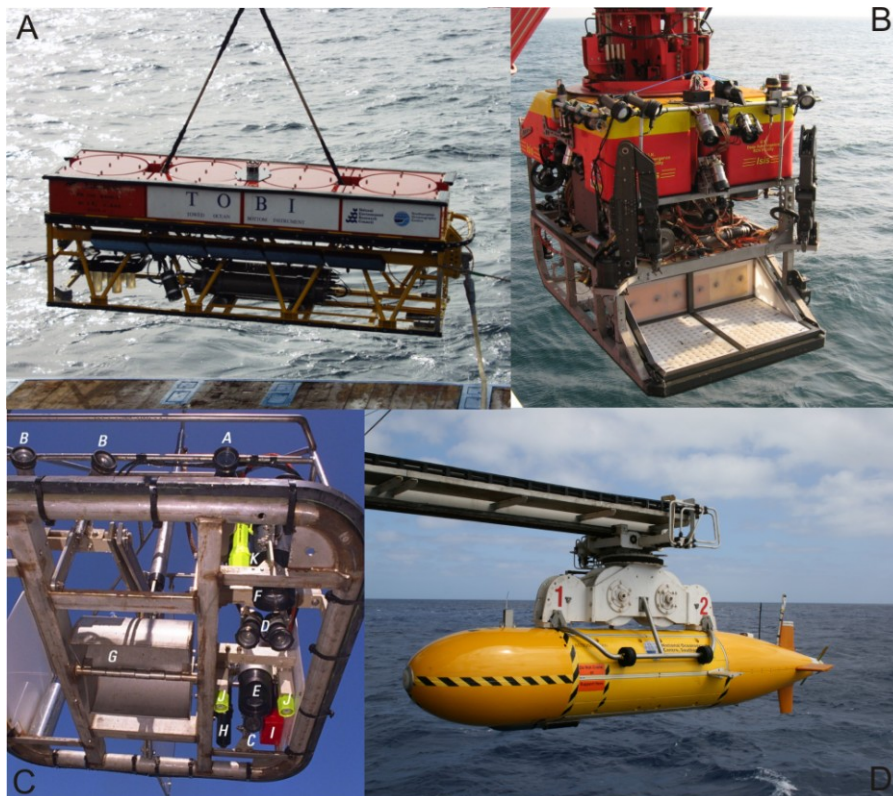


Figure 4.2 Some examples of habitat mapping equipment used in cold-water coral research. a. The 30kHz TOBI side-scan sonar (image V. Huvenne); b. The deep-water ROV *Isis*; c. The US Geological Survey SEABed Observation and Sampling System (SEABOSS) (Valentine *et al.* 2000); d. The deep-water AUV Autosub with mounted high-resolution EM2000 multibeam system (Image S. McPhail).

C. Video and photographic surveys

Visual surveys are a very valuable tool in habitat mapping, as they often give a first appreciation of the seabed in terms of physical substrate and biota. A wide range of instruments is available, running from simple, hopper-type photo cameras (e.g. Mienis *et al.* 2006; USGS 2008) to sophisticated high-resolution digital video systems mounted on platforms such as ROVs or AUVs (e.g. Foubert *et al.* 2005). As with the towed side-scan sonars, accurately recording the vehicle's position may be challenging. When mapped against other datasets (e.g. bathymetry), the video tracks often can be 'repositioned' or alternatively, USBL navigation systems can be used on the platform. The fields of view covered by video and photographic systems are on the order of 5 m², but obviously vary depending on the distance off the seabed. For quantitative analysis, it is necessary to have a correct measure of the field of view. The use of laser pointers may help, but is not always sufficient in heterogeneous coral habitats (see also Section 2.2.3). As with MBES, there is a trade-off between the distance from the substrate and the size of species that can be resolved and identified. Thus while lower resolution visual surveys may allow the overall habitat type to be identified, higher resolution images will almost always be needed for megafaunal identification (e.g. Roberts *et al.* 2008).

Data analysis methods range from purely descriptive techniques, which rely heavily on the experience of the observer, to fully quantitative methods. Video transects can be divided in equal-length intervals, followed by scoring of the relative abundances of different species (e.g. Jonsson *et al.* 2004). Still photographs and video mosaics (correctly balanced for image distortions) can be used as point quadrants, and quantified in terms of percentage cover or species counts. Alternatively, image analysis techniques, as described for backscatter/sidescan sonar data, may also be used for photographic imagery to enhance and automate part of the interpretation (Jerosch *et al.* 2007).

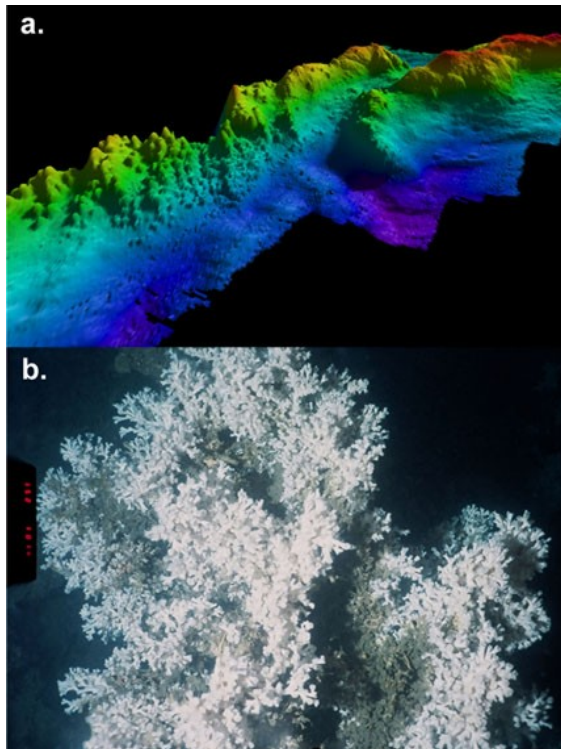


Figure 4.3 (a) Digital terrain model derived from multibeam echounder survey showing many small seabed mounds formed by *Lophelia pertusa* in the Mingulay reef complex. (b) Colony of *Lophelia pertusa*. Figure adapted from Roberts *et al.* (2005).

D. Sampling

In addition to video and photography, actual seabed samples are still necessary to fully groundtruth habitat maps and acoustic data sets. A large number of sampling tools are available, with a varying level of control concerning the actual seabed habitat sampled. They range from dredges and boxcores, TV-guided grabs (Fig. 4.2c) to ROV- and manned submersible-based pushcoring and species sampling. It is clear that a minimal disturbance of the seabed is preferred from a conservation perspective, however, bulk samples such as boxcores or large, sealed grabs may be necessary to best describe ecological communities (e.g. Henry & Roberts 2007).

E. Data integration and map presentation

In order to create the final habitat maps, all datasets have to be integrated. This includes the coverage data (bathymetry, backscatter/side-scan, and derived data), sampling results and also information concerning physical oceanography (temperatures, current speeds, water densities etc.) which is vital to fully understand coral habitats and their ecology. In addition, data on human impacts and use of cold-water habitats can be incorporated. The ideal tool for this integration is a Geographical Information System (GIS). A GIS is a geographical database that allows spatial representation, queries, (spatial)

statistics and correlations between data sets that are geographically positioned, used in context of an overall rigorous data management system. Web-based versions can be used for outreach and information sharing (e.g. www.uncw.edu/oculina and www.ub.edu/hermes). Coverage data can be classified into potential habitats, ‘marine landscapes’ or acoustic zonations using multivariate statistics and parameters such as slope, aspect, backscatter strength, or a Bathymetric Position Index (BPI) calculated from multibeam or backscatter data at various scales. Some of the more advanced analyses include geostatistical techniques and correlations used for the interpolation (and extrapolation) of point-based ground-truthing information onto coverage-wide grids (e.g. Jerosch *et al.* 2006; Verfaillie *et al.* 2009).

4.1.2 Existing cold-water coral habitat mapping work

To date, few cold-water coral sites have been mapped to the extent of including interpretations of the different associated habitats. In most cases, acoustic data such as multibeam bathymetry forms the background upon which video interpretations are plotted (e.g. Fosså *et al.* 2005; Wienberg *et al.* 2008). Visual interpretation of the acoustic data (e.g. sidescan sonar or multibeam backscatter) may lead to coverage-wide substrate maps, or may include biotic interpretations and result in habitat maps *sensu stricto* (e.g. Freiwald *et al.* 2002; Huvenne *et al.* 2005; Roberts *et al.* 2005; see Fig. 4.4). However, the degree of detail and the methods used often vary greatly between studies and the classification schemes employed are generally designed for the specific location under investigation. Comparison between studies and areas is difficult, and many sites have not been mapped at all. Renewed and more extensive mapping efforts are necessary, and the recent development of unmanned underwater vehicles (ROV, AUV or hybrids) opens up further opportunities with this respect. Deep-water sites can now be mapped in great detail, in a time-efficient way.

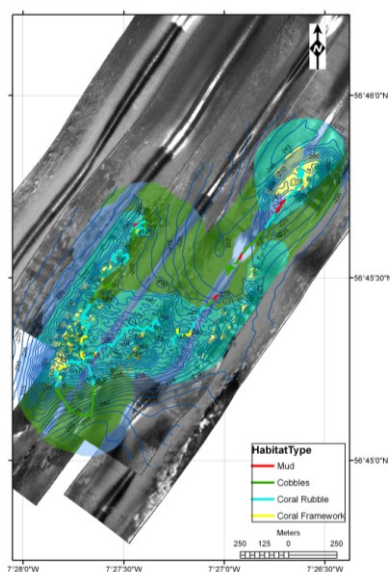


Figure 4.4 Habitat map of the Mingulay 5S *Lophelia* reef, Scotland, based on side-scan sonar, multibeam bathymetry and ROV *Isis* video data. Four seabed habitats were identified and mapped in a 200 m zone around the ROV track, side-scan sonar artefacts are shaded in grey. After Green (2007).

4.1.3 Classification schemes and scales

Several universal habitat classification schemes do exist, although they are not always very well adapted to incorporate the deep-sea environment and the complexity of cold-water coral habitats. Examples include EUNIS (EUNIS 2002) and CMECS (Madden & Grossman 2007) and the classification proposed by Greene *et al.* (2007). In terms of cold-water coral reefs, research has shown that besides the live coral framework, the apron of dead coral rubble around the framework and the surrounding sediments are important biodiversity-rich habitats as well (Henry & Roberts 2007). Therefore appropriate classes for such habitats should be added to the relevant schemes. Live and dead coral framework also form microhabitats for meiofauna and smaller communities (Raes & Vanreusel 2006). Most schemes have a hierarchical, nested structure to describe the seabed at different levels of detail. Naturally, a habitat mapping result will depend on the scale of the survey and the resolution of the data available, and on the purpose of the map.

4.1.4 Mapping for conservation

In order to set up effective management and protection schemes, high quality benthic and/or habitat maps are essential, both at a large scale, indicating coral occurrence within ocean basins (e.g. NRC 2002; Morgan *et al.* 2006; Lumsden *et al.* 2007), and at a more local scale (e.g. Reed *et al.* 2005) detailing the spatial distribution of coral vitality and status (e.g. 'pristine' vs. damaged). Too often management decisions have to be based on inadequate information. Further development of predictive habitat mapping techniques is necessary to guide the exploration for unknown CWC areas (see Section 4.2 below). Integration with socio-economical data sets such as fisheries activities and bycatch should give a more complete picture of the pressures and status of cold-water coral areas. In addition, as management schemes become established, it will become important to monitor coral status and recovery with repeated surveys and habitat mapping efforts.

4.1.5 Habitat mapping aims and objectives

The overall aim and roles of habitat mapping within TRACES are to:

- underpin the specific science themes, especially 'linkages & connectivity' and 'biodiversity and biogeography'
- investigate spatial patterns of cold-water coral communities at different scales
- support conservation actions, identifying undocumented cold-water coral areas and areas for protection
- provide input to and validate the results of habitat suitability modelling

- investigate key environmental parameters that could be controlling cold-water coral and associated species' distributions (in relation to the 'biodiversity and biogeography' science theme)

These aims can be formulated into the following objectives:

- to agree on common mapping methods and classification schemes for cold-water coral habitat mapping in the Atlantic, working at a variety of scales. This will be based on a review of existing mapping experiences from well-documented sites and must take into account the appropriate mapping approaches for different coral types (e.g. scleractinian coral carbonate mounds and reefs on the Irish, Norwegian & Florida margin, gorgonian coral 'forests' and biostromes on the Canadian margin or patchy coral occurrences on seamounts and canyon flanks)
- to elaborate existing habitat classification systems where necessary such that cold-water coral associated habitats can be represented accurately. Again this will follow from a review of existing classification schemes and their application in cold-water coral areas.
- to create detailed habitat maps for TRACES key sites and co-ordinated pooling of data to create base maps for use by multiple project partners
- to compare the habitat structure at different cold-water coral sites throughout the Atlantic (in terms of surface area of different habitats, patchiness etc.) and to establish the relationships between those habitat structures and the underlying physical environment
- to map and inventory cold-water coral occurrences and human impacts, based on a geodatabase and GIS
- to monitor the temporal variability in cold-water coral habitat structure at selected sites (affected and non-affected by human activities) through repeated mapping.

4.1.6 Standardisation and trans-Atlantic opportunities

Working on a trans-Atlantic scale, standardising methods and approaches will increase the potential for comparative studies over the entire basin. It will create the opportunity to identify common ('universal') spatial patterns in cold-water coral habitats - either for similar species at different sides of the Atlantic, or even for entirely disparate species. The broad-scale collaboration between European, US, Canadian and South American research groups opens up a broad equipment pool, including the newest technological advances, which will increase the capacities for high-resolution and high-quality mapping.

4.2 *Predictive habitat mapping*

The geographical distribution of cold-water corals will be influenced by a combination of different physical, chemical and biological factors. Predictive modelling approaches can be used to generate habitat suitability maps,

producing representations of geographical areas that match species' requirements based on several environmental parameters (Guisan & Zimmermann 2000; Hirzel *et al.* 2002; Phillips *et al.* 2006). Cold-water corals are ideally suited for predictive modelling approaches because of their sessile nature and longevity. However, the majority of predictive mapping approaches (e.g. General Linear Modelling and Principal Component Analysis) require information on both the presence and absence of species (Guisan & Zimmermann 2000). In the deep-sea, absence data is often unavailable or unreliable. The majority of research expeditions are targeted towards areas with known coral occurrences, and sampling methodologies often vary between expeditions. The patchiness of deep-sea habitats also limits confidence for assessing the absence of cold-water corals, which could be easily missed because sampling methods have such a limited spatial coverage.

Ecological-niche factor analysis was developed to address both the paucity and unreliability associated with absence data in predictive modelling (ENFA; Hirzel *et al.* 2002). This technique assumes that a given species has a non-random distribution within an eco-geographical variable and that the majority of individuals would occupy the optimal range. By using only presence data, ENFA calculates habitat suitability based on the niche width of a species in relation to eco-geographical variables, thereby producing useful statistics related to the species niche and predicted habitat suitability over large spatial areas (Hirzel *et al.* 2002; Hirzel & Arlettaz 2003). This approach has been used in several terrestrial studies (e.g. Zaniwski *et al.* 2002; Hirzel & Arlettaz 2003; Reutter *et al.* 2003; Hirzel *et al.* 2004; Santos *et al.* 2006) but to date only relatively few deep-sea studies, for example: (1) investigating the distribution of cold-water gorgonian corals (Leverette & Metaxas 2005; Bryan & Metaxas 2007) ; (2) evaluating the distribution of cold-water corals on seamounts (Tittensor *et al.* 2009); (3) deriving eco-geographical data from multibeam bathymetry and using ENFA to determine habitat suitability for squat lobsters (Wilson *et al.* 2007) and (4) a study attempting both global and regional north east Atlantic ENFA for *Lophelia pertusa* (Davies *et al.* 2008).

4.2.1 Limitations

Several limitations must be considered when applying predictive models to deep-sea species:

1. Many eco-geographical variables are only available at coarse spatial and temporal resolutions, which reduces the quality of modelled predictions (Osborne *et al.* 2001; Gibson *et al.* 2004). In one recent deep-sea study, there were inconsistencies between the known thermal tolerance of *L. pertusa*, which ranges between 4-12 °C (Roberts *et al.* 2003) and those extracted from gridded temperature data (Davies *et al.* 2008). This was due to the low resolution of the gridded temperature dataset used, because areas where there might be rapid change in temperature over small spatial scales could not be resolved.

2. Not all eco-geographic data are available in gridded form that extends over the spatial area required for predictive modelling. One example important for scleractinian corals is aragonite saturation state (Guinotte *et al.* 2006; Turley *et al.* 2007). At present, the data coverage for aragonite and other variables (e.g. dissolved organic carbon, pH, alkalinity) has not extended into northern, notably Arctic, latitudes partly as a result of the complex hydrography of this area and also under-sampling of the variables required to model aragonite saturation.
3. Sampling bias will probably skew predictive outcomes for many deep-sea species. Research into cold-water coral habitats has so far been mostly carried out in the north east Atlantic and Mediterranean Sea, which has skewed the known spatial distribution towards these areas. Cold-water corals have been documented in all ocean basins, but their distributions are very probably under-represented outside the north east Atlantic.
4. The relative paucity of presence points at the global scale, and indeed outside of the north east Atlantic is not ideal for ENFA. Predictive models are sensitive to the number of presence points incorporated into the analysis but success differs between approaches (e.g. Stockwell & Peterson 2002; Elith *et al.* 2006; Bryan & Metaxas 2007). Yet at present, there has been no conclusive test of the amount of presence points required for many predictive modelling approaches. For instance, Hirzel *et al.* (2001) showed that when the sample size was reduced from 1200 to 300 there appeared to be no adverse effect on their ENFA results, although care should be taken in assuming such a situation would therefore apply across the broader spatial scales considered by TRACES.
5. Predictive maps show potentially suitable habitat where environmental conditions are similar to areas where the species in question has been found, but this does not mean that the species is actually present within that area. In the north east Atlantic, *L. pertusa* is the primary reef framework-forming species (Roberts *et al.* 2006). Yet in some parts of that region, there may remain barriers to colonisation, such as dispersal pathways that are blocked (Guisan & Zimmermann 2000) or at smaller scales biotic interactions in the form of competitive exclusion.

4.2.2 Standardisation, conservation and trans-Atlantic relevance

Over the last few years, the impact of anthropogenic activities on cold-water coral ecosystems has become an international concern. In particular, bottom trawling has been identified as probably the most severe immediate threat facing cold-water corals (Hall-Spencer *et al.* 2002; Gage *et al.* 2005; Grehan *et al.* 2005; Roberts *et al.* 2006). This has led to substantial publicity and lobbying to ban bottom trawling in areas of coral habitat (Davies *et al.* 2007; De Santo & Jones 2007). In December 2006, a moratorium on High Seas bottom trawling was discussed at the United Nations General Assembly. Although these discussions failed to establish such a moratorium, progress was made towards conserving vulnerable deep-sea ecosystems. In particular, the UNGA called upon member states and regional fisheries management organisations (RFMOs) to close down bottom fishing in areas where

seamounts, hydrothermal vents, and cold-water corals are known or *are likely* to occur based on scientific information (UNGA Resolution 61/105).

Clearly, the current generation of predictive models is constrained by the limited geographical coverage and resolution of eco-geographical variables (e.g., temperature and aragonite saturation state along the Nordic Margin). However, if the resolution and geographical coverage of these variables are improved and further presence points are incorporated into databases predictive modelling would become increasingly accurate. With the flow of data that TRACES could provide, this technique would become a valuable tool for understanding the habitat requirements of cold-water corals as well as those for other deep-water species. In addition, validation of models may be conducted, further increasing the accuracy of the predictions and developing our understanding of the main drivers behind the distribution of cold-water corals. The TRACES study area encompasses the only area of the world's oceans that is predicted to remain supersaturated (at cold-water coral depths) in aragonite through to the end of the century (Guinotte *et al.* 2006). This area therefore has high conservation value as it may be one of the last refuge areas from ocean acidification. The next generation of predictive analyses need to bring together seamount, canyons and continental shelf occurrences to further develop our understanding of cold-water coral distribution throughout the world.

4.2.3 Predictive mapping objectives

1. Distributional data
 - Survey current literature to develop comprehensive databases for major coral species. Potentially develop a comprehensive international species database.
 - Develop a centralised presence databases and investigate potential for equivalent absence database for coral species.
2. Eco-geographical data
 - Develop the next generation of global environmental data from existing sources and liaise with other projects and institutes to develop these where the data do not exist. Key variables include depth, temperature, hydrodynamic data, aragonite/calcite saturation state, nutrient levels.
 - Centralise eco-geographical data, assessing data with respects to coverage and quality.
 - Develop high resolution local environmental data from known coral areas to better understand local environmental tolerance, and link between habitat quality and coral abundance.
3. Models
 - Assess models by reviewing available techniques and advising on a standard operating practice to ensure comparison between model iterations.

- Feed models into existing cruise plans, identifying areas where no sampling effort has been conducted for validation purposes.
4. Policy
- Involve relevant policy makers at early stage of research.
 - Ensure modelled data are available to policy makers, NGOs and conservation scientists to facilitate on-going implementation of UN General Assembly resolution 61/105.

4.3 Oceanography and food supply

4.3.1 Introduction

Many hydrographic phenomena can significantly influence cold-water coral habitats exerting control through three major processes:

- i) the supply of organic matter (food) and nutrients to the coral system
- ii) the near-seabed current regime controlling sedimentation and re-suspension
- iii) the mixing of gametes and dispersal of larvae

For these reasons ‘oceanography and food supply’ is a cross-theme contribution to the TRACES programme. These hydrographic controls occur over a wide spectrum of temporal and spatial scales (Figure 4.5). As the time-space scales cascade to smaller levels so, in parallel, the character of the hydrographic influence also changes. Therefore, the overall control on coral distribution and functioning by abiotic factors is highly complex with large time and spatial scale processes controlling overall pelagic food supply and small scale processes controlling food supply to individual coral habitats.

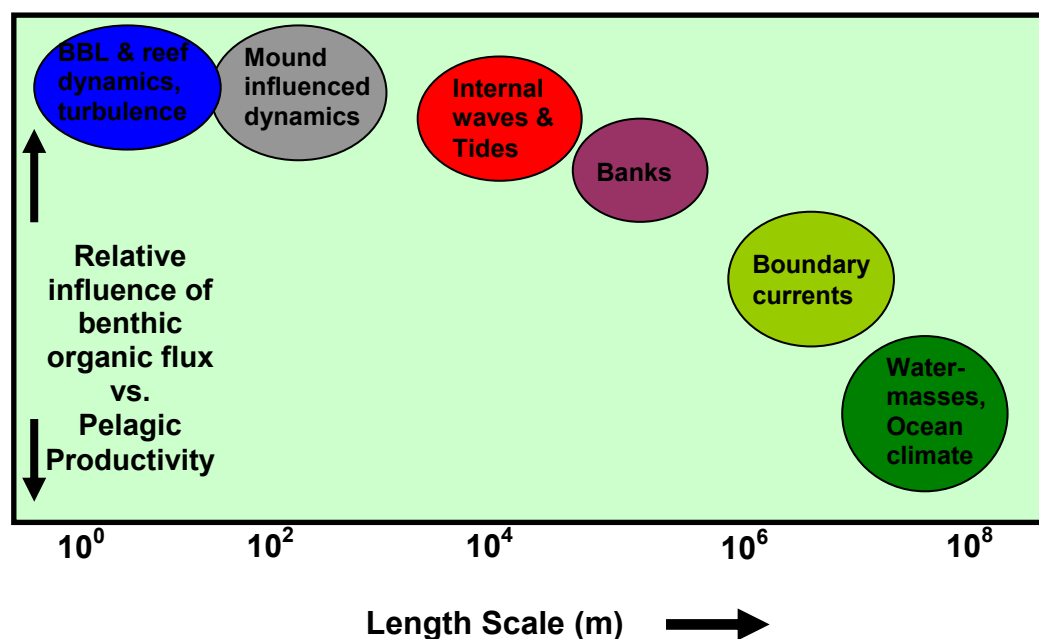


Figure 4.5 Hydrographic processes that control coral ecosystem functioning. The indicative length scale of the process is given on the horizontal axis and the vertical scale represents the relative influence of the hydrodynamics on the flux of organic matter to the gross overlying primary productivity.

The distribution of primary productivity in the surface ocean is controlled at the largest spatial length scales, those of the ocean basin, both by current (gyre) systems and ocean-atmosphere interactions (wind-driven circulation). As azooxanthellate species, cold-water corals have a distinct distribution relative to their tropical counterparts, and are strongly coupled to increased primary productivity in surface waters (e.g. Freiwald 2002; Roberts *et al.*

2006). Large western boundary currents, such as the Gulf Stream, are also the major nutrient streams to the sub-polar NE Atlantic (Pelegri *et al.* 2005) where, for example, the majority of *Lophelia pertusa* records have been made.

At intermediate length scales, dynamical processes that occur at the continental margin may produce 'hotspots' of primary productivity (e.g. Frederiksen *et al.* 1992), fuelled by the vertical fluxes of nutrients due to either upwelling processes or vertical mixing by internal waves (e.g. Pingree *et al.* 1986; Sharples *et al.* 2007). In addition, boundary currents, together with the action of tidal period currents at the continental margin, provide a means of along and down-slope transport of organic material. Thiem *et al.* (2006) have shown the role of bottom boundary layer friction in driving transport of material down the continental slope, hence increasing particle fluxes to *Lophelia* reef systems off Norway. Large submarine banks may also retain organic material over them and this material may be delivered to the coral carbonate mounds at their margin through similar processes (White *et al.* 2005). In addition, internal waves and other baroclinic tidal period motions may generate large organic matter fluxes through re-suspension and significant along- and cross-slope advection of material (Frederiksen *et al.* 1992; White 2007; White *et al.* 2007). For example at the Mingulay reef complex off Scotland downwelling promoted by an internal wave impinging on local rocky topography provides regular, pulses of food material on the turn of the tide (Davies *et al.* 2009).

At the scale of individual reefs and coral colonies, benthic boundary layer dynamics control the flux of nutrients and organic matter that have been brought into the region by larger scale processes. These dynamics therefore have a profound effect on the smaller scale habitat distribution. For example, processes that accelerate the near bottom flow will enhance fluxes (e.g. Genin *et al.* 1986). Increased turbulence levels will probably be generated by the presence of scleractinian coral reef structures and asymmetry in flow strength and turbulence generation with impinging flow direction are likely to lead to the evolution of different reef forms such as isolated patches, elongated reef ridges, or the large coral carbonate mound formations. Small spatial scale variability in flow around reef structures is complex and will cause heterogeneity in the facies, habitat and faunal distribution (e.g. Dorschel *et al.* 2007; Henry *et al.* submitted).

Food sources and supply: There have been comparatively few studies on food sources and supply of cold-water corals, and these have concentrated primarily on the north east and, less so, north west Atlantic. Therefore questions on the spatial and temporal variability of food supply still exist. Aquarium and field observations have shown that *Lophelia pertusa* may capture live zooplankton up to 2 cm in length (Mortensen *et al.* 2001), but fatty acid and stable nitrogen isotope signatures suggest that cold-water Scleractinia from the north east Atlantic may also feed on detrital particulate organic matter, albeit in different proportions (Duineveld *et al.* 2004; Kiriakoulakis *et al.* 2005; Duineveld *et al.* 2007). For example, Kiriakoulakis *et al.* (2005) showed that *Lophelia pertusa* may rely more on zooplankton

than *Madrepora oculata* as the former had higher $\delta^{15}\text{N}$ values and higher amounts of mesozooplankton biomarkers than the latter, although no studies for tissue assimilation efficiencies exist. Further lipid analysis comparing *L. pertusa* from the New England Seamounts, Rockall and the Mingulay Reef Complex implies this that species has some dietary flexibility in terms of zooplankton prey (Dodds *et al.* in press).

Studies in the north west Atlantic show that different cold-water coral species occupy different trophic niches; some seem to rely more on fresh organic particles (e.g. *Paragorgia arborea*), others may supplement their food with zooplankton and/or more degraded material (Sherwood *et al.* 2008b). This study suggested that the fine interaction of substrate with oceanographic regime (currents, tides) modulates food availability and quality, thus controlling the feeding habits of the corals, but no long-term detailed oceanographic measurements were carried to examine this further. The importance of food quality in the functioning of these deep-water ecosystems has been noted before, but little information is available. Kiriakoulakis *et al.* (2004, 2007) reported relatively high concentrations of lipid-rich, fresh suspended particles, in the benthic boundary layer of many cold-water coral habitats of the NE Atlantic (i.e. Darwin Mounds, Porcupine Bank and Seabight and Rockall Bank). Furthermore, over the Rockall Bank, long term benthic lander measurements have shown the extended supply of fresh, phytoplankton-rich material arriving at the seabed at ~800 m depth between February and July (Duineveld *et al.* 2007). Clearly more studies are needed in order to better constrain the spatial and temporal variability of the food sources and supply to cold-water coral ecosystems.

Historical Changes: Climate change and its effects on oceanographic conditions across the Atlantic is a key aspect of the TRACES Climate Records theme. The development of large coral carbonate mounds in the north east Atlantic must imply that these areas have provided oceanographic conditions conducive to coral growth repeatedly through time. Such conditions include circulation patterns and water column structure, particularly the depth of the permanent thermocline which, at the continental margin, coincides in depth with enhanced wave energy and increased residual flow strength (White 2007; White & Dorschel 2008). Changes in the location of the gyres and the strength of overturning circulation in the sub-polar gyre will therefore alter the vertical structure of the ocean and hence other characteristics, including vertical stratification, the depth of enhanced currents and the overlying surface productivity regime. It is, however, important to note that the time scales of change vary immensely, ranging between:

- geological timescales such as glacial/interglacial periodicity (~100 kYr)
- scales of order 1000 years, related to the Meridional Overturning Circulation timescales and rapid climate exchanges
- Multi-decadal timescales of order 60-70 years, such as the Atlantic Meridional Oscillation (AMO) and other associated feedbacks with the warm-cold water conversion within the sub-polar gyre occurring at higher frequency
- Multi-year variability related to processes such as El Niño or the NAO.

These long term variability cycles will not be uniform across the whole Atlantic basin and hence knowledge is required not just of the timing and duration of climatic changes, but of their regional expression. Here the use of climate proxies from coral skeletons, as discussed in Section 3, can be utilised to quantify these regional changes.

4.3.2 Methodology

The wide spectrum of oceanographic processes highlighted in Figure 4.5 requires a large number of measurement and modelling techniques to describe the dynamics and likely organic matter supply to a reef system.

Lander systems: A large amount of hydrographic information has been collected by using benthic lander in different cold-water coral settings such as the Norwegian Margin and Belgica mounds (Roberts *et al.* 2005) or the Pelagia and Logachev Mounds (Mienis *et al.* 2007). Such systems can typically deploy or measure:

- currents at high resolution near the seabed as well as above the benthic boundary layer, turbulence estimates
- common hydrographic variables such as temperature, salinity, fluorescence, turbidity and oxygen
- particle fluxes through use of sediment traps
- acoustic backscatter for turbidity measurements
- photographic and video footage
- settlement panels for biological experiments
- other more complex sampling systems such as *in situ* benthic chambers and sediment profiling systems.

An advantage of lander systems is that they are stand alone units that can make long term (up to 1 year) measurements at a site. During TRACES, we envisage benthic landers forming a central aspect of the long term monitoring at selected key sampling sites. Standardisation of instruments and methodology for these key monitoring sites will be required. One disadvantage of large scale landers is that they are typically deployed in a free fall mode or released acoustically within 25 m of the seabed. For deep reef ecosystems, therefore, the precise location of the lander in relation to the intra-reef habitat is not known. This has important implications for data interpretation as the flow variability within a cold-water coral habitats will be highly complex and spatially variable (e.g. Dorschel *et al.* 2007). Video-guided landers or deployment of small ‘microlanders’ by submersibles and ROVs both alleviate this problem.

Moorings and historical data: Conventional current meter moorings and thermistor arrays have an important role to play in characterising local hydrography. In addition, there are historical datasets from different oceanographic or biogeographic regimes of the Atlantic. Such an approach on the north west European margin has been successfully taken to quantify the

important dynamics for coral ecosystems, e.g. White (2007) for the influence of baroclinic tidal motions and boundary currents, Dullo *et al.* (2008) for relationships to water mass distributions or Thiem *et al.* (2006) for process studies to look at organic matter fluxes at the continental margin.

Potential datasets that can be used during TRACES include:

- WOCE current meter archive for Eulerian measurements and the ARGO float archive for both deep currents and water mass structure.
- Numerous data banks for temperature and salinity data (e.g. ICES, NOAA, BODC etc.)
- Continuous Plankton Recorder (CPR) data for zoo- and phytoplankton abundances for the last 50-60 years, the last 15 years of which have been calibrated/validated against satellite ocean color measurements (Raitsos *et al.* 2005).

Biogeochemical sampling: In order to assess the quality of organic matter available to corals, it is appropriate to use a properly inclusive sampling approach. Sediment traps, deployed on long-term landers capture sinking particulate organic matter (POM_{sink}) and allow flux rates to be estimated. Nevertheless, sediment traps are often compromised by complex hydrodynamics, and do not necessarily trap the suspended POM (POM_{susp}) used by the corals and other epifauna. For this reason, it is essential to collect POM_{susp} by using high volume stand-alone pumps (SAPs), which pump hundreds of litres of water through a large filter (Kiriakoulakis *et al.* 2004, 2007). The pumps can be deployed on a wire close to coral habitats or, preferably, using a small lander frame and deploying by ROV or submersible on the seafloor. Finally, it is also important to collect sediments around the coral system to assess the contribution of resuspended material to the POM_{sink} and POM_{susp} . Organic matter quality is assessed through bulk analyses (e.g. C/N, pyrolysis) and by measurement of the molecular composition of the POM (pigments, lipids, amino acids etc., Kiriakoulakis *et al.* 2004).

In order to assess the trophic status of the corals themselves, stable isotope analysis both of carbon and nitrogen, provide important information on feeding status (e.g. Kiriakoulakis *et al.* 2005; Duineveld *et al.* 2007; Sherwood *et al.* 2008b). To date there have been few trophic studies of corals, but there clearly is variability in their diet, depending on location, and probably, time of year (see Section 4.2.1, Food Sources and Supply). Nevertheless, in concert with lipid analyses, it is possible to qualitatively assess the dominant food sources (e.g. fresh detritus vs. degraded detritus vs. zooplankton).

4.3.3 Objectives and tasks

This section reviews physical oceanographic methodologies that can be used to address the research questions generated by the two TRACES workshops.

Oceanographic Questions

- 1) *What is the role of the basin scale circulation on the dispersal of coral larvae? Are there barriers to the gene flow, both vertically and horizontally, between locations within the Atlantic?*

A range of ocean circulation models is available to determine mean circulation pathways and the variability of same, for the Atlantic. Such models have been validated with the use of satellite altimetry and drifting buoy data, particularly that from the ARGO program.

We can use known circulation patterns and their variability to map, statistically, larval flow pathways for different spawning periods and larval stage duration. The use of ARGO and satellite altimetry data can be used to derive mean values of horizontal diffusion to superimpose on the mean or seasonally varying circulation, allowing a form of random dispersion. Additional biological complexity might be added by using satellite and ecosystem model-derived chlorophyll or plankton abundance/distributions as a proxy for potential energy supply. In addition, results from Niche Factor Analysis (NFA) modelling may be used to estimate likely suitability and survivability of larvae along transport pathways and final settlement locations.

The role of the boundary currents at both the European and American Atlantic margins is of particular interest. On the European margin these comprise Mediterranean Outflow and north east Atlantic poleward flowing slope current whereas along the North American margin are the Gulf Stream and the Deep Western Boundary Current.

- 2) *What are the mechanisms that transport organic matter from the pelagic to the reef ecosystem and are differences in these mechanisms reflected in the cold-water coral habitats and/or their associated communities?*
- 3) *Are regional changes in organic matter quality reflected in coral distribution and what is the role of irregular topographic features in concentrating or modulating food sources?*

Historical datasets relating to water mass structure, biological components and current measurements, together with process studies, can be used to assess the dominant oceanographic processes occurring at target sites across the Atlantic. Such data synthesis can be used for habitat or Niche Factor Analysis modelling and for comparing to biogeographic datasets collated with the TRACES biodiversity and linkages/connectivity themes.

- 4) *Can we use circulation and ecosystems models, as well as other indicator data (e.g. teleconnection pattern indices, CPR plankton data), to predict circulation/productivity changes and relate these climatic changes in N Atlantic circulation and productivity to palaeo records contained within coral skeletons?*
- 5) *Do coral reef ecosystems of different structural character (mounds vs isolated reefs/ridges etc.) represent different hydrodynamic control (residual vs tidal flow dominance, turbulence levels etc.)*

5 Policy

5.1 Introduction - ideas for development and discussion

The policy component of TRACES underlies, supports, and ultimately implements the scientific findings that evolve from the programme. The policies and systems that contribute towards biodiversity conservation at domestic and international scales in the marine environment are in a dynamic state of development. In the EU, traditional instruments that cover biodiversity management and conservation such as the Habitats Directive, are developing in tandem with reforms to the management of marine environments and maritime industries. Commitments and targets for biodiversity conservation and marine protected area (MPA) implementation at domestic and international levels are imminent. However, the science to support MPA development, especially in deep-water, is still at an early stage. In addition, there is a considerable reform agenda emerging in the fisheries policy environment as the concept of ecosystem based management is progressively brought into practice.

Therefore, as the science programme in TRACES evolves, so too does the policy and regulatory environment in the marine sphere. The reforms to domestic and international law cover a wide array of sectors (e.g. fisheries, aquaculture, shipping and renewable energy), introduce the concept of marine spatial planning and move towards spatially based conservation reform. This parallels increasing use of the seas by existing and new industries, and increasing competition for space in the marine environment.

Such changes and reforms introduce challenges for policy makers and scientists alike. While TRACES maintains a focus specifically on the ecology and palaeoceanography of cold-water corals, it is critical to both understand how evolving policy will affect the conservation of these habitats, and how new research findings can help inform policy development. This section will present an initial list of policy orientated research questions that will inform discussion and feed into the developing TRACES research agenda.

Biodiversity beyond national jurisdiction cannot be protected effectively unless countries cooperate. For management measures to be implemented, coordination is essential across sectors and States. Institutional and governance mechanisms for ensuring such cooperation are required and should be identified in the research planning stage. There is extensive discussion currently occurring in this area and the focus here will be on how this applies specifically to cold-water corals.

5.2 TRACES policy research agenda

The questions outlined below are split between three major issues: (1) Marine policy processes relevant to TRACES; (2) Developing regional governance case studies and (3) Means by which basic scientific research and policy may be integrated.

5.2.1 Issue 1: Evolving marine policy process relevant to TRACES

Understanding the development of domestic and international law as it applies to deep-sea biodiversity is critical for orienting the science towards management and conservation measures. This is a complex, diverse and rapidly evolving topic. It is heterogeneous, with policy initiatives, regulatory measures and instruments being developed and applied at different rates across different sectors. Policy development is not uniform but varies at temporal and spatial scales based on socio-political, economic and environmental factors. It will be important for TRACES to map the existing policy climate and policy development trajectory. However, it would be beyond the scope of the project to understand every possible domestic and international initiative. This phase should develop a specific framework and methodology to examine and map evolving policy issues of relevance to cold-water corals and the TRACES programme.

Research questions to include:

1. Review of the role and development of international conventions relevant to high seas biodiversity that specifically apply to areas beyond national jurisdiction.
 - Convention on Biological Diversity (as it may inform conservation of high seas biodiversity and sustainable use of its components)
 - UNCLOS and associated instruments (i.e. UNCLOS jurisdictions, Seabed exploitation and minerals development, bioprospecting, dumping, ocean modification)
 - The UN Fish Stocks Agreement (UNFSA) and regional fishery management organisations in the Atlantic
 - FAO Compliance Agreement
 - MARPOL
 - London Convention and 1996 Protocol
 - Convention on International Trade in Endangered Species (CITES)
 - Regional Seas Agreements e.g. OSPAR Convention, Barcelona Convention
2. Examine the standing and trajectory of soft law approaches to high seas biodiversity and cold water corals
 - The evolution of the UN General Assembly Resolution 61/105 and actions to prevent significant adverse impacts from fishing to vulnerable marine ecosystems, including cold water corals, in areas beyond national jurisdiction.
 - WSSD Johannesburg Declaration
 - FAO instruments: IPOA, Code of Conduct for Responsible Fisheries
 - Role of UNEP
3. What are the activities and responses from actors and sectors that have interests in areas beyond national jurisdiction?

- Fisheries
 - Shipping
 - Deep-sea mining
 - NGOs
 - Bioprospecting
 - Research scientists
 - The public's attitudes and values towards cold-water corals
 - Governments
4. Status of MPAs in international law
 - Current developments
 - Coordination between instruments
 - Private initiatives versus public (government) sponsored initiatives
 5. Policy processes and regulatory instruments at the European Union level
 - Marine Strategy Directive and Maritime Policy (cognisant of marine planning and bills at national level)
 - Common Fisheries Policy
 - Habitats and Birds Directive - Natura 2000
 - EIA Directive
 - SEA decisions
 - EU directives and regulations regarding shipping and pollution
 6. Policy processes and regulatory instruments in Canada
 - Canadian Fisheries Act (1867), Section 35(1), with Federal authority established by the Constitution Act (1982)
 - Canadian Oceans Act (1997)
 - National Marine Conservation Act (2002)
 7. Policy processes and regulatory instruments in the USA
 - Roles of the National Oceanographic and Atmospheric Administration (NOAA, part of the US Department of Commerce) and Regional Fishery Management Councils in developing coral conservation in the US exclusive economic zone
 - Review relevant legislation including: Magnuson-Stevens Fishery Conservation and Management Act as re-authorised in 2006 (PL 109-479); National Marine Sanctuaries Act
 - Emerging policy frameworks under the Interagency Ocean Policy Task Force (2009), including marine spatial planning as they may relate to cold-water coral habitats.

5.2.2 Issue 2: Regional governance case studies

The overall aim would be to specify several case studies that analyse the interactions between regulations, policy and sectoral activities. Case studies should investigate management options and link with the results of TRACES science outputs.

- What locations would provide an appropriate basis for detailed policy-science-management case studies? What scales should we focus on? What support is there for applications?
- What methods could be used to assess and analyse governance arrangements and science outputs?
- What experience do partners have that could help focus case studies?

5.2.3 Issue 3: Integration of science and policy research

The issue of science and policy integration is an important topic in broader marine science and specifically in the development of management and conservation measures for cold-water corals. The focus should be on the interaction of science and policy within TRACES and the export of research into policy forums.

- What theoretical and analytical approaches can we bring to the programme?
- What policy instruments can be used to implement TRACES outputs?
- What is happening in other arenas? For example in research projects and forums in Europe, US and Canadian jurisdictions that already attempt to link science and policy output?
- What mechanisms are being used to engage relevant policy makers?

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