# Ageing methods for protected deep-sea corals:

## a review and recommendation for an ageing study

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***Cover image:*** *Solitary colony of Bathypathes in situ, Louisville Ridge [Deep towed Imaging System, NIWA]*

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# Executive summary

Deep-sea corals are a highly diverse group of marine organisms several of which are characterised by their overall slow growth and extreme longevity. Due to their fragile forms, skeletal composition, and location, they are vulnerable to various anthropogenic threats with some groups expected to have little to no ability to recover. Impacts include; fishing such as bottom trawling and bottom long-lining, mineral exploration and deep-sea mining. There are also the environmental impacts predicted from climate change including sea water warming and ocean acidification.  To better inform risk assessments for these deep-sea corals, a knowledge of their age and growth is key to understanding coral regeneration times following trawl disturbances or other damage. This report presents outputs for year one of the Conservation Services Programme, Department of Conservation Project POP2017-07, and includes a literature review describing the methods to age coral species and a recommendation to obtain accurate age and growth data for a key protected coral species.

We review the main methods applied to measure age and growth of deep-sea corals.  These can be split into three key applications: (1) direct observation e.g., in situ measurements or in-aquaria experiments of linear growth or surface extensions; polyp addition rate; estimation of calcification rates (e.g., using the buoyant weight technique), (2) enumeration of skeletal growth bands and (3) radiometric analyses. The advantages and disadvantages of each method are reviewed. Overall (1) direct observation studies were few, due to time constraints and cost of research in the deepsea; (2) growth band counts were not valuable for certain coral species with porous skeletons, hollow branches, or colonial matrix-like morphologies (e.g., gorgonian bubblegum corals and branching stony corals), but were appropriate for corals containing clear banding patterns in cross section (e.g., gorgonian octocorals such as bamboo corals; and some stony cup corals); and (3) radiometric analyses had been applied to several coral groups, but success of the dating techniques (i.e., radiocarbon ($^{14}$C) vs. lead 210 ($^{210}$Pb) vs. uranium / thorium dating (U/Th)) is dependent upon local environmental conditions and the carbonate mineralogy of the coral.

We recommend next steps for coral ageing research in the New Zealand region and detail a method most appropriate to apply to obtain accurate age and growth data for a previously determined ‘High Risk’ protected coral species, specifically the Antipatharian black coral genus Bathypathes (Family Schizopathidae). The analytical method we propose is radiocarbon ($^{14}$C) dating of base and tip regions of the colony combined with growth ring counts from around 10 basal sections for selected specimens of species *B. alternata* or *B. patula*. The micro-milling of material, and the interpretation of results would be carried out in Year 2 of the project.

The recommendations build on the recent risk assessment that identified deep-sea species such as black corals (at the order level Antipatharia, and the genus *Bathypathes*), and the gorgonian coral genus *Paragorgia*, as being at high risk from the effects of bottom trawling. Most reef-building scleractinian corals, as well as other gorgonian coral taxa, were assessed as medium risk, and cup corals and hydrocorals were relatively low risk. These results were consistent with expectations based on the form and biology of the corals, their depth and distribution patterns, and knowledge of trawling impacts, both past and predicted.  The research will address the risk assessment recommendations.

# 1 Background

Knowledge of the age and growth of protected deep-sea coral species (also referred to as cold-water corals) for the New Zealand region has been identified as key to understanding coral regeneration times following trawl disturbances (Williams *et al.* 2010) or other damage. Regeneration of fauna relates to the time that would be required for a colony to grow back to its unfished state. Coral form and ecological sensitivity are important components of defining the risk of impacts, and therefore protected deep-sea coral groups need to be aged to inform future risk assessments and the development of appropriate management options for these groups.

As part of an earlier Conservation Services Programme (CSP), Department of Conservation (DOC) Project POP2013-05, a pilot ecological risk assessment (ERA) for protected corals in New Zealand was developed by Clark *et al.* (2014). The risk assessment examined the extent of the impact due to the fishing activity (determined by the susceptibility of the unit to the fishing activities), and the productivity of the unit which determines the recovery potential. Susceptibility of the corals is assessed by three aspects (availability, encounterability, and selectivity), and a single productivity aspect. Risk assessments such as these are key tools for informing management approaches for protected corals in that they provide a better understanding of the various aspects and characteristics of coral species and the fisheries that contribute to risk determination.

Also under the CSP POP2103-05 project, Anderson *et al.* (2014) predicted the distribution of protected deep-sea corals in relation to areas where they are at risk of interactions with commercial trawl gear targeting orange roughy and oreo species on the Chatham Rise. The modelling showed that a substantial overlap between predicted coral habitat and the 20-year trawl footprint (>50%) occurs across the entire EEZ for *Goniocorella dumosa*, with lesser overlaps (<25%) for *Enallopsammia rostrata*, *Primnoa* spp., and *Bathypathes* spp. On the Chatham Rise, overlaps of >50% occur for *Goniocorella dumosa*, *S. variabilis*, *Madrepora oculata*, and all genera of antipatharians except for *Bathypathes* spp. For all taxa, however, substantial areas of suitable habitat are predicted to exist across the Exclusive Economic Zone (EEZ) outside of the historic trawl footprint.

These results, together with various studies on trawling impacts, knowledge of current and predicted coral distributions, and morphological information on the shape and size of corals, all helped the risk assessment to determine the “selectivity” of a trawling encounter. Biological data such as age, growth, reproduction, colonisation, and dispersal were used to rank the “productivity” of a coral species or group, which reflects its ability to recover from trawling. There have been several studies on benthic community composition following the cessation of fishing (Clark & Rowden 2009, Althaus *et al.* 2009, Clark *et al.* 2010, Williams *et al.* 2010) that inform risk assessments. Results indicate that recovery of fished habitats comprising deep-sea stony coral reef (*S. variabilis*) is likely to take centuries, as there have been no indications of stony coral settlement or growth after periods of up to 10 years.

Clark *et al.* (2014) identified that deep-sea protected species such as black corals (at the order level Antipatharia, and the genus *Bathypathes*), and the gorgonian coral genus *Paragorgia*, were two species groups at high risk from the effects of bottom trawling. Most reef-building scleractinian corals, as well as other gorgonian coral taxa, were medium risk, and cup corals and hydrocorals were relatively low risk. These results were consistent with expectations based on the form and biology of the corals, their depth and distribution patterns, and knowledge of trawling impacts, both past and predicted.

The key limitation of this pilot ERA was data paucity on coral productivity. This relates directly to the recoverability of corals from disturbance, which is a key factor in developing more robust ERAs for protected corals in New Zealand waters. A key priority in filling this information gap is research to determine the age and growth characteristics (especially growth rates) of key New Zealand protected deep-sea coral species such as the black corals (e.g., *Bathypathes* spp), as well as select gorgonian octocoral groups highlighted by the pilot ERA as high risk, such as the primnoid seafan, and species in the bubblegum coral genus *Paragorgia*.

In Section 1: '**Ageing methods for protected deep-sea corals: A review'** we update and summarise recent methods applied to successfully age deep-sea corals. Age and growth parameters of coral species from the literature are presented and methods used to age the corals evaluated. International studies are described along with New Zealand studies carried out on two gorgonian octocorals, a bubblegum coral specimen and four bamboo coral specimens, on several samples of the scleractinian stony branching coral *S. variabilis*, and recently for two *Leiopathes* black corals as part of a Marsden Project study (Neil H, Sinclair D, Hitt N unpubl. data).

The review expands our knowledge of the life history (age and growth) of the deep-sea corals for our region summarised previously in Consalvey *et al.* (2006) and by Neil *in* Tracey *et al.* (2013). These two reports were funded by the Department of Conservation and Ministry for Primary Industries respectively.

Section 2: presents our '**Recommendations**'. We describe both the proposed methodology to determine the age and growth characteristics of a key high risk New Zealand deep-sea coral species, and the study species itself, the black coral *Bathypathes* (Family Schizopathidae). The selection of a priority species to age is based on the risk assessment priority list and the literature review, and was also coupled with availability of samples (location and total numbers), and complementary research under the paleoclimate Marsden project, (*Corals, currents, and phytoplankton: Reconstructing 3000 years of circulation and marine productivity in the world's largest ocean gyre,* NIW1602). The samples will be selected from existing specimens collected by fisheries observers and researchers, and held in the NIWA Invertebrate Collection (NIC).

This document meets the reporting requirements for Year One of the Conservation Services Programme (CSP), Department of Conservation (DOC) Project POP2017-07 Objective to "Develop a methodology to determine the age and growth characteristics of key high risk New Zealand deep-sea (cold-water) coral species".

# 2 Section 1: Ageing methods for protected deep-sea corals: A review

## 2.1 Introduction

Deep-sea corals (Phylum Cnidaria), also referred to as cold-water corals, are an abundant and diverse group that exist in cold, aphotic environments of the world's oceans. They are found globally at depths ranging from hundreds to thousands of metres, and generally require hard substrate to settle on and grow, along with good current flow to provide suitable food to thrive (Freiwald and Roberts 2005). As such, deep-sea corals often populate underwater features including steep continental shelves, seamounts, knolls, drop-offs, ridges, and canyons in regions of high currents (Rogers *et al.* 2007, Tracey *et al.* 2011; Anderson *et al.* 2014.). In these environments, deep-sea corals play key ecological roles by supporting an array of marine organisms via the creation of habitat, nursery grounds, shelter, and refuge (Freiwald and Roberts 2005, Purser *et al.* 2013). Black corals along with various species of gorgonian octocorals are increasingly recognized as key species within deep coral ecosystems that provide structure and habitat, much like branching stony corals (Etnoyer and Warrenchuk 2007).

Despite the challenging and costly nature of deep-sea exploration, current research on deep-sea corals has progressed in the last 20 years. In the New Zealand region research has focused on taxonomy, age and growth studies, spatial distribution, predictive mapping tools, and assessing responses to anthropogenic stressors such as ocean acidification (Tracey *et al.* 2011; 2013; 2016; Anderson *et al.* 2014; Gammon 2016).

Deep-sea corals are typically characterised by both long life and slow growth. Various ageing methods have revealed that some corals are thousands of years old and continue to grow today (Prouty *et al.* 2011). For instance, the black coral *Leiopathes* displays ages of over 2,000 years (Roark *et al.* 2006, Roark *et al.* 2009, Carriero-Silva *et al.* 2013) and colonies of the stony coral *Lophelia pertusa* and *Solenosmilia variabilis* have been found to be continuously growing in reef form for 9,000 and 10,744 years, respectively (Fallon *et al.* 2014, Neil *et al.* in review).

Corals also exhibit a variety of growth strategies and their structural forms can be as individual colonies or clusters of individual colonies. Several are bushy, tree or whip-like, or they can build complex three-dimensional reef structures. Modular organisms, such as trees and corals, grow by the addition of modules (i.e., more polyps or leaves) which can result in an increase in body size and extremely long life spans, a concept described by Lartraud *et al.* (2017). Those authors also discuss applying some of the techniques developed for trees (e.g., annual growth ring count).

Growth rates have been recorded for multiple deep-sea corals and reveal that growth is slow, ranging from as little as microns to perhaps 1–2 cm per year (Sherwood and Edinger 2009, Roark *et al.* 2009, Carriero-Silva *et al.* 2013, Prouty *et al.* 2016; Tracey *et al.* 2011). For the stony coral *S. variabilis*, reported growth rates from radiocarbon dating methods indicate that it would take 2,000–3,000 years to build just one metre of reef (Neil *et al.* in review, Tracey *et al.* 2013, Fallon *et al.* 2014). Growth rates in corals have also been shown to vary throughout their lifespans. For instance, it is commonly observed that corals undergo an initial period of rapid growth to allow colonization, followed by decreased growth rates with age (Mortensen 2001, Brooke and Young 2009, Roark *et al.* 2009). This trend, however, is not consistent across all deep-sea corals; instead, some larger corals have also exhibited higher growth rates than smaller individuals, likely due to an increased available surface for food uptake (Roark *et al.* 2005). Variation in growth both within a coral and between different corals is likely attributable to environmental influences. Factors such as temperature, pH, salinity, food availability, sedimentation, hydrography, and the geomorphology or substrate of the seabed (e.g., bedrock, seamount top or flank), have been all shown to affect growth in deep-sea corals (Mortensen 2001, Mortensen and Buhl-Mortensen 2005, Tracey *et al.* 2007, Thresher 2009, Jantzen *et al.* 2013, Tracey *et al.* 2013, Thresher *et al.* 2016).

The slow-growing yet long-lived nature of deep-sea corals make them especially vulnerable to a variety of anthropogenic stressors. Ocean acidification, for instance, is projected to greatly impact those corals composed of calcium carbonate (e.g., stony corals and certain gorgonian octocorals), as decreases in pH will likely alter skeletal composition and compromise growth (Tracey *et al.* 2013; Bostock *et al.* 2015; Gammon 2016; Gammon *et al.* submitted). Bottom trawling and bottom long-ling methods serve as major threats to deep-sea corals, with all groups recorded as common bycatch from these fishing events in the New Zealand region (Clark *et al.* 2014; Tracey *et al.* 2017). Deep-sea corals are also at risk of damage from equipment and sedimentation impacts from oil, gas, and mineral exploration and telecommunication industries and are sometimes even purposefully harvested for their economic value (e.g., jewellery) (Roark *et al.* 2006). The high rate of destruction coupled with the fragile life history traits of deep-sea corals has serious implications for coral resilience and ability to recovery (Tracey *et al.* 2013). Monitoring of newly protected habitats on the Chatham Rise have revealed no occurrences of recovery over a period of ten years; instead, it is thought that recovery will take centuries, if at all (Clark *et al.* 2014). Because of this, conservation efforts to prevent population collapse and extinction have been initiated, for example in regions the US (Hourigan *et al.* 2017).

Recognizing these threats to deep-sea corals, the 2010 amendment of Schedule 7A of the Wildlife Act 1953 protects all hard corals, including: black corals (all species in the order Antipatharia); gorgonian octocorals in the order Alcyonacea (previously known as Order Gorgonacea); stony corals (all species in the order Scleractinia); and hydrocorals (all species in the family Stylasteridae).

These key protected hard coral groups differ in both skeletal composition and growth forms. For instance, both reef-forming stony corals, the stylasterid hydrocorals, and some tree-like gorgonian octocorals such as *Paragorgia* spp. have skeletons composed of calcium carbonate, making them particularly vulnerable to ocean acidification (Tracey *et al.* 2013; Bostock *et al.* 2015). In contrast, black corals have proteinaceous skeletons (Love *et al.* 2007).

Because growth and age are important life characteristics that have implications for coral resilience, ageing methods are extremely valuable. Ageing can be complex, however, because not only are deep-sea corals inaccessible to easily observe for long periods *in situ*, they also exhibit great diversity in growth and morphology (Stoddart 1969, Tracey *et al.* 2013). As such, a universal ageing method does not exist, but rather a variety of methods are used to accurately describe the age and growth rate of deep-sea corals. The methods include measuring growth by (1) direct observations; (2) the enumeration of growth bands from coral skeletons; and (3) the use of radiometric dating to trace isotopes in coral skeletons. Often, multiple methods are used for age validation, which can result in the most accurate estimates of growth rate and age (e.g., Thresher *et al.* 2004, Tracey *et al.* 2007, Sherwood and Edinger 2009). In addition to providing critical information about the life history of corals, ageing is valuable because deep-sea corals can act as environmental archives, revealing past oceanographic conditions and climatic events (Smith *et al.* 1997, Sherwood *et al.* 2005, Williams *et al.* 2006, Thresher *et al.* 2016). For instance, isotopic ratios of elements in coral skeletons can reveal ocean circulation patterns, cooling events, and sediment or nutrient fluxes (Mikkelsen *et al.* 1982, Druffel *et al.* 1990, Magini *et al.* 1998, Tracey *et al.* 2003, Thresher *et al.* 2004, Magini *et al.* 2010). Because of this, deep-sea corals have the potential to inform otherwise unknown past environmental conditions in the deep ocean, which is of particular interest in light of the present changing climate.

Here, we provide a comprehensive review of methods currently used to age deep-sea corals, specifically for the protected coral groups (i.e., Scleractinia, Antipatharia, Alcyonacea and Stylasteridae). We first describe each method (e.g., direct observations, enumeration of growth bands, and radiometric analyses) with their advantages and disadvantages, and for each method, give examples of key protected deep-sea coral groups where these methods have been applied. We then summarise available growth and age information for all studies done to date for the protected deep-sea coral groups (Appendix 1). The table is adapted from Tracey *et al.* (2013) and Clark *et al.* (2014). Also presented in Appendix 1 is a small amount of ageing study data summarised for two non-protected coral groups (Families Zoanthidae and Pennatulacea).

Lastly, based on our findings, we recommend which method may be most appropriate for obtaining accurate age and growth data for key deep-sea protected coral species in the New Zealand region (Appendix 2).

## 2.2 Age and growth methods

In the following sections, we present ageing methods used for deep-sea corals. When examining the key protected coral groups that each method has been applied to, only stony corals, black corals and gorgonian octocorals are considered, as there have been no ageing or growth studies to date for hydrocorals. Growth in deep-sea corals is classified mainly by linear extension and radial growth. Taking an example of a coral branch, linear extension refers to growth on the vertical axis, describing how tall or long the branch has grown out**.** Radial growth, by contrast, describes the diameter of the coral branch, measuring growth on the horizontal axis (e.g., thickness). Other measurements, including buoyant weight and polyp additions, have been used to study growth, but are not as widespread and therefore do not offer a good comparative measure (e.g., in Orejas *et al.* 2008, Orejas *et al.* 2011a, Orejas *et al.* 2011b, Sabatier *et al.* 2012, Gammon 2016, Tracey *et al.* 2016, Gammon *et al.* submitted).

### 2.2.1 Direct observations

Direct observations involve observing individual corals overtime either *in situ* or in aquaria and measuring growth from observation (e.g., photographs, videos). Another strategy for direct observations includes taking advantage of manmade structures of a known age that contain deep-sea corals, which allows the extrapolation of age and growth rate. This has been done with both telegraph cables and oil rigs that have returned to the surface colonized with deep-sea coral communities (Duncan 1877, Bell and Smith 1999, Gass and Roberts 2006). There are advantages to using direct observations to age deep-sea corals, namely that the observation of the coral in its natural habitat may give clues about growth patterns that would otherwise be lost. This method requires opportunistic events or it is costly (i.e., exploration of the deep-sea requires a remotely operated vehicle or manned submersible) and requires multiple monitoring visits over a very long time to observe any signs of growth, as growth rates in deep-sea coral are extremely slow.

In the New Zealand region growth rates of 3.9 cm $y^{-1}$ have been obtained for shallow (fiord) cold water black coral *Antipathes aperta* (Grange & Singleton 1988). There are a few direct observation studies available for gorgonians, primarily those examining time series photographs and videos for *Primnoa* spp., *Paramuricea placomus*, and the bubblegum coral *Paragoria arborea* in the North Atlantic (Mortensen and Buhl-Mortensen 2005, Lundalv *et al.* 2012, Bennecke *et al.* 2016*)*, and gorgonian octocoral *Calcigorgia spiculifera* in the North Pacific (Stone *et al.* 2017). Most of the direct observation studies, however, have been carried out on stony corals. For instance, *in situ* measurement and video analyses have been carried out for *Lophelia pertusa* and reveal a linear extension growth rate of 0.7–3.77 mm $y^{-1}$ (Brooke and Young 2009, Lundalv *et al.* 2012). There have also been a number of studies measuring growth of *L. pertusa* and *Madrepora oculata* based on observations in aquaria over periods of eight months to two years, where growth rate was found to be from 5.5–18 mm $y^{-1}$ (Mortensen and Rapp 1988, Mortensen 2001, Orejas *et al.* 2008, Orejas *et al.* 2011b). However, those growth rates for *L. pertusa* in aquaria studies were much higher than those *in situ* (2x–6x). The New Zealand aquaria study on *S. variabilis* found no treatment effect between the pH reflecting the region's current conditions (7.88) and an end-of-century scenario (7.65), on the growth rates of corals which were seen to be highly variable, ranging from 0.583 to 3.068 mm $y^{-1}$ (Gammon 2016; Tracey *et al.* 2016; Gammon *et al.* submitted).

### 2.2.2 Enumeration of growth bands

Growth bands in deep-sea coral skeletons, which are formed repeatedly over discrete time periods, can be used to determine ages and growth rates. This method involves counting bands or zones formed over a given distance of skeleton, and is comparable to counting the rings of trees or fish otoliths. To view such growth bands, it is necessary to section a skeleton fragment with a diamond-edged saw, polish the section on a lapidary wheel, and finally embed it in epoxy resin on glass slides for viewing with microscopy (Andrews *et al.* 2002, Mortensen and Buhl-Mortensen 2005, Tracey *et al.* 2007). To obtain a clearer resolution of banding pattern, coral growth bands can also either be fluoresced or can be fixed and stained prior to sectioning (e.g., calcein stain developed for the organic matrix of the red precious coral *Corallium rubrum*) (Tracey *et al.* 2003, Marschal *et al.* 2004).

The use of the enumeration of periodic growth bands or increments as an ageing method can be seen as reasonably straight forward, however complex banding patterns can place serious limitations on this method (Rogers *et al.* 2007). In addition, if growth zones contain high organic content, fixatives can interact to dehydrate or denature certain bands, which results in a decreased resolution between growth zones (Sánchez *et al.* 2004). Therefore, skeletal composition and morphological complexity are important considerations when applying this method. For instance, the skeletons of bubblegum corals are porous, which makes it hard to identify growth rings, and consequently, confident estimates of growth rate have not been obtained for these gorgonians using solely growth band counts (Griffin and Druffel 1989, Tracey *et al.* 2003, Andrews *et al.* 2005). It is also difficult to age stony corals using growth band counts due to their complex morphology, the branches are often hollow and so it is only the cup or calyce region of the branching or solitary form that can be examined for growth increments (e.g., see Hamel *et al.* 2010, who obtained age estimates from skeletal patterns in the cup coral *Flabellum alabastrum*).

Instead, enumeration of growth bands is ideal for deep-sea corals that have a high contrast between growth bands, and has proved successful for bamboo corals and black corals (Roark *et al.* 2005, Love *et al.* 2007, Rogers *et al.* 2007, Tracey *et al.* 2007, Noe *et al.* 2008). However even in these high contrast corals there are potential limitations to this method, as it is often difficult to distinguish which bands are annual. For instance, zones may exhibit lunar periodicity or be a product of food or sediment flux, thus occurring based on seasonal cycles rather than annual cycles (Risk *et al.* 2002, Roark *et al.* 2005, Tracey *et al.* 2007, Fallon *et al.* 2014). Misinterpretation of growth bands may lead to inaccurate age and growth estimations. In addition, corals may have more than one point of growth, and bands can also vary based on environmental conditions and surrounding water movement, which can further confound results (Risk *et al.* 2002, Matsumoto 2007, Noe *et al.* 2008).

The majority of studies that have successfully applied counting of growth bands to determine ageing and growth rate are for gorgonian octocorals. Ages for a variety of gorgonians have been obtained based on radial growth rates calculated from enumeration of growth bands, and these include 400 year old *Keratoisis* bamboo corals, 100 year old *Primnoa* spp., and 60 year old *Lepidisis* spp. (Mortensen and Buhl-Mortensen 2005, Sherwood *et al.* 2005, Thresher *et al.* 2004, Tracey *et al.* 2007, Thresher *et al.* 2007, Sherwood and Edinger 2009). Black corals have also been successfully aged using growth counts, with ages from 150 years old to 480 years old for *Antipathes dendrochristos* and *Leiopathes glaberrima*, respectively (Love *et al.* 2007, Williams *et al.* 2007). In a study of the black coral *Stauropathes arctica* ring counts of 55–58 were obtained (Sherwood & Edinger 2009), with the authors noting that radiocarbon dating constrained these ages to 55 and 82 years respectively. Growth rates of black corals via growth band enumeration reveal low radial growth from 0.008–0.140 µm $y^{-1}$ (Love *et al.* 2007, Prouty *et al.* 2011). The gorgonian bubblegum corals (e.g., *Paragorgia*) and red precious corals (e.g., *Corallium*), however, have not been aged successfully using growth band counts due to inherent complex or poorly defined banding patterns (Griffin and Druffel 1989, Andrews *et al.* 2005).

### 2.2.3 Radiometric analyses

Radiometric dating of deep-sea corals takes advantage of trace amounts of radioactive isotopes incorporated into the coral skeleton during formation. This technique measures the decay (i.e., via a known constant rate) of the isotope. Radiometric dating assumes that there has been no exchange of the element between the skeleton and environment since formation (Curtis 1966). Deep-sea corals are particularly at risk of contamination as they are generally coated with iron and magnesium oxides that can absorb additional isotopes like carbon, thorium, uranium, lead, etc. (Cheng *et al.* 2000, Sabatier *et al.* 2012). These newly introduced isotopes are not part of the closed system decay within the coral skeleton, but may be detected during the analyses, resulting in erroneous age and growth information (Lomitschka and Mangini 1999, Cheng *et al.* 2000, Sabatier *et al.* 2012). Thorough cleaning processes are therefore required for all radiometric analyses in order to avoid contamination, and this has been applied to New Zealand samples thus far (Neil *et al.* in review and NIWA unpub. data). Accurate dating also relies on the application of corrections to data, in which models account for various limitations of each dating method to allow the most accurate age to be obtained; however, this stage offers additional potential error inherent of modelling (Stuber and Polach 1977, Schroder-Ritzaru 2005, Noe *et al.* 2008, Chen *et al.* 2000). While there are a number of radiometric dating techniques, the three main methods employed to date deep-sea corals include radiocarbon(14C) dating, lead-210 (210Pb) dating and uranium-thorium (U/Th) dating, as described in the following sections.

### Radiocarbon $^{14}C$ dating

The most common radiometric method used in deep-sea corals is dating with the radiocarbon ($^{14}C$) isotope. This method which relies on the fact that a very small amount of natural carbon in the atmosphere is radioactive in the form of $^{14}C$ and this is incorporated into the coral skeleton when it forms its calcium carbonate or protein and chitin (Adkins *et al.* 2002, Tracey *et al.* 2003, Consalvey *et al.* 2006). Because the half-life of radiocarbon is known to be 5,730 years, this method can be used to reliably age specimens to 50,000 years ago; beyond that, the activity of $^{14}C$ becomes too tiny to detect (Coleman 1991, Sheridan 1995). During the 1950s–60s, there was rapid increase of atmospheric $^{14}C$ resulting from the testing of nuclear devices; this so-called “bomb carbon” can also be used as a tool to calibrate ages, providing a reference point for more recent samples (Coleman 1991, Tracey *et al.* 2003, Roark *et al.* 2009; Sherwood & Edinger, 2009).

Prior to analyses, samples should be properly cleaned (e.g., acid leached) of black crusts and endolithic activity to remove any younger contaminant $^{14}C$, which may alter results (Adkins *et al.* 2002; Neil *et al.* in review). Following this, samples are prepared via acidification or combustion (e.g., conversion of skeletal carbons to $CO_2$) and converted to graphite (Adkins *et al.* 2002, Roark *et al.* 2006). The graphite targets are then analysed by Accelerator Mass Spectrometry (AMS) and provide information about the percentage of modern radiocarbon in the sample. To convert the AMS radiocarbon results to dates requires several corrections, assumptions and calibrations (Stuiver and Polach 1977, Adkins *et al.* 2002, Roark *et al.* 2005).

Radiocarbon dating of deep-sea corals has some limitations (Donahue *et al.* 1990). As a result of ocean circulation, the radiocarbon age of the water in the oceans is significantly older than the atmosphere, the so called “marine reservoir age” (Tracey *et al.* 2003, Consalvey *et al.* 2006, Roark *et* *al.* 2006, Noe *et al.* 2008). Errors in the reservoir age can have significant effects on coral age estimates; for instance, a 10% error has been estimated to add 85 years for age estimates of the black coral *Leiopathes* spp. (Carriero-Silva *et al.* 2013). Correcting for reservoir ages requires knowledge of surrounding waters and assumes constant ratios of radiocarbon in the water; however, these levels may be altered by mixing within the ocean, localised upwelling events and productivity blooms, all of which can alter carbon cycle transformations and coral skeletal composition of $^{14}$C (Bowman 1995, Thresher *et al.* 2004, Thresher *et al.* 2007, Roark *et al.* 2005, Consalvey *et al.* 2006). The resultant confounding data can prove hard to analyse, as exemplified in a study by Thresher *et al.* (2004). Here, $^{14}$C-dating was employed in combination with growth band counts and U/Th-dating (described later) for bamboo corals of *Keratoisis* spp. and revealed ages that were not in agreement with the latter two methods. This difference was attributed to a variable $^{14}$C reservoir age, which was likely due to cooling events due to upwelling of deep waters to where the coral was growing. This was further supported by temperature proxies. Radiocarbon reservoir ages are poorly known in the deep sea around New Zealand with only limited water samples measured in this region (Sikes *et al.* 2008, Key *et al.* 1996, 2004). It also appears that the complex oceanography of this region with downwelling events can significantly alter the $^{14}$C signal of the waters, introducing bomb radiocarbon to depths greater than 600 m. Waters below 800 m appear to be unaffected by bomb radiocarbon, but this is likely to change with time and ocean circulation (Sikes *et al.* 2008).

A final consideration with $^{14}$C-dating is the lack of knowledge on how deep-sea corals feed and incorporate carbon when growing, which could potentially further confound age and growth models (Tracey *et al.* 2003, Consalvey *et al.* 2006).

Once the radiocarbon reservoir correction has been applied to the sample, the radiocarbon age must be calibrated to the global marine calibration curve (currently MARINE13; Reimer *et al.* 2013). This is because the radiocarbon age does not have a 1:1 relationship to the calendar age as the production of $^{14}$C in the atmosphere changes through time. There are number of different software programs that can be used to undertake this calibration including CALIB (http://calib.org/) and Oxcal (https://c14.arch.ox.ac.uk/oxcal.html). For background see: https://c14.arch.ox.ac.uk/calibration.html

Other approaches have been to date the inner and outer zones, or the base and the tips of corals and determine the age difference directly (e.g., see Neil *et al.* in review, Tracey *et al.* 2003), especially in regions where the radiocarbon reservoir age may be unknown.

Despite apparent disadvantages, radiocarbon dating has been successfully used on a number of coral species, including stony corals, black corals and gorgonian octocorals (Druffel *et al.* 1990, Roark *et al.* 2006, Carriero-Silva *et al.* 2013, Prouty *et al.* 2016, Neil *et al.* in review). For stony corals in the New Zealand region, $^{14}$C-dating has been mostly focused on *S. variabilis.* Samples from other key branching stony coral species in our region (*Goniocorella dumosa*, *Madrepora oculata*) are currently being radiocarbon dated but the results are not yet available (author's unpublished data). The studies on *S. variabilis* have revealed extreme longevity, ageing individual corals to 75–666 years old and coral colonies to 9,000–10,744 years (Fallon *et al.* 2014, Tracey *et al.* 2014, Neil *et al.* in review). $^{14}$C-dating for black corals have revealed extremely slow growth, with multiple reported radial growth rates of less than 10 µm/yr in *Leiopathes* spp. (Roark *et al.* 2006, Roark *et al.* 2009, Prouty *et al.* 2011, Carriero-Silva *et al.* 2013). For gorgonian octocorals, $^{14}$C-dating has been successful on a number of different species, with the majority focusing on the *Keratoisis* bamboo coral. $^{14}$C-dating has also revealed fairly consistent radial and linear growth rates for the bamboo coral, ranging from ~5–200 µm/yr and 0.2–1 cm/yr, respectively, with variations likely attributable to environmental or habitat variation (Roark *et al.* 2005, Sherwood *et al.* 2005, Noe and Dullo 2006, Noe *et al.* 2008, Sherwood and Edinger 2009). For the bubblegum gorgonian (*Paragorgia arborea*), where growth band counts have previously failed to produce ageing information, $^{14}$C-dating has been able to accurately define growth as 15–25 mm/yr to reveal an approximate age between 300–500 years (Tracey *et al.* 2003). Contrary to growth band counts, whose accuracy relies on coral morphological characteristics, the effectiveness of $^{14}$C-dating instead appears to be dependent on local environmental variability, which can potentially alter levels of oceanic radiocarbon.

## Lead-210 dating

Lead-210 ($^{210}$Pb) dating is another radiometric technique that can be used to provide valid estimates of age and growth for deep-sea corals. This method measures the radioactive decay of $^{210}$Pb incorporated into the coral skeleton from the environment at the time of formation (Andrews *et al.* 2002, 2009, Tracey *et al.* 2007). With a relatively short half-life of 22.3 years, the build in $^{210}$Pb activity takes about 120 years to reach secular equilibrium with radium ($^{226}$Ra). Typically, $^{210}$Pb activity is analysed along in a radial pattern within the thickest part of the colony or along the growth axis of the coral skeleton in a time series transect. The assumption is made that the uptake of $^{210}$Pb by the skeleton is constant over time and that the average growth rate of the coral is estimated by fitting a radioactive decay curve to the $^{210}$Pb activity. Radium-226 is also incorporated to the skeleton and will also create some in situ $^{210}$Pb activity. This “supported” $^{210}$Pb is estimated from the 226Ra activity in skeletal parts that are older (>100 years, Robinson *et al.* 2014). Typically, this activity is negligible, but can be back calculated to adjust for supported and unsupported $^{210}$Pb activities.

In general, this method involves proper cleaning of samples (e.g., removal of leachable lead) and use alpha-spectrometry (LMS) to assay samples for $^{210}$Pb activity via polonium-210, with emphasis on exogenous $^{210}$Pb levels in relation to $^{226}$Ra activity, which can be used to provide valid estimates of age and growth (detailed methods given in Andrews *et al.* 2002, 2009, Sabatier *et al.* 2012, Adkins *et al.* 2004). As such, this method is more appropriate for dating corals that are less than 100 years old (Andrews *et al.* 2002, 2009, Tracey *et al.* 2007, Sabatier *et al.* 2012). For instance, Andrews *et al.* (2005) found that both the gorgonian bamboo and precious corals were over one hundred years old based on the fact that the $^{210}$Pb:$^{226}$Ra activity ration was in equilibrium (ratio =1.0). While still informative, ages and growth may be better estimated through the use of other radiometric techniques. A potential disadvantage for use of $^{210}$Pb-dating is the assumption of constant uptake from the sea water through time and this may not be the case for some corals. For example, inconsistent patterns of $^{210}$Pb:$^{226}$Ra activity have been measured in coral skeletons that are attributed to complex coral growth patterns, variable uptake, an open system to radionuclides, or some combination of these factors (*see* Figure 10, Andrews *et al.* 2009). Poorly calcified coral, such a *Paragorgia* spp. or sea whips (Wilson *et al.* 2002, Andrews *et al.* 2005), have been shown to exhibit such problems for $^{210}$Pb dating.

Lead-210 dating has been successfully applied in the determination of age and growth for protected deep-sea corals. Currently, only one study has used $^{210}$Pb-dating to assess age and growth in stony corals, where linear and radial growth rates and ages of *Desmophyllum cristagalii* and *Enallopsammia rostrata* revealed samples were over 100 years old (Adkins *et al.* 2004). In black corals, $^{210}$Pb-dating has been applied to two species, *Antipathes dendrochristos* and *Leiopathes glaberrima* (Williams *et al.* 2006, Love *et al.* 2007, Williams *et al.* 2007). For *A. dendrochristos*, $^{210}$Pb dating was employed to clarify the use of ambiguous growth band counts to determine age — counting criteria revealed two potential interpretations of banding patterns that provided age estimates of either 30 or 300 years, which led to growth rate estimates that differed by orders of magnitude (Love *et al.* 2007). In this case, $^{210}$Pb-dating revealed the accurate age for the coral was 30 years and confirmed the faster growth pattern was annual — the smaller radial growth bands were attributed to lunar periodicity or nutrient fluxes (Love *et al.* 2007). Overall, the majority of $^{210}$Pb-dating methods have been applied to gorgonian octocorals and have been generally combined with other methods, like $^{14}$C dating (both bomb produced and true pre-1950 radiocarbon dating). $^{210}$Pb-dating has been successfully applied to various bamboo coral (e.g. *Lepidisis* and *Keratoisis* spp.), red tree coral (*Primnoa resedaeformis (*now *P. pacifica* in the Pacific Ocean)), and *Corallium* spp. (Druffel *et al.* 1990, Andrews *et al.* 2002, 2005, 2009, Thresher *et al.* 2004, Sherwood *et al.* 2005, Thresher *et al.* 2007, Tracey *et al.* 2005, Sherwood and Edinger 2009). Precise ages of less than 200 years were revealed with $^{210}$Pb-dating, and linear and radial growth rates were found to be low across all tested gorgonians (*see* Appendix 1, e.g., Andrews *et al.* 2002; Prouty et al 2017).

## Uranium/Thorium dating

Uranium-thorium (U/Th) dating is the final radiometric dating technique that has been shown to give high precision ages on modern aragonitic corals (Cheng *et al.* 2000). Unlike the $^{14}$C and $^{210}$Pb radiometric dating methods this technique does not measure the accumulation of a stable end-member decay product, but instead the age is based on the degree to which secular equilibrium has been restored between $^{230}$Th and its radioactive parent $^{234}$U within a sample and can date a specimen to over 500,000 years ago with an uncertainty of <1% (Edwards *et al.* 1987, Goldstein *et al.* 2001). Uranium is soluble in sea water and thus all organisms that grow in seawater incorporate some uranium at a level of parts per billion to parts per million. In contrast thorium is insoluble and therefore should not be incorporated in the organism's skeleton. However, deep-sea corals tend to have higher thorium absorbed on the outside of their skeletons through the precipitation of metal oxides (e.g., from the surrounding water and detritus, which discolour the skeleton) (Chen *et al.* 2000). The concentration of the long lived $^{232}$Th is therefore also monitored to assess the contribution of $^{230}$Th not from uranium decay (Cheng *et al.* 2000). It is recommended that rigorous cleaning methods are used to remove excess thorium (Lomitschka and Mangini 1999, Cheng *et al.* 2000, Schroder-Ritzau *et al.* 2005, Sabatier *et al.* 2012) prior to the measurement of $^{230}$Th, $^{232}$Th, $^{234}$U and $^{238}$U using thermal ionization mass spectrometry (described in detail in Edwards 1988, Chen *et al.* 1989, Cheng *et al.* 2000). The effects of diagenesis (chemical alteration of the carbonate skeletons) can be monitored using the ratio of $^{234}$U: $^{238}$U (Robinson *et al.* 2014).

While limitations to this method include the reliance on constant uranium and thorium oceanic levels and rigorous cleaning, this method is advantageous over $^{14}$C-dating as it does not require radiocarbon reservoir corrections and calibrations (e.g., the marine reservoir effect, and variations in the radiocarbon calibration curve) and is advantageous over $^{210}$Pb-dating as it can date much older specimens. However, there are drawbacks to this method. To date, it hasn't been possible to use it on calcitic corals, such as bamboo corals, because uranium concentrations are very low (e.g., in bamboo coral calcite uranium comprises ~0.03 ppm (Sinclair *et al.* 2011)), although with new more sensitive analytical techniques it is now possible to measure lower concentrations of U isotopes. It has also been found that uranium can be easily diagenetically altered by open system behaviour (e.g., exchange of U and Th with the surrounding environment) in calcitic gorgonian and stylasterid hydrocorals, thus producing erroneous ages (Robinson *et al.* 2007; Sinclair *et al.* 2011; Robinson *et al.* 2014).

Compared to other radiometric analyses, U/Th-dating has been applied to the protected coral groups less frequently, but appears to be increasing in use with time. Currently, this method has been applied to only one black coral, where in combination with $^{14}$C-dating it revealed the slow-growing and long-lived nature of black corals in the Tasman Sea (Komugabe *et al.* 2014). There is also only one instance of U/Th-dating of calcitic gorgonian octocorals, where it was successfully used in conjunction with growth band counts to age the bamboo coral *Keratoisis* to be about 400 years old based on a growth rate of 0.005 mm/yr (Thresher *et al.* 2004). Lastly, U/Th-dating has been applied to various stony corals, with most work focusing on *Desmophyllum cristagalli* and *Lophelia pertusa* (Cheng *et al.* 2000, Risk *et al.* 2002, Pons-Branchu *et al.* 2005, Schroder-Ritzrau 2005). U/Th-dating applied to *D. cristagalli* has yielded linear extension rates ranging from of 0.1–3.1 mm/yr, which have been validated using $^{14}$C-dating (Cheng *et al.* 2000, Risk *et al.* 2002). For *L. pertusa,* a precise and fairly constrained age range was determined between 82–211 years, using U/Th dating (Pons-Brachu *et al.* 2005). U/Th dating has also revealed that deep-sea corals existing in the Mid-Atlantic Ridge and the western Mediterranean Sea have been growing continuously for 53,500 years (Schroder-Ritzrau 2005). While there are only limited studies using U/Th to date age and growth rates in modern corals there have been many studies using this method to understand paleoceanographic information from fossil scleractinian corals (Robinson *et al.* 2014).

### 2.2.4 Amino acid racemization

A final, yet uncommon, method for obtaining age and growth data from deep-sea corals uses amino acid racemization, specifically aspartic acid racemization (Goodfriend 1997, Sherwood *et al.* 2006). This method relies on different configurations of amino acids (e.g., “L” versus “D”) and takes advantage of the fact that living organisms tend to keep their amino acids in the “L” configuration (Bada 1975). However, when an organism dies, amino acids undergo racemization, in which amino acid configuration control ceases and the ratio of D:L amino acids approaches one (Bada 1975). This method is achieved through reverse-phase high performance liquid chromatography (methods given in detail in Kaufman and Manley 1998, Sherwood *et al.* 2006). Racemization rates, however, can be affected by the surrounding environment (e.g., temperature, humidity) and may also depend on the amino acid composition (Bada 1975). This restricts this method to organisms with known environmental histories. Despite this, this method proves advantageous because amino acid composition in modern day corals has been found to be the same as in fossils, suggesting that this method is not sensitive like radiometric dating to errors that may arise from contamination (Sherwood *et al.* 2006). There is only one instance of this method applied to any of the protected coral groups, where Sherwood *et al.* (2006) used aspartic acid racemization along with $^{14}$C-dating to age *Primnoa resedaeformis*. Here, radial growth rates of 0.06 mm/yr were observed and ages of ~700 years old were extrapolated. In addition, Sherwood *et al.* (2006) found that D/L-aspartic acid dating exhibited better constraints on age estimates than $^{14}$C-dating, and suggested that this method may be beneficial to use to screen samples for further radiometric analyses.

# 3 Section 2: Recommendations

The recommendations in this report build on the recent ecological risk assessment (ERA) carried out by Clark *et al.* (2014), along with information on the spatial distribution of available samples, and a thorough literature review (Section 1). The biological age and growth data that we recommend be obtained will be used to rank the productivity of a coral species or group, which reflects its ability to recover from trawling.

The ERA identified deep-sea species such as black corals (at the order level Antipatharia, and the genus *Bathypathes*) and the gorgonian coral (genus *Paragorgia*) as being at high risk from the effects of bottom trawling. Most reef-building scleractinian corals, as well as other gorgonian coral taxa, were assessed as medium risk in the ERA, and cup corals and hydrocorals were relatively low risk.

These results were consistent with expectations based on the form and biology of the corals, their depth and distribution patterns, and knowledge of trawling impacts, both past and predicted.

The black coral genus *Bathypathes* is widely distributed in the New Zealand region. The key species listed in Opresko *et al.* (2014) are *Bathypathes alternate*, *B. bifida*, and *B. patula*. The NIWA invertebrate collection (NIC) currently holds the following number of available specimen samples for these species: *B. alternata* = 29; *B. bifida* = 2; *B. patula* = 79, with 67 *Bathypathes* spp. yet to be described. The largest specimens held for *B. alternata* or *B. patula* will most likely be the species we select to age as they have been identified to species level, are robust enough to provide sufficient material for milling and sectioning to count basal zones, and a number of the specimens were collected from the Chatham Rise region (Figure 1), where modern $^{14}C$ reservoir age data are available for the surrounding waters (Sikes *et al.* 2008).

The literature review describes methods that have been successfully applied to provide age and growth rate estimates for a number of protected coral groups (Appendix 1). No single method was universally appropriate, and each has advantages and limitations based on experimental design, coral characteristics and local environmental variability (Appendix 2). Direct observation studies *in situ* were sparse as they are costly and require repeated monitoring over long periods of time to observe any changes in growth. Success of ageing through the enumeration of growth bands depends largely on coral morphological characteristics; as such, this method is ideal for corals that have distinct banding patterns (e.g., bamboo corals), as opposed to corals having complex growth, hollow branches, or porous skeletons (e.g., stony corals, bubblegum corals). Radiometric analyses, in contrast, generally are not sensitive to coral characteristics, but are rather more dependent upon local environmental conditions that control surrounding levels of isotopes. Each radiometric analysis has limitations which should be considered when selecting such methods.

For $^{14}C$-dating, knowledge of the local marine reservoir effect and other potential influencers of fluctuating oceanic carbon levels must be taken into consideration. For $^{210}Pb$-dating, older specimen (e.g., over 100 years old) may not be able to be precisely dated due to $^{210}Pb$-$^{226}Ra$ equilibrium constraints. Uranium/Thorium (U/Th)-dating has been applied to modern deep-sea corals to a lesser extent (but there are many studies analysing fossil corals), but may be better at overcoming the limitations of the $^{14}C$ and $^{210}Pb$ dating methods, noting that it is important to understand the coral's mineralogy and is difficult to apply to non-aragonitic corals due to the lower uranium content and issues of alteration by diagenesis from open system behaviour (e.g., the exchange of U and Th between the ocean and the skeleton). In general, a combination of methods is preferred in order to validate ageing and growth. As deep-sea corals are highly vulnerable and continue to face anthropogenic threats, determining the growth and longevity is extremely valuable to protect these organisms.

## 3.1 Selected study species and methodology

For the study we propose the Antipatharian black coral genus *Bathypathes (species B. alternata* or *B. patula)* be aged by applying the analytical method of radiocarbon ($^{14}C$) dating in tandem with preparing around 10 thin basal sections to obtain zone counts. We would age two colonies and obtain four $^{14}C$ dates per colony from the base and growing tip region to obtain radial and linear growth estimates. The methods of Tracey *et al.* (2007) and Sherwood & Edinger (2009) would be followed.

Analytical costs for $^{14}C$ dating (~$800 per sample, or potentially less if an Australian Laboratory is used), the micro-milling of material, and the interpretation of results will be covered out of the funds in Year 2 of the Project. Initially we recommend we focus on corals from Chatham Rise, from where we have the modern $^{14}C$ reservoir age, but we would also like to test corals from different regions to assess the variability in the growth rates for different regions with different oceanography and food availability.

We have proposed this method to enable comparisons with other ongoing studies and previous work that has been undertaken in New Zealand and elsewhere in the world, and also based on the review of the ageing methods presented in Appendix 2 where the success of the chosen methods was highlighted. According to the literature, these methods have worked well for black corals in other parts of the world (e.g., see Sherwood & Edinger 2009). Finally, the radiocarbon dating analyses can easily be undertaken either locally (Rafter Laboratory, GNS) or at the Radiocarbon Dating Laboratory, Australian National University, Melbourne. The preparation of basal and tip thin sections to obtain count zones can be carried out at NIWA (following the bamboo coral thin sectioning method described by Tracey *et al.* (2007)).

## 3.2 Complementary research

Previous growth rate data has been obtained using $^{14}C$ dating from two bamboo octocoral species (*Lepidisis sp*. and *Keratoisis sp*. (Tracey *et al.* 2007) and a reef-forming stony branching coral (*S. variabiis* (Neil *et al.* in review). This DOC project will complement a number of other ongoing studies that are undertaking age and growth analyses on other deep-sea corals from the New Zealand region. It will also complement growth data currently being obtained for other key black coral species (three *Leiopathes secunda; one Antipathella fiordensis;* and two unknown *Antipatharia*) from contrasting water masses north (Bay of Plenty) and southwest of New Zealand as part of a paleoclimate Marsden funded project: *Corals, currents, and phytoplankton: Reconstructing 3000 years of circulation and marine productivity in the world's largest ocean gyre,* (NIW1602). NIWA and Victoria University of Wellington are carrying out the paleoclimate study and thus far the bases of the black coral colonies have been cut and sampled for $^{14}C$ dates. Preliminary results showed the uncalibrated age ranges from the inner to outer zone of 3250 to 1173 $^{14}C$ years — approximately 2000 years old (sample 35104); and from 1960 to 506 $^{14}C$ years — approximately 1500 years old (sample 64334), (Neil H, Sinclair D, Hitt N unpubl. data). We are working collaboratively with the Marsden Project, and will incorporate their black coral age data with the aims of this DOC Project.

We have recently secured NIWA funding to radiocarbon date and age two key deep-sea stony branching corals *Madrepora oculata* from the Northwest Chatham Rise Graveyard Knolls, Northeast Chatham Rise Andes Knolls, and East Coast North Island region Ritchie Hills region, and *Goniocorella dumosa* from the Graveyard Knolls. We hope these funds may also cover obtaining $^{14}C$ age data for the primnoid octocoral *Primnoa notialis* (specifically from the Chatham Rise samples*).*

The combination of all of these age and growth research projects will provide the region with a significantly improved dataset of age data for key high risk New Zealand deep-sea coral species.

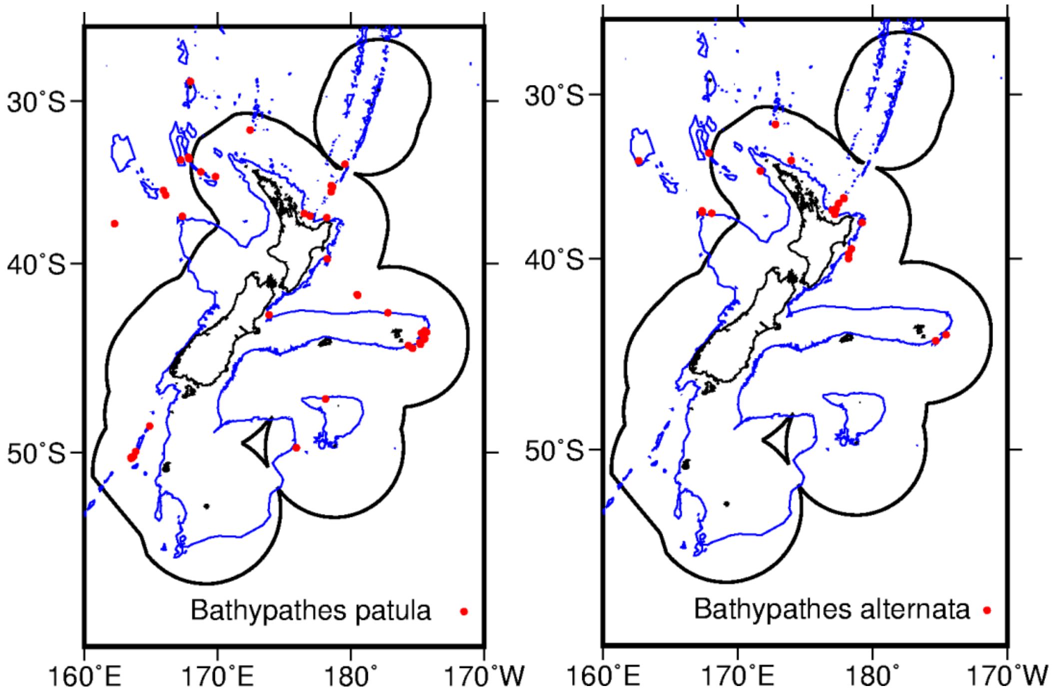

**Figure 3-1: Distribution map for the New Zealand region of the two black coral species proposed to be aged: *Bathypathes* species, *B. patula* and *B. alternata*.**

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# Appendix A Summary of current age and growth data for deep-sea corals, adapted from Tracey *et al.* 2013 and Clark *et al.* 2014.

The appendix is divided by coral group (i.e., for the protected corals Scleractinia, Antipatharia, Alcyonacea, and Stylasteridae). A small amount of age data is included for the non-protected coral groups (Families Zoanthidae and Pennatulacea). Location and depth of collection, age (in years), growth (in mm/yr), growth parameter measured (e.g., linear, radial), ageing method, and a citation reference are provided for each coral species

**PROTECTED CORAL GROUPS**

| Coral species | Location of collection (with depth in metres of collection) | Age (years old) | Growth (mm/yr) | Growth parameter measured | Method | Reference |
|---|---|---|---|---|---|---|
| **Stony Corals (Scleractinia)** | | | | | | |
| *Desmophyllum cristagalli* | Northwest Spain, Atlantic Ocean (940-990) | | 6.35 | Linear extension | Man-made structure of known age | Duncan 1877 |
| *Desmophyllum cristagalli* | Pacific, Atlantic, Southern Ocean (420-2200) | 7–535 | 0.1–3.1 | Linear extension | U/Th dating | Chen *et al.* 2000 |
| *Desmophyllum cristagalli* | Baltimore Canyon, Atlantic Ocean | >200 | 0.5–1.0 | Linear extension | 14C dating; U/Th dating | Risk *et al.* 2002 |
| *Desmophyllum cristagalli* | South Pacific Ocean | | 0.5–2 | Linear extension | 210Pb dating | Adkins *et al.* 2004 |
| *Enallopsammia rostrata* | North Atlantic Ocean | >100 | 0.07<br>5 | Radial growth<br>Linear extension | 210Pb dating | Adkins *et al.* 2004 |
| *Enallopsammia rostrata* | Bermuda, Atlantic (1410) | 560–630 | 0.87–0.98 | Linear extension | 14C dating; 210Pb dating | Lee *et al.* 2017 |
| *Lophelia pertusa* | Northwest Spain, Atlantic Ocean (940–990) | | 7.408 | Linear extension | Man-made structure of known age | Duncan 1877 |
| *Lophelia pertusa* | Rockwall Bank, Scotland, Atlantic Ocean (800) | | 6 | Linear extension | From man-made structure of known age | Wilson 1979 |
| *Lophelia pertusa* | Norway, Atlantic Ocean (300) | | 25 | Linear extension | C&O stable isotopes (assuming annual periodicity) | Mikkelsen *et al.* 1982 |
| *Lophelia pertusa* | Norway, Atlantic Ocean (250) | 520 | 19 | Linear extension | C&O stable isotopes (assuming annual periodicity) | Freiwald *et al.* 1997 |

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|---|---|---|---|---|---|---|
| *Lophelia pertusa* | Norway, Atlantic Ocean (200-250)<br>Trondhjem Biological Station, Norway (maintained in aquaria) | | 5.5<br>2.6 | Linear extension<br>Linear extension | C&O stable isotopes (assuming annual periodicity)<br>Observation in live aquaria over 18 mo | Mortensen & Rapp 1998 |
| *Lophelia pertusa* | Oil storage buoy in the North Sea (60-109) | | 26 | Linear extension | From man–made structure of known age | Bell and Smith 1999 |
| *Lophelia pertusa* | Bergen Aquarium, Norway (maintained in aquaria) | | 1.3–9.4 | Linear extension | Observations of live coral grown in aquaria | Mortensen 2000, 2001 |
| *Lophelia pertusa* | Sea of the Hebrides, Eastern Atlantic Ocean (220) | 86–211 | 2.2–5.0 | Linear extension | U/Th dating | Pons–Branchu *et al.* 2005 |
| *Lophelia pertusa* | Oil and gas platforms in the North Sea (94–115) | | 0.4–3.3 | Radial growth | From man–made structure of known age, video analyses | Gass & Roberts 2006 |
| *Lophelia pertusa* | Cap de Creus Canyon, Mediterranean Sea (214–218, maintained in aquaria) | | 15–17 | Linear extension | Observation in live aquaria over 15 mo | Orejas *et al.* 2008 |
| *Lophelia pertusa* | Viosca Knoll, Gulf of Mexico (430–520) | | 2.44–3.77 | Linear extension | *In situ* measurements of transplanted (and stained) live coral | Brooke & Young 2009 |
| *Lophelia pertusa* | Island of Malta, Mediterranean Sea (300) | | 8.76 | Linear extension | Observation in live aquaria over 1 year | Orejas *et al.* 2011b |
| *Lophelia pertusa* | | | 0.7 | Linear extension | *in situ* video analysis | Lundalv *et al.* 2012 |
| *Lophelia pertusa* | Rost Reef, Arctic Circle (350) | | 8 | Linear extension | 210Pb dating | Sabatier *et al.* 2012 |
| *Lophelia* sp. | | >20–9000 | 1–35 | | Various methods | Summarised in Tracey *et al.* 2014 |
| *Madrepora oculata* | | | 3–18 | Linear extension | Observation in live aquaria over 15 mo | Orejas *et al.* 2008 |
| *Madrepora oculata* | Cap de Creus Canyon, Mediterranean Sea (250, maintained in aquaria) | | 51.1 | Linear extension | Observation in live aquaria over 2 years | Orejas *et al.* 2011b |
| *Madrepora oculata* | Rost Reef, Arctic Circle (350) | 3 | 14.4 | Linear extension | 210 Pb dating | Sabatier *et al.* 2012 |
| *Solenosmilia variabilis* | Tasmanian seamounts, Australia, South Pacific Ocean (958–1454) | 75–120<br>47400 (colony ) | 0.84–1.25<br>0.27 | Linear extension<br>Accumulation rate | Growth band counts; 14C dating | Fallon *et al.* 2014 |

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|---|---|---|---|---|---|---|
| *Solenosmilia variabilis* | Louisville Seamount chain, New Zealand, South Pacific Ocean (910-1448) | | 0.53-3.068 | Linear extension | Observation in live aquaria over 1 year | Tracey *et al.* 2016, Gammon 2016 |
| *Solenosmilia variabilis* | New Zealand seamounts, South Pacific Ocean (1019–1250) | 150–660 | 0.25–1.3 | Linear extension | 14C dating | Neil *et al.* in review |
| Various stony corals | North East Atlantic (77–1951) | 900–53500 | | | U/Th dating | Schroder-Ritzrau *et al.* 2005 |
| **Black corals (Antipatharia)** | | | | | | |
| *Antipathes dendrochristos* | Anacapa Island Passaga, California, USA, Pacific Ocean (106) | 30<br>140 | 1–1.25*$10^{-4}$<br>0.10–0.14 | Radial growth<br>Radial growth | Growth band counts; 210Pb dating<br>Growth band counts; 14C dating | Love *et al.* 2007 |
| *Antipathes dichotoma* | Lahaina, Hawaii, USA, Pacific Ocean (50) | 15–109 | 0.13–1.14 | Radial growth | 14 C dating | Roark *et al.* 2006 |
| Black coral | Norfolk Ridge, Tasman Sea (560) | 300–330 | 0.002–0.1 | Radial growth | 14C dating; U/Th dating | Komugabe *et al.* 2014 |
| *Leiopathes glaberrima* | Makapuu deep-sea coral bed, Hawaii, USA, Pacific Ocean (450) | 2377 | 0.005 | Radial growth | 14C dating | Roark *et al.* 2006 |
| *Leiopathes glaberrima* | North-central Gulf of Mexico (307–369) | 198 | 0.0145 | Radial growth | 210Pb dating | Williams *et al.* 2006 |
| *Leiopathes glaberrima* | Jacksonville Lithoherms, USA, Atlantic Ocean (527) | 198–483 | | | Growth band counts; 210Pb dating | Williams *et al.* 2007 |
| *Leiopathes sp.* | Hawaii, USA, Pacific Ocean (300–500) | | < 0.005 | Radial growth | 14C dating | Roark *et al.* 2009 |
| *Leiopathes* sp. | De Soto Slope, Gulf of Mexico (304–317) | >2000 | 0.008–0.022 | Radial growth | Growth band counts; 14C dating | Prouty *et al.* 2011 |
| *Leiopathes sp.* | Condo and Acor seamounts, Azores, Atlantic Oceann (290–370) | 265–2320 | 0.005–0.03 | Radial growth | 14C dating | Carriero-Silva *et al.* 2013 |
| *Stauropathes arctica* | Newfoundland and Labrador, Atlantic Ocean (812–876) | 55–82 | 0.033–0.066 | Radial growth | Bomb 14C dating | Sherwood & Edinger 2009 |
| **Gorgonian octocorals (Alyconacea/Gorgonacea)** | | | | | | |
| Bamboo coral | | | | | | |

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|---|---|---|---|---|---|---|
| *Acanella arbuscula* | Newfoundland and Labrador, Atlantic Ocean (526) | 30 | 0.02–0.070<br>3–10 | Radial growth<br>Linear extension | Growth band counts; 14C dating | Sherwood *et al.* 2005, Sherwood & Edinger 2009 |
| *Echinisis* | Antarctica (699) | | 0.012 | | 14C dating | Thresher et al 2009 |
| *Keratoisis ornata* | Newfoundland and Labrador, Atlantic Ocean (601–1193) | 94–200 | 0.053–0.075<br>9.3–10 | Radial growth<br>Linear extension | 14C dating; 210Pb dating | Sherwood *et al.* 2005, Sherwood & Edinger 2009 |
| *Keratoisis* spp. | Cascade Plataeu of Tasmania, Australia, South Pacific Ocean (1000) | 316–400 | 0.005 | Radial growh | Growth band counts; 14C dating; 210Pb dating; U/Th dating; Mg:Ca ratios | Thresher *et al.* 2004 |
| *Keratoisis* sp. | Davidson Seamount, California, USA, Pacific Ocean (1425) | 56-220<br>>200 | 1.9–4.4<br>0.05–0.11 | Linear extension<br>Radial growth | Growth band counts<br>Growth band counts (assuming annual periodicity); 210Pb dating | Andrews *et al.* 2005 |
| *Keratoisis* sp. | Urry Knoll, Chatham Rise, New Zealand, South Pacific Ocean (594–770) | 305 | 0.4 | Linear extension | 14C dating | Noe and Dullo 2006 |
| *Keratoisis* sp. | Snares Shelf, Campbell Plateau, New Zealand, South Pacific Ocean (935) | 38 | 0.22 | Radial growth | Growth band counts (SEM) | Tracey *et al.* 2007 |
| *Keratoisis* spp. | Chatham Rise, New Zealand, South Pacific Ocean (680) | | 0.23–0.64<br>5 | Linear extension<br>Vertical growth | Growth band counts; 14C dating | Noe *et al.* 2008 |
| *Keratoisis* sp. | Antarctica (2119–2592) | | 0.0155 | | 14C dating | Thresher et al 2009 |
| *Lepidisis* sp. | New Zealand seamounts, South Pacific Ocean (638–1030) | 7–58 | 0.15–0.32<br>21.5–57 | Radial growth<br>Linear extension | Growth band counts (SEM); 210Pb dating<br>Growth band counts (SEM) | Tracey *et al.* 2007<br>Tracey *et al.* 2007 |
| Various bamboo corals | Warwick Seamount, Gulf of Alaska (700) | 75 – 208 | 0.05–0.16 | Radial growth | Growth band counts; Sr:Ca ratios; 14C dating | Roark *et al.* 2005 |
| Bubblegum coral | | | | | | |
| *Paragorgia arborea* | New Zealand seamounts, South Pacific Ocean | 300–500 | 15–25 | Radial growth | 14C dating | Tracey *et al.* 2003 |
| *Paragorgia arborea* | Newfoundland and Labrador, Atlantic Ocean (414) | 80 | 0.830<br>16.2 | Radial growth<br>Linear extension | 14C dating | Sherwood *et al.* 2005, Sherwood & Edinger 2009 |

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|---|---|---|---|---|---|---|
| *Paragorgia arborea* | Northeast Channel Coral Conservation Area, Gulf of Maine, Atlantic Ocean (863) | | 37 | Linear extension | In situ measurements with 3D photogrammetrirc reconstructions | Bennecke *et al.* 2016 |
| *Paragorgia* sp. | Davidson Seamount, California, USA, Pacific Ocean (1313) | 9–14 | 60–90 | Linear extension | Growth counts (subjective, stated by authors) | Andrews *et al.* 2005 |
| Red coral | | | | | | |
| *Corallium noibe* | Little Bahama Bank, Atlantic Ocean (640) | 135 | 0.13 | Radial growth | 14C dating | Griffin & Druffel 1989 |
| *Corallium niobe* | Little Bahama Bank, Atlantic Ocean (600) | 180 | 0.11 | Radial growth | 210Pb dating; 14C dating | Druffel *et al.* 1990 |
| *Corallium rubrum* | Marseilles, France and Medes Islands, Spain, Atlantic Ocean (25–62) | 16–18 | 0.35 | Radial growth | Growth band counts, visualized by calcein–stained organic matrix | Marschal *et al.* 2004 |
| *Corallium secundum* | Makapuu deep–sea coral bed, Hawaii, USA, Pacific Ocean (450) | 68–77 | 0.170 | Radial growth | 14C dating | Roark *et al.* 2006 |
| *Corallium* sp. | Davidson Seamount, California, USA, Pacific Ocean (1482) | ~30 | 9–11 | Linear extension | Growth band counts | Andrews *et al.* 2005 |
| Other gorgonians | | | | | | |
| *Chrysogorgia* sp. | Mississippi Canyon, Gulf of Mexico (1049–1094) | 464 | 0.0052–0.0015 | Radial growth | 14C dating | Prouty *et al.* 2016 |
| *Paramuricea biscaya* | Mississippi Canyon, Gulf of Mexico (882–1852) | 187–599 | 0.0003–0.016 | Radial growth | 14C dating | Prouty *et al.* 2016 |
| *Paramuricea placomus* | | | 4–5 | Linear extension | *in situ* video analysis | Lundalv *et al.* 2012 |
| *Paramuricea* sp. | Mississippi Canyon, Gulf of Mexico (1040–1050) | 168–215 | 0.0056–0.0039 | Radial growth | 14C dating | Prouty *et al.* 2016 |
| *Paramuricea* spp. | Newfoundland and Labrador, Atlantic Ocean (814–850) | 71–103 | 0.092–0.205<br>5.6–5.8 | Radial growth<br>Linear extension | 14C dating | Sherwood *et al.* 2005, Sherwood & Edinger 2009 |
| *Primnoa arborea* | | 180 | 10<br>20–60 | Linear extension<br>Linear extension | Assumed annual growth rate from previous studies<br>Time-series photographs | Mortensen & Buhl-Mortensen 2005 |
| *Primnoa pacifica* | Japan, Pacific Ocean (385–505) | 40 | 0.19–0.37 | Radial growth | Growth band counts (assuming annual periodicity) | Matsumoto 2007 |
| *Primnoa resedaeformis* | Southeast Alaska, Pacific Ocean (>200) | 112 | 16–23.2<br>0.36 | Linear extension<br>Radial growth | Growth band counts (CAT scan); 210Pb dating | Andrews *et al.* 2002 |

| | | | | | | |
|---|---|---|---|---|---|---|
| *Primnoa resedaeformis* | Northeast Channel, Gulf of Maine, Atlantic Ocean (450) | >300 | 0.044<br>1.5–2.5 | Radial growth<br>Linear extension | 14C dating and comparison of live specimens | Risk *et al.* 2002 |
| *Primnoa resedaeformis* | Northeast Channel, Gulf of Maine, Atlantic Ocean (246–630) | 61 | 17<br><0.5 | Linear extension<br>Radial growth | Growth band counts | Mortensen & Buhl-Mortensen 2005 |
| *Primnoa resedaeformis* | Newfoundland and Labrador, Atlantic Ocean (257–640) | 18–100 | 0.083–0.215<br>10–26.1 | Radial growth<br>Linear extension | Growth band counts | Sherwood *et al.* 2005, Sherwood & Edinger 2009 |
| *Primnoa resedaeformis* | Northeast Channel, Gulf of Maine, Atlantic Ocean (250–475) | 700 | 0.06 | Radial growth | 14C dating; aspartic acid racemization | Sherwood *et al.* 2006 |
| *Primnoa resedaeformis* | Northeast Channel Coral Conservation Area, Gulf of Maine, Atlantic Ocean (863) | | 16–27 | Linear extension | In situ measurements with 3D photogrammetrirc reconstructions | Bennecke *et al.* 2016 |
| **Hydrocorals (Stylasteridae)** | | | | | | |
| No studies to date. | | | | | | |

**OTHER CORAL GROUPS (non-protected)**

| Coral species | Location of collection (with depth in meters of collection) | Age (years old) | Growth (mm/yr) | Growth parameter measured | Method | Reference |
|---|---|---|---|---|---|---|
| **Zoanthids (Zoanthidae)** | | | | | | |
| *Gerardia* sp. | Little Bahama Bank, Atlantic Ocean (632) | >3000 | 0.005 | Radial growth | 14C dating | Griffin & Druffel 1989 |
| *Gerardia* sp. | Little Bahama Bank, Atlantic Ocean (620) | 1800 | | | 14C dating | Druffel *et al.* 1995 |
| *Gerardia* sp. | Bahamas, Atlantic Ocean | 250 | | | Aspartic acid racemization | Goodfriend 1997 |
| *Gerardia* sp. | Makapuu deep-sea coral bed, Hawaii, USA, Pacific Ocean (630) | 807 | 0.0015 | Radial growth | 14C dating | Roark 2006 |
| *Gerardia* sp. | Souther Hawiian Archipelago, Pacific Ocean (380–466) | 950 | 0.0041 | Radial growth | 14C dating | Parrish & Roark 2009 |
| | | | 2.2 | Linear extension | 14C dating | |

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|---|---|---|---|---|---|---|
| *Gerardia* sp. | Hawaii, USA, Pacific Ocean (300–500) | 300–2700 | 0.0035–0.0025 | Radial growth | 14C dating | Roark 2009 |
| **Sea pens (Pennatulacea)** |  |  |  |  |  |  |
| *Halipteris willemoesi* | Bering Sea (142–248) | 7–44 | 36–61<br>0.145 | Linear extension<br>Radial growth | Growth band counts | Wilson *et al.* 2002 |

# Appendix B Advantages and disadvantages for ageing methods, with protected coral groups for which method was successfully applied.

| Method | Advantage | Disadvantages | Recommendations |
|---|---|---|---|
| **Direct observations** | | | |
| *in situ* | -Can observe coral growing in natural habitat | -Costly (e.g., ROV, manned submersible, research vessel)<br>-Requires multiple observations over a long period of time to observe growth | This method would be appropriately applied to all protected corals. |
| In aquaria | -Can monitor coral frequently<br>-Can obtain finer detail of growth (e.g., buoyant weights, polyp additions) | -May not reflect growth in natural habitat<br>-Requires long period of time to observe growth | |
| From ‘man-made’ structure of known age | -Know period of time of growth with certainty<br>-Relatively easy method | -May not reflect growth in natural habitats (e.g., changed local environments) | |
| **Enumeration of growth bands** | | | |
| Unstained | -Methodology relatively straight forward<br>-Comparatively not costly | -Complex growth rings can complicate age and growth estimates<br>-Periodicity of bands may be unknown | This method depends upon coral morphological traits and would be appropriately applied to corals with clear banding patterns (e.g., black, bamboo corals) but not for complex morphological/growth band corals (e.g., stony, bubblegum corals). |
| Stained | -Growth bands made easier to visualize | -Some fixatives may dehydrate or denature organic content of bands, making it hard to visualize<br>-Periodicity of bands may be unknown | |

| | | | |
|---|---|---|---|
| **Radiometric analyses** | | | |
| Isotope ratios | -Can characterize growth (i.e., periods of fast/slow growth) and reveal environmental conditions (e.g., temperature) | -Cannot reveal age information | This method is appropriate to apply to all protected corals in order to obtain detailed growth information. |
| 14C dating | -Can date old samples (50,000 ya) | -Consideration must be taken for marine reservoir effect<br>-Possible contamination | These radiometric analyses would be appropriately applied to all protected corals but success may vary based on local environmental variations. $^{14}$C and U/Th-dating are more appropriate for older specimens. |
| 210Pb dating | | -Cannot date older samples (>100 yr)<br>-Possible contamination | |
| U/TH dating | -Can date old samples (500,000 ya) | -Possible contamination | |
| **Amino acid racemization** | | | |
| D/L-Asp racemization | -Constant amino acid levels overtime | -Rate of racemization sensitive to temperature, humidity (fossil condition) | This method has only been tested on one protected coral, but may be appropriate for screening corals for further radiometric dating. |