New Zealand: Southwest Pacific Region

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Abstract

The New Zealand region, in the South Pacific, supports a diverse and abundant deep-sea coral fauna. In particular, framework-forming scleractinians that can form reefs can support diverse benthic assemblages. In this chapter, we first set the broader environmental scene by describing the geological and bathymetric setting of the region and its complex oceanography at both the surface and in the deep sea. We then describe current knowledge of the biology and ecology of the reef-forming species, before discussing the various threats to them from the exploitation of natural resources for commercial use, as well as a changing regime of temperature and ocean acidification due to climate change. Key knowledge gaps for the region include coral distribution data in areas without commercial fishing, information on coral age and growth, and an evaluation of the efficacy of existing protections for cold-water corals.

Keywords

Deep sea · Marine geology · Seabed mapping · Scleractinian corals · Species distribution · Predictive habitat modelling · Coral age and growth · Reproduction · Genetic connectivity · Fishing impacts

9.1 Introduction

The New Zealand region (Fig. 9.1) supports a diverse and abundant deep-sea coral fauna (Cairns 1995, 2007; Gordon 2009), where corals are important components of deep-sea ecosystems, providing habitat and refuge for a variety of invertebrate and fish species. In particular, the calcifying, framework-forming scleractinians (branching stony corals) that can form reefs (referred to as reef-corals here, and the subject group of this chapter) are a widespread and abundant group in New Zealand waters (Tracey et al. 2011) that can support diverse benthic assemblages (Clark and Rowden 2009).

In this chapter, we first set the broader environmental scene by describing the geomorphology and bathymetry of the region and its complex oceanography at both the surface and in the deep sea—thus focusing on the key elements that define the environmental characteristics of deep-sea coral-reef habitat. We then describe current knowledge of the ecology of the reef-forming species, before discussing the various threats to them from the exploitation of natural resources for commercial use, as well as a changing regime of temperature and ocean acidification (OA) due to climate change. Key knowledge gaps are then highlighted.

9.2 Geology and Bathymetric Setting

The geological history of New Zealand and its tectonic activity have resulted in a complex topography composed of a number of distinct bathymetric features including seamounts, rises, volcanic ridges, plateaus, submarine canyons, deep troughs, and abyssal plains (Fig. 9.1). Many of these features have rocky hard substrata which can support reef-coral species, especially seamount features which are widespread throughout the region as a result of subduction processes along the tectonic plate boundary, or intraplate volcanism which was common in the Cenozoic and has ages of 10–40 million years (Rowden et al. 2005; Timm et al. 2010).

The age of the reef-corals, both live and dead components of the reef matrix, is described in Sect. 9.5.2. However, linked with the active geological history of the New Zealand region are occurrences on land of fossil coral thickets in the southern part of the North Island (see Squires 1964). Records include a thicket of *Goniocorella dumosa* in mudstones, with foraminifera data indicating an age of Late

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E. Cordes, F. Mienis (eds.), *Cold-Water Coral Reefs of the World*, Coral Reefs of the World 19,
https://doi.org/10.1007/978-3-031-40897-7_9

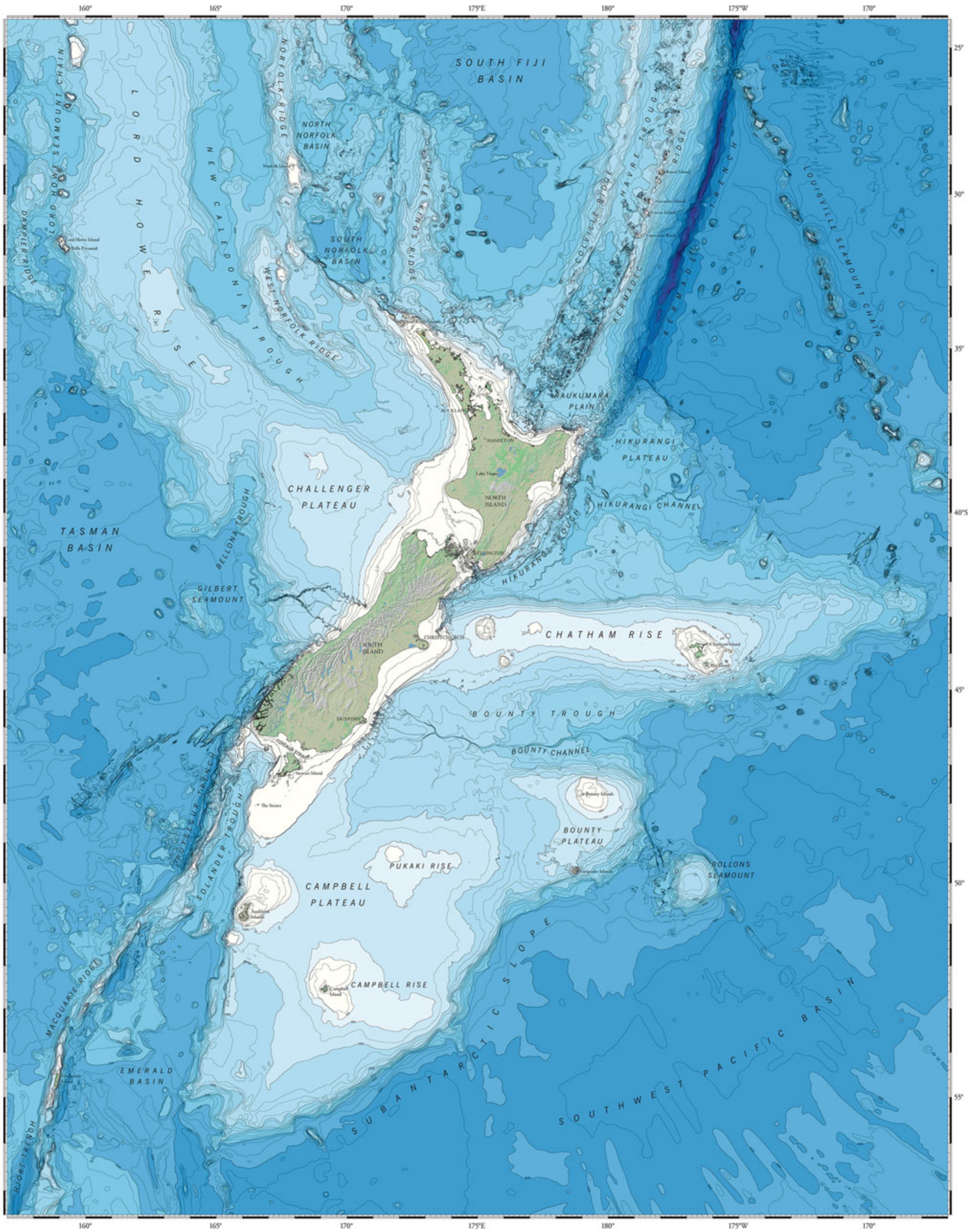

Fig. 9.1 Bathymetry map of the New Zealand region (Mitchell et al. 2012)

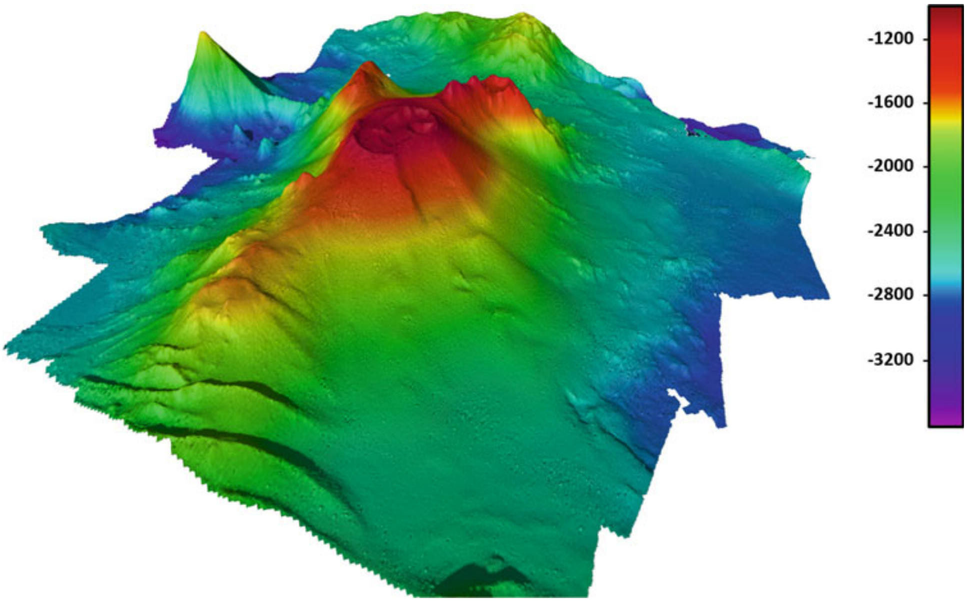

Fig. 9.2 Digital terrain model derived from multi-beam echosounder bathymetric data showing the 'Sonne' Seamount feature, located in the Kermadec (Rangitahua) region, northern New Zealand

Miocene and deposition in around 300 m of water (Wells 1986).

Multi-beam echosounder (MBES) data are synthesised into a bathymetric map of the ocean floor, which reveals the geomorphology at regional scales. The use of these instruments since the start of the millenium has significantly increased our knowledge of the distribution of seafloor features around New Zealand (Rowden et al. 2005). MBES data have been used to produce detailed maps of deep-sea coral-reef habitats on topographical features such as hills, knolls, seamounts, guyots, calderas, and ridges (Fig. 9.2).

Most reef-corals in the region are found associated with seamount summits and flanks and thrive between depths of 400 and 1500 m (e.g., Clark and Rowden 2009; Tracey et al. 2011), and results of habitat suitability modelling studies show that factors of seamount feature and seafloor slope are key drivers of reef-coral distributions (Anderson et al. 2014). However, reef-corals can often have a patchy distribution on a seamount feature and highly detailed and accurate bathymetric and backscatter data are required to produce more resolved estimates of their distribution (Anderson et al. 2016a). The use of such data in habitat modelling studies indicates that relatively high abundances of reef-coral are generally predicted to be restricted to elevated ridge- and cone-like features on seamounts (Rowden et al. 2017).

9.3 Oceanography

The New Zealand landmass sits at the crossroads between warm, nutrient-poor, subtropical surface waters flowing in from the north, and cool, nutrient-rich, subantarctic surface waters flowing in from the south. The complex bathymetry exerts controls over many of the oceanographic currents (Chiswell et al. 2015). Figure 9.3 shows the present understanding of the water masses and key ocean currents in the region as summarised by Chiswell et al. (2015) and Stevens et al. (2021). The region is fed with Subtropical Water from the north by the East Australia Current and the Tasman Front, which becomes the East Auckland Current (EAUC). This current merges with highly modified Subtropical Water (STW) from the south in flows associated with the Subtropical Front that forms the Southland Current, which is the local name for the Subtropical Front (SAF) as it runs up the New Zealand South Island east coast. The front separates modified STW inshore and Subantarctic Water (SAW) offshore (Sutton 2003). While the current is formed by Pacific Ocean regional processes, fluctuations are predominately wind-driven (Chiswell 1996). There is also a much smaller contribution directly from the Tasman Sea to the west, although this is relatively weak in terms of energetics (Chiswell et al. 2015). How these currents affect the shelf region varies in both space and time and depends on a confluence of drivers, one being tides (Stanton et al. 2001).

The variability in regional currents influences the distribution of deep-sea corals through their influence on dispersal of coral larvae, food delivery, and sediment redistribution (Miller and Gunasekera 2017).Deep-sea reef-corals are also affected by surface currents and eddies that influence and enhance primary productivity, which is the ultimate source of food at the seafloor (Stevens et al. 2021). For example, surface currents form the Subtropical Front (STF), the position of which is influenced by the Chatham Rise, a plateau between Te Waipounamu (the South Island) and the Chatham

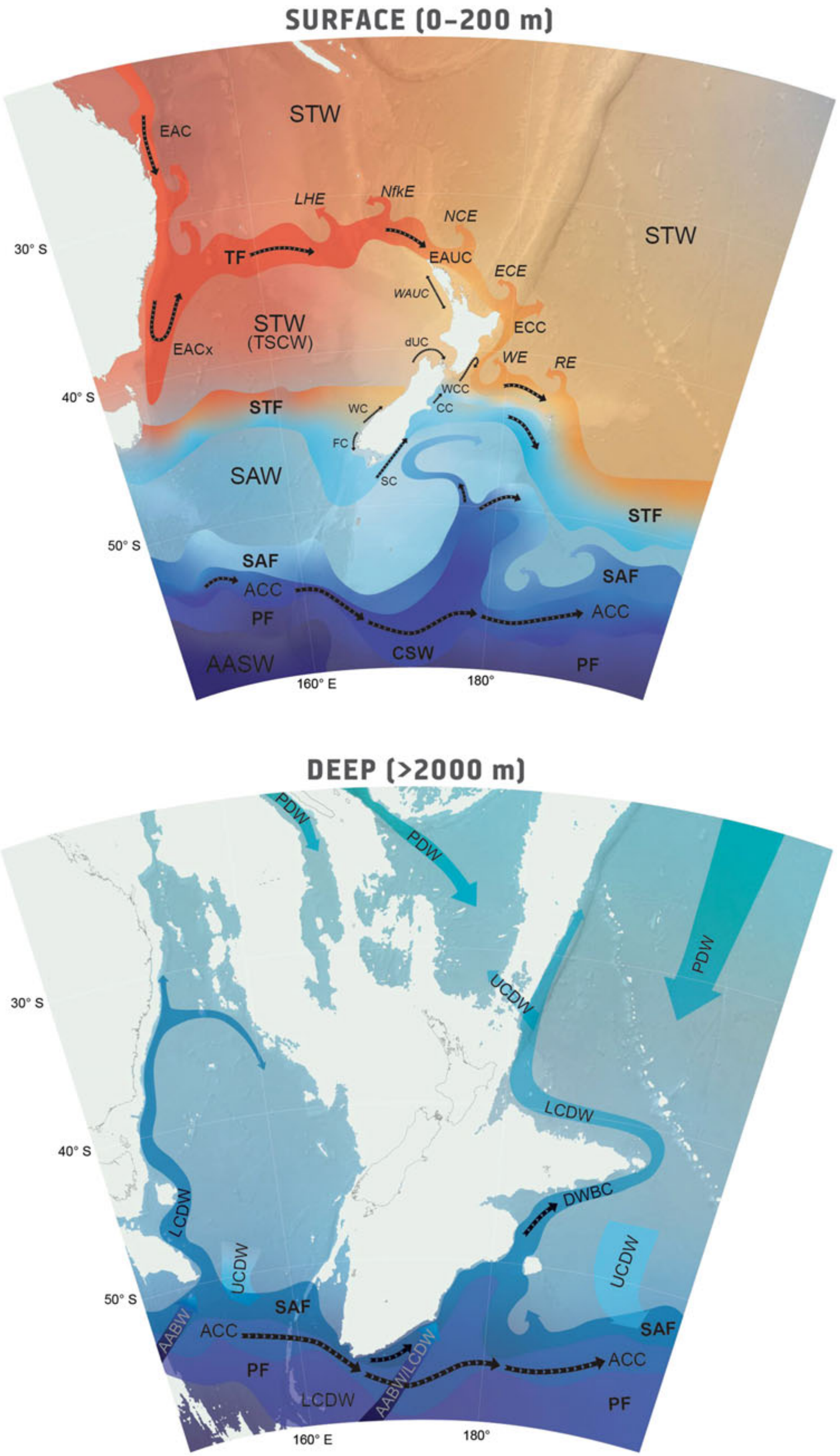

Fig. 9.3 Description of the oceanography around New Zealand (from Chiswell et al. 2015). Key ocean currents in the top image are the Subtropical Surface Waters (STW), Subantarctic Waters (SAW), Subantarctic Front (SAF), East Auckland Current (EAUC), and the Subtropical Front (STF). In the bottom image Pacific Deep Water (PDW) are old waters with low oxygen and high nutrients and they flow south from the North Pacific. Circumpolar Deep Water (CDW) flows in directly from the Southern Ocean in the Deep Western Boundary Current, the main flow of water into the South Pacific. SAF is the northern edge of the Antarctic Circumpolar Current (ACC). Polar Front (PF) is another ACC front

Islands (also called Rekohu/Wharekauri) (Fig. 9.1). The front is the meeting point of Subtropical surface waters and Subantarctic waters sourced from the Southern Ocean, which results in a region of high nutrients and therefore high primary productivity. The reef-coral *Goniocorella dumosa* is abundant on the Chatham Rise, where it is associated with the position of the STF (Chiswell et al. 2015).

The environmental characteristics of the water masses at depth, including temperature, salinity, dissolved oxygen, nitrate and phosphate, and carbonate content, along with variations in these variables, specifically the aragonite saturation state, all influence the distribution of corals (see section below).

9.4 Reef-Corals

9.4.1 Description

There are six key species of scleractinian reef-corals in New Zealand waters (Cairns 1995; Tracey et al. 2011): *Solenosmilia variabilis* (Family: Caryophylliidae); *Madrepora oculata* (Family: Oculinidae); *Enallopsammia rostrata* and *E. pusilla* (*E. marenzelleri*) (Family: Dendrophylliidae), which are also found globally (Roberts et al. 2009); *Goniocorella dumosa* (Family: Caryophylliidae) which is found only in the Indo-Pacific and New Zealand regions; and *Oculina virgosa* (Family: Oculinidae) which is located in New Zealand and New Caledonian waters (Kitahara and Cairns in press).

The living and dead frameworks of most of these species form reef-like structures (Fig. 9.4) that provide habitat for other fauna (see Sect. 9.7). In the literature, the structures are variously described as 3D matrices, coppices, bioherms, and thickets.

The continuous and semi-continuous patches of reef-coral habitat are often topographically constrained, and their size can vary considerably from square metres to square kilometres. The species *S. variabilis* and *M. oculata,* for example, typically form reef-like 3D matrix structures, on the Graveyard Seamount complex on Chatham Rise that can range from 100 m^2 to 0.05 km^2 (derived from Clark et al. 2021) and be up to 2–3 m high on unfished seamounts (Fig. 9.4). On the large guyots of the Louisville Seamount Chain, reefs of *S. variabilis* range from 600 m^2 to 0.04 km^2 (Rowden et al. 2017). These reefs on the Louisville and Graveyard seamounts are smaller than those reported on seamounts off Tasmania, Australia (*see* location in Box insert Fig. 9.15), (0.02–1.16 km^2, Williams et al. 2020a, b).

In contrast to the reef structures formed by *S. variabilis,* the two *Enallopsammia* species and *G. dumosa* form thickets or dense clumps of individual colonies less than 0.5 m high and these can be located on seamounts but also intermittently scattered over distances of 50 km on the continental slope (Rowden et al. 2014a, b). On the crest of the Chatham Rise concentrations of glauconite and phosphate nodules (Chatham Rock Phosphate Ltd 2014) provide suitable hard substrate for *G. dumosa* (Fig. 9.5), in a typically muddy-sand sediment environment (Rowden et al. 2014a, b).

Oculina virgosa is a more sparsely branched species which can also form thicket-like structures that are sometimes continuous when along a ridge. The species has a more northern distribution than the other species and can be found quite shallow, often observed by divers on cliff overhangs (Tracey and Hjorvarsdottir 2019).

As well as reefs and/or thickets made up of a mixture of live and dead coral framework, extensive areas of dead matrix can occasionally be found at the periphery of some reefs, such as on some seamounts of the Louisville Seamount Chain where they occur at greater depths than live coral (Clark et al. 2015). The dead matrix occurs on both fished and unfished seamounts and their present distribution is possibly due to a major oceanographic event in the past, changes in sea-level, or a gradual deepening of the seamounts with age through tectonic movement (Clark et al. 2015). The dead matrix can also form habitat for other invertebrates (see below) and also off Tasmania (Thresher et al. 2014). The reef-corals provide habitat for other fauna not only at the spatial scales described above, but also at the scale of their individual colony structures.

While the focus of this chapter is on the reef-corals, other coral groups found in abundance throughout the region also provide habitat e.g., large tree-like gorgonian octocoral taxa *Paragorgia* and *Primnoa* (Sánchez 2005; Cairns 2016; Thresher et al. 2014), and bushy black corals such as *Dendrobathypathes* and *Telopathes* (Opresko et al. 2014).

9.4.2 Distribution

The distribution of reef-corals collected in the New Zealand region is shown in Fig. 9.6.

Records indicate that most of the reef-coral species are widely distributed through the region in temperate water masses. They occur primarily at depths of 200 to over 2000 m, with elevated abundance at 800 to 1000 m (Tracey et al. 2011). The exception is *Oculina virgosa,* which is found primarily in warmer northern latitudes, and unlike the other species it extends into a shallow water environment (Tracey et al. 2011).

Areas with high incidences of seamounts and ridges and where reef species have been frequently observed include the Kermadec, Colville, Three Kings, Norfolk, and Macquarie ridges, the East Coast North Island, and seamount features in the Chatham Rise region such as the Graveyard and Andes complexes (Tracey et al. 2011).

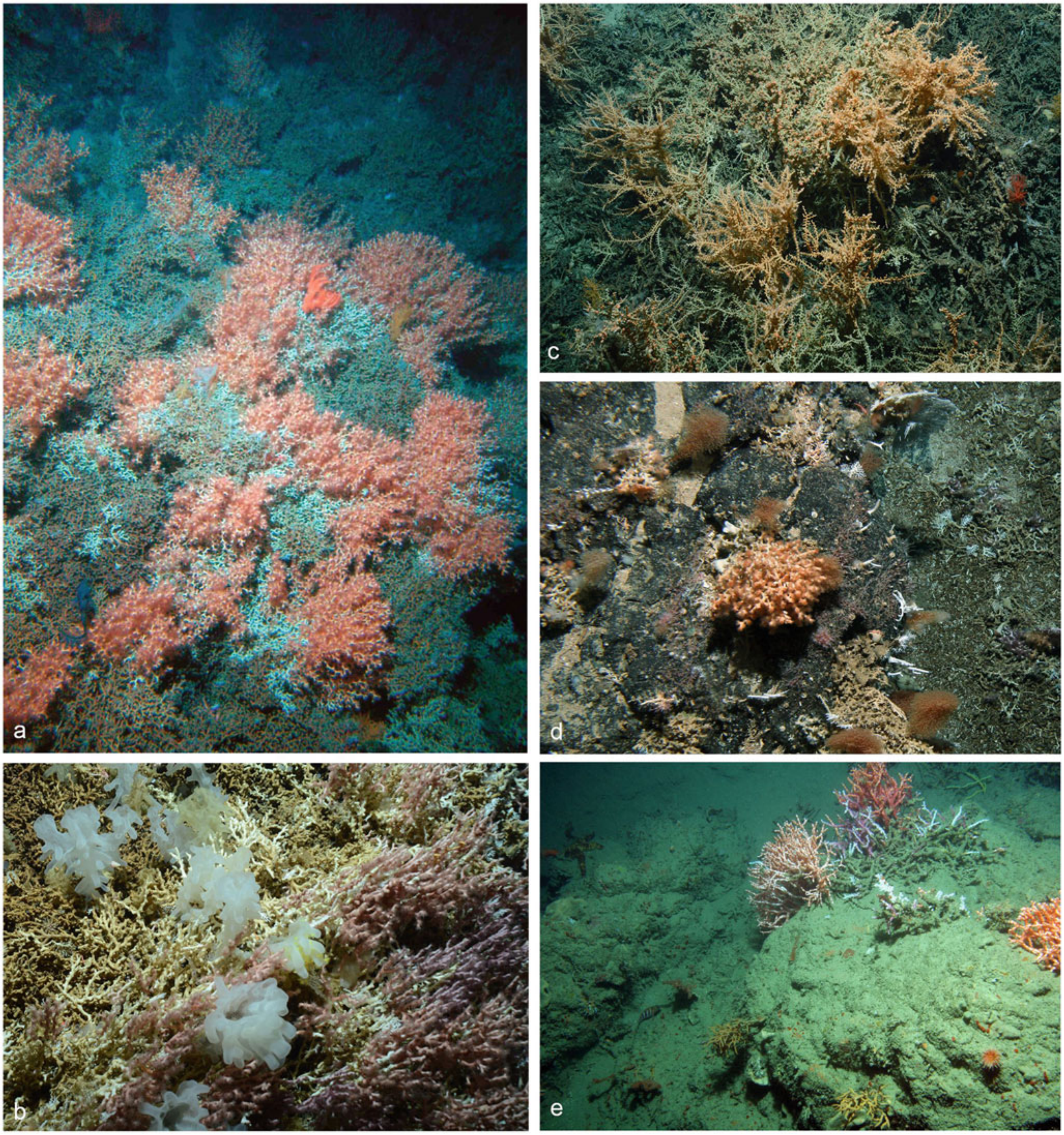

Fig. 9.4 Key habitat-forming coral-reef species found in the New Zealand region: *Solenosmilia variabilis* (**a**) (visible are abundant live coral heads and dead coral matrix), *Enallopsammia rostrata* (**b**), *Madrepora oculata* (**c**) *Goniocorella dumosa* (**d**), and *Oculina virgosa* (**e**). Live and dead reef is clearly visible in images a-c. The more clump-like thicket structures are shown for *G. dumosa* and *O. virgosa*. (Images NIWA)

9.4.3 Predicting Reef-Coral Habitats

Physical sampling efforts in the deep sea around New Zealand have been extensive, but there are still many gaps in our knowledge about the distribution of benthic species. A range of modelling methods to predict habitat suitability and species distributions for corals, including scleractinians, in unsampled or poorly sampled areas have been developed and applied to the New Zealand region and the wider Southwest Pacific Ocean (Tracey et al. 2011; Baird

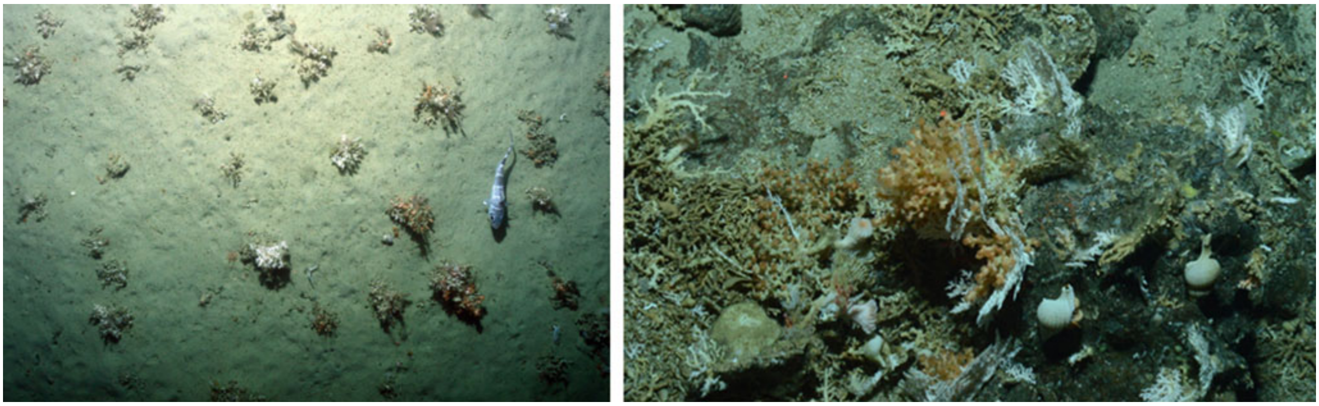

Fig. 9.5 In situ image of *Goniocorella dumosa* attached to phosphate nodules (Left), and on a hard substrate, seamount flank, Chatham Rise, eastern New Zealand waters (Right). (Images NIWA)

et al. 2013; Anderson et al. 2014, 2015, 2016a, b; Rowden et al. 2015, 2017; Stephenson et al. 2018; Georgian et al. 2019). Some of these studies have utilised predictions of future oceanographic conditions from Earth System Models to identify deep coral habitats at risk from commercial fishing activities and potential future climactic refugia (Anderson et al. 2015). Other studies have focussed on specific sites and individual seamounts, using detailed drop-camera surveys to provide coral presence data and local oceanographic information along with terrain variables derived from MBES surveys (Rowden et al. 2017). Results from two different model approaches are shown in Fig. 9.7.

Results from the various regional-scale modelling studies generally predict faunal distributions across similar seabed areas. Anderson et al. (2016a) used two habitat suitability modelling techniques, boosted regression trees, and maximum entropy, to describe the distribution for Vulnerable Marine Ecosystem indicator taxa in the New Zealand area and adjacent seas, including four of the reef-corals discussed in this chapter. For *G. dumosa* the highest habitat suitability indices were over the Chatham Rise, parts of the Challenger and Campbell plateaus, some regions north of New Zealand, and much of the Louisville Seamount Chain. In contrast, the pattern for the three deeper living species *S. variabilis*, *E. rostrata,* and *M. oculata* showed areas of greatest suitability situated primarily in deeper parts of the Campbell Plateau as well as the fringes of the Chatham Rise and other features in the west and north of the region, at latitudes of 30 to 35 degrees S. A similar pattern was shown for *S. variabilis* in the Georgian et al. (2019) study (Fig. 9.7).

These modelling studies indicate that the distributions of reef-coral habitats are dependent primarily on the predicator variables dynamic topography (a proxy for large-scale current patterns) and temperature (Fig. 9.8), with seabed slope, seamount, ocean chemistry (specifically aragonite), and dissolved organic matter representing further important variables (e.g., Anderson et al. 2015, 2016a).

9.5 Coral Biology

9.5.1 Physiology

Deep-sea corals form calcium-carbonate skeletons consisting of the minerals aragonite, calcite, and high magnesium calcite. As with other deep-sea reef-corals, the scleractinians in New Zealand waters are all made of aragonite (Guinotte et al. 2006; Thresher et al. 2011a, b; Bostock et al. 2015).

In the New Zealand region 85% of the reef-corals (*S. variabilis*, *E. rostrata*, *G. dumosa*, *M. oculata,* and *O. virgosa*) are found above the Aragonite Saturation Horizon (ASH), which sits between depths of 1050 and 1250 m (shallower south of Chatham Rise and deeper north of Chatham Rise; Bostock et al. 2015). However, part of the distribution of *S. variabilis* occurs below the ASH. This species appears to be more resilient to undersaturation of aragonite than other reef-coral species (Bostock et al. 2015). Nevertheless, because aragonite is relatively more soluble than some of the other minerals in coral skeletons, these New Zealand species can be susceptible to dissolution with climate change. Because of their physiology, coral mortality will also occur if conditions such as oxygen and temperature are sub-optimal.

9.5.2 Age

From radiocarbon dating (^{14}C), colony ages of various reef-coral species have been obtained for the New Zealand region (Fig. 9.9). The age of *S. variabilis* species has been assessed

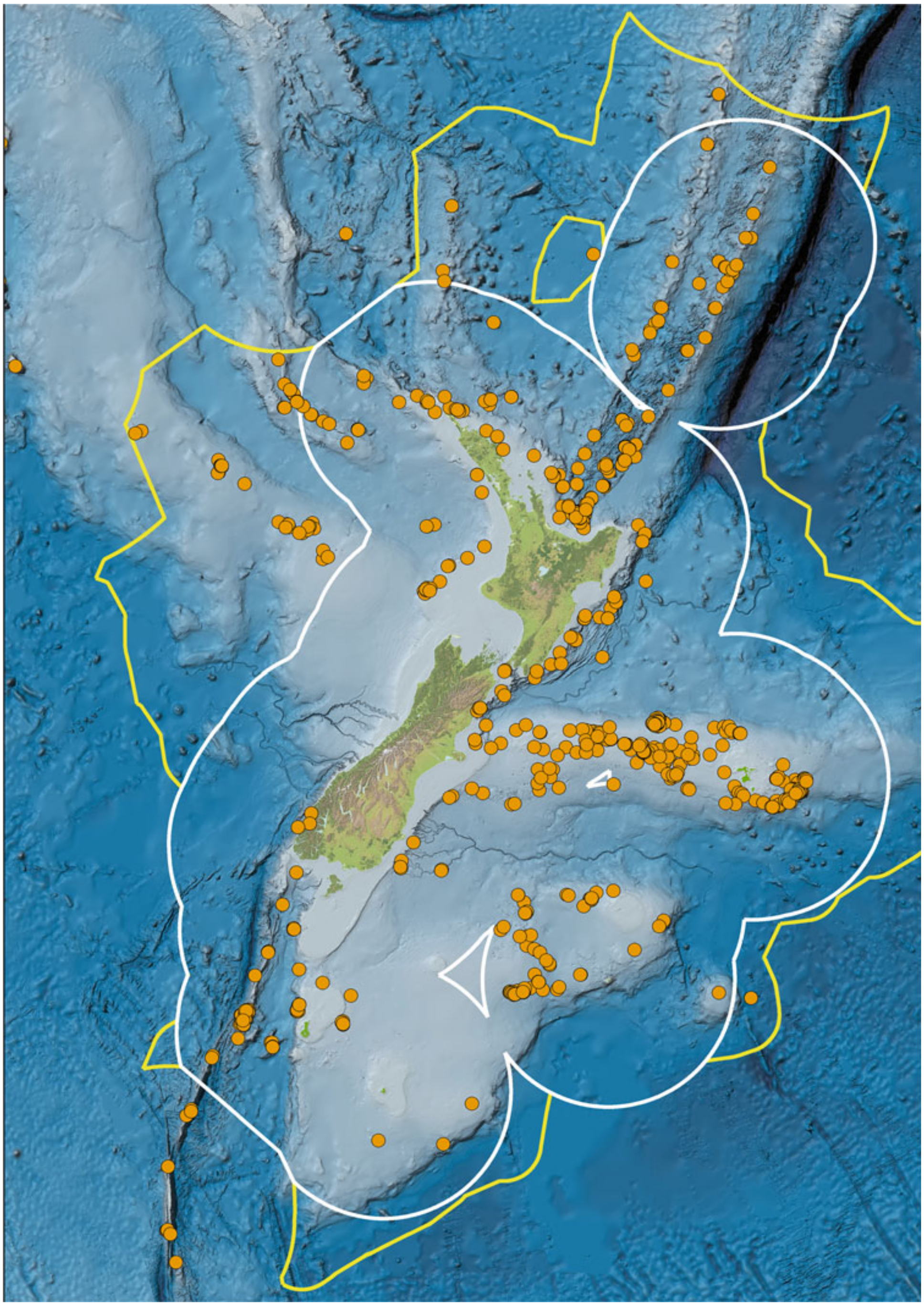

Fig. 9.6 Distribution of reef-coral records in the New Zealand region. The white line shows the Exclusive Economic Zone (EEZ) and the yellow line the Extended Continental Shelf (ECS)

for ‘long dead’ (old and discoloured manganese coated matrix), ‘recently dead’ (no polyps but white-grey skeleton), and live branch sections of coral sampled from seamounts on the Chatham Rise and Louisville Seamount Chain. Overall, linear growth rates for *S. variabilis* ranged from 0.25 to 1.3 mm year^{-1}. Using a conservative estimate of matrix height of ~20 cm, it could take hundreds of years (~150–660 years) for a colony to attain this height, or ~2000 years, to build a colony diameter of 1 m (NIWA unpub. data; Tracey et al. 2019). Similar growth rates were reported for *S. variabilis* on seamounts off Tasmania, Australia, ranging from 0.84 to 1.25 mm year^{-1} linear extension (Fallon et al. 2014).

Other New Zealand reef-coral species show similar growth rates to *S. variabilis* but colony ages differ. For the Chatham Rise and Bay of Plenty areas, *M. oculata* colony ages determined by ^{14}C ranged from 752 to 1123 years, with overall growth rates of 0.39–0.8 mm year^{-1}. For *G. dumosa* from the Chatham Rise, ^{14}C colony ages were

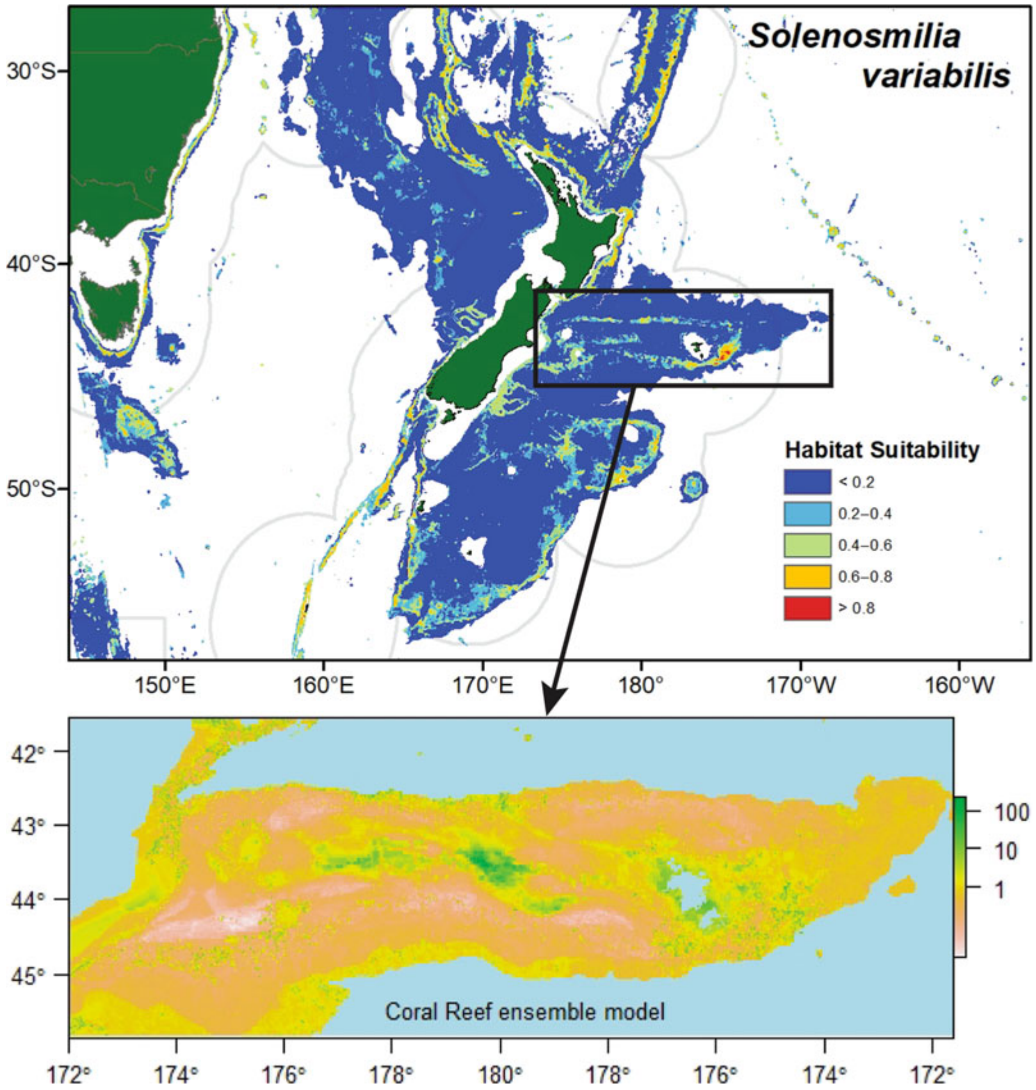

Fig. 9.7 Habitat suitability models: Top: Ensemble model habitat suitability map for the stony coral *Solenosmilia variabilis* in the southwest Pacific Ocean (modified from Georgian et al. 2019). Bottom: Ensemble model predictions of abundance (individuals 1000 m^{-2}) on the Chatham Rise for four coral-reef species as a group: *Enallopsammia rostrata*, *Madrepora oculata*, *Solenosmilia variabilis, and Goniocorella dumosa* (from Bowden et al. 2019)

372–422 years, and linear growth was estimated to be 0.48 mm year^{-1} (Tracey et al. 2019).

As noted in Sect. 9.4.1, the flanks of several Louisville Ridge seamounts have extensive areas of dead coral matrix (Clark et al. 2015). The age of the apparent coral die-off events that have occurred was estimated at over 10,000 radiocarbon (^{14}C) years, which coincides with a time of significant oceanographic change in the New Zealand region (Bostock et al. 2013). The oldest reef matrix age in Tasmanian waters, located in a different water mass (*see* location in Box insert Fig. 9.15), was radiocarbon dated to be a lot older, 47,400 radiocarbon years (Fallon et al. 2014). This age estimate, while treated with caution by the authors as the measured results were at the limit of radiocarbon dating, suggested the Tasmanian seamounts have been occupied by *S. variabilis* since before the Last Glacial Maximum.

9.5.3 Reproduction

In New Zealand waters the reproduction of *S. variabilis*, *M. oculata*, *G. dumosa*, and *E. rostrata* are thought to exhibit seasonality, with fertilisation occurring after the austral summer in April/May in synchrony with increased food availability (Burgess and Babcock 2005). No studies have been carried out on the reproduction of *O. virgosa*, and so it is uncertain whether this species exhibits a similar reproductive cycle to *O. varicosa,* which occurs off the east coast of Florida. For the latter species, the gametogenic cycle appears

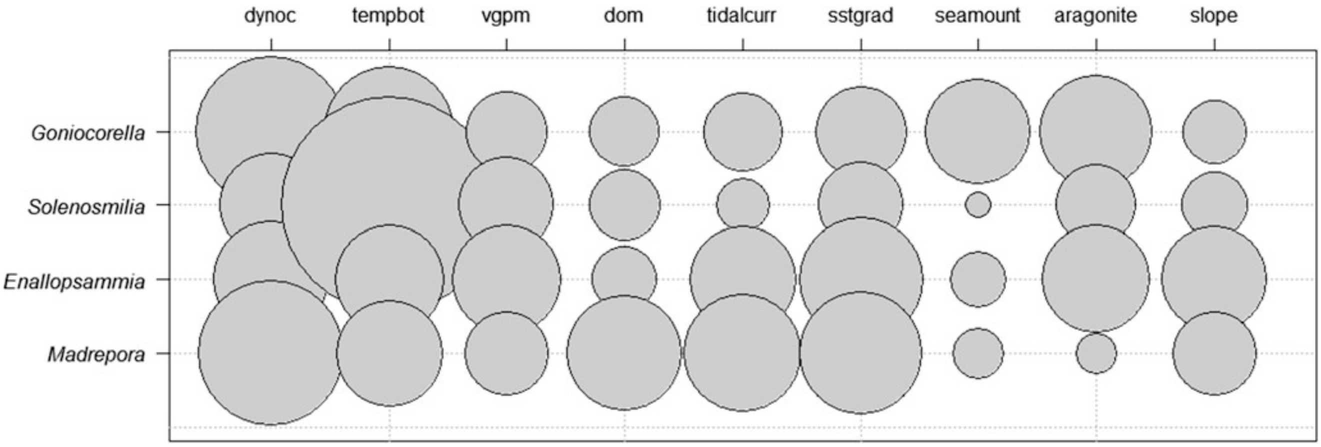

Fig. 9.8 The relative influence of explanatory variables on the predictive models for four reef-forming coral taxa (revised from Anderson et al. 2014). Variable descriptions are: Dynoc: dynamic topography; tempbot: bottom temperature; vgpm: surface water primary productivity; dom: dissolved organic matter; tidalcurr: tidal current velocity; sstgrad: sea surface temperature gradient; seamount: on or off a seamount; aragonite: seafloor aragonite saturation state; calcite: seafloor calcite saturation state; slope: seafloor slope

to begin in early boreal summer, with spawning occurring during late boreal summer/fall (Brooke and Young 2003).

Previously, New Zealand reef-corals were believed to be broadcast spawners and spawn gametes (Burgess and Babcock 2005), but recent research is suggesting one species may instead be a brooder (e.g., see Waller et al. 2023). In September 2020, colonies of *G. dumosa* held in aquaria at NIWA were observed to spawn towards the end of a sedimentation experiment, releasing brooded larvae. Larvae from a spawning event have not been observed before for any deep-sea coral in New Zealand waters, and never for this species. Indeed, spawning events have only been observed for a handful of reef-corals globally (Waller 2005; Waller et al. 2023) even for very well-studied species like *Lophelia pertusa* (Larsson et al. 2014). Some of the larvae settled after only 24 h (Fig. 9.10). Subsequent research from this serendipitous observation of *G. dumosa* describing aspects of brooding, larval behaviour, settlement medium, fecundity, length of larval phase prior to settlement, and possible settlement cues is now completed and the paper describing the science is in review).

9.5.4 Genetics

There have been a few genetic studies of the reef-coral species off New Zealand, but they indicate that connectivity patterns are not uniform across the species and in some cases have varied between studies, molecular markers applied, or geographical areas sampled. For example, low connectivity was observed for *S. variabilis* with local structure noted between seamounts off New Zealand and Tasmania (Miller and Gunasekera 2017). In contrast, genetic differentiation was observed for the same species at the province and regional scales, as well as the geomorphic feature scale (i.e., between seamounts, plateaus, ridges, etc.) by Zeng et al. (2017). This study also detected genetic structure amongst regions and geomorphic features, but not between provinces, for *G. dumosa*. For *M. oculata* only limited regional structure was observed. Zeng et al. (2017) also recorded a significant isolation-by-depth pattern for *G. dumosa* and *M. oculata*, and an isolation-by-distance pattern for microsatellite variation in *S. variabilis*. This study attributed the observed spatial patterns of genetic structure/connectivity primarily to the influence of currents and oceanographic fronts. Zeng et al. (2020) in a subsequent seascape analysis study found that dynamic topography (*G. dumosa*), sea surface temperature and surface water primary productivity (*M. oculata*), and tidal current speed (*S. variabilis*) were the most important variables explaining patterns of genetic structure observed in these reef-coral species. At the population level, factors related to current and food source explained the genetic structure in all species, whilst at the geomorphic features level, factors related to food source and topography were most important. Environmental variation in these parameters may be acting as a barrier to gene flow at different scales. The study of Zeng et al. (2020) highlights the utility of seascape genetic studies to better understand the processes shaping the genetic structure of organisms and to identify environmental factors that can be used to locate sites for the protection of deep-sea corals (see Sect. 9.8).

There are limited genetic data available for *E. rostrata*, with analysis findings being somewhat ambiguous and highlighting the need for further genetic data (Holland et al.

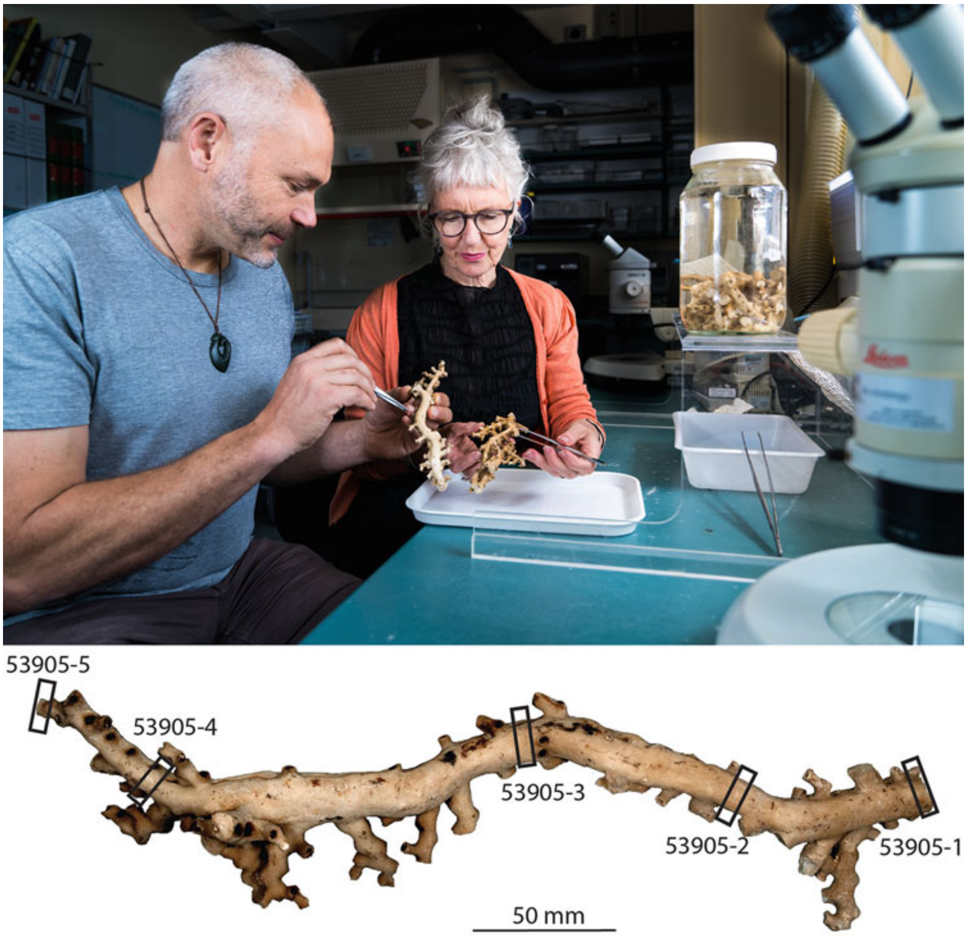

Fig. 9.9 NIWA staff Peter Marriott and Di Tracey examining a *Madrepora oculata* specimen selected for transverse sectioning and subsequent radiocarbon dating (Top). *M. oculata* branch showing the various sample sites where section cuts were made for sample milling along the colony to estimate linear and step-wise growth (Bottom). (NIWA images). Note: *M. oculata* displays three different morphologies in New Zealand waters. One (pictured above) has calices that alternate sympodially on each side of thick branches in a flute-like orientation (Cairns 1995)

2020). No studies on the genetic structure of *O. virgosa* populations have been carried out to date.

9.6 Reef-Corals as Habitat

Deep-sea reef-corals in general are known to provide habitat for other fauna, including a range of invertebrates and fish (Rogers 1999; Krieger and Wing 2002; Stone 2006; Mortensen et al. 2008; D'Onghia et al. 2010; Soffker et al. 2011; Rooper et al. 2019; Henderson et al. 2020; Schnabel and Mills 2019). These associations can be highly dependent (i.e., associated fauna not found outside of coral habitat) or spatially and temporally variable in their strength (e.g., used as nursery grounds for limited periods of time).

9.6.1 Invertebrates

One of the most commonly observed associations is between eunicid polychaetes and scleractinian corals. Eunicids form parchment-like tubes on the matrix of reef-corals, and the corals commonly calcify over the tubes (Mueller et al. 2013). Three species in this family have been observed to form their tubes on *S. variabilis* in the New Zealand region (Schnabel and Mills 2019). However, nothing is known about the potential enhancement of calcification and reef growth for New Zealand coral species.

Ophiuroid assemblages sampled from *S. variabilis* coral reefs off Australia and New Zealand are distinct from those of seamount habitats and from continental slope (O'Hara et al. 2008). The coral-associated ophiuroids were generally in the coral matrix rather than on the top of the reef. The species found in the matrix lack the specialised hook-like arm spines that species living on arborescent corals usually possess. Instead, the ophiuroids of the coral reef typically had long flexible arms used for filter- or deposit-feeding.

Other echinoderms such as brisingid seastars and echinoids are regularly seen on live reef-corals. Stevenson et al. (2018) examined echinoid distributions off France, Australia, and New Zealand. The New Zealand records were primarily from seamounts, and 43% of observations

Fig. 9.10 Left: Sectioned *G. dumosa* corallite showing several planulae larvae ready to be released. Image shows 4 of the 10 larvae in this single polyp. Right: Recently settled larva on a dead branch area of *G. dumosa* showing a newly formed corallite with tentacles extending from the calice area and coenenchyme forming at the base region of the pedicel. (NIWA images)

were associated with live coral reef. *Dermechinus horridus*, a common echinoid on seamounts off New Zealand and Tasmania, was found primarily distributed amongst dense live coral, potentially because of a likely suspension-feeding mode where living on elevated coral matrix is an advantage (Stevenson et al. 2018).

Galatheoid squat lobsters, including the globally distributed *Munida* species, are frequently encountered throughout the region, but some species are distinctly 'seamount associated' species (Rowden et al. 2010). For example, *M. isos* is often observed in high abundance in the living and dead-standing reef-coral matrix (Schnabel 2020) as well as in accumulations of coral rubble at the base of the reef (Fig. 9.11).

An analysis of megabenthos assemblages off Tasmania between ~700 and 4000 m on the rocky continental margin (Thresher et al. 2014) showed species richness was highest at intermediate depths (1000–1300 m), as a result of an extensive coral-reef habitat comprising both live and dead *Solenosmilia variabilis*. The community associated with this habitat was similar to that off New Zealand. They included brisingid seastars, *Dermechinus horridus*, octocorals, sponges, and crinoids on the surface of the coral, while common interstitial organisms included galatheid squat lobsters, shrimps, crabs, worms, and ophiuroids. Overall, the observed depth zonation in this region appeared to be based in part on changing species assemblages with depth, but also an underlying reef-coral biota that was common across all depths.

9.6.2 Fish

Compared to elsewhere, there has been limited research looking at the nature of associations between fish and reef-corals in New Zealand. Seamounts with high densities of reef-corals often host large populations of commercial fish species, including orange roughy (*Hoplostethus atlanticus*), alfonsino (*Beryx splendens*, and black cardinalfish (*Epigonus telescopus*)). A study of research trawl catches from the Graveyard Seamounts complex showed that the composition and abundance of fish populations can vary between seamounts on the kilometre scale (Tracey et al. 2012), in contrast to observed differences in fish communities and abundance between widely distributed seamounts at ocean-basin scales and influenced by different water masses (Clark et al. 2010c). However, the specificity of the associations among fishes and corals are uncertain, including the extent to which these corals might provide biogenic structure for shelter, feeding, spawning, or as nursery sites (Morrison et al. 2014; Clark and Dunn 2012; Jones et al. 2016). A recent study used video surveys from six seamounts on the Chatham Rise to examine the habitat associations of demersal fish including those with reef-corals. Over 4000 individual fish and their associations with a range of habitats were recorded and showed significant and consistent associations between certain fish species and the deep-sea coral-reef matrix (Simmons 2016; Tracey and Hjorvarsdottir 2019).

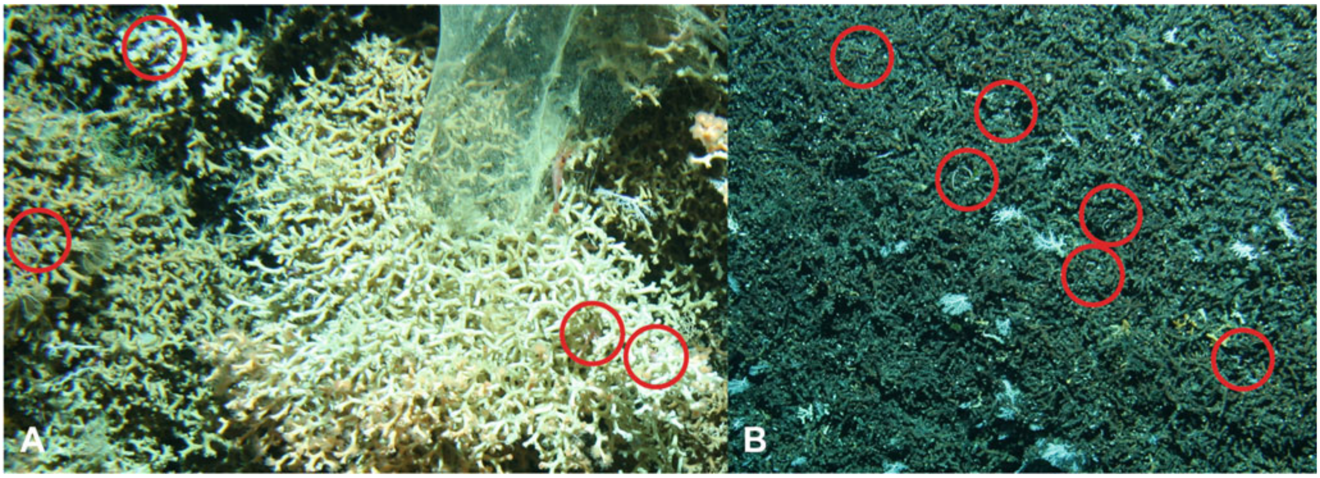

Fig. 9.11 Squat lobsters (red circle) identified in live and dead matrix (**a**) as well as on dead coral rubble at the base of the reef (**b**). (NIWA image)

9.6.3 Microbes

Microbial communities associated with deep-sea corals are beginning to be studied worldwide, and it appears they can be important contributors to the coral host's function (e.g., see Vega Thurber et al. 2008). As an indication of their functional importance, microbes may help the coral host adjust to prevailing environmental conditions (e.g., see research by Röthig et al. (2017) on the deep-sea coral *Eguchipsammia fistula*, a cup-like form of stony coral, and a species abundant in the New Zealand region). Using 16S rRNA gene amplicon sequencing, the microbiome for *G. dumosa* colonies collected from two contrasting habitats of the Chatham Rise, a sedimented and a hard-bottom environment, is currently being researched to see if the microbiome adjusts and supports the coral holobiont under changing environmental conditions. It is anticipated that this work will be able to assess how stress from different sedimentation levels might manifest itself as a change in the coral microbiome community, thereby acting as a proxy of host health.

9.7 Threats and Outlook

The reef-coral species focused on here are protected species within the New Zealand EEZ (New Zealand Wildlife Act 1953) and are also considered vulnerable marine ecosystem (VME) indicator taxa in the South Pacific Regional Fishery Management Organisation (SPRFMO) region (Parker et al. 2009). S. *variabilis, M. oculata, G. dumosa*, and *E. rostrata* are all considered ‘At Risk’ and ‘Declining’ according to the New Zealand Threat Classification (Freeman et al. 2013).

Due to their fragile skeletal composition, erect growth form and habitat preferences (e.g., seamounts) deep-sea reef-coral species are vulnerable to various physical disturbances, such as trawling and potential seabed mining (Clark et al. 2016). In the following sections, threats to reef-coral species from various sources in the region are described.

9.7.1 Fishing Impact

A number of studies have investigated the effects of bottom trawling on deep-sea macro-invertebrate assemblages (including reef-corals) around New Zealand and Australia (e.g., Koslow et al. 2001; Clark & O'Driscoll 2003; Anderson & Clark 2003; Clark and Rowden 2009; Althaus et al. 2009; Clark et al. 2010a, b, 2019a; Williams et al. 2020a, b). These studies have demonstrated appreciable impacts from trawling, with changes in the extent of the reef matrix on fished seamounts, as well as changes in community composition and diversity associated with the reef-corals and reductions in relative abundance of certain taxa. The matrix of *S. variabilis* on seamounts can have a vertical extent of several metres, and combined with its brittle skeletal structure, heavy ground gear from bottom trawling can have a severe impact after only a few passes with a trawl (Fig. 9.12). The reduction from 20 to 50% coral cover on unfished seamounts to levels of 1–5% on fished features can occur after less than 10 trawls.

Over the period of 20 years where time series of surveys have been carried out, there is little or no evidence of recovery of the reef-coral species (Althaus et al. 2009; Williams et al. 2010; Clark et al. 2019a; Goode et al. 2020) (***see* Box on seamount recovery**) although remnant patches occur on most fished seamounts which may aid localised recovery of them (Clark et al. 2021).

More detailed analyses of trawl effort in certain areas and on individual seamounts have also been carried out for the

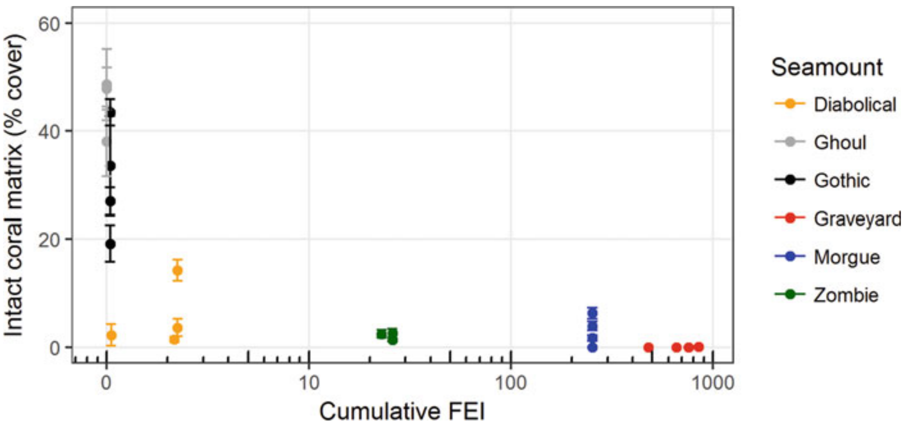

Fig. 9.12 Plot of decreasing reef-coral matrix (Y axis; mean per cent cover measured in individual seabed photographs, from six seamounts on the Chatham Rise over time), in relation to increasing fishing effort (Fishing Effects Index; FEI) (X axis) (from Clark et al. 2019a)

New Zealand EEZ, to ascertain how much fishing occurs in such habitat, and how its distribution compares with the likely or known distribution of corals. This work combined data on the trawl footprint of commercial deep-sea fisheries and records of reef-corals (Clark et al. 2014a, b). The trawl footprint shows a clear overlap between reef-like corals and targeted tows for orange roughy on various seamount features of the Chatham Rise in depths of 800 to 1000 m (Fig. 9.13).

The spatial extent of the corals or suitable habitat (such as seamount features or from habitat suitability models) in relation to the distribution of commercial trawling (trawl footprint) is regularly quantified (e.g., Anderson et al. 2014; Baird and Wood 2018) as well as analyses of bycatch in commercial fisheries (e.g., Anderson et al. 2017). Similar overlap-type analyses of predicted changes in distributions due to climate change are also evaluated (e.g., Anderson et al. 2020).

9.7.2 Sedimentation

The direct physical effects of human activities in the deep sea, such as bottom contact fisheries, are relatively well documented globally and around New Zealand (see Clark et al. 2016). Indirect effects, however, are not, and a major concern for the sustainability of reef-corals is the possible impact of sedimentation from plumes generated by trawling or potential seabed mining that can extend over a wide area. Current studies focused on the Chatham Rise are using a combination of field survey experimentation with in situ field observations, and laboratory-based experiments to determine the effects of various levels of suspended sediment

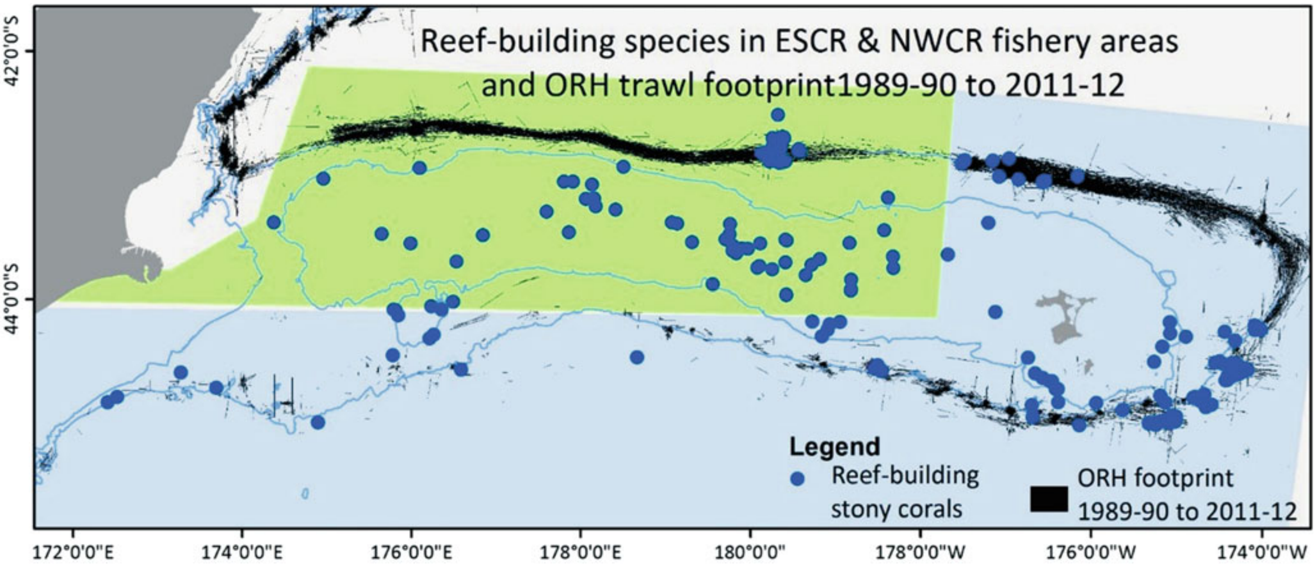

Fig. 9.13 Plot of the location of reef-corals on the Chatham Rise overlain is the trawl footprint for orange roughy (ORH) for the fishing years 1989 to 2012 (from Clark et al. 2014a, b). East South Chatham Rise (ESCR) = blue rectangle, Northwest Chatham Rise (NWCR) = Green rectangle

on benthic corals and sponges, including *G. dumosa* (Clark et al. 2018).

The laboratory programme has involved holding live *G. dumosa* in tanks and exposing them to various levels and duration of suspended sediment concentrations from 0 to 500 mg l^{-1} of particles. Data from experiments including pulses of sediment and continuous exposure for up to 4 weeks indicate that *G. dumosa* is resilient to levels of 100 mg l^{-1} or less for periods of several weeks, and also to 500 mg l^{-1} if exposure was not constant (i.e., pulses were also tested). With constant exposure effects included death of some coral polyps and tissue atrophy, and changes in respiration rates for periods of time (Mobilia 2021, NIWA unpublished data).

9.7.3 Ocean Climate

Cumulative impacts are an important consideration for the management of deep-sea corals. Along with impacts from fishing and potential seabed mining, other threats faced by these corals in the New Zealand region include those resulting from, or associated with, climate change. Numerous global studies describe how climate change could significantly shift and reduce the availability of suitable habitats for deep-sea species by 2100 (see Sweetman et al. 2017 for an overview). While there has been limited research in the New Zealand region to investigate impacts of climate change on deep-sea fauna, work by Thresher et al. (2015), Anderson et al. (2015), Bostock et al. (2015), Gammon et al. (2018), Mikaloff-Fletcher et al. (2017), and Law et al. (2018) predict a rapid shoaling of the ASH in the region that represents a significant threat to deep-sea corals in construction and maintenance of their skeletons. Deep-sea coral geochemistry archives are being used to reconstruct New Zealand's baseline ocean dynamics to help trace the changing health of the marine environment (Davis et al. 2021; Hitt et al. 2020; Hitt 2021).

9.7.3.1 Temperature

A general trend in recent decades of increasing surface water temperatures has been exacerbated by marine heatwaves, notably off the south-east coast of New Zealand's North Island in 2017 and 2018, where surface temperatures were up to 4 °C above average, and warmer water reached deeper (down to 200 m) than the mixed layer (Sutton and Bowen 2019). Ocean warming research is showing less phytoplankton production in the Tasman Sea associated with a warming environment as deep as 850 m, but conversely there is more in the mixed waters of the subtropical front east of New Zealand (Chiswell and Sutton 2020). The surface water changes will likely impact *O. virgosa*, but the deeper warming may also have effects on the other New Zealand reef-corals.

Habitat suitability modelling indicates that the distribution of reef-coral habitat is only weakly dependent on surface water primary productivity (phytoplankton) and dissolved organic matter (see Fig. 9.8). Even so, the aforementioned changes in phytoplankton production, as a result of future ocean warming, could impact strongly upon reef-coral distribution in New Zealand waters as temperature is a strong predictor variable. It is worth noting here that productivity is likely driven by several local dynamics such as phytoplankton community structure, sea surface temperature, upwelling, and gyre circulation and that there is natural variation in these variables on a variety of timescales (Hitt 2021).

9.7.3.2 Ocean Chemistry

With their delicate aragonitic skeleton, scleractinian reef-corals will be under threat from ocean acidification (Law et al. 2017). Few studies have taken place on ocean acidification impacts on deep-sea corals, and laboratory aquaria experiments, while they can be problematic in terms of cost or knowledge of food availability (Büscher et al. 2017), are often the only option. Gammon et al. (2018) investigated impacts from a change in pH from current conditions (7.88) and an end-of-century scenario (7.65), on the skeletons of *S. variabilis* from New Zealand waters. This in-aquaria research showed loss of coenenchyme tissue, but no significant changes in growth rates or respiration with the reduced pH. The loss of coenenchyme indicated a reallocation of energy with physiological processes (e.g., growth and respiration) being maintained at the expense of coenenchyme production (Gammon et al. 2018).

Water chemistry and carbonate mineralogy have a strong influence on the distribution of deep-sea reef-corals (Feely et al. 2012), and like elsewhere, New Zealand corals are at risk from future changes in these parameters (Law et al. 2018). The depth of ASH has already shallowed since pre-industrial times by 50–100 m over much of the New Zealand region (Mikaloff-Fletcher et al. 2017). This shallowing has demonstrable implications for the habitat range of marine organisms with aragonite shells or exoskeletons and will contribute to a decline in suitable habitat for reef-corals at depths where aragonite levels in the water column will decrease, and thereby impact the deep-sea ecosystems and biodiversity they support (Anderson et al. 2015; Bostock et al. 2015). The shallower regions of the Chatham Rise may provide refugia for reef-corals from the impact of changes in ocean acidification (Bostock et al. 2015).

9.8 Future Directions

While research on reef-corals in the New Zealand region has grown substantially in the last 10–15 years, there still remain significant limitations in knowledge. A recent gap analysis by Hjorvarsdottir and Tracey (2017) and research needs identified by Anderson et al. (2018) covered six gap categories: Biological, Environmental, Spatial, Modelling, Threat and Pressure, and Data, Management and Communication. These gap analyses formed the basis of a Draft Medium-Term Research Plan for Protected Coral Species which will guide future research efforts for New Zealand waters, when finalised (DOC 2023). Below we highlight some issues that relate to some of the threats posed to reef-corals.

Deep-sea reef-coral species have protected status in the New Zealand EEZ but are nonetheless subjected to impacts from human activities, in particular bottom trawling (see Sects. 9.7.1 and 9.7.2). Thus, the status of being a protected species does not by itself guarantee that these species, and the functions they perform, are conserved. The key for effective conservation is to ensure that species, communities, and populations are maintained above a level where adverse effects (from human impacts but also natural factors) do not risk the sustainability of these biological entities (Freeman and Cryer 2019). Inside the New Zealand EEZ there are Benthic Protection Areas (BPAs) (Helson et al. 2010) and Seamount Closure Areas (SCAs) (Brodie and Clark 2003) where bottom trawling and dredging are prohibited, which will protect reef-corals in those areas. However, it is uncertain if these closed areas together constitute an adequate connected network of suitably representative areas that will ensure that reef-coral populations are sustained across the region. Studies to date suggest that these BPAs and SCAs are potentially inadequate for maintaining the genetic structure and diversity of *S. variabilis*, *M. oculata*, and *G. dumosa* populations (Zeng et al. 2017, 2020), but clearly further work is required to establish the efficacy of the current protection measures (and see Clark et al. 2019b). For example, while monitoring of reef-coral populations has taken place for some seamounts in the Graveyard Seamount Complex, there is currently no widespread deep-sea monitoring programme to track the stability or otherwise of coral populations.

While there are many records for reef-corals in the New Zealand region (Fig. 9.6), most of these have come from fishery by-catch surveys or research surveys that focused on particular areas/habitats, making the records spatially biased. This results in distributional gaps in sampling, particularly for depths greater than 2000 m, where the information on coral species composition is sparse or lacking entirely. Additional surveys (both direct physical sampling and less-destructive seafloor imagery) would provide a better understanding of the distribution of reef-corals and their population structure, as well as improve knowledge of population connectivity (through more genetic studies). Data from such additional sampling will also help test and improve the predictive habitat suitability modelling that has already been carried out for reef-corals in the New Zealand region. These data would also help to reveal the response of corals to changes in carbonate saturation horizon depth. Furthermore, future surveys should include quantitative density and biomass data to more accurately reflect the relative importance of coral species in different areas. Achieving this will require a shift towards sampling with submersibles, remotely-operated vehicles (ROVs), and autonomous underwater vehicles (AUVs) to support these quantitative analyses.

A preliminary ecological risk assessment of bottom trawl fishing impacts on deep-sea corals on the Chatham Rise (Clark et al. 2014) concluded that, although vulnerability criteria could be assessed reasonably well, data on coral productivity was limited. This highlighted the need for research to improve knowledge of age and growth characteristics of many deep-sea coral species. Similarly, there is little information on reproductive biology of these corals. Although obtaining this information is often challenging for deep-sea corals, research in this area is increasing (e.g., Feehan and Waller 2015; Tracey et al. 2021; Waller et al. 2023) to determine spawning patterns, and hence how coral communities may grow or recolonise impacted areas.

The above knowledge gap issues are just some of those detailed in the draft research plan published by the New Zealand Department of Conservation. The extent of the research needed ensures the sustainability of deep-sea reef-coral groups is challenging. There is an urgent need to better understand the ecology of deep-sea corals in the region and evaluate the nature and extent of natural and human impacts. It will require more sampling to address distributional gaps, improve data on abundance (both on coral-reef density and biomass), data on coral productivity, and long-term monitoring programmes.

Recovery Box/Spotlight

A number of the deep-sea reef-corals that are found around New Zealand are broadly distributed in the South Pacific Ocean (Cairns 1995; Tracey et al. 2011; Anderson et al. 2016a, b). Off the Australian island of Tasmania, in particular, seamount and knoll features have very similar coral assemblages to those described in this chapter for New Zealand, where benthic communities are dominated by the reef-corals *Solenosmilia variabilis* and *Madrepora oculata* (Thresher et al. 2014; Williams et al. 2010; Fig. 9.14).

(continued)

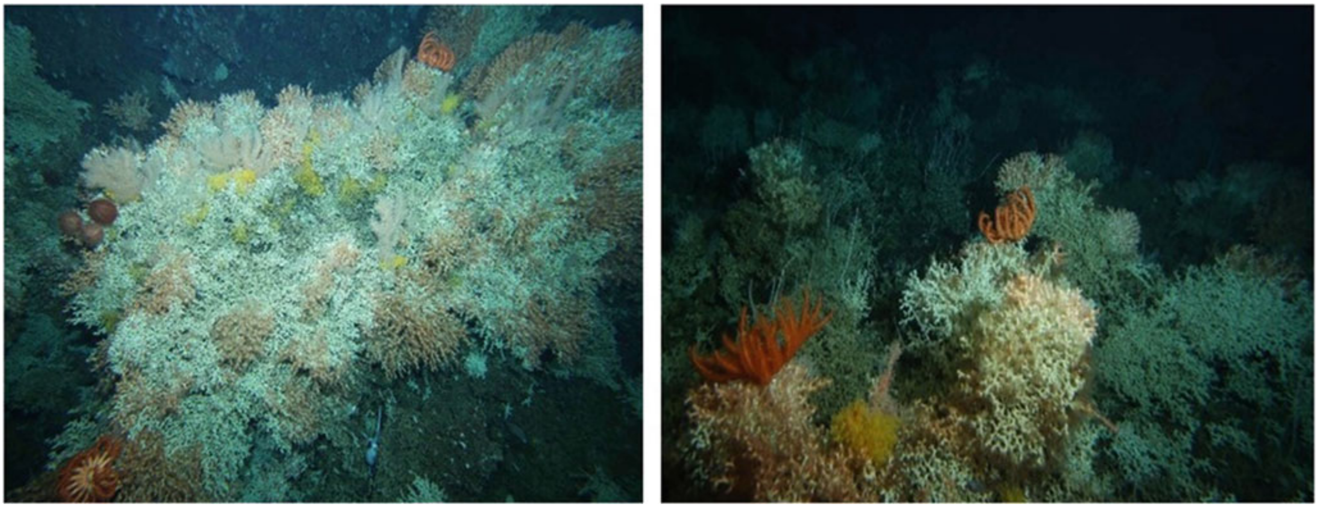

Fig. 9.14 *Solenosmilia variabilis* reef-coral on the summit of seamounts off southern Tasmania (Images courtesy of Alan Williams, CSIRO, Hobart)

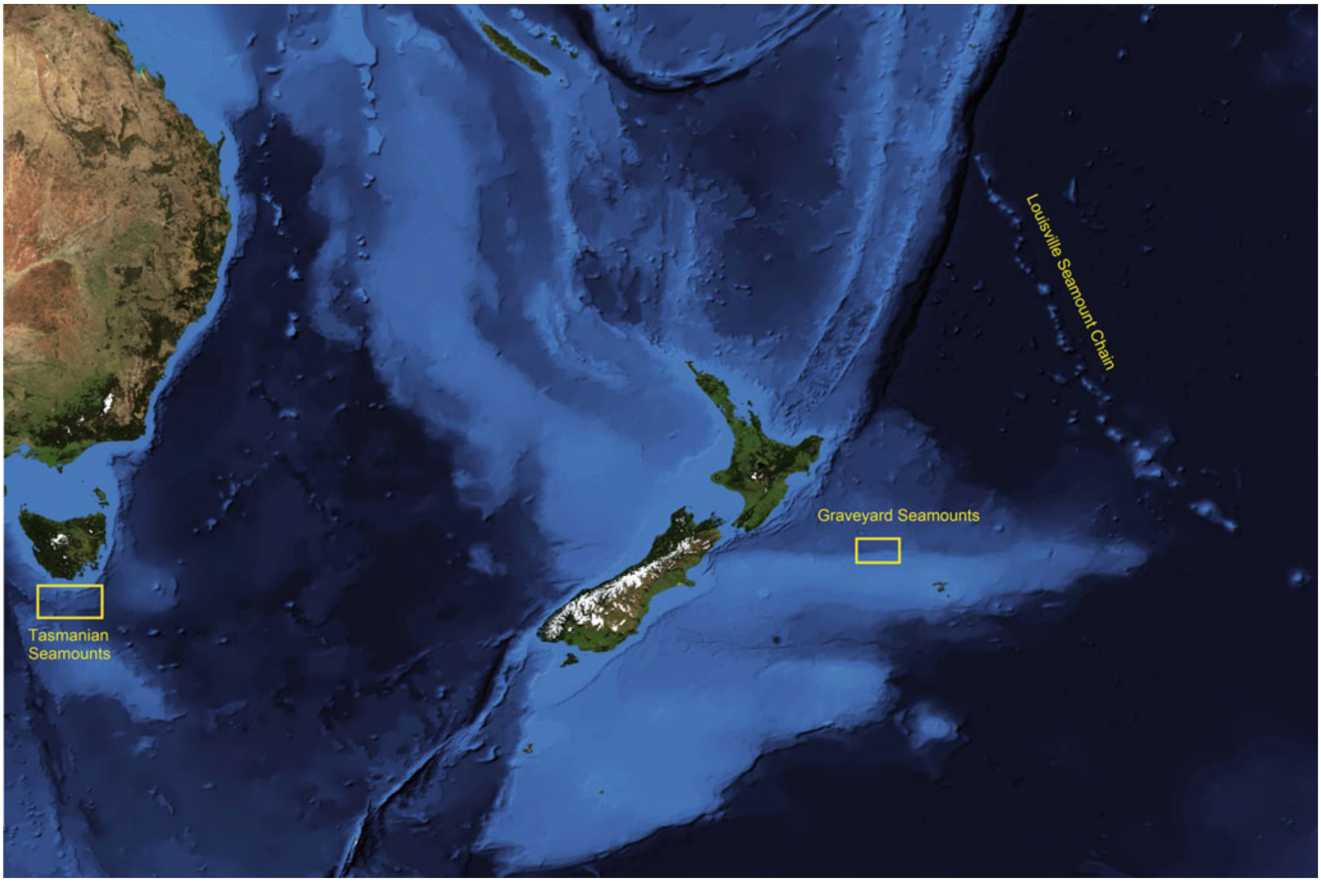

Fig. 9.15 The general location of the Tasmanian seamounts off southern Australia, and of the Graveyard Seamounts off New Zealand

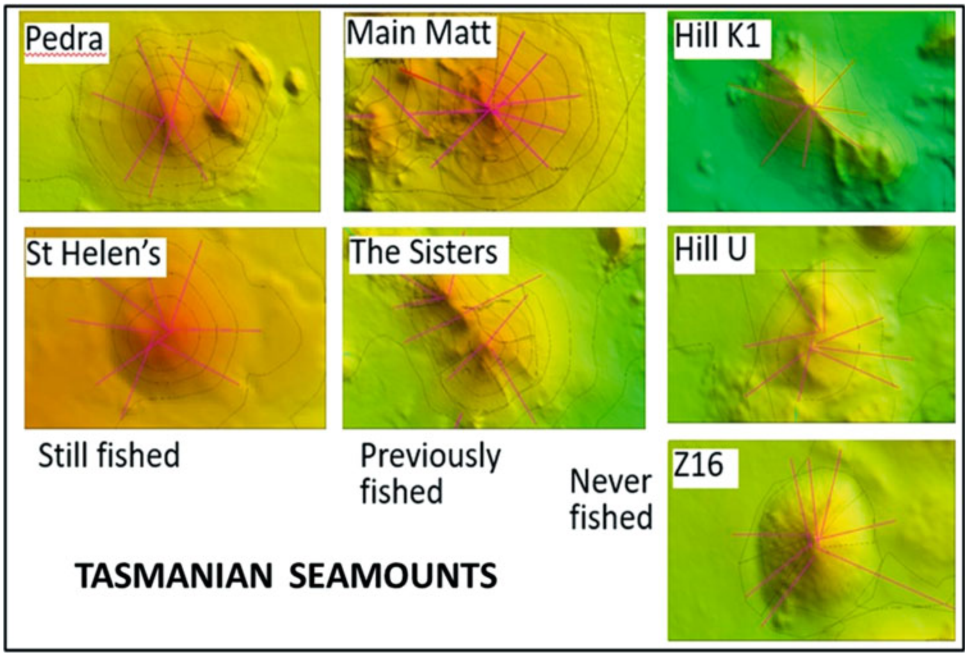

Fig. 9.16 Core set of seamounts surveyed over time off southern Tasmania. Depths range from 600 m (red) through 1200 m (yellow) to 1700 m (green). The DTM is 3× vertical exaggeration. North is to the top of the page. The red lines show photographic transect lines from a survey in 2018

Another feature in common between Australia and New Zealand is the occurrence of bottom trawl fisheries for orange roughy, and both countries have undertaken research into the effects of trawling on corals and other benthic invertebrates on seamounts. A key objective of this research has been to examine the resilience of the corals to trawling pressure and to understand the dynamics of recovery post-trawling when a number of seamounts off New Zealand and southern Tasmania (Fig. 9.15) were closed to trawling in the 1990s and early 2000s (Brodie and Clark 2003; Koslow et al. 2001). Time series of surveys have been carried out in both areas to monitor changes over time.

Both areas have seamount/knoll features in close proximity (within km-10 s km), of broadly similar size (1–10 km^2) and depth ranges (700–1200 m summit depths) and contrasting fishing states. This situation has enabled 'compare and contrast' photographic studies of features that have continually been fished, some previously fished and then closed, and others that have remained unfished (Figs. 9.16 and 9.17).

Comparison of benthic communities on fished and unfished seamounts has shown strong contrast and demonstrated clearly that bottom trawling can damage the coral-reef structure, and repeated trawling can leave a seamount almost without any live intact reef (Koslow et al. 2001; Clark and Rowden 2009; Althaus et al. 2009; Clark et al. 2016). The results are not unexpected, given the fragility of these reef-coral structures (Clark et al. 2010b), but a key management issue arising from this research is whether such communities can recover if management action closes an area to trawling, and if so, over what sort of time period?

Repeat photographic surveys have been carried out on the Graveyard seamounts in 2001, 2006, 2009, 2015, and 2020. Repeat surveys of Tasmanian seamounts have occurred in 1998, 2007, and 2018. The 5-survey series off New Zealand and 3-survey comparison off Tasmania each spanning about 20 years, respectively, reveal the same patterns: (1) there are consistent and strong differences in faunal diversity and abundance between fished and unfished seamounts; (2) various faunal groups exhibit different responses over time, but the benthic communities of fished and then closed seamounts show little indication of steps towards recovery; and (3) the reef-corals only persist in areas where trawling was not possible because of rough bottom, or in remnant patches in-between trawling regions (Clark et al. 2019a; Williams et al. 2020a, b; Goode et al. 2020).

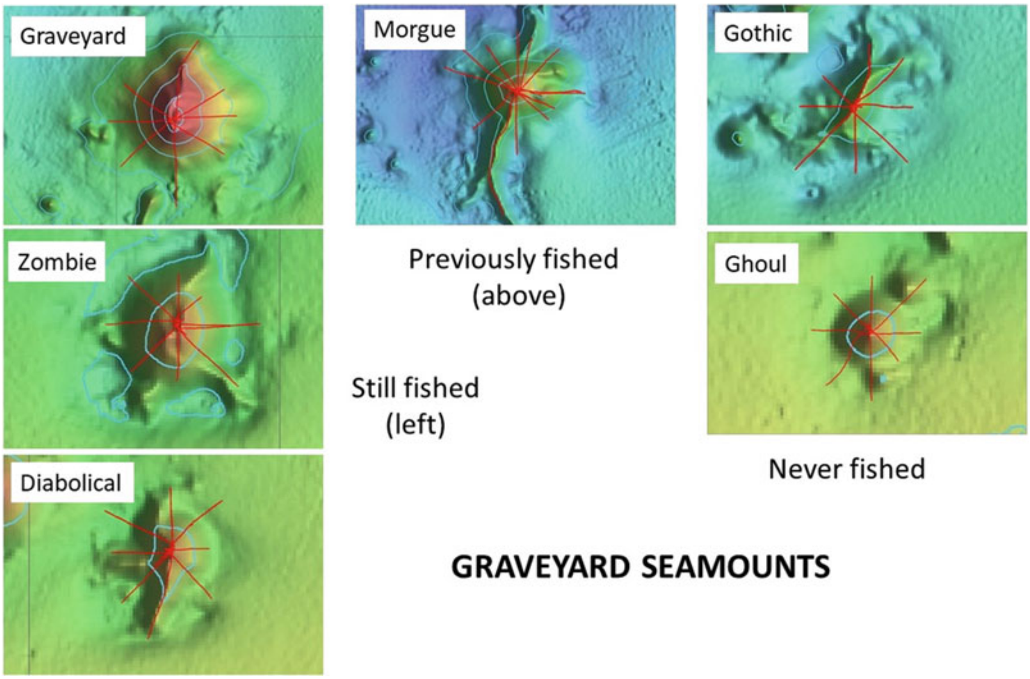

Fig. 9.17 Core set of seamounts surveyed over time off New Zealand. Depths range from 750 m (reddish) through 1000 m (green) to 1200 m (blue). The DTM is 3× vertical exaggeration. North is to the top of the page. The red lines show photographic transect lines from a survey in 2015

Acknowledgements A key source of information used for this chapter is a recent report on the 'State of Knowledge of Deep-sea Corals in the New Zealand Region' compiled by Tracey and Hjorvarsdottir (2019). We acknowledge the many contributors of that report, Erika Mackay, Kareen Schnabel, Rob Stewart, Owen Anderson, Jennifer Beaumont, Kevin Mackay (all NIWA) for the provision of figures and images used in this chapter, Stephen Cairns for his dedication to the taxonomic descriptions of the region's scleractinian reef-corals, as well as more recent research efforts by NIWA scientists that continue to contribute to an improved understanding of deep-sea reef-corals in New Zealand waters. Various New Zealand Government agencies have funded deep-sea coral research over the years, these include the Department of Conservation, Fisheries New Zealand, and Ministry for Business Innovation and Employment. Finally, our thanks to Erik Cordes and Furu Mienis for their significant effort in leading this Cold-Water Corals volume in the 'Coral Reefs of the World' series.

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