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Coralline algae of New Zealand: a summary of recent research and the current state of knowledge

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Coralline red algae (Rhodophyta, orders Corallinales, Hapalidiales, and Sporolithales) are considered ecosystem engineers for the functional roles they perform, including providing habitats and niches that support a high diversity and abundance of marine animals and algae. As calcifying organisms, coralline algae are vulnerable to global climate change, particularly to the impacts of ocean acidification, and also vulnerable to the impacts of a range of human activities including physical disruption from trawling, dredging, anchoring, as well as people trampling over rocky reefs, and from reductions in water quality, alterations to water movement, and aquaculture installations.

Research funded through the Biodiversity Research Advisory Group (ZBD200105, ZBD200407, ZBD200903, ZBD201407) has built baseline information on the diversity and distribution of coralline algae of New Zealand, contributing specimens and data to national herbaria to enable further systematic research. The research has revealed very high species and generic diversity within the New Zealand region with 141 species predicted to occur in the region, and particularly high diversity in the south (99 species predicted). Significant progress has been made on documenting and understanding distributions of corallines in New Zealand (e.g., geographic: northern, central and southern; ecological: rhodoliths, Foveaux Strait oyster beds), although more information is needed about regional differences, habitat requirements at a species level, and the ecological services that individual species provide.

Globally the taxonomy of coralline algae is in flux with many new discoveries disrupting previous understanding of relationships, and generic and specific boundaries. Research over the past decade has clearly established that sequence data and phylogenetic analyses are essential for the characterisation of coralline algae. Morpho-anatomical characters are in many cases insufficiently informative, leading to the misapplication of generic and specific concepts when identifying specimens. It is now clear that many names have been incorrectly applied to coralline algae in New Zealand, where the identification has been based solely on morphological and/or anatomical features and all such identifications need to be reviewed in the light of these findings. The discoveries globally and in New Zealand provide additional challenges when interpreting experimental and field investigations of coralline algae. Unless voucher material has been retained, or sequence data are available, the identity of species used for experiments in many cases cannot be confirmed. There is currently no genetic evidence of species in the genera *Harveylithon*, *Heteroderma*, *Hydrolithon*, *Lithoporella*, *Lithophyllum*, *Melobesia*, *Mesophyllum*, *Phymatolithon*, *Porolithon*, and *Spongites* in New Zealand.

The ecosystem services provided by coralline algae as well as their potential vulnerability to changing global climate are well documented and include roles in habitat provision and in larval settlement of species such as pāua (*Haliotis iris)*. New Zealand coralline algae forming rhodolith beds have been recognised as providing an important biogenic habitat and are considered to form 'small natural features', ecosystems that 'support a diverse fauna and flora and provide ecosystem services disproportionate to their size', although these remain poorly documented in terms of distribution, extent, and functional roles. The coralline turfs of rocky reefs are structurally complex and home to extremely diverse and productive macrofaunal assemblages which are known to support juvenile fish populations.

Given the importance of this group of organisms in coastal ecosystems of New Zealand it is important to understand how changing environmental conditions may be affecting them. To do this, it will be necessary to better understand species-specific attributes (e.g., physiology, reproduction, competitive abilities, and susceptibility to key stressors). This in turn requires further research, involving targeted collection programmes, multigene phylogenetic analyses, and morpho-anatomical characterisation.

1. INTRODUCTION

1.1 Overview: Introduction to coralline algae

Coralline red algae belong to the Rhodophyta, sub-class Corallinophycidae. They are currently classified into three orders: Corallinales (Silva & Johansen 1986), Hapalidiales (Nelson et al. 2015), and Sporolithales (Le Gall et al. 2010), and are characterised by containing extracellular calcium carbonate (Le Gall & Saunders 2007). There are three distinct forms of coralline algae: geniculate, non-geniculate, and rhodoliths (Figure 1). Geniculate coralline algae have alternating segments that are calcified (intergenicula) and non-calcified (genicula). They are often referred to as articulated coralline algae and can form dense turfs over suitable substrates.

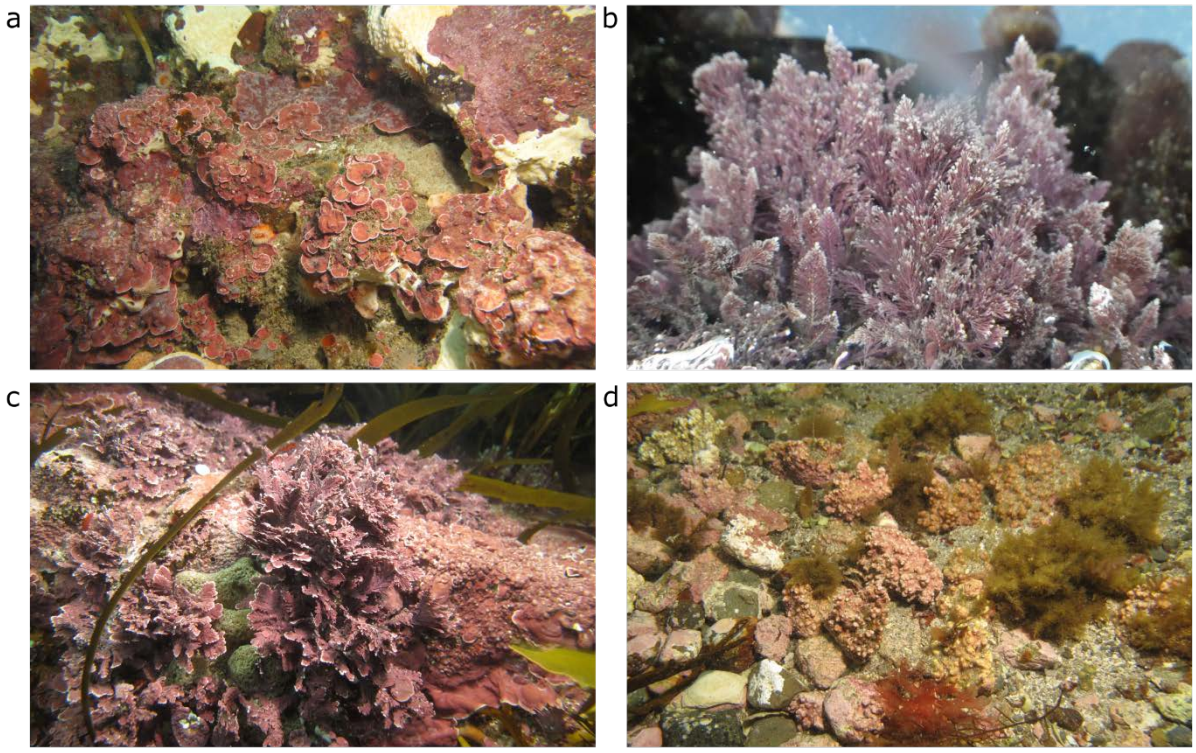

Figure 1: Field images of a) non-geniculate coralline algae, b) geniculate coralline algae, c) both geniculate and non-geniculate coralline algae, and d) rhodoliths (free-living, non-geniculate coralline). Photo credits: Roberta D'Archino, Wendy Nelson and Brenton Twist.

Non-geniculate coralline algae are completely calcified, typically prostrate, and found growing on a wide range of substrates. They are sometimes referred to as encrusting or crustose coralline algae because of their growth form. Non-geniculate coralline algae can exhibit a range of different external morphologies (Figure 2), and a single species may display multiple morphologies (e.g., Steneck 1986; Woelkerling et al. 1993). Rhodoliths (or maerl) are a free-living growth form of non-geniculate coralline algae and are not attached to any fixed substrate. They can be moved around on the sea floor by water motion and exhibit a range of morphologies including smooth, warty, and delicate branching forms. Rhodoliths often form extensive beds on the sea floor (e.g., Amado-Filho et al. 2012).

Coralline algae have been referred to as foundation species and ecosystem engineers for their ability to modify characteristics of the surrounding marine environment and the functional roles they perform (Jones et al. 1994; Foster 2001; Crain & Bertness 2006; Daleo et al. 2006; Nelson 2009; McCoy & Kamenos 2015). Coralline algae play an important role in the formation and stabilisation of reef systems by cementing together and weighing down loose material (Bosence 1983; Adey 1998; Chisholm 2000; Payri & Cabioch 2004). They are often early colonisers of reef systems and play an important role in

recovery of biodiversity post disturbance (Asnaghi et al. 2015). Coralline algae enhance the settlement of larvae of a number of benthic invertebrate species, such as abalone (Day & Branch 2000; Roberts 2001), sea snails (Spotorno-Oliveira et al. 2015), sea urchins (Pearce & Scheibling 1990; Day & Branch 2000), and coral species (Morse et al. 1996; Whalan et al. 2012). Furthermore, preferential settlement of larvae on certain coralline alga species over others (i.e., species-specificity of settlement) has been demonstrated for some invertebrate species (Morse et al. 1988; Daume et al. 1999b; Roberts et al. 2004).

Geniculate coralline algae provide surfaces for settlement of microphytobenthos and trap particles for epiphytic filter-feeding taxa. They can host a large number of small invertebrates by providing settlement sites, protection from wave action, reduced predation, and desiccation protection in intertidal environments (Brown & Taylor 1999; Kelaher 2002; Cowles et al. 2009; Berthelsen et al. 2014). Likewise, non-geniculate coralline algae provide many cracks and crevices for a large number of grazing and burrowing cryptofauna (Steller et al. 2003; Chenelot et al. 2011). The settlement and germination of several fleshy macroalgal species has also been demonstrated to be inhibited by chemical compounds produced by coralline algae (Johnson & Mann 1986; Suzuki et al. 1998; Kim et al. 2004; Vermeij et al. 2011). However, recent evidence suggests that although non-geniculate coralline algae inhibit spore settlement of some fleshy macroalgae, spores of macroalgae readily settle on the genicula of articulated coralline algae (Parada et al. 2017). Rhodolith beds form a three-dimensional habitat that can support high densities of invertebrates, seaweeds and juvenile fish (Bosence 1979; Steller et al. 2003; Hinojosa-Arango & Riosmena-Rodríguez 2004; Nelson et al. 2014; Riosmena-Rodríguez et al. 2017). In the NE Atlantic rhodolith beds have been found to harbour 30% of the regional algal flora, compared to that found associated with kelp (ca 10%) and seagrass (ca 5%) (Peña et al. 2014). Rhodoliths have also been shown to act as an endolithic (living within) reservoir and seed bank for many microalgal species such as ecologically important dinoflagellates (Krayesky-Self et al. 2017; Fredericq et al. 2019). Overall, coralline algae provide important habitat and niche space that supports a high diversity and abundance of marine flora and fauna.

These ecosystem engineers have colonised a wide range of temperature, light, and wave environments (Aguirre et al. 2000). They are found from the tropics to polar regions and from the intertidal to the limits of the euphotic zone (Steneck 1986; Nelson 2009). In temperate regions coralline algae are a major component of shallow rocky reefs (Adey 1964, 1965; Steneck 1986; Daume et al. 1999a*;* Roberts et al. 2002) and are one of the most productive habitats in these regions (Mann 1973; Harrer et al. 2013), whereas in the tropics they are considered to be critical components of coral reef ecosystems (Littler 1973; Steneck & Adey 1976; Adey 1978; Bosence 1983; Chisholm 2000; Fabricius & De'ath 2001; Dean et al. 2015). Coralline algae can also be abundant on soft substrata in the form of rhodolith beds or on cobble and shell substrata (Steller & Foster 1995; Marrack 1999; Foster 2001; Bosence 2003; Nelson et al. 2015), and in some locations these are very extensive, for example on the coast of Brazil, where rhodolith beds extend over 20 000 km^2 (Amado-Filho et al. 2012). They are a significant component of communities at mesophotic depths (ca. 30–150 m depth depending on the region) where other photosynthetic organisms are in low abundance or absent (Adey & Macintyre 1973; Roberts et al. 2002; Spalding et al. 2003, 2019; Richards et al. 2018b). The deepest recorded macroalgae are non-geniculate corallines at 268 m (Littler et al. 1985).

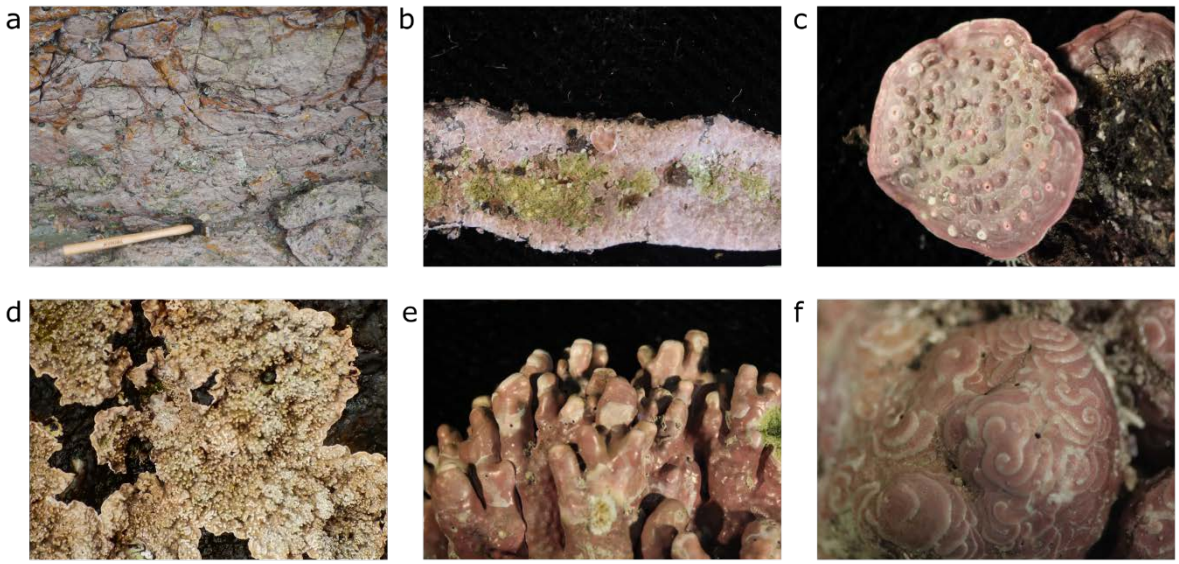

Figure 2: Growth forms of non-geniculate coralline algae: a) smooth encrusting on rock (epilithic), b) encrusting on fleshy macroalgae (epiphytic), c) discoid — thin encrusting discs, d) warty — short protuberances, e) fruticose — long flattened or cylindrical branches, and f) layered — obvious layering. Photo credits: Wendy Nelson and Brenton Twist.

The distribution of individual species of coralline algae is affected by species-specific physiological responses to abiotic factors such as light levels, temperature, and wave exposure, among many other environmental parameters (Padilla 1984; Minnery 1990; Daume et al. 1999a; Fabricius & De'ath 2001; Martone et al. 2010; Guenther & Martone 2014; Dean et al. 2015). Coralline algae can dominate in areas of high disturbance or high stress where other macroalgae are absent (Dethier 1994; Steneck & Dethier 1994; Airoldi 2000), including habitats that experience severe sand scouring (Kendrick 1991), intensive wave action (Airoldi 2000), and high herbivory (Underwood, 1980; Steneck & Dethier 1994). There are few rocky photic habitats in which coralline algae are absent (Steneck 1986). In contrast, rhodoliths occurring on soft substrata normally require specific environmental conditions, particularly gentle slopes, moderate flow, and low sedimentation (Steller & Foster 1995; Foster 2001; Wilson et al. 2004).

Coralline algae have been assessed as a major store of global carbon, and their role in global carbon budgets, as well as their utility as indicators of past climatic conditions, have been the subject of recent research. Carbonate sequestration (the long-term capture and storage of atmospheric CO_2) by rhodolith beds is considered to be comparable to that of coral reefs in both productivity and extent (Amado-Filho et al. 2012). Van der Heijden & Kamenos (2015) have calculated that coralline algae have 'production rates similar to mangroves, salt marshes and seagrasses representing an as yet unquantified but significant carbon store'. Coralline algae are also being used to interpret other aspects of environmental and ecosystem change. Some coralline algae lay down regular growth bands and thus can serve as recorders of past climatic conditions (e.g., Halfar et al. 2008; Halfar et al. 2011; Kamenos et al. 2017). As scientists and policy makers look towards global carbon stores in the marine environment, understanding the scale and nature of this carbon storage function has become increasingly important (Hill et al. 2015).

As calcifying organisms, coralline algae are potentially vulnerable to global climate change, particularly to the impacts of ocean acidification (OA) (e.g., Kuffner et al. 2008; Kroeker et al. 2013). It is anticipated that OA will primarily result in a reduction in net calcification rates and growth (e.g., Cornwall et al. 2013a ,2013b, 2014). Temperate coralline algae may be less sensitive to OA than those at tropical latitudes (Jokiel et al. 2008; Fabricius et al. 2015) because the increased mortality and reduced recruitment rates in tropical corallines under lower pH were not observed in similar

experiments on temperate coralline algae (Cornwall et al. 2013a, 2013b, 2014; James et al. 2014: Roleda et al. 2015). Responses are likely to be both species-specific and habitat-dependent, for example, slower seawater velocities allow corallines to exert a greater influence on the surrounding pH (Hurd et al. 2011; Cornwall et al. 2013a, 2013b, 2015; Law et al. 2017).

Coralline algae have also been shown to be vulnerable to the impacts of a range of human activities including physical disruption from trampling (e.g., Brown & Taylor 1999), trawling, dredging, and anchoring (Hall-Spencer & Moore 2000), as well as from reductions in water quality (e.g., Wilson et al. 2004; Riul et al. 2008), alterations to water movement, and aquaculture installations such as shellfish rafts and lines, and fish cages (Hall-Spencer et al. 2003, 2006). Rhodoliths are considered to be particularly vulnerable given their fragility and slow growth rates (0.05–2 mm/yr) (e.g., Wilson et al. 2004). Fragmentation from physical disruptions has significant impacts on the communities associated with rhodolith beds. For example, Steller et al. (2003) found that the diversity and abundance of species associated with rhodoliths increase as the complexity (branching density) and the space available (thallus volume) within the bed increases. MacDiarmid et al. (2013) identified rhodolith beds as being sensitive biogenic marine habitats in New Zealand. The contributions made by small natural features (SNFs), ecosystems that 'support a diverse fauna and flora and provide ecosystem services disproportionate to their size', are reviewed by Lundquist et al. (2017) who note that rhodolith beds are a poorly recognised macroalgal SNF.

The ecological roles and ecosystem contributions of coralline algae have often been overlooked, best exemplified by some ecological literature crudely referring to it as 'pink paint'. This may be a consequence of occurring as understorey species beneath the canopy of fleshy macroalgae and also reflect the difficulty of identifying species in the field and collecting samples that are very firmly attached to rock substrates. Early studies of coralline algal diversity, distribution, and ecology (e.g., Adey 1964; Littler 1973; Bosence 1976) used taxonomic descriptions based on morphological and anatomical features (morpho-anatomical features) to identify species (e.g., Foslie 1906; Woelkerling 1988). However, this approach has been shown to be problematic because coralline algae are reported to exhibit both phenotypic plasticity and also convergent morphologies (Woelkerling et al. 1993). This has led to the increasing use of phylogenetic techniques to identify coralline algae over the past decade. DNA sequence data from type specimens (the material on which the species name and description is based) has enabled major progress, clarifying the application of names and also relationships within the group (e.g., Le Gall & Saunders 2007; Broom et al. 2008; Gabrielson et al. 2011; Hind et al. 2014a, 2014b; Nelson et al. 2015; Caragnano et al. 2018; Peña et al. 2018). This research has shown that many generic and species names have been misapplied, with very serious implications when interpreting earlier work based on morphology and anatomy. Globally the documentation of the diversity and phylogeny of coralline algae using modern phylogenetic approaches is still in its infancy (Hernandez-Kantun et al. 2016; Melbourne et al. 2017; Peña et al. 2018).

All research based on species-specific attributes relies on correct species assignments; for example, in ecological and physiological research when investigating species-specific responses of coralline algae to disturbances (Noisette et al. 2013; Cornwall et al. 2017) and the ecosystem functions they perform (McCoy & Kamenos 2015). Mis-identification of coralline algae based on incorrect or inadequate taxonomic descriptions has been shown to mislead biodiversity and ecological studies, due to incorrect estimates of species diversity (Hind et al. 2014b). To conduct repeatable and sound research, it is important that the research keeps abreast of emerging taxonomic discoveries, particularly in a rapidly developing field; incorrectly applied names can have profound impacts on the interpretation of field and experimental studies on coralline algae. Documenting the diversity, phylogeny, and geographic and ecological distributions of species is a key step in being able to fully understand the roles coralline algae play in the diverse array of habitats within which they are found.

1.2 Objectives

Research funded through the Biodiversity Research Advisory Group (ZBD200105, ZBD200407, ZBD200903, ZBD201407) has been focused on building baseline information on the diversity of the

coralline algae of New Zealand, contributing specimens and data to national herbaria to enable further systematic research, and the eventual description of new genera and species, leading to improved understanding of the diversity and distribution of coralline algae around New Zealand. For the research focused on diversity, the New Zealand region was divided into three broad zones (Figure 3), northern, central and southern regions.

The objectives of ZBD201407 were:
1. document critical baseline information on the biodiversity of coralline algae in southern New Zealand using morphological and molecular identification,
2. develop coralline reference collection from habitats and regions predicted to experience stress from ocean acidification, and
3. prepare identification guide for coralline algae of southern New Zealand.

The first two objectives have been met through research conducted in southern New Zealand (e.g., Twist 2019), with collections from a wide range of habitats, including in association with key sites associated with the MBIE-funded CARIM research project (Coastal Acidification: Rate, impacts and management). Given the nature of the discoveries about diversity made during this research, and following discussion with Fisheries New Zealand, it was agreed that the preparation of an identification guide would not be appropriate.

The previous two projects on diversity of coralline algae in New Zealand (ZBD200105, ZBD200407) for central and northern New Zealand, respectively, did not include the preparation of an AEBR. Thus, it was agreed that this Report would be prepared to provide a summary of research to date and, specifically, to present an overview of the roles and ecological importance of coralline algae, provide a summary of research outcomes from projects on the diversity of coralline algae funded through the Biodiversity Research Advisory Group, and to summarise the state of knowledge about coralline algae in New Zealand.

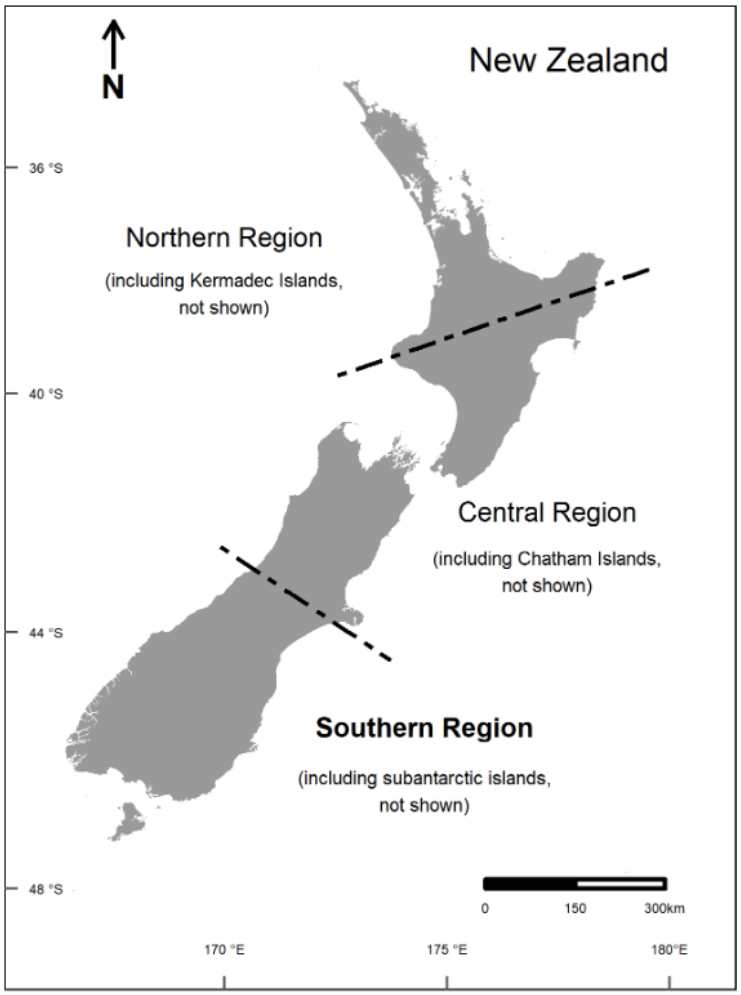

Figure 3: Map showing the location of the southern study region with respect to the previously studied central (Harvey et al. 2005) and northern (Farr et al. 2009) regions.

1.3 Contributions from New Zealand coralline research projects

This research has made important contributions to increasing our understanding of coralline algae in New Zealand, including:

a) enhanced national collections of coralline algae, providing a baseline for current and future research, from extensive field work from a wide range of collection sites within the region (northern region, 86 mainland sites plus 5 sites in the Kermadec Islands; central region, 85 sites; southern region, 110 sites),

b) a best practice guide developed for the care of herbarium collections of coralline algae (Appendix 1),

c) a baseline summary and analysis of the taxonomic diversity of coralline algae in the New Zealand region (Woelkerling & Nelson 2004),

d) two popular guides to coralline algae for the central (Harvey et al. 2005) and northern (Farr et al. 2009) regions,

e) a review of the contributions of calcified algae to coastal ecosystems and their vulnerability to change (Nelson 2009),

f) genetic data and phylogenetic analyses, which contribute critical information about the identity and diversity of New Zealand species, and contributions to global understanding of phylogenetic relationships, including the description of a new order of coralline algae, insights from genomic studies, and contributions to the NSF Red Algal Tree of Life programme (e.g., Broom et al. 2008; Kim et al. 2015; Nelson et al. 2015; Lee et al. 2018; Twist 2019; Twist et al. [in prep]),

g) research on rhodolith beds in the Bay of Islands (Nelson et al. 2012, 2014; Neill et al. 2015),

h) contributions to global syntheses on rhodoliths, including a summary of diversity and distribution of rhodoliths in the South Pacific and at mesophotic depths (Nelson & Neill 2017; Riosmena-Rodríguez et al. 2017; Spalding et al. 2019),

i) scientific advice for policy development on sensitive marine habitats, particularly with respect to rhodoliths (MacDiarmid et al. 2013),

j) specimens for skeletal carbonate mineralogical analyses (Smith et al. 2012),

k) baseline information about coralline algal diversity for the CARIM project and PhD investigations (responses of coralline algae to ocean acidification, A. Kluibenscheld, University of Otago; physiological responses of coralline algae to ocean acidification, H. Nguyen, University of Otago),

l) description of new taxa from New Zealand (e.g., *Corallinapetra novaezelandiae*, *Jania sphaeroramosa)* (Nelson et al. 2015; Twist et al. 2018).

The methods employed in the coralline projects have been published in a range of publications:
a) field collecting, sorting, and morpho-anatomical characterisation (Harvey et al. 2005; Farr et al. 2009),

b) genetic and phylogenetic methods (Broom et al. 2008; Kim et al. 2015; Nelson et al. 2015; Lee et al. 2018; Twist 2019; Twist et al. [in prep]),

c) description of new species (Nelson et al. 2015; Twist et al. 2018),

d) ecological research methods including diversity and community analyses (Nelson et al. 2012, Neill et al. 2015; Twist 2019),

e) investigations of the role of coralline algae in biogenic habitats (Nelson et al. 2012, 2014; Neill et al. 2015; Twist 2019).

2. TAXONOMY OF CORALLINE ALGAE

2.1 Classification and identification of coralline algae

The application of stable taxonomic names and descriptions is essential for reproducible science; the correct assignment of species names is critical for data to be compared between studies, regardless of their focus (e.g., ecology, physiology, biochemistry, paleoclimate studies). Consistently applied species concepts are also crucial for monitoring long-term trends and for predicting future changes in communities and ecosystems.

The identification of coralline algae has been regarded as challenging for a number of reasons. Field sampling can be difficult, particularly removing tightly appressed non-geniculate specimens from rocky substrates. Species recognition in the field is problematic. It has been understood that corallines, particularly non-geniculate species, exhibit both significant morphological convergence as well as

phenotypic plasticity. Although, traditionally, coralline algae have been defined by morphological and anatomical features including their general external appearance and shape, or growth form (e.g., discoid, encrusting, fruticose, foliose, layered, lumpy, warty), it has been recognised that a single species may display multiple growth forms depending on habitat, stage of development (Farr et al. 2009).

The corallines have life histories typical of red algae, with an alternation of haploid gametophytes (male and female thalli) alternating with a diploid sporophyte generation that produces tetraspores. Fertilised female thalli bear the carposporophyte generation (Farr et al. 2009). The type, arrangement, and features of reproductive structures are considered to be critical anatomical features for identifying coralline algae, particularly for non-geniculate species. The gametes and spores of corallines are found in uniporate conceptacles (Figure 4 a-c, Figure 5), hollow chambers housing spores or gametes with a single pore in the roof through which the spores or gametes are released; multiporate conceptacles (Figure 4 d-e, Figure 4 c), hollow chambers in which tetraspores are produced with multiple pores in the chamber roof; and calcified compartments (Figure 4 f, Figure 5), calcified structures that produce tetraspores that may be solitary or grouped together forming a sorus [plural = sori]. The tetrasporangia may be divided either cruciately or zonately (Figure 5).

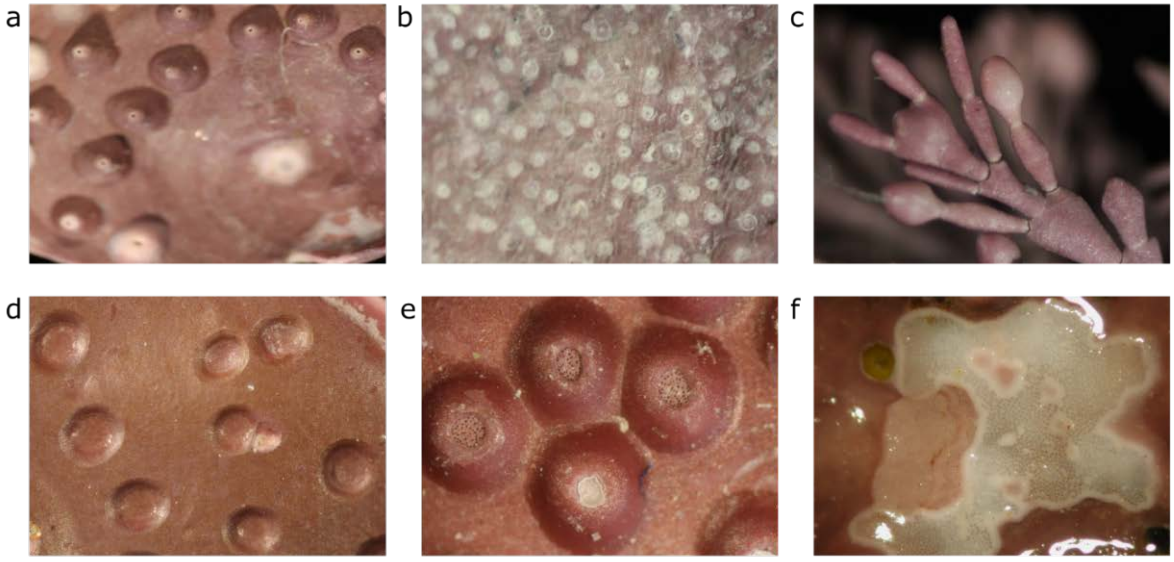

Figure 4: Reproductive structures: a) uniporate conceptacles – pointed dome, b) uniporate conceptacles – flush, c) conceptacles – geniculate, d) multiporate conceptacles – flat tops, e) multiporate conceptacles – volcano, and f) sori – calcified compartments. Photographs: Kate Neill and Brenton Twist.

Other key anatomical features used in distinguishing species include the presence or absence of cell fusions and pit connections (Figure 5), the presence or absence of an apical plug at the conceptacle pore, and the shape of cells on the upper surface of the thallus. To determine many of these features, and other anatomical characteristics, it is necessary to decalcify samples, embed them in resin, and section before examining them microscopically. The requirement for fertile samples and the challenges of determining key anatomical features have long been seen as barriers to easy identification of coralline algae (Harvey et al. 2005; Farr et al. 2009).

Globally the taxonomy of coralline algae is in flux as new discoveries disrupt previous understanding of relationships, with new orders, genera, and species described in the past decade and new understanding of generic and specific boundaries. Prior to 2010 only one order of coralline algae was recognised, the Corallinales, established by Silva & Johansen (1986). Le Gall & Saunders (2007) proposed the subclass Corallinophycidae within the Florideophyceae, based on a nuclear DNA sequence phylogeny, initially comprised of the orders Corallinales and Rhodogorgonales (Fredericq & Norris 1995). All members of the sub-class share the anatomical feature (found between adjacent cells) of proteinaceous pit plugs, with two cap layers and with the outer cap an enlarged dome-like layer. The

order Sporolithales was segregated from Corallinales by Le Gall et al. (2010), who recognised this order as monophyletic and sufficiently genetically divergent from other members of the sub-class. Members of the Sporolithales also possess a distinctive reproductive character, namely, cruciately divided tetrasporangia that are produced in calcified compartments. The order Hapalidiales was established on the basis of its phylogenetic relationships within the Corallinophycidae and the possession of distinctive tetrasporangial conceptacles by Nelson et al. (2015), based on data obtained in studies of Corallinophycideae from the central and northern regions of New Zealand. Nelson et al. (2015) also emended the circumscription of the Corallinales.

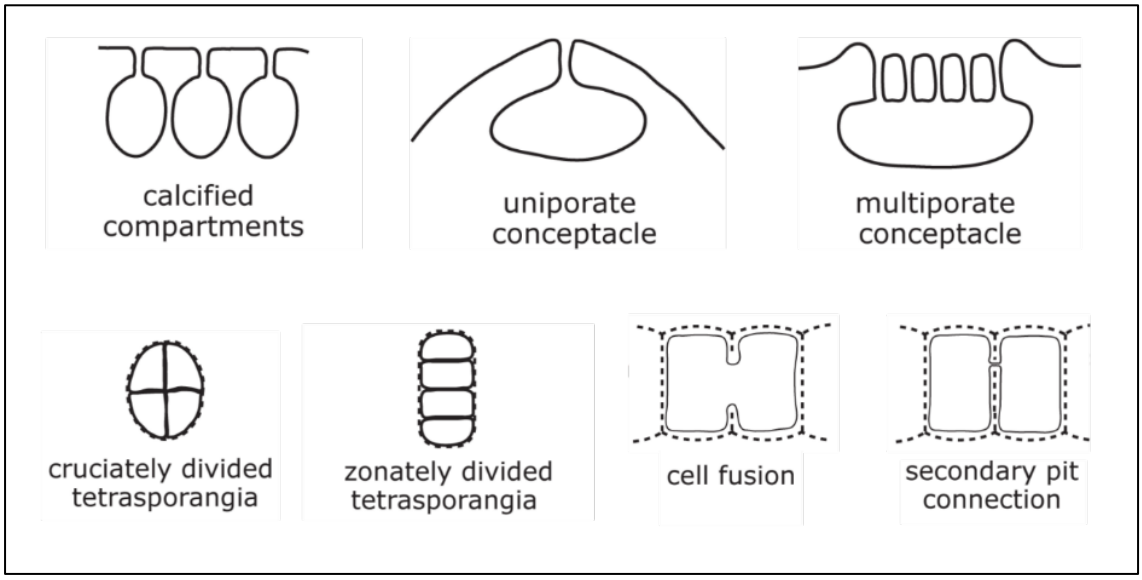

Figure 5: Diagram of conceptacles and compartments (top row), tetrasporangia divisions (bottom left), and cellular connections (bottom right) used to distinguish coralline algae into separate orders. Figure adapted from Farr et al. (2009).

Nelson et al. (2015) also noted that, on the basis of both reproductive anatomy and genetic differences, the genus *Corallinapetra* is likely to require a separate order. They refrained from describing this order given the paucity of material available at that stage (a single collection from northern New Zealand). The proposal to establish a new order and family (Corallinapetrales, Corallinapetraceae) is being presented to an international phycological conference in May 2019 (Jeong et al. 2019). Table 1 summarises key anatomical and morphological features of the three currently recognised orders of coralline algae.

Table 1: Anatomical and reproductive characteristics of members of the three currently recognised coralline orders (after Nelson et al. 2015).

Character	**Corallinales**	**Hapalidiales**	**Sporolithales**
Tetrasporangial conceptacles	uniporate conceptacles	multiporate conceptacles	calcified compartments
Division of tetrasporangia	zonate	zonate	cruciate
Males, females, carposporophytes	uniporate conceptacles	uniporate conceptacles	uniporate conceptacles
Apical plugs	absent	present	present
Cell connections	secondary pit connections or cell fusions	cell fusions (not in *Choreonema*)	secondary pit connections and cell fusions

Research on coralline algal systematics over the past decade, both in New Zealand and internationally, has clearly established that sequence data and phylogenetic analyses are essential for the characterisation of genera and species (Gabrielson et al. 2011; Martone et al. 2012; Hind et al. 2014a, 2014b, 2015, 2016; Sissini et al. 2014; Adey et al. 2015; Hernandez-Kantun et al. 2015, 2016; Nelson et al. 2015; van der Merwe et al. 2015; Caragnano et al. 2018). Morpho-anatomical characterisations have been shown to be misleading and have 'resulted in frequent species misidentifications and, worse, polyphyletic genera' (Richards et al. 2017). Richards et al. (2018a) concluded that, only when a baseline picture of all the species and their morpho-anatomical variations are known for a given area, can identifications based on morphology alone be used. Until then, phylogenetic based approaches are recommended when identifying species for future biodiversity, physiological, or ecological studies to avoid misidentification which could lead to highly variable results and incorrect conclusions depending on the nature of the study. There is clear evidence of the problems in coralline taxonomy with multiple entries in GenBank under single species names for both geniculate and non-geniculate taxa such as *Spongites yendoi* and *Sporolithon durum*. Progress on sequencing type specimens (particularly generitype material, i.e., the holotype of the type species of the genus, is leading to greater clarity about coralline genera and their delimitation (Adey et al. 2015; Peña et al. 2018; Richards et al. 2017, 2018a, 2018b; Gabrielson et al. 2018).

2.2 Taxonomy of New Zealand coralline algae

Until recently the coralline algae had received the least attention of all macroalgal groups in New Zealand (Nelson et al. 2002; Nelson et al. 2015). There have been over 80 species and infraspecific taxa of coralline algae reported from New Zealand, with the first described by Lamouroux (1821) from collections made in Dusky Sound, Fiordland. In 2004 Woelkerling & Nelson summarised the state of knowledge for New Zealand coralline algae, indicating the dearth of accurate taxonomic information and the confused nomenclature (including the use of incorrect superfluous names). Thirty species described based on New Zealand type material are listed in Tables 2 and 3 (geniculate taxa and non-geniculate taxa, respectively). The identity of many of these remains unknown.

Table 2: Current status and disposition of taxa of geniculate coralline algae based on New Zealand region types.

Epithet	Basionym	Disposition of taxon
armata	*Corallina armata* Hook.f. & Harv.	Status as a distinct species uncertain
crassa	*Jania crassa* J.V.Lamour.	Status as a distinct species uncertain
elegans	*Cheilosporum elegans* Aresch.	Status as a distinct species uncertain; sometimes considered a synonym of *C. sagittatum*
hombronii	*Jania hombronii* Mont.	Generic placement uncertain; status as a distinct species uncertain
longiarticulata	*Jania novae-zealandiae* var. *longiarticulata* Harv.	Generic placement uncertain; status as a distinct taxon uncertain
novae-zelandiae	*Jania novae-zelandiae* Harv.	Generic placement uncertain; status as a distinct species uncertain
pistillaris	*Jania pistillaris* Mont.	Generic placement uncertain; status as a distinct species uncertain
sphaeroramosa	*Jania sphaeroramosa* Twist, J.E.Sutherl. & W.A.Nelson	Generic placement confirmed by sequence data

Table 3: Current status and disposition of taxa of non-geniculate coralline algae based on New Zealand region types.

Epithet	Basionym	Disposition of taxon
asperulum	*Lithothamnion asperulum* f. *asperulum* (Foslie) Foslie	Generic placement uncertain; status as a distinct species uncertain
aucklandicum	*Lithothamnion fumigatum* f. *aucklandicum L. aucklandicum* (Foslie) Foslie	Possibly heterotypic synonym of *Mesophyllum engelhartii*
carpophylli	*Melobesia carpophylli* Heydrich	Generic placement uncertain; status as a distinct species uncertain
caulerpae	*Melobesia caulerpae* Foslie	Possible heterotypic synonym of *Pneophyllum coronatum*
chathamense	*Lithothamnion chathamense* Foslie	Taxon of indeterminate status both at genus and species levels
cladophorae	*Schmitziella cladophorae* V.J.Chapm.	Possible heterotypic synonym of *Melobesia membranacea*
cystocarpideum	*Lithothamnion cystocarpideum* Foslie	Generic placement uncertain; status as a distinct species uncertain
detrusum	*Lithophyllum detrusum* Foslie	Generic placement uncertain; status as a distinct species uncertain
explanatum	*Lithophyllum explanatum* Foslie	Generic placement uncertain; status as a distinct species uncertain
geppii	*Lithothamnion geppii;* as *geppiorum* Me Lemoine	Generic placement uncertain; status as a distinct species uncertain
haptericolum	*Lithothamnion haptericolum;* as *haptericola Foslie* in Algae Base	Generic placement uncertain; status as a distinct species uncertain
incisa	*Lithothamnion patena* f. *incisa* (basionym); *L. incisa* (Foslie) Foslie	Generic placement uncertain; status as a distinct species uncertain
insigne	*Lithothamnion insigne* Foslie	Generic placement uncertain; status as a distinct species uncertain
jugatum	*Lithophyllum jugatum* Foslie	Generic placement uncertain; status as a distinct species uncertain
leptura	*Melobesia leptura* Foslie	Possible heterotypic synonym of *Pneophyllum fragile*
monostromaticum	*Lithothamnion monostromaticum* Foslie	Generic placement uncertain; status as a distinct species uncertain
novaezelandiae	*Corallinapetra novaezelandiae* T.J.Farr, W.A.Nelson & J.E.Sutherl.	Generic placement confirmed by sequence data
novae-zeelandiae	*Lithothamnion novae-zeelandiae* Heydrich	Generic placement uncertain; status as a distinct species uncertain
novae-zeelandiae	*Melobesia novae-zeelandiae* Heydrich	Generic placement uncertain; status as a distinct species uncertain
patena	*Melobesia patena* Hook.f. & Harv.	Considered to be a distinct species/generitype of *Synarthrophyton*
rhizomae	*Lithophyllum rhizomae* Heydrich	Generic placement uncertain; status as a distinct species uncertain
schielianum	*Synarthrophyton schielianum* Woelk. & M.S.Foster	Generic placement uncertain
tuberculatum	*Lithophyllum tuberculatum* Foslie	Generic placement uncertain; status as a distinct species uncertain

Following the 2004 summary, two studies were conducted on coralline algae in the central (Harvey et al. 2005) and northern (Farr et al. 2009) parts of the New Zealand region. Work in central New Zealand focused solely on non-geniculate coralline algae and relied heavily on morpho-anatomical features to distinguish species, with international expert advice provided by Drs William Woelkerling and Adele Harvey (Harvey et al. 2005). As work progressed and extended to the northern region, the value of phylogenetic techniques became clearer, given the difficulty in distinguishing species using morpho-anatomical features and the greater availability and cheaper cost of DNA sequencing (Farr et al. 2009). Genetic protocols were developed (e.g., Broom et al. 2008) and refined for the extraction and amplification of material from coralline algae specimens. The work on coralline algae in northern New Zealand combined these refined phylogenetic techniques with morpho-anatomical data and incorporated both geniculate and non-geniculate coralline algae specimens (Farr et al. 2009).

As a consequence of research over the past decade, it is now clear that many names applied to coralline algae in these earlier New Zealand studies were incorrect. These errors are, in part, a result of insufficiently informative morpho-anatomical characters, leading to the misapplication of generic and specific concepts when identifying specimens. They are also a result of poorly understood generic and specific boundaries. For example, previously, *Spongites* and *Pneophyllum* have been distinguished from each other by the mode of their tetra/bisporangial conceptacle roof development and, in Australia and New Zealand, the substratum type was used to assign specimens to either *Pneophyllum* (epiphytic) or *Spongites* (epilithic, epizoic, or unattached) in New Zealand and South Australia (Woelkerling 1996; Farr et al. 2009). According to Caragnano et al. (2018), this assignment by habitat has led to misidentifications and to the polyphyletic outcomes seen in DNA sequence analyses. The lack of comparative molecular data globally at the time of these prior studies further compounded this issue, making placements of specimens in a global context difficult. However, over the past few years, the increased global taxonomic research on coralline algae has provided critical data to enable the establishment of robust phylogenies and clarification of taxonomic concepts for genera and species (e.g., Hernandez-Kantun et al. 2016; Caragnano et al. 2018).

2.3 Diversity in southern New Zealand

Prior to the project on southern New Zealand, there were major gaps in collections particularly around the South Island and Subantarctic islands (Antipodes, Bounties, Snares, Auckland, and Campbell islands). Based on overall macroalgal diversity patterns for the country, it was anticipated that there would be lower diversity of corallines in southern New Zealand than in northern regions. The intention was to document diversity using molecular sequence data as a route to distinguish taxa, and also to focus on some ecological aspects of coralline distribution.

A total of 796 samples of coralline algae were collected from the 110 collection sites around southern New Zealand (Figure 6), many of which were remote and difficult to access. Collections of corallines were made from a variety of habitats within South Westland, Fiordland, Southland, Otago, Stewart Island and the Subantarctic Islands, and intensive sampling was undertaken at two sites in Moeraki and Karitāne. At the site in Moeraki, which is under mātaitai reserve management, there are large boulders interspersed in sand which allowed repeatable sampling. [A mātaitai reserve is a customary managed fishery of significant importance to local iwi, where commercial fishing is prohibited and in which bylaws concerning recreational fishing activities can be set (Fisheries Act 1996).] The Karitāne site, a typical example of shallow rocky reefs of southern New Zealand, is in Butterfly Bay on the Huriawa Peninsula (Shears & Babcock 2007; Hepburn et al. 2011). The reef at Butterfly Bay extends from the intertidal down to a depth of ca. 12 m before reaching a sandy bottom, like many rocky reefs in this part of New Zealand. This area is currently under taiāpure management (East Otago Taiāpure) and has been a focus of much scientific research, particularly around algal, benthic invertebrate, and ocean acidification monitoring (e.g., Hepburn et al. 2011; Desmond et al. 2015). [A taiāpure allows for commercial fishing and therefore bylaws can be set on both commercial and recreational fishing activities in the area (Fisheries Act 1996).]

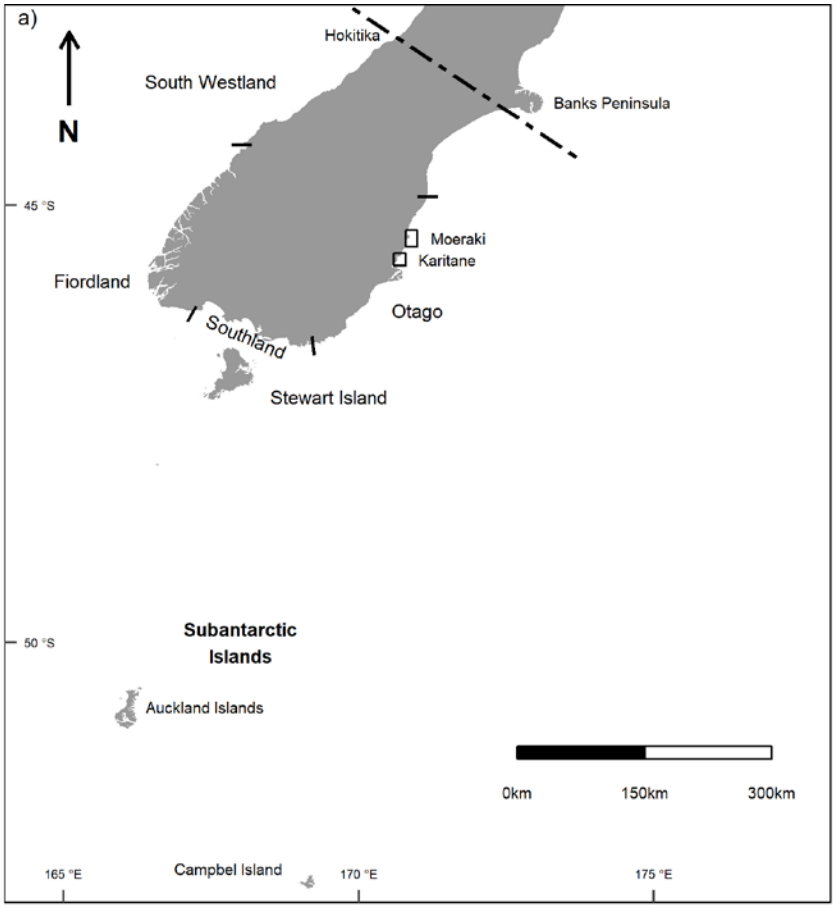

Figure 6: Southern New Zealand study region with each of the sampling areas labelled. Sites where extensive sampling was undertaken at Moeraki and Karitāne are indicated.

Molecular approaches were employed for species identification; phylogenetic analyses based on DNA sequence data from the *psb*A gene were employed for species delimitation, supplemented by *rbc*L sequence data to clarify relationships between taxa. For the southern region, 450 sequences were used in the phylogenetic analyses, and the resulting *psb*A datasets, excluding outgroups, were all 862 bp in length with 175 sequences for the analysis of southern Corallinales and 275 sequences for southern Hapalidiales. Recently developed species delimitation methods were implemented. These approaches have been developed for inferring species boundaries and are based on assessing discrepancies between intraspecific and interspecific sequence variation (e.g., Pons et al. 2006; Puillandre et al. 2012; Fujisawa & Barraclough 2013; Zhang et al. 2013). These methods have been successfully used in a wide range of studies to separate species, with results often being congruent with other lines of evidence such as morpho-anatomical features and biogeography (Melbourne et al. 2017; Buchanan & Zuccarello 2018; Hoshino et al. 2018; Torrano-Silva et al. 2018). Typically, multiple (usually three) species delimitation approaches are used to assign final phylogenetically derived species boundaries (Blair & Bryson 2017; Hoshino et al. 2018). Three single-locus species delimitation methods were implemented: (1) a distance-based method, Automatic Barcode Gap Discovery (ABGD; Puillandre et al. 2012); (2) an ultrametric tree-based method, Generalised Mixed Yule Coalescent (GMYC; Pons et al. 2006; Fujisawa & Barraclough 2013); and (3) a tree-based method, Poisson Tree Processes (PTP; Zhang et al. 2013). These were compared with the approach implemented by Nelson et al. (2015). Each method employs a slightly different approach to independently provide assessment of potential species groupings.

A high level of diversity was revealed in southern New Zealand with 77 species identified based on molecular sequence data. Most of the diversity identified in the southern region was in the orders Hapalidiales and Corallinales, with only one member of the order Sporolithales being identified in southern New Zealand (**Error! Reference source not found.** 4). Although the diversity was high when

considered at a regional level, it was also high at smaller scales; 17 species were found at small spatial scales at two sites in the southern region where intensive sampling was undertaken, at both Moeraki (50 m^2 area) and the Karitāne site (0.02 km^2 area).

The phylogenetic analyses revealed that the majority of taxa distinguished with sequence data from the southern region do not have currently accepted species names, and many do not belong to currently recognised genera. In the absence of available formal names, a naming system was developed by Twist (2019) for each of the species clades determined by the delimitation methods. The name is constructed of the order name, a genus number, and a species number for all entities without appropriate taxonomic names (e.g., Corallinales Genus 1 species 2, for the second species in the first genus belonging to the order Corallinales). A representative specimen, based on sequence quality, was then selected for each phylogenetically derived species, and the above naming system applied to this specimen on all phylogenetic trees in all subsequent phylogenetic analyses in which that taxon was included. Branch support values were used in determining the boundaries of genera when applying this naming system. These are preliminary genus assignments, and further lines of evidence (e.g., information on shared morpho-anatomical features and placement in a wider global context) are needed to fully support the delimitations of genera. For data lodged in GenBank and specimens registered in the NIWA Specify database, the naming system was modified to conform to the Department of Conservation naming system (Townsend et al. 2008). Both these naming systems and how they relate are listed in Appendix 2.

2.4 Diversity in the New Zealand region

The discovery of high diversity in southern New Zealand, coupled with the major international developments in coralline taxonomy, provided an opportunity to re-evaluate the diversity of coralline algae for the New Zealand region as a whole. The sequence data for southern corallines were combined with 486 sequences from northern and central New Zealand regions in the orders Hapalidiales and Corallinales. The resulting *psb*A datasets, excluding outgroups, were all 862 bp in length and included 441 sequences for Corallinales NZ and 493 sequences for Hapalidiales NZ.

The diversity of coralline algal species was found to be highest in the southern region. There were substantially more species belonging to the order Hapalidiales in the southern region than in the northern and central New Zealand regions, either individually or combined (47 compared with 16 and 21, respectively). In contrast, the same number of Corallinales species were found in northern and southern New Zealand (29), whereas fewer were recorded in central New Zealand (18 species). This difference was unlikely to be due to a greater number of habitats sampled in the southern region, because a range of intertidal and subtidal habitats on varying substrate types with different degrees of exposure were sampled across all regions. However, there were fewer DNA sequences available from central (130) and northern (384) New Zealand locations than those obtained in this study from the southern region (536), which potentially confounds this comparison. In addition, the central coralline study focused solely on non-geniculate taxa.

For robust comparisons of diversity, non-parametric incidence-based asymptotic estimators were used to estimate the total number of species expected, based on the frequencies of rare species in the original sampling (Chao et al. 2009). These approaches have been widely used in a number of studies to estimate species richness (e.g., Colwell & Coddington, 1994; Woodcock et al. 2013; Ashton et al. 2015; Thormann et al. 2016). In the calculation of these estimators, site is typically used as the sampling unit. However, this was impractical in this study due to differences in sampling intensity and area among sites, and therefore sequences were used as the sampling unit in these analyses. The expected total number of species was estimated using the Chao2 estimator (Chao 1987), and the first and second order Jackknife (Jack1 & Jack2) using the '*specpool'* function in the R package 'vegan' (R Core Team 2017). A species accumulation curve (SAC) was constructed using the Chao2 estimator to visualise the relationship between total number of sequences sampled and the increase in number of species discovered, using consensus results from the species delimitation methods that were employed. The curve and 95% confidence interval were calculated using a permutational approach (Oksanen et al. 2017). Table 5 presents the predicted diversity number of coralline algal species estimated for areas of

different spatial scales within the New Zealand region, under the assumption that sampling continued in similar habitats to those previously sampled (using the Chao2 incidence-based species estimator).

Table 4: Number of coralline algal species from three study regions around the New Zealand coast identified by phylogenetic analyses from the orders Corallinales, Hapalidiales, and Sporolithales, and the number of species estimated using Chao2 incidence-based species estimators rounded down to the nearest integer (in brackets). *n* = the number of sequences used in analyses.

	South (*n*= 535)	Central (*n*= 130)	Northern (*n*= 384)	NZ wide (*n*= 1049)
Corallinales	29 (44)	18 (30)	29 (31)	57 (62)
Hapalidiales	47 (54)	21 (27)	16 (18)	61 (75)
Sporolithales	1 *	3 (3)	4 (4)	4 (4)
Total	77 (99)	42 (60)	49 (53)	122 (141)

* No incidence-based species estimator was calculated because only one individual was found.

For the New Zealand flora, in the Corallinales, there are members of 6 genera that are currently recognised — *Amphiroa* (1 species), *Arthrocardia* (3 species), *Corallina* (1 species), *Jania* (8 species), *Mastophora* (1 species), *Pneophyllum* (11 species), and an additional 16 genera without current names. In the Hapalidiales, the majority of genera (30) do not have current names. There is a single species in *Lithothamnion*, *L. crispatum*, and a single species of *Synarthrophyton*, *S. patena* (the generitype), as well as the parasite *Choreonema thuretii*. The latter species is not included in the phylogenetic analyses of species because no *psb*A or *rbc*L sequence data are available. Within the Sporolithales, there are species of *Sporolithon* (2 species) and *Heydrichia* (1 species) in New Zealand, and there is also an undescribed genus. The ordinal placement of the genus *Corallinapetra* was initially unclear, but work describing a new order and family for this genus is underway (Jeong et al. 2019). (Refer Appendix 2 for summary of currently recognised coralline algae genera found in New Zealand.)

Table 5: Number of coralline algal species estimated for areas of different spatial scale within the New Zealand region, under the assumption that sampling continued in similar habitats to those previously sampled using the Chao2 incidence-based species estimator.

Area	Chao2 estimator	Approximate Area (km^2)
New Zealand	141	4 083 744
Southern region	99	1 546 666
Central region	60	1 181 536
Northern region	53	1 309 602
Karitāne site	33	0.02
Moeraki site	25	0.00005

The consequences of these analyses are significant. There is currently no genetic evidence of species in the genera *Harveylithon*, *Heteroderma*, *Hydrolithon*, *Lithoporella*, *Lithophyllum*, *Melobesia*, *Mesophyllum*, *Phymatolithon*, *Porolithon*, and *Spongites* in New Zealand. There are also significant issues relating the results of these analyses to earlier species identifications, for example, the name *Mesophyllum erubescens* (Foslie) M.Lemoine has been assigned previously to multiple specimens collected in New Zealand, but it is now revealed to have been applied incorrectly to multiple, phylogenetically unrelated taxa that have convergent morphologies. There are names that have been used in the New Zealand flora where the identification has been based solely on morphological and/or anatomical features, and at present there is no way to verify the presence of these taxa. All such identifications need to be reviewed in the light of these findings. The situation for members of the Hapalidiales in New Zealand is the most problematic, with a large number of genetically distinct, but undescribed, genera.

3. ECOLOGY OF CORALLINE ALGAE IN NEW ZEALAND

3.1 Distribution of coralline algae in New Zealand

The taxonomic discoveries outlined in section 2 have meant that our understanding of the species of coralline algae present in New Zealand and their distributions has had to be re-evaluated. Despite the ecological importance of coralline algae, few studies have examined the factors influencing community composition across large spatial scales, particularly in a modern context using DNA based species identification. An important first step in the ability to predict distributions of coralline algae to understand how changing environmental conditions may affect them, is to determine the environmental conditions in which coralline algal communities are found (Keddy 1992; McCoy & Kamenos 2015). Understanding the abiotic factors associated with the community composition can help predict where specific assemblages may occur, and how they may change with changing conditions.

New Zealand regional distribution

(summarised from Twist 2019)

Species data from phylogenetic analyses (outlined in section 2) were the basis for community analysesof distributional information from the three New Zealand regional studies. Hierarchical clustering techniques were used to group collection sites that had similar combinations of species of corallines (i.e., communities of coralline algae), and indicator analysis was used to determine species significantly associated with each cluster. Hierarchical clustering has a wide range of transformations available for different data types and has been commonly implemented in ecological studies (Boesch 1977; McKenna 2003). To minimise the effect of rare species on the analyses, all species that had fewer than three occurrences were removed from the data matrix (Marchant 2002; Oldeland et al. 2010). Sites with fewer than three species present were removed from the analyses, because they were unlikely to group efficiently and could distort the formation of significant clusters (De Cáceres et al. 2010). In addition, sites from the Subantarctic islands, Chatham Islands, and Kermadec Islands were removed from the analyses due to a lack of environmental data available at these sites. The remaining dataset consisted of 84 sites containing 57 distinct species of coralline algae from around the New Zealand coast. The hierarchical cluster analysis identified seven distinct groups or communities of coralline algae (
Figure).

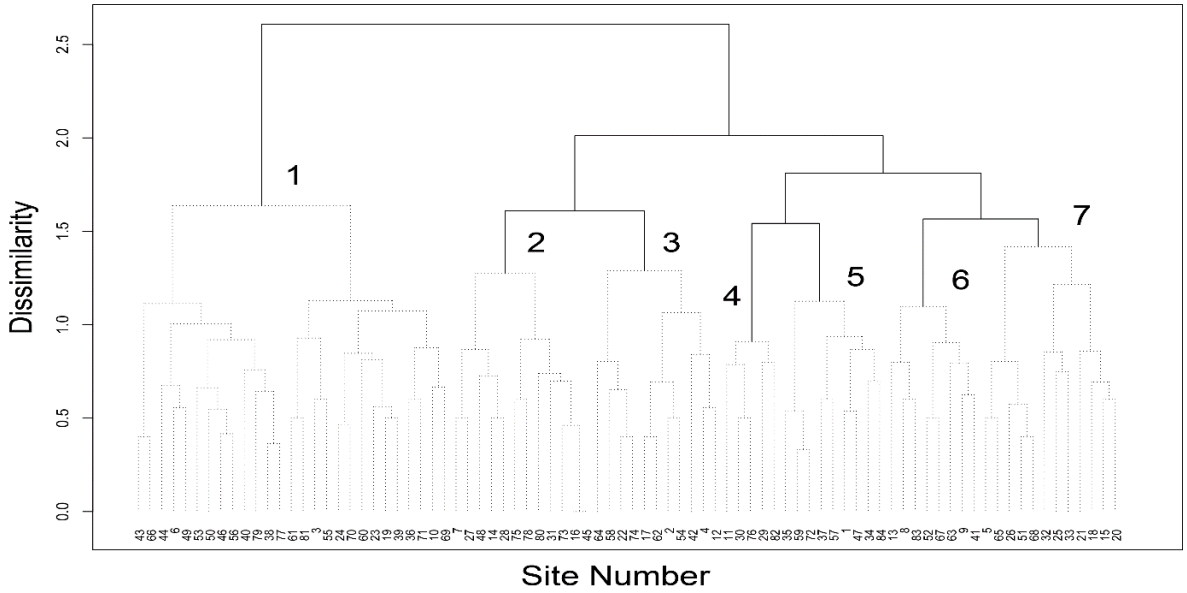

Figure 7: Hierarchical cluster analysis dendrogram of coralline algae sites from around the New Zealand coast. Cluster analysis was performed with Ward's clustering algorithm on Jaccard transformed species matrix. Group significance was assessed using SIMPROF routine (999 simulations), and significant (p<0.05) cluster groups indicated by numbering and dotted lines.

These derived cluster groups were located in different regions around the New Zealand coast (Figure 8) and different coralline taxa were significantly associated with each cluster (for results of indicator analysis refer to Twist 2019). Some groups appear to be geographically restricted, with sites mainly occurring in the southern region (e.g., Groups 2, 6, and 7). Group 2 was best characterised by both geniculate and non-geniculate members of the order Corallinales as revealed by indicator analysis on the derived groups. Members of the order Hapalidiales were particularly represented in Groups 6 and 7. Group 3 was also restricted to the South Island and Stewart Island and was best explained by non-geniculate corallines of the orders Corallinales and Hapalidiales. Group 1 contained the greatest number of sites and the majority of these were located in the northern half of the North Island. This group was best characterised by a range of non-geniculate species from the orders Corallinales and Hapalidiales. Group 5, also found at sites located in the northern half of the North Island, was the second smallest group and was best characterised by members from only the Corallinales, particularly by several geniculate species. Group 4, which included sites located in central and northern New Zealand, was characterised by the rhodolith forming species, *Sporolithon durum*.

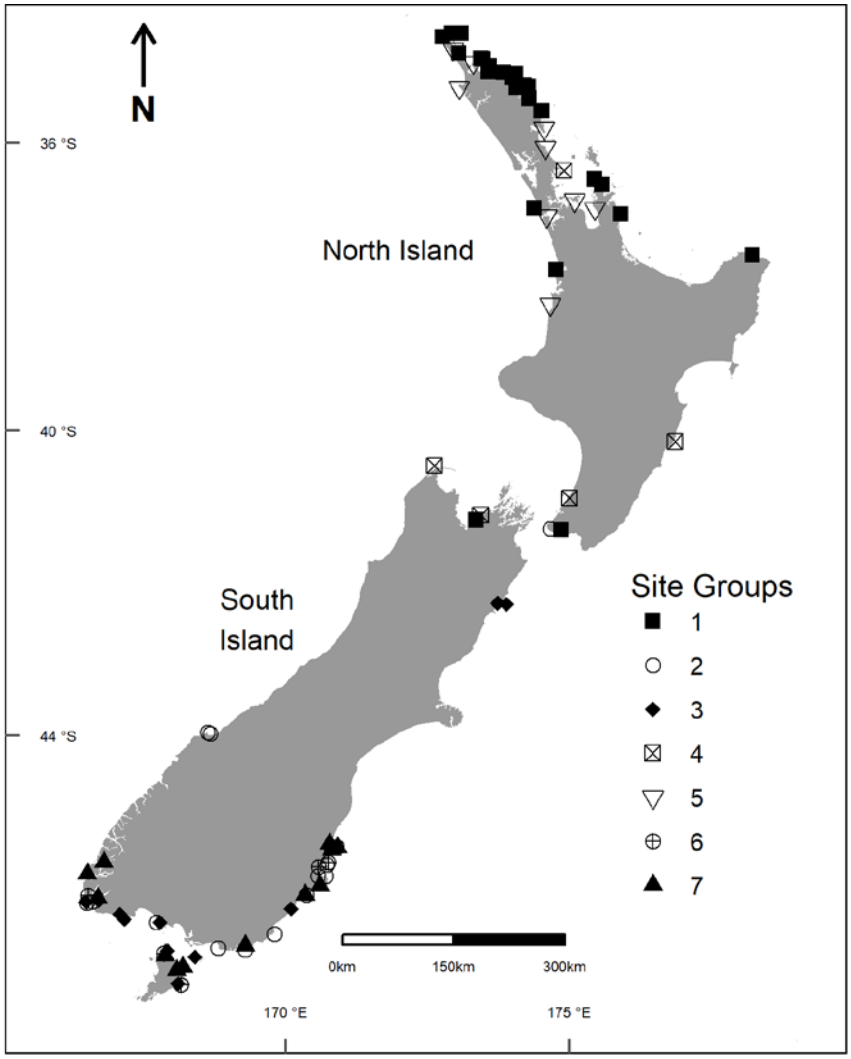

Figure 8: Coralline algae site clusters determined from hierarchical clustering techniques around the New Zealand coast.

Constrained ordination techniques were employed to relate multivariate clusters, as defined above, to selected environmental parameters (Figure 9). The environmental variables for each coralline collection site were recorded or calculated from GPS coordinates. These included, after the removal of highly correlated variables, mean wave height (offshore wave model), wind-derived fetch (calculated from wind direction data and GPS data), sea surface temperature (satellite measurements), turbidity (satellite measurements), and light at the seabed (calculated from PAR [photosynthetically active radiation] and depth measurements).

Of the environmental parameters selected, sea surface temperature (SST, 8.4% variance explained) and light at the seabed (2.9% variance explained) were the variables found to be significantly correlated (dbRDA, permutational test, pseudo-F = 4.56, $p < 0.001$) with these community groupings across the New Zealand region. Differences in tolerances of individual species to SST could result in the differences in coralline algal community composition around the New Zealand coast observed in this study. For example, the community composition of Group 1, largely restricted to northern New Zealand, was explained by higher SST and best explained by two particular species, indicating these species may have a preference for warm water temperatures. In contrast, community Group 3, located in southern New Zealand, is characterised by low SST and best explained by a single species which may indicate its sensitivity to warm water. However, little, if any, physiological information exists on individual coralline algae species in New Zealand, and further investigations are needed to fully understand tolerances of individual coralline species to SST.

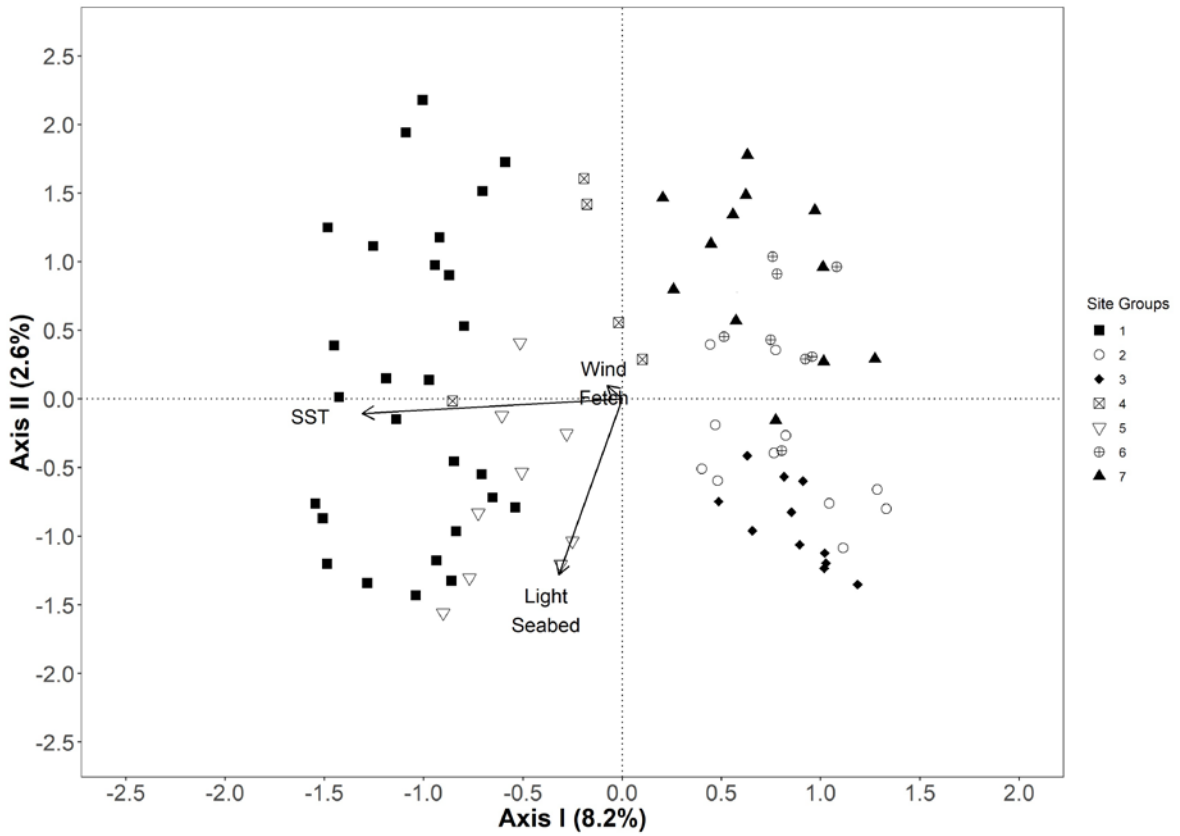

Figure 9: Distance-based redundancy analysis (RDA) plot showing the relationship between significant environmental explanatory variables and coralline algal community composition. Axis I (8.2% variance explained) and Axis II (2.6% variance explained). Arrows indicate the strength of the association by the length of the line and direction of the gradient with the arrow head indicating an increase. Site groups were identified using hierarchical cluster analysis

The second most important variable identified for explaining community composition was light at the seabed, although it accounted for only a small amount of variation (2.9%). Sites included in the analyses of this study rarely exceeded a depth of 12 m (with one site being located at 17 m), and this narrow depth range could explain why a stronger relationship between light at the seabed and coralline algal community composition was not seen. Despite this limited depth distribution, light at the seabed did explain some of the variation and can still be considered to have a role in structuring coralline algal communities. Community Group 7 was explained by low light at the seabed. Sites within this group were located in southern New Zealand and were also primarily subtidal. In contrast, community Group 3 was best explained by high light conditions, and sites in this group were primarily intertidal. Little information exists on the physiology of individual coralline species in New Zealand and further investigation would be needed to determine whether the species characteristics of these community groups show differences in light tolerance. Other factors, such as desiccation stress in the intertidal zone, known to increase mortality of coralline algae (Padilla 1984; Martone et al. 2010), could account for some of the variance in community composition explained by the light at the seabed variable.

Although a wide range of different exposure sites were examined (0.9 to 3.1 m mean wave height and 0.001 to 0.425 wind fetch values), wave conditions and exposure indices did not appear to be influential in driving coralline algal community composition. Wind fetch (an indication of local wind-derived sea conditions) was a significant variable in the analysis, but it explained very little variation (0.6%) in the community composition of coralline algae and cannot be considered as having a large influence in

structuring the coralline algal community. The resilience of coralline algae to mechanical stress may enable species to tolerate a wide range of wave exposures, and this may explain why no strong associations with wave and exposure indices were observed in this study. The encrusting growth form of many coralline algae and their strong calcium carbonate structure makes them extremely tolerant of mechanical stress caused by wave action (Adey & Macintyre 1973). Upright geniculate coralline algae have also been shown to be well adapted to resist damage from wave exposure due to strong calcified segments separated by flexible joints which bend to reduce drag (Martone 2007; Martone & Denny 2008).

Only a small proportion (11.9%) of the variance in coralline algal community composition was explained by the measured environmental variables, indicating that other unmeasured factors (environmental, biotic, or habitat variables) could be influential. Information on habitat, whether the site was primarily sand, cobble, or rocky reef, was missing for several sites in this study and was therefore not included in the analyses. Habitat type — the position of the reef, reef flat vs reef slope — is important in structuring the community of coralline algae in tropical coral reefs (Dean et al. 2015).

Several aspects of the data availability and quality are likely to have affected the outcomes of the analyses; in particular, the large species diversity detected, the different collection effort between sites (including the narrower focus in the central region), and the differences in the size of the area in which collections were made. These factors resulted in the majority of sites having a low proportion of the total species found. Furthermore, this study used presence-absence data rather than abundance data. The use of abundance data to complement presence-absence analyses has been recommended because certain environmental conditions may be needed for a species to occur in an area, whereas others might affect how abundant a species is (Blanchet et al. 2014).

Despite the issues with data availability or quality, this study has identified that distinct community groups of coralline algae are distributed along the New Zealand coastline, and that at least three environmental variables have an influence on their occurrence, although wind-derived fetch explained very small amounts of variation. This information can be used by future research efforts; for example, habitat suitability modelling to predict the distribution of coralline algal communities in unsampled space, as well as in the future under changing environmental conditions (e.g., Degraer et al. 2008; Monk et al. 2010; Rengstorf et al. 2013).

Community structure at local spatial scales

(summarised from Twist 2019)

Patterns in the community structure of coralline algae were examined at local spatial scales to determine whether these patterns could give an indication of processes that structure these communities. The abundances of individual species of coralline algae were examined on a series of boulders under similar abiotic conditions with, and without, the presence of a large grazing invertebrate (pāua; *Haliotis iris* Martyn, 1784). Surrounded by sand, habitat that is unsuitable for coralline algae, these boulders were considered ‘marine islands’. It was hypothesised that biotic interactions between species of coralline algae, primarily competitive interactions, would be the major driving force controlling coralline community structure on these ‘marine islands’ at this local spatial scale, given that biotic interactions are thought to be more relevant at small scales (Bycroft et al. 1993; McGill 2010). In addition, it was hypothesised that grazer-mediated biotic interactions would influence the community structure and distribution of abundances of coralline algae on boulders with and without pāua (i.e., biotic interactions would occur between coralline algae species and pāua). This is based on the assumption that the differences would be a consequence of grazing by pāua because grazing can favour those species more resistant to grazing and change competitive interactions among species (Steneck et al. 1991; McCoy & Pfister 2014).

Quantitative information on the distribution of coralline species was obtained using the line intersect transect method; a method developed for vegetative studies by Canfield (1941) and first used in the marine environment for studies on coral by Loya and Slobodkin (1971). It has recently been successfully employed for collecting quantitative information on coralline algae in tropical coral reefs by Dean et al. (2015). The line transect method results in more precise estimates of percentage cover than that of quadrat sampling, where estimates of cover are often subjective and can vary greatly between individual recorders (Hanley 1978). Additionally, the use of quadrats to estimate the abundance of individual coralline algal species can be extremely challenging due to difficulties in determining the area of individuals as a consequence of overlapping crust boundaries. Dethier et al. (1993) have shown the line intersect method is preferable to point intercept methods because it is unlikely to under-sample rarer species. Samples of each individual specimen recorded across the length of the transect were removed with a hammer and chisel and later stored in silica gel for genetic identification.

A total of 17 species with varying levels of abundance were identified from 70 samples collected from the six boulders sampled in Moeraki. Many of these species presented similar external morphology. For example, four separate species belonging to different genera in the Corallinales and Hapalidiales all exhibited a range of morphologies, from smooth to lumpy in appearance, and all possessed similar reproductive structures, visible when examined under a microscope at some stages of their life cycle. Species richness was similar across all boulders with six to seven species being identified from each boulder community. The percentage cover of the most abundant coralline algae species from a given boulder community ranged from 57.8% to 22.2%. Two species (one Corallinales, one Hapalidiales) had the highest abundance across the study site when all boulders were combined with 21.5% and 19.2% percentage cover, respectively. A high number of species had a low abundance across the study site, with 9 out of 17 species having less than 3% cover.

Species co-occurrence patterns were found to be no different than would be expected by chance which indicated, on average, that species pairs were not aggregated (positive co-occurrence) nor were segregated (negative co-occurrence). This result suggests that neither biotic interactions among coralline algae species nor abiotic factors are structuring the coralline algal communities. The distribution of abundance of species across the boulder communities indicated three theoretical models (each describing a different relationship between species identity and relative abundance) fit the data, dependent on the boulder community. All these theoretical models suggest that some sort of competitive interactions between coralline algae species may be responsible for structuring abundances, with few abundant species and many rare. No difference in community composition was observed between algal communities of boulders containing high densities of pāua and those of boulders without the grazer. This result suggests that grazing by adult pāua does not influence coralline algal community structure, including via interactions among algal species. However, it must be noted that observations during this research suggest these adult pāua were not actively grazing over the coralline surfaces.

3.2 Functional roles

Habitat provision

On many rocky shores, turf-forming geniculate coralline algae are a major component of algal assemblages (e.g., Stewart 1982; Akioka et al. 1999; Kelaher 2002). Extremely diverse and productive macrofaunal assemblages have been recorded within the habitat provided by the densely packed fronds of coralline turf (e.g., Hicks 1971; Taylor 1998; Akioka et al. 1999; Cowles et al. 2009). Kelaher (2002) found that the physical structure of the coralline turf was extremely important to the biodiversity of the associated macrofaunal assemblage, noting that these habitats may provide a refuge from desiccation, predation, and wave action. Coralline turf provided the best refuge for mobile invertebrates from fish predation in a variety of intertidal tidepool habitats tested by Coull & Wells (1983).

The small mobile invertebrates (under 10 mm in length) typical of these coralline turf assemblages play a number of important ecological roles, including serving as a pathway for energy and materials to flow from primary producers to predators such as small fishes (Taylor 1998). In northeastern New Zealand, coralline turf assemblages have been shown to support high densities of juvenile carangid, mullid, and sparid fishes (Choat & Kingett 1982). Cowles et al. (2009) investigated the density, biomass, and productivity of small (0.5–8.0 mm) mobile invertebrates within a wide variety of coastal habitats in temperate northeastern New Zealand. They found that the structurally complex and food-rich coralline turf, and also stranded seaweed wrack, supported the highest densities, estimated biomasses, and estimated productivities of small mobile invertebrates.

The effects of coralline host species identity and spatial variability on animals inhabiting subtidal coralline turfs was examined by Berthelsen et al. (2014). They compared the assemblages of small (1–8 mm) mobile invertebrates associated with five coralline turf species across a number of subtidal rocky reefs in northeastern New Zealand. The faunal assemblages in the coralline turfs were dominated by arthropods, gastropods, and polychaetes, and the fauna were both abundant (average of 16 000 to 80 000 ind.m^{-2}) and diverse (129 taxa in total). They found host identity had little effect on total abundance and richness of the fauna and a moderate effect on taxonomic composition. Of the environmental factors measured, wave exposure and depth had the greatest explanatory power on assemblage-level properties.

Brown & Taylor (1999) investigated the impacts on macrofauna from different intensities of human trampling of geniculate coralline turfs within the Cape Rodney to Okakari Point Marine Reserve, north-eastern New Zealand. They looked at impacts at the time of trampling disturbance and after 3 months. They found there was a strong negative effect of trampling on total animal densities 2 days after the experimental trampling had ceased, with densities at the highest trampling intensity declining to 50% of control values. There was no apparent effect of trampling on total animal densities after 3 months. They found polychaetes were particularly susceptible to low levels of trampling.

Larval settlement

Particular chemical cues from non-geniculate coralline algae have been shown to induce larval settlement in diverse taxa that have chemosensory systems including sea urchins, abalones, limpets, scleractinian corals, and octocorals, and, for some, this settlement induction has been found to be species-specific (e.g., Daume et al. 1999b; Roberts 2001; Roberts et al. 2004; Harrington et al. 2004; O'Leary et al. 2012). There has been some debate about the role of biofilms in the settlement cues. Experimental testing has shown that the biofilm is not always the source of the settlement induction, for example, the Roberts et al. (2010) examination of the settlement of the pāua, *Haliotis iris*, on the non-geniculate coralline *Phymatolithon repandum*; and the Tebben et al. (2015) examination of the induction of coral larvae settlement by non-geniculate corallines.

3.3 Ecological case studies

Rhodolith beds in the Bay of Islands

(summarised from results of ZBD200903, Nelson et al. 2012, 2014; Neill et al. 2015)

The ecology of subtidal rhodolith beds was investigated in the Bay of Islands. This study characterised two rhodolith species (*Lithothamnion crispatum* and *Sporolithon durum*), examined the structure and physical characteristics of beds at two locations (Kahuwhera Bay and Te Miko Reef) (Figures 10–12), and documented their associated biodiversity. The rhodolith beds were mapped using a combination of techniques, and the physical characteristics of the habitats were assessed and compared with adjacent areas outside the rhodolith beds. The rhodolith beds differed significantly in terms of water motion, sediment characteristics, and light levels; Te Miko Reef had characteristics regarded as typical of rhodolith assemblages (i.e., in clear water and rhodoliths were clearly visible sitting on top of the substrate in a more-or-less single layer over rhodolith- and shell-derived gravel), and Kahuwhera Bay was atypical

with respect to sediments and water clarity (i.e., fine sediments suspended in the water column and covering rhodoliths and associated biota, and live rhodoliths were in a more-or-less single layer overlaying grey to blackened rhodoliths in a darkly coloured rhodolith/sediment sublayer) (Figure 12).

Figure 10: Map of the Bay of Islands indicating the position of the two study locations, Kahuwhera Bay and Te Miko Reef.

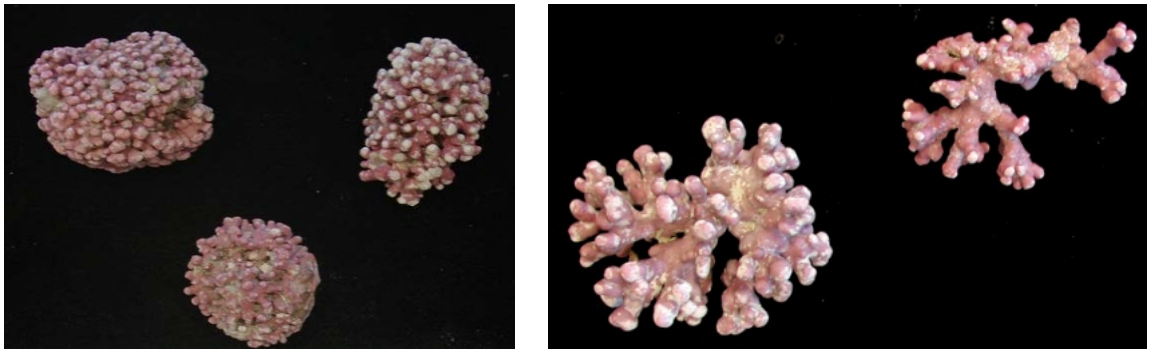

Figure 11: Two rhodolith species. Left: *Lithothamnion crispatum*, maximum size approximately 4 cm. Right: *Sporolithon durum*, maximum size approximately 7 cm.

The biodiversity of the rhodolith beds was investigated by sampling (1) invertebrates at three levels of association (epifauna, infauna, and cryptofauna), (2) macroalgae, (3) fishes, as well as recording the biogenic and non-biogenic substrates. The study discovered a number of undescribed taxa, new records for the New Zealand region, and range extensions of species known elsewhere. More than double the number of invertebrate taxa were present in the rhodolith beds than found outside the beds. Both rhodolith beds harboured high diversity of associated macroalgae and invertebrates, but faunal composition differed significantly between sites, with significant differences in infaunal composition of cores taken inside and outside the rhodolith beds. Significant differences were also found in epifaunal species composition between sites within the rhodolith beds as well as significant seasonal variation. More sponges and echinoderms were found inside the rhodolith bed at Kahuwhera Bay than either of the two sites within the Te Miko Reef location and significantly more molluscs were inside the rhodolith

beds at Te Miko Reef than at the other site. More macroalgae were found inside rhodolith beds than outside beds, and the species composition differed markedly inside and outside the beds.

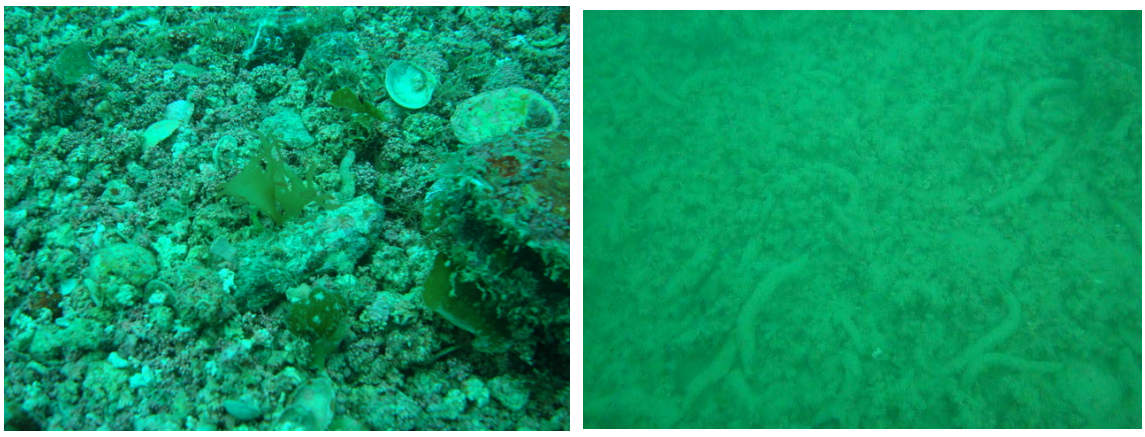

Figure 12: Subtidal rhodolith beds: Te Miko Reef (left), Kahuwhera Bay (right)

The effects of changes in temperature in combination with the effects of lowered pH, predicted to occur as a consequence of climate change, were investigated in both species of rhodolith by examining responses to two pH levels and three temperatures. Both rhodolith species were found to be vulnerable to the impacts of increasing temperature and decreasing pH. There was a significant difference between the effects of treatments on the two species and further statistical analysis showed significant interaction between temperature and pH level on growth. Overall, the greatest effect on growth rate occurred with the combination of high temperature (25° C) and low pH (7.65) on *Lithothamnion crispatum* which showed negative growth, indicating probable dissolution. In experiments investigating other environmental stressors, temperature was found to be more important for the survival and growth of the rhodolith species examined than the effects of burial, light, and fragmentation.

Biogenic reefs in Foveaux Strait

(summarised from Twist 2019)

Despite the important roles coralline algae can play in reef systems, there has been very little attention paid to coralline algae in biogenic reef environments other than rhodolith beds. Foveaux Strait, located in southern New Zealand between the South Island and Stewart Island (46°35'21.6" S, 168°03'46.4" E), is characterised by shallow depths (average of 20–30 m) and strong currents. There are important commercial fisheries in the area for oysters (*Ostrea chilensis*) and blue cod (*Parapercis colias*). The oysters are associated with biogenic reefs, primarily structured by bryozoans, and sponges (Cullen 1962; Cranfield et al. 1999). Internationally, the dredging of biogenic reefs has often been associated with degradation and loss of these important habitats (e.g., Hall-Spencer & Moore 2000; Thrush & Dayton 2002; Chuenpagdee et al. 2003). However, studies by Cranfield et al. (2003, 2004) in Foveaux Strait have shown persistence and recovery from dredging of the biogenic reefs within 3–5 years. The health of the biogenic reefs has been shown to be associated with increased abundances of oysters and blue cod (Cranfield et al. 2001; Cranfield et al. 2003); thus, understanding the composition and distribution of components of the reef systems is important. Research to date has focused on oyster stock assessments (Cranfield 1968; Michael et al. 2013), changes in the distribution of biogenic reefs affected by dredging (Cranfield et al. 1999; Cranfield et al. 2003), and the different macrofaunal assemblages associated with the habitat (Cranfield et al. 2004). To date there has been no evaluation of coralline algae in the reefs.

Based on the ecological roles coralline algae perform in other biogenic systems — such as cementing together materials that are used as habitat by sessile species, maintaining structural integrity and thus preventing species removal by extreme environmental conditions, and providing settlement sites for invertebrate larvae — these algae are potentially critical components for the Foveaux Strait reef systems. However, before these potential roles can be examined, it is necessary to understand the distribution of corallines in the strait and the environmental and habitat factors influencing this distribution. Coralline algae surveys were carried out in conjunction with the oyster industry-funded 2017 Foveaux Strait oyster stock assessment dredge surveys (Figure 13). Dredge landings were subsampled and the percentage cover of coralline algae over the substrate was estimated. From this information the density of coralline algae across the strait was calculated, and the distribution of coralline algae was examined in relation to five environmental and habitat factors. These factors included depth, sediment type (sand, bryozoan hash, shell hash, or cobbles), density of oysters, the eastern or western side of the strait (proxy for current strength), and community type (derived from invertebrate bycatch recorded in dredge survey).

Coralline algae were found growing on a variety of surfaces, from cobbles to different types of shells, as well as on a range of living organisms, including oysters (Figure 14). These calcifying algae were found to be distributed across almost the entire area of Foveaux Strait and ranged in abundance from zero in some western areas, to 38.3% in south western and south eastern areas (Figure 15).

Figure 13. Dredged sample from the Foveaux Strait oyster fishery (left) and a subsample (right).

Figure 14. Oysters with non-geniculate coralline algae.

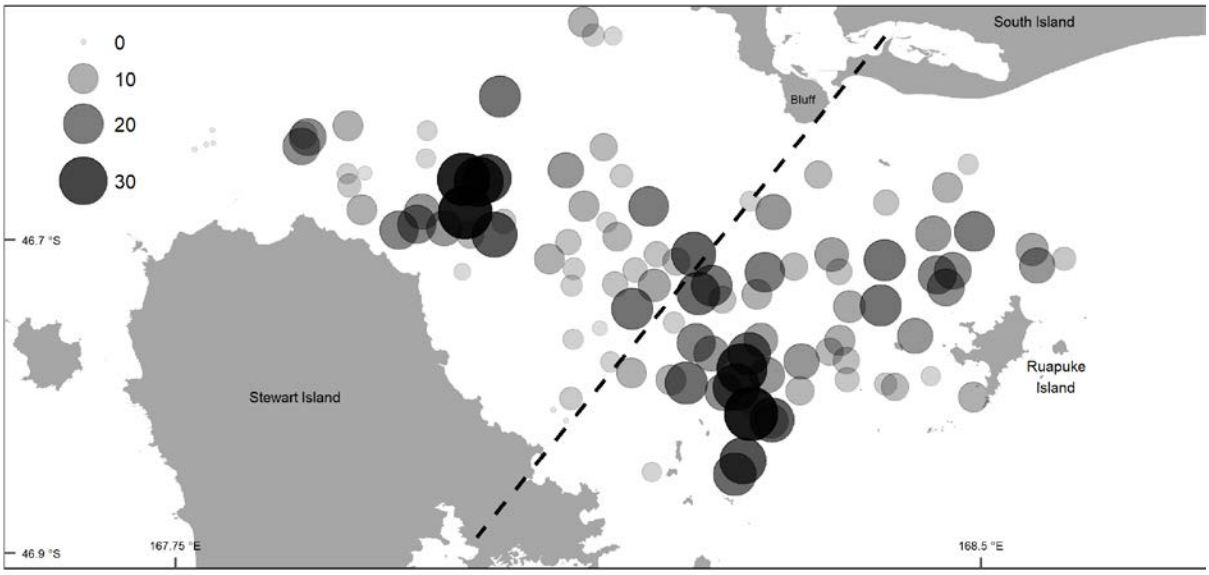

Figure 15: Distribution of coralline algae across the Foveaux Strait biogenic environment in southern New Zealand. The size and shade of the points represent the percentage cover of coralline algae over a 370 m survey tow. The dashed line represents a division of the strait between eastern and western areas.

Depth was the most important environmental variable associated with coralline algal abundance, with corallines likely to be at the highest abundance at around 29 m depth; abundance was lower in shallower and deeper depths, although shallow depths (under 14 m) were not sampled. This depth association is likely a function of the available light affecting growth and survival of these photosynthetic organisms. Sediment type was also important in explaining coralline algal abundance in Foveaux Strait, with a lower abundance likely in areas with bryozoan hash compared with cobble to gravel sediment types. This relationship with substrate type is possibly due to a lower amount of suitable settlement substrata for coralline algal growth in bryozoan hash. Finally, a positive relationship between oyster density and coralline algae populations occurred, but this relationship was relatively weak, and the reasons for the association unclear. This association could be due to preferential larval settlement and growth of oysters on coralline algae, or vice versa, or that associations are simply a result of shared environmental and habitat preferences.

Although this research has established new understanding of the distribution within Foveaux Strait, a finer scale approach is needed to further investigate coralline algae and environmental/habitat relationships. A detailed examination of whether oysters have preferential larval settlement and growth on coralline algae is needed. Studies on oysters have shown settlement on a range of substrata, from gregarious settlement (settlement on or among individuals of their own species) to settlement on biofilm-covered substrate (Bonar et al. 1990; Zimme-Faust & Tamburri 1994; Anderson 1996). However, to date, no studies have been published on the potential role of coralline algae for oyster larvae settlement, despite evidence from other shellfish species (e.g., pāua, Daume et al. 1999b; and scallops, Steller & Cáceres-Martínez 2009) of preferential settlement of larvae on corallines. Further investigations should examine the other reasons for a coralline algae-oyster relationship and the distribution of coralline algae in different biogenic reef communities across Foveaux Strait.

Responses to global change

Law et al. (2017) provided a synthesis of published information about the threat posed by ocean acidification in New Zealand marine ecosystems. International studies have suggested that coralline algae may be amongst the most vulnerable calcifying organisms to reduced pH in a future ocean (e.g., Kuffner et al. 2008; Kroeker et al. 2013). New Zealand research on selected species of coralline algae

suggests that OA will result primarily in a reduction in net calcification rates and growth, possibly due to increased dissolution of calcium carbonate at lower pH (Cornwall et al. 2013b; Cornwall et al. 2014). Despite intensive international research effort, the mechanisms responsible for the decline in coralline algal calcification due to OA have not been identified (McCoy and Kamenos 2015). Laboratory studies of recruitment in New Zealand coralline algae showed little effect of reduced pH (7.65, Cornwall et al. 2013b; Roleda et al. 2015), in contrast with results from field studies along volcanic vent sites in Papua New Guinea where recruitment was reduced to under 20% at pH of under 7.8 (Fabricius et al. 2015). There is evidence that the effects of OA may be habitat-dependent. Corallines exert greater metabolic influence at lower seawater velocities, moderating the impact of OA with increasing pH at their surface (Hurd et al. 2011; Cornwall et al. 2013a; Cornwall et al. 2014; Cornwall et al. 2015).

There may be a buffering effect of pH on calcifying species within dense macroalgal beds (Figure 16): the attenuation of flow in these coastal habitats combined with an increase in pH during the daytime (Cornwall et al. 2015; Cornwall et al. 2013b; Hurd 2015). It is also possible that the pH fluctuations experienced in the field may enhance the negative impacts of reduced pH on growth and calcification of juvenile and adult coralline algae (Cornwall et al. 2013a; Roleda et al. 2015).

Ocean acidification will not be acting in isolation but will rather be interacting with other aspects of global change and anthropogenic drivers. It is likely that both communities and individual species will display differing degrees of perturbation in the face of environmental change and also from the cumulative impacts of stressors.

Figure 16: Non-geniculate corallines forming understorey beneath the canopy formed by large brown algae.

4. DISCUSSION

The research conducted on coralline algae in New Zealand over the past 15 years has revealed very high species and generic diversity within the New Zealand region. Southern New Zealand has been shown to have particularly high diversity. Although significant progress has been made on documenting and understanding the geographic and ecological distributions of corallines in New Zealand, more

information is needed about regional differences through to habitat requirements at a species level. The research conducted to investigate diversity at local (small) spatial scales has also resulted in important discoveries, and these results coupled with predictions of potential diversity based on sampling effort have clearly shown that further sampling is required in New Zealand. Twist (2019) reported that there are 18 singleton species (i.e., species known from a single collection) represented in the southern New Zealand datasets and 29 in New Zealand-wide datasets – that is, almost a quarter of the species discovered to date are known from single collections. On the basis of such limited material, it is not possible to understand the ecological or geographic distributions of these 'singleton' species nor to characterise them morphologically or anatomically. In addition, analyses indicate that additional taxa remain to be discovered (at least ca. 20 species, see Table 4).

Clearly there are very important issues facing coralline taxonomy both globally and within New Zealand. Progress is seriously constrained by inadequate understanding of generic and species concepts. Although systematic research on coralline algae has been revolutionised by the application of molecular sequencing tools and phylogenetic analyses, more work is required, particularly to characterise type material. The use of ancient DNA approaches (i.e., protocols used to obtain sequence data from very old specimens) and next generation sequencing methods to obtain data from type material of red algae, including corallines, is yielding critical new information, enabling for example, the examination of fossil corallines (Hughey et al. 2008), as well as the clarification of type concepts (summarised by Hughey & Gabrielson 2012; Hind et al. 2014b; Hughey et al. 2014). However, obtaining sequence data from type material requires not only access to herbarium material (with some herbaria reluctant to allow destructive sampling of type material), but also access to facilities where appropriate ancient DNA protocols can be followed. For some species, type material is not available, or cannot be identified with certainty. Hughey & Gabrielson (2012) argue that the designation of epitypes (i.e., specimen selected to serve as an interpretative type when holotype material is not available or ambiguous) with contemporary material has to be seen as a "last resort, not an alternative to sequencing type material" and, at the very least, based on topotype material (i.e., a specimen collected at the locality at which the original type was obtained). To deal with the current bottlenecks that are constraining progress in coralline taxonomic research, it may be that the selection of epitypes accompanied by sequence data will help resolve some of the current impediments to progress, namely the correct application of genus and species concepts.

The research in New Zealand has made significant contributions to the global perspective on the coralline algae with the description of the order Hapalidiales and the discovery of the enigmatic genus *Corallinapetra*. It is clear to us that further research, involving targeted collection programmes, multigene phylogenetic analyses, and morpho-anatomical characterisation, is needed before the relationships and diversity of the Corallinophycidae in New Zealand will be fully understood.

The discoveries globally and in New Zealand provide additional challenges when interpreting experimental and field investigations of coralline algae. The findings reported here from Twist (2019) of high diversity at small spatial scales are particularly challenging and suggest that approaches to sampling diversity of coralline algae need to be reviewed. There are also significant challenges relating the newly discovered diversity to earlier published accounts of coralline algae. Unless voucher material has been retained, or sequence data are available, the identity of species used for experiments in many cases cannot be confirmed, and thus conclusions regarding species specificity cannot be validated.

The species concepts of most of the coralline algae described, based on type specimens collected from the New Zealand region (Woelkerling & Nelson 2004), remain unclear, and these names are not in current use. The identity of these taxa needs to be resolved as the next step in clarifying the taxonomy of New Zealand coralline algae.

The targeted collections made in southern New Zealand (and some opportunistic specimens collected from the Subantarctic region) have enabled better distributional records, more complete reference collections, and a better understanding of the overall diversity of coralline algae in the region.

Given the evidence of species-specific responses of coralline algae and their vulnerability to environmental change (combined with their importance in global ecosystems), there is some urgency in addressing taxonomic issues in this group to enable more accurate identifications for further assessments of the distribution and ecological roles of coralline algae.

5. POTENTIAL MANAGEMENT IMPLICATIONS

Given the importance of this group of organisms in coastal ecosystems of New Zealand it is important to understand how changing environmental conditions may be affecting them. To do this, it will be necessary to better understand species-specific attributes (e.g., physiology, reproduction, competitive abilities, and susceptibility to key stressors). This in turn requires taxonomic research and additional collections from throughout the New Zealand region.

The ecosystem services provided by coralline algae as well as their potential vulnerability to changing global climate have been outlined in a number of published reviews (e.g., Nelson 2009; McCoy & Kamenos 2015). In New Zealand, coralline algae rhodolith beds have been recognised as providing an important biogenic habitat (MacDiarmid et al. 2013). Rhodolith beds are considered to form 'small natural features', ecosystems that 'support a diverse fauna and flora and provide ecosystem services disproportionate to their size'. In New Zealand these remain poorly documented in terms of distribution, extent, and functional roles. The coralline turfs of rocky reefs are structurally complex and home to extremely diverse and productive macrofaunal assemblages (Cowles et al. 2009). After examining the impacts of trampling on invertebrates inhabiting intertidal geniculate coralline algae, Brown & Taylor (1999) concluded that, in the light of the abundance and importance of these invertebrates and their vulnerability to even low levels of trampling, effective marine protection in some places may need to address this through exclusion or restriction of access.

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APPENDIX 1: HERBARIUM CARE FOR NON-GENICULATE CORALLINE RED ALGAE

1. Introduction

This guide has been produced to assist herbarium collection managers to care for non-geniculate ('crustose') coralline red algae by providing advice on best practice to ensure the ongoing value of specimens for scientific study and to enable storage of permanent voucher material.

[This is an updated version of a guide prepared by Adele Harvey and William Woelkerling (La Trobe University, Melbourne), and Tracy Farr, Kate Neill, and Wendy Nelson (NIWA, Wellington), Jenn Dalen (Museum of New Zealand Te Papa Tongarewa).]

Coralline red algae have vegetative cell walls that are impregnated with calcium carbonate, giving them a distinctive appearance. There are two types of corallines – non-geniculate species are completely calcified, whereas geniculate species produce branches consisting of alternating calcified and non-calcified segments. This segmentation can be seen easily with the unaided eye. The branches of geniculate species are extremely fragile when dried; non-calcified portions readily break, and entire specimens can quickly become reduced to small fragments. The procedures and suggestions given here for non-geniculate coralline red algae also apply to geniculate coralline red algae.

Many non-geniculate corallines look like pink rocks or crusts, but colour and appearance can vary greatly both between species and within species. Because of this variation, identification to genus or species is seldom possible from simple visual inspection of intact individuals. The full identification of most specimens requires sub-samples to be embedded and sectioned to examine internal anatomy and reproductive structures, both of which are important for genus and species determination. It is often possible to obtain necessary information for identification from dried individuals, but alcohol preserved material always yields superior preparations and more readily interpreted slides. Rapidly dried specimens (i.e., in silica gel) are required for DNA extraction.

Non-geniculate coralline algae can grow attached to almost any kind of substrate, or live unattached on the sea floor. The most common substrates are other algae and rocks. Fully mature individuals of some species may be less than 0.1 mm in greatest dimension, whereas individuals of other species may be over 1 metre in size. A single herbarium collection of a small species may contain thousands of individuals growing on a single host alga or stone, whereas for some larger species, only part of a single individual may make up a herbarium collection.

Because individuals are calcified, most are also brittle. This means that particular procedures need to be employed to ensure that individuals do not become badly fragmented as a consequence of herbarium storage, thereby rendering them largely or entirely useless as vouchers or for use in taxonomic research. The remainder of this document expands on the above overview and provides some general background information about the significance of these algae in the world's oceans.

2. Collection, preservation, and processing for herbarium storage

Specimens of non-geniculate corallines need to be collected, preserved, sorted, and processed for incorporation into the herbarium. Their care and storage in herbaria, however, requires a different approach than taken with most other macroscopic algae because they are calcified, and many grow firmly attached to rocks or animals.

Collection and preservation

Specimens with any associated substrate are collected intertidally or subtidally and rough-sorted on the shore before preservation, usually into groups:

- rocks;
- molluscs, sponges, other animals
- plant material (algal and seagrass hosts); and

- delicate or easily fragmented corallines.

A label with relevant collection data should be placed with each sample or sub-sample. Any samples slated for molecular analysis should be separated before the rest of the collection is preserved in formalin. Samples for molecular analysis are preserved either by air drying, drying in silica gel, or placement directly in 100% ethanol. Silica gel preserved specimens generally yield the best success for molecular sequencing.

Remaining material is then preserved in formalin as soon as possible after sorting to ensure quality herbarium collections and to minimise deterioration of non-calcified reproductive structures. Material slated for formalin preservation is placed in heavy-duty polythene bags with labels containing relevant collecting information. A small amount (about 10–15 ml) of full strength formalin is then added to each bag, which then is immediately sealed, usually with rubber bands. The bags are then placed in screw-top black plastic barrels or similar containers (away from light) for storage and transport.

***CAUTION**: formalin is hazardous and should be used only in well-ventilated areas, preferably with an extractor fan or fume-hood.*

It is valuable to indicate the method of preservation used for each herbarium collection. This information will greatly assist subsequently in deciding which material is most suited for molecular analyses and which material is best used for other work. In general, formalin preserved material is not suited for molecular analyses.

Processing for herbarium storage

Formalin preserved material requires further processing and sorting into individual collections before incorporation into an herbarium. Wherever possible, each herbarium collection should include some liquid-preserved reproductive material for use for embedding, sectioning, and identification. Formalin should not be used for long-term preservation, not only because it is hazardous, but also because corallines and host material eventually become soft and fall apart after extended periods. A glycerol-ethanol-water solution (1:7:2) is excellent for long-term storage.

A solution of 1:7:2 glycerol-ethanol-water is easily prepared by adding 100 ml of glycerol to 900 ml of 70% ethanol.

After initial preservation in formalin, all rough-sorted material must be washed thoroughly of all formalin in a fume hood. This is achieved by rinsing the material in a continuous flow-through container for at least 1 hour or until all detectable formalin is gone. Material should then be fine-sorted to become individual herbarium collections. Usually each collection will consist of more than one individual. A variety of strainers, sieves, and baskets to hold the samples are very useful at this stage.

All individuals that look superficially the same and occur on the same substrate should be grouped together as a collection. This does not guarantee that each collection contains only one species, but lessens the chances of any particular collection containing a mixture of taxa. Individuals that look the same but occur on different substrates should be treated as separate collections (e.g., two different host species of algae, on rock vs on shells or other substrates). Similarly, individuals that clearly differ in growth-form should be treated as separate collections unless there is an obvious gradient from growth-form to growth-form amongst the individuals in the sample.

When processing attached plants for the herbarium, it is important to retain some of the substrate with the specimens. Removal of the substrate almost always leads to the loss of the basal layers of the coralline specimen and thus of anatomical information that may be of value for identification. It also commonly leads to the fragmentation of specimens, and consequently a lowering of the quality of the herbarium collection.

CAUTION: *Pre-existing (older) collections made up of individuals on more than one substrate, or containing a mixture of non-intergrading growth-forms, should not be subdivided into several collections without the advice of a taxonomic expert on non-geniculate corallines. There may be good historical or other reasons for keeping such older mixed collections intact in the herbarium.*

Once fine-sorting is completed, each collection can be further processed for long-term preservation in glycerol-ethanol and/or air dried. For each collection it is highly desirable to have some material preserved in glass jars in a glycerol-ethanol-water solution because such material is far superior to dried material for the subsequent examination of non-calcified reproductive structures (important for species identification) and for studying how structures develop.

Do not overcrowd or compress material in the jar because this inhibits penetration of the glycerol-alcohol solution and damages the coralline material. Jar lids should be lined with an insert that creates a seal when screwed onto the jar to prevent or minimise evaporation. As a general rule, keep up to two 250 ml (or 500 ml) screw-cap jars worth of material and air-dry any excess material.

Collections on stones too big for the jars may have to be broken up at this stage (using a hammer, chisel, and cutting board). It is also a good idea at this time to get rid of any unnecessary host material before putting the corallines in jars. Keep enough material to be able to identify the host.

Each collection is given an individual collection number written on adhesive labels in pencil (as ink will dissolve/run if the jar leaks). One is placed on the jar lid and one on the side of the jar. This helps when several jars are open. (Note: the labels will not stick on to a jar covered in glycerol). Attach the labels with permanent tape to be certain they do not fall off. A piece of permanent/waterproof paper with the collection number written in pencil is also placed inside the jar. This helps if the other labels are dislodged or lost.

After the coralline material and labels are in the jar, completely fill the jar with the glycerol-alcohol solution. Jar lids are then screwed down and checked for leakage by turning on their side. In addition, a labelled box is prepared for each collection. This is used to store any air-dried material, scanning electron microscope (SEM) stubs, embedded material, glass slides, notes, etc.

Collection details will normally be recorded on to computer and labels printed out. Labels should include information such the Herbarium, collection locality, depth collected, date collected, names of collectors, details on any associated substrate (on rock, on ‘so-and-so’ [name of host organism], etc.), and the collection number.

Labels are photocopied in duplicate (photocopied material does not smudge if the jars leak). One label is glued to the top of a rectangular box and the other is placed inside the box.

3. Identification of non-geniculate coralline algae

Most collections cannot be readily identified, even to genus level, from external features because of the wide variation in growth-form, and because the same growth-form can occur in widely different taxa. With rare exceptions, reliable specimen identification is possible only when reproductive structures are present. In non-geniculate corallines, reproductive structures occur in chambers known as conceptacles or in specialised structures known as sporangial compartments.

Identification requires decalcification, embedding, and sectioning for microscopic examination of the vegetative and reproductive structures. Sometimes, fragments are needed for examination with a scanning electron microscope.

When loaning specimens, it is essential that permission be given to remove small portions of material for identification purposes. Otherwise, it will not be possible to determine which species the material belongs to or to confirm the accuracy of a pre-existing identification.

Permanent slides with sections showing diagnostic characters are usually prepared during the identification process, and representative slides should be returned with the material to minimise the need for further removal during subsequent loans. However, additional removal is sometimes needed, and thus permission to do so should be given with each loan.

Not all slides made are worth saving, as many will not be suitable for use in identification. Thus there is no value in insisting that all slides be returned. Fragments examined with the electron microscope also can be returned but should be so identified.

In many species, conceptacles and sporangial compartments will be evident to the unaided eye. Conceptacles, when evident, commonly look like small bumps on the surface that may be either dome-like or flat-topped. They may have a single pore or have a number of pores through which reproductive structures are released. Depending on the specimen, a few to many conceptacles may be evident.

Sporangial compartments are not visible individually. However, they often are aggregated into large groups that can be distinguished from the surrounding plant surface by slight differences in height, texture, or colour. An aggregated group of sporangial compartments is commonly called a sorus.

Herbarium specimens that lack evident conceptacles or sporangial compartments are not necessarily sterile. Sporangial compartments that are not aggregated into sori are almost impossible to detect without embedding and sectioning. Sometimes, conceptacles are flush with the plant surface and are very difficult to detect without a good stereomicroscope or without embedding and sectioning. In other specimens, older conceptacles and sori can become buried but still provide sufficient information to allow accurate identification after embedding and sectioning.

Unnamed specimens that are not reproductive and cannot otherwise be identified are of very limited value as herbarium preparations. Unless such specimens are known to represent vouchers for published studies, or retention can be justified on other grounds (e.g., early collections of potential historical interest), consideration should be given to discarding them. Unnamed, unidentifiable specimens should not be discarded without first consulting a taxonomic expert on the group who is familiar with the literature from the region from which such specimens were collected.

4. Storage and maintenance issues

Because the classification of corallines has yet to fully stabilise, the manner in which specimens are grouped in the herbarium requires careful consideration. The system used must be obvious both to collection managers and to those who might make use of the specimens. It is essential to keep track of the history of names applied to a specimen and to know where specimens that have had different names are currently located in the herbarium. Many specimens in herbaria are cited in the literature under misapplied names, and it is essential that those who need to examine them at some future date can trace these in the herbarium.

In arranging collections of a particular species or infraspecific taxon in the herbarium, there is little value in taking growth-form into account. If any within-taxon arrangement were to be considered, it would be more valuable to base this on geographic region than on growth-form, reproductive state (male, female, sporangial), and the like.

All parts of a collection should be clearly and appropriately labelled (jars, accompanying box, slide boxes, SEM stubs, etc) and where possible stored together in a single box representing a single herbarium preparation. Several such collections can be grouped together in a large box or carton on a single herbarium shelf. However, regulations concerning storage of collections in alcohol may mean that the wet-preserved material has to be stored separately from all the other collection material.

Liquid preservation

Whenever possible, collections should be stored in a glycerol:ethanol:water solution (1:7:2). This prevents the non-calcified structures (which are important for identification) from drying out or becoming distorted, and also ensures longer term preservation. The glycerol impregnates the algae and affords some protection from desiccation even if complete alcohol evaporation occurs because of a faulty seal in the jar lid or a faulty thread on the jar. Potential evaporation can be minimised if jars are completely filled with liquid before initial herbarium storage. If evaporation is detected, the material should be placed in a new jar with a new lid and re-immersed in glycerol-alcohol.

Air-dried specimens

Air-dried specimens are not as useful for subsequent detailed morphological-anatomical study as liquid-preserved specimens, for reasons already mentioned. However, air-dried material that has not been preserved in formalin can be used for molecular analyses, and any such material should be clearly labelled to indicate that it has not been previously preserved.

Air-dried material, unlike liquid preserved material, will maintain its colour for a period of time if stored in darkness. Over time, however, the colour of many specimens can change and ultimately can be lost due to gradual pigment deterioration.

Air drying generally is used for any excess material not preserved in glycerol-alcohol after initial formalin preservation, and for particularly large specimens to show the habit of intact individuals. There is no advantage in storing air-dried material in silica gel over a long term; eventually the silica becomes saturated with moisture and this can then adversely affect the specimens.

Pressed specimens on herbarium sheets

Coralline red algae should never be stored as pressed specimens on herbarium sheets. They should be stored in boxes. Storage on herbarium sheets promotes fragmentation and renders many specimens useless in the longer term. This is particularly true of smaller epiphytic species and of geniculate corallines.

Storage in boxes not only minimises fragmentation, but also retains any fragments with the collection from which they originated. Such fragments are useful for scanning electron microscopy and, in the absence of liquid-preserved material, they also are useful for embedding and sectioning.

Storage of prepared slides and of stubs used in scanning electron microscopy

Prepared slides are best stored with the collection from which they originated. Storing them separately is more complicated and increases the workload when specimens are requested for loan. Individual slides should be placed in small cardboard holders; groups of slides can be placed in small plastic slide boxes. Both protect the slides from breakage. Scanning electron microscope (SEM) stubs should also be stored with the collection from which the material originated. Stubs should be placed individually in packets or containers to prevent damage.

Mixtures of species in a collection

Collections containing more than one species inevitably occur as a consequence of the large variability and overlap of growth forms displayed by non-geniculate corallines and/or as a consequence of two or more species sharing the same substrate. Species mixtures, when discovered, can be handled in several ways.

1. For mixtures in which individuals of each species can easily be identified and segregated (e.g., mixtures of rhodoliths or mixtures of parts of larger plants lacking a substrate), the different components should be separated into two (or more) collections. The original herbarium number should be retained for one component/species and new numbers given to the segregate collections. All collections should be cross-referenced by number and name, and should be annotated to indicate that they once formed part of a single collection.

2. For mixtures of small, encrusting epiphytic species on a single substrate (e.g., a host alga or seagrass blades), it is virtually impossible to separate individuals of each species from the others. In such cases, slides showing the diagnostic features of each component species need to be prepared. The host material can then be divided arbitrarily into several portions and new collections formed, each with a component slide representing one of the species present. The original herbarium number should be retained for one component and new numbers given to the segregate collections. All collections should be cross-referenced by number and name, and should be annotated to indicate that they once formed part of a single collection and that a mixture of species is present in the collection.

3. For mixtures growing on a substrate that cannot be easily divided without damage to the corallines (e.g., many pāua/abalone and other mollusc shells, some stones), the substrate should be left intact. Representative individuals on the substrate should be marked and linked to prepared slides (also marked) showing the diagnostic features of the species. Marking can be achieved by using a small, brightly coloured sticker attached with alcohol-proof glue. On the specimen, this is best done by allowing the piece to dry out a little first before adding a dollop of glue and the sticker. The glue is allowed to dry for 10–20 seconds before the specimen is replaced in the alcohol/glycerol jar.

Collections containing mixtures of species that cannot be separated due to the nature of the substrate present a major problem in that the material cannot be divided up and distributed through the herbarium. There is no easy solution. One way is to store the collection under the name of the most abundant species and to retain the original herbarium number for that species. Other species present can then be given separate herbarium numbers, which need to be clearly marked on the prepared slides. An annotation sheet then should be prepared explaining which species have what numbers and indicating the symbols/stickers used to flag the individuals on the common substrate. Copies of the annotation sheet can then be made and filed under each relevant species in the herbarium. Each copy needs to also indicate where the actual specimen is filed.

5. Loan issues

When preparing a collection of non-geniculate coralline algae for loan, the following are recommended.

1. Any dried material, prepared glass slides, and stubs used previously for scanning electron microscopy are subject to breakage/fragmentation during shipment. Special care should be taken to pack material in such a manner that it cannot move or rattle during shipment.

- Dried specimens should be wrapped in tissue and placed in a small box. Fill any remaining space in the box with packing material.
- Glass slides are best shipped in individual cardboard holders, not in slide boxes. The cardboard holders should be wrapped in bubble plastic and grouped together in a box.
- SEM stubs should be placed individually in packets, which then can be placed in a protective box. Fill any remaining space in the box with packing material.

2. When posting liquid-preserved material, make sure you comply with shipping regulations both internally and internationally.

Do not ship liquid-preserved material in glass. Remove material to be sent from the jar, wrap in tissue soaked in glycerol-alcohol, and firmly seal each piece in a heavy-duty plastic bag or a leak-proof plastic container. If a leak-proof plastic container is used, make certain the specimens cannot shift about within the container during shipment. Movement leads to fragmentation.

For double protection against leakage from polythene bags during shipment, place all bags in a larger heavy-duty bag with added tissues and firmly seal the outer bag. To avoid possible specimen damage during shipment, pack the plastic bags in a box cushioned with packing material.

3. It may not be necessary to ship all of the liquid preserved material if a representative portion will do. The person requesting the loan should be asked about this. Shipping only part of the collection saves money and ensures that at least part of the collection remains intact should a shipment be lost in transit.

4. If possible, photograph the collection before shipment, and include a copy of the photo with the loan.

5. Be certain to give the borrower permission to use small pieces for embedding and sectioning and for scanning electron microscopy. Reasons for this have been explained in the section dealing with the identification of non-geniculate coralline algae.

6. For customs purposes, it is most appropriate to indicate that the contents are 'Dead Marine Algae for Scientific Study'**.** Do not use the word 'coralline' in the customs information as this can lead to the confiscation of the shipment on the mistaken impression that coral animal material is involved.

7. Provide the borrower with a full set of instructions for packing the material and any additional slides and stubs for the return shipment. Many borrowers will not be experienced packers and shippers.

APPENDIX 2: NAMING SYSTEM

Species clade naming system used in Twist 2019 compared to that used in Specify and GenBank. Algae number (e.g. NZC) of representative specimen of each clade indicated in brackets.

Species clade (Twist 2019)	Species naming in Specify and GenBank
Amphiroa_anceps	*Amphiroa anceps* (NZC2344)
Arthrocardia_sp1	*Arthrocardia* sp. A (NZC2540: Arthrocardia_sp.1 sensu Twist 2019)
Arthrocardia_sp2	*Arthrocardia* sp. B (NZC2343: Arthrocardia_sp.2 sensu Twist 2019)
Arthrocardia_sp3	*Arthrocardia* sp. C (NZC5029: Arthrocardia_sp.3 sensu Twist 2019)
Corallina_caespitosa	*Corallina caespitosa* (NZC2537) (now *C. ferreyrae*)
Corallinales_Gen1_sp1	Corallinales sp. A (NZC5546: Corallinales_Gen1_sp.1 sensu Twist 2019)
Corallinales_Gen2_sp1	Corallinales sp. B (NZC5472: Corallinales_Gen2_sp.1 sensu Twist 2019)
Corallinales_Gen3_sp1	Corallinales sp. C (NZC2266: Corallinales_Gen3_sp.1 sensu Twist 2019)
Corallinales_Gen4_sp1	Corallinales sp. D (NZC5138: Corallinales_Gen4_sp.1 sensu Twist 2019)
Corallinales_Gen4_sp2	Corallinales sp. E (NZC5484: Corallinales_Gen4_sp.2 sensu Twist 2019)
Corallinales_Gen5_sp1	Corallinales sp. F (NZC2025: Corallinales_Gen5_sp.1 sensu Twist 2019)
Corallinales_Gen5_sp2	Corallinales sp. G (NZC2009: Corallinales_Gen5_sp.2 sensu Twist 2019)
Corallinales_Gen6_sp1	Corallinales sp. H (NZC5378: Corallinales_Gen6_sp.1 sensu Twist 2019)
Corallinales_Gen6_sp2	Corallinales sp. I (NZC5243: Corallinales_Gen6_sp.2 sensu Twist 2019)
Corallinales_Gen6_sp3	Corallinales sp. J (NZC5217: Corallinales_Gen6_sp.3 sensu Twist 2019)
Corallinales_Gen7_sp1	Corallinales sp. K (NZC2412: Corallinales_Gen7_sp.1 sensu Twist 2019)
Corallinales_Gen8_sp1	Corallinales sp. L (NZC2125: Corallinales_Gen8_sp.1 sensu Twist 2019)
Corallinales_Gen8_sp2	Corallinales sp. M (NZC5333: Corallinales_Gen8_sp.2 sensu Twist 2019)

Species clade (Twist 2019)	Species naming in Specify and GenBank
Corallinales_Gen8_sp3	Corallinales sp. N (NZC0781: Corallinales_Gen8_sp.3 sensu Twist 2019)
Corallinales_Gen8_sp4	Corallinales sp. O (NZC2122: Corallinales_Gen8_sp.4 sensu Twist 2019)
Corallinales_Gen8_sp5	Corallinales sp. P (NZC0090: Corallinales_Gen8_sp.5 sensu Twist 2019)
Corallinales_Gen9_sp1	Corallinales sp. Q (NZC0667: Corallinales_Gen9_sp.1 sensu Twist 2019)
Corallinales_Gen10_sp1	Corallinales sp. R (NZC2328: Corallinales_Gen10_sp.1 sensu Twist 2019)
Corallinales_Gen11_sp1	Corallinales sp. S (ASN200: Corallinales_Gen11_sp.1 sensu Twist 2019)
Corallinales_Gen12_sp1	Corallinales sp. T (NZC2573: Corallinales_Gen12_sp.1 sensu Twist 2019)
Corallinales_Gen13_sp1	Corallinales sp. U (NZC2055: Corallinales_Gen13_sp.1 sensu Twist 2019)
Corallinales_Gen14_sp1	Corallinales sp. V (NZC2576: Corallinales_Gen14_sp.1 sensu Twist 2019)
Corallinales_Gen15_sp1	Corallinales sp. W (NZC5673: Corallinales_Gen15_sp.1 sensu Twist 2019)
Corallinales_Gen15_sp2	Corallinales sp. X (NZC0314: Corallinales_Gen15_sp.2 sensu Twist 2019)
Corallinales_Gen15_sp3	Corallinales sp. Y (NZC2302: Corallinales_Gen15_sp.3 sensu Twist 2019)
Corallinales_Gen15_sp4	Corallinales sp. Z (NZC5418: Corallinales_Gen15_sp.4 sensu Twist 2019)
Corallinales_Gen15_sp5	Corallinales sp. ZA (NZC2352: Corallinales_Gen15_sp.5 sensu Twist 2019)
Corallinales_Gen16_sp1	Corallinales sp. ZB (NZC2270: Corallinales_Gen16_sp.1 sensu Twist 2019)
Corallinales_Gen16_sp2	Corallinales sp. ZC (NZC2409: Corallinales_Gen16_sp.2 sensu Twist 2019)
Corallinales_Gen16_sp3	Corallinales sp. ZD (NZC2127: Corallinales_Gen16_sp.3 sensu Twist 2019)
Corallinales_Gen16_sp4	Corallinales sp. ZE (NZC2590: Corallinales_Gen16_sp.4 sensu Twist 2019)
Corallinales_Gen16_sp5	Corallinales sp. ZF (NZC5562: Corallinales_Gen16_sp.5 sensu Twist 2019)

Species clade (Twist 2019)	Species naming in Specify and GenBank
Corallinales_Gen16_sp6	Corallinales sp. ZG (NZC5022: Corallinales_Gen16_sp.6 sensu Twist 2019)
Corallinapetra	*Corallinapetra novaezelandiae* (NZC2381)
Hapalidiales_Gen1_sp1	Hapalidiales sp. A (NZC5251B: Hapalidiales_Gen1_sp.1 sensu Twist 2019)
Hapalidiales_Gen1_sp2	Hapalidiales sp. B (NZC5574: Hapalidiales_Gen1_sp.2 sensu Twist 2019)
Hapalidiales_Gen1_sp3	Hapalidiales sp. C (NZC5470: Hapalidiales_Gen1_sp.3 sensu Twist 2019)
Hapalidiales_Gen1_sp4	Hapalidiales sp. D (NZC5447: Hapalidiales_Gen1_sp.4 sensu Twist 2019)
Hapalidiales_Gen1_sp5	Hapalidiales sp. E (NZC5224: Hapalidiales_Gen1_sp.5 sensu Twist 2019)
Hapalidiales_Gen2_sp1	Hapalidiales sp. F (NZC2238: Hapalidiales_Gen2_sp.1 sensu Twist 2019)
Hapalidiales_Gen2_sp2	Hapalidiales sp. G (NZC5623: Hapalidiales_Gen2_sp.2 sensu Twist 2019)
Hapalidiales_Gen3_sp1	Hapalidiales sp. H (NZC5294: Hapalidiales_Gen3_sp.1 sensu Twist 2019)
Hapalidiales_Gen3_sp2	Hapalidiales sp. I (NZC2013: Hapalidiales_Gen3_sp.2 sensu Twist 2019)
Hapalidiales_Gen4_sp1	Hapalidiales sp. J (NZC2041: Hapalidiales_Gen4_sp.1 sensu Twist 2019)
Hapalidiales_Gen5_sp1	Hapalidiales sp. K (NZC5440: Hapalidiales_Gen5_sp.1 sensu Twist 2019)
Hapalidiales_Gen6_sp1	Hapalidiales sp. L (NZC0847: Hapalidiales_Gen6_sp.1 sensu Twist 2019)
Hapalidiales_Gen6_sp2	Hapalidiales sp. M (NZC2369: Hapalidiales_Gen6_sp.2 sensu Twist 2019)
Hapalidiales_Gen6_sp3	Hapalidiales sp. N (NZC5345: Hapalidiales_Gen6_sp.3 sensu Twist 2019)
Hapalidiales_Gen6_sp4	Hapalidiales sp. O (NZC2406: Hapalidiales_Gen6_sp.4 sensu Twist 2019)
Hapalidiales_Gen7_sp1	Hapalidiales sp. P (NZC5362A: Hapalidiales_Gen7_sp.1 sensu Twist 2019)
Hapalidiales_Gen7_sp2	Hapalidiales sp. Q (NZC5379: Hapalidiales_Gen7_sp.2 sensu Twist 2019)
Hapalidiales_Gen7_sp3	Hapalidiales sp. R (NZC5306: Hapalidiales_Gen7_sp.3 sensu Twist 2019)
Hapalidiales_Gen7_sp4	Hapalidiales sp. S (TC17874: Hapalidiales_Gen7_sp.4 sensu Twist 2019)

Species clade (Twist 2019)	Species naming in Specify and GenBank
Hapalidiales_Gen7_sp5	Hapalidiales sp. T (NZC5406: Hapalidiales_Gen7_sp.5 sensu Twist 2019)
Hapalidiales_Gen7_sp6	Hapalidiales sp. U (NZC5290B: Hapalidiales_Gen7_sp.6 sensu Twist 2019)
Hapalidiales_Gen7_sp7	Hapalidiales sp. V (NZC2311: Hapalidiales_Gen7_sp.7 sensu Twist 2019)
Hapalidiales_Gen8_sp1	Hapalidiales sp. W (NZC0875: Hapalidiales_Gen8_sp.1 sensu Twist 2019)
Hapalidiales_Gen9_sp1	Hapalidiales sp. X (NZC4004: Hapalidiales_Gen9_sp.1 sensu Twist 2019)
Hapalidiales_Gen10_sp1	Hapalidiales sp. Y (NZC5202: Hapalidiales_Gen10_sp.1 sensu Twist 2019)
Hapalidiales_Gen11_sp1	Hapalidiales sp. Z (NZC5245: Hapalidiales_Gen11_sp.1 sensu Twist 2019)
Hapalidiales_Gen12_sp1	Hapalidiales sp. ZA (NZC5368: Hapalidiales_Gen12_sp.1 sensu Twist 2019)
Hapalidiales_Gen12_sp2	Hapalidiales sp. ZB (NZC5362B: Hapalidiales_Gen12_sp.2 sensu Twist 2019)
Hapalidiales_Gen12_sp3	Hapalidiales sp. ZC (NZC0476: Hapalidiales_Gen12_sp.3 sensu Twist 2019)
Hapalidiales_Gen13_sp1	Hapalidiales sp. ZD (NZC5080: Hapalidiales_Gen13_sp.1 sensu Twist 2019)
Hapalidiales_Gen14_sp1	Hapalidiales sp. ZE (NZC5469: Hapalidiales_Gen14_sp.1 sensu Twist 2019)
Hapalidiales_Gen15_sp1	Hapalidiales sp. ZF (NZC5361: Hapalidiales_Gen15_sp.1 sensu Twist 2019)
Hapalidiales_Gen16_sp1	Hapalidiales sp. ZG (NZC5425A: Hapalidiales_Gen16_sp.1 sensu Twist 2019)
Hapalidiales_Gen17_sp1	Hapalidiales sp. ZH (NZC5501: Hapalidiales_Gen17_sp.1 sensu Twist 2019)
Hapalidiales_Gen18_sp1	Hapalidiales sp. ZI (NZC5079: Hapalidiales_Gen18_sp.1 sensu Twist 2019)
Hapalidiales_Gen19_sp1	Hapalidiales sp. ZJ (TC18093: Hapalidiales_Gen19_sp.1 sensu Twist 2019)
Hapalidiales_Gen20_sp1	Hapalidiales sp. ZK (NZC5354: Hapalidiales_Gen20_sp.1 sensu Twist 2019)
Hapalidiales_Gen21_sp1	Hapalidiales sp. ZL (NZC5429: Hapalidiales_Gen21_sp.1 sensu Twist 2019)
Hapalidiales_Gen21_sp2	Hapalidiales sp. ZM (TC18097: Hapalidiales_Gen21_sp.2 sensu Twist 2019)
Hapalidiales_Gen22_sp1	Hapalidiales sp. ZN (NZC5548: Hapalidiales_Gen22_sp.1 sensu Twist 2019)

Species clade (Twist 2019)	Species naming in Specify and GenBank
Hapalidiales_Gen22_sp2	Hapalidiales sp. ZO (NZC2371: Hapalidiales_Gen22_sp.2 sensu Twist 2019)
Hapalidiales_Gen22_sp3	Hapalidiales sp. ZP (NZC5698A: Hapalidiales_Gen22_sp.3 sensu Twist 2019)
Hapalidiales_Gen23_sp1	Hapalidiales sp. ZQ (NZC5095: Hapalidiales_Gen23_sp.1 sensu Twist 2019)
Hapalidiales_Gen24_sp1	Hapalidiales sp. ZR (NZC5308B: Hapalidiales_Gen24_sp.1 sensu Twist 2019)
Hapalidiales_Gen25_sp1	Hapalidiales sp. ZS (NZC2093: Hapalidiales_Gen25_sp.1 sensu Twist 2019)
Hapalidiales_Gen25_sp2	Hapalidiales sp. ZT (NZC5056: Hapalidiales_Gen25_sp.2 sensu Twist 2019)
Hapalidiales_Gen26_sp1	Hapalidiales sp. ZU (NZC5140: Hapalidiales_Gen26_sp.1 sensu Twist 2019)
Hapalidiales_Gen27_sp1	Hapalidiales sp. ZV (NZC5221: Hapalidiales_Gen27_sp.1 sensu Twist 2019)
Hapalidiales_Gen27_sp3	Hapalidiales sp. ZX (NZC5223: Hapalidiales_Gen27_sp.3 sensu Twist 2019)
Hapalidiales_Gen28_sp1	Hapalidiales sp. ZY (NZC5397B: Hapalidiales_Gen28_sp.1 sensu Twist 2019)
Hapalidiales_Gen28_sp2	Hapalidiales sp. ZZ (NZC5500: Hapalidiales_Gen28_sp.2 sensu Twist 2019)
Hapalidiales_Gen29_sp1	Hapalidiales sp. YA (NZC5036: Hapalidiales_Gen29_sp.1 sensu Twist 2019)
Hapalidiales_Gen30_sp1	Hapalidiales sp. YB (NZC0745: Hapalidiales_Gen30_sp.1 sensu Twist 2019)
Hapalidiales_Gen30_sp2	Hapalidiales sp. YC (NZC5028: Hapalidiales_Gen30_sp.2 sensu Twist 2019)
Hapalidiales_Gen30_sp3	Hapalidiales sp. YD (NZC5292: Hapalidiales_Gen30_sp.3 sensu Twist 2019)
Hapalidiales_Gen30_sp4	Hapalidiales sp. YE (NZC2354: Hapalidiales_Gen30_sp.4 sensu Twist 2019)
Hapalidiales_Gen30_sp5	Hapalidiales sp. YF (NZC2342: Hapalidiales_Gen30_sp.5 sensu Twist 2019)
Hapalidiales_Gen31_sp1	Hapalidiales sp. YG (NZC5241: Hapalidiales_Gen31_sp.1 sensu Twist 2019)
Hapalidiales_Gen32_sp1	Hapalidiales sp. ZW (NZC2317: Hapalidiales_Gen32_sp.1 sensu Twist 2019)

Species clade (Twist 2019)	Species naming in Specify and GenBank
Heydrichia_homalopasta	*Heydrichia homalopasta* (NZC2111)
Jania_rosea4	*Jania* sp. A (NZC5426: *Jania*_rosea4 sensu Twist 2019)
Jania_rosea1	*Jania* sp. B (WELT A029085: *Jania*_rosea1 sensu Twist 2019)
Jania_rosea2	*Jania* sp. E (NZC5062: *Jania*_rosea2 sensu Twist 2019)
Jania_rosea3	*Jania* sp. F (NZC5006: *Jania*_rosea3 sensu Twist 2019)
Jania_sagittata	*Jania sagittata* (NZC2216)
Jania_sp1	*Jania* sp. C (WELT A029128: *Jania*_sp.1 sensu Twist 2019)
Jania_sp2	*Jania* sp. J (WELT A029133: *Jania*_sp.2 sensu Twist 2019)
Jania_sphaeroramosa	*Jania sphaeroramosa (NZC5234)*
Lithothamnion_crispatum	*Lithothamnion crispatum (NZC2411)*
Mastophora_pacifica	*Mastophora pacifica* (NZC2000)
Pneophyllum_sp1	*Pneophyllum* sp. A (NZC2023: *Pneophyllum*_sp.1 sensu Twist 2019)
Pneophyllum_sp10	*Pneophyllum* sp. J (NZC5720: *Pneophyllum*_sp.10 sensu Twist 2019)
Pneophyllum_sp11	*Pneophyllum* sp. K (NZC2019: *Pneophyllum*_sp.11 sensu Twist 2019)
Pneophyllum_sp2	*Pneophyllum* sp. B (NZC5564: *Pneophyllum*_sp.2 sensu Twist 2019)
Pneophyllum_sp3	*Pneophyllum* sp. C (ASN195: *Pneophyllum*_sp.3 sensu Twist 2019)
Pneophyllum_sp4	*Pneophyllum* sp. D (NZC0507: *Pneophyllum*_sp.4 sensu Twist 2019)
Pneophyllum_sp5	*Pneophyllum* sp. E (NZC5323: *Pneophyllum*_sp.5 sensu Twist 2019)
Pneophyllum_sp6	*Pneophyllum* sp. F (NZC0627: *Pneophyllum*_sp.6 sensu Twist 2019)
Pneophyllum_sp7	*Pneophyllum* sp. G (NZC0730: *Pneophyllum*_sp.7 sensu Twist 2019)

Species clade (Twist 2019)	Species naming in Specify and GenBank
Pneophyllum_sp8	*Pneophyllum* sp. H (NZC5746C: *Pneophyllum*_sp.8 sensu Twist 2019)
Pneophyllum_sp9	*Pneophyllum* sp. I (NZC5063: *Pneophyllum*_sp.9 sensu Twist 2019)
Sporolithales_gen1_sp1	*Sporolithales* sp. A (NZC2014: *Sporolithales*_gen1_sp.1 sensu Twist 2019)
Sporolithon_durum_epilithic	*Sporolithon* sp. A (WELT A029440: epilithic)
Sporolithon_durum_rhodolith	*Sporolithon* sp. B (WELT A029433: rhodolith sensu Twist 2019)
Synarthrophyton_patena	*Synarthrophyton patena* (NZC5537A)

APPENDIX 3: SUMMARY OF CURRENTLY RECOGNISED CORALLINE ALGAE GENERA FOUND IN NEW ZEALAND

Corallinales:

Amphiroa J.V.Lamour.
Amphiroa anceps (Lam.) Decne is known from northern New Zealand (Kermadec Islands, northern North Island). As noted by Farr et al. (2009), molecular data show that *A. anceps* from New Zealand is closely related to, but distinct from *A. anceps* from Australia (type locality is "...les mers Australes ou de la Nouvelle Hollande" [Australia]), and further work clarifying the identity and relationships of the New Zealand species is required.

Arthrocardia Decne.
Three species of *Arthrocardia* have been distinguished in the phylogenetic analyses, two from northern New Zealand and one from southern New Zealand. Previously two species of *Arthrocardia* had been reported from New Zealand: *A. corymbosa* (type locality South Africa) and *A. wardii* (type locality Victoria, Australia). It is now clear that these names do not apply to New Zealand species and work is required to characterise these taxa.

Corallina L.
A single species name has been used in New Zealand recently, *C. officinalis* L. However, the use of this name has changed over the past decade with New Zealand material considered to be part of *C. caespitosa* R.H.Walker, J.Brodie & L.M.Irvine (Walker et al. 2009), and most recently transferred to *C. ferreyrae* E.Y.Dawson, Acleto & Foldvik (Bustamente et al. 2019).

Farr et al. (2009) noted the diversity within *Corallina* in New Zealand, referring to six "spacer" taxa that were able to be distinguished using *psb*A-*trn*L spacer sequence data. Further work is required to understand the extent and distribution of diversity within *Corallina* around New Zealand, and also the identity of *C. armata* Hook.f. & Harv. (refer Table 2).

Jania J.V.Lamour.
Eight species of *Jania* from New Zealand can be distinguished on the basis of molecular sequence data. Two of these are well defined both genetically and morphologically: *J. sagittata* (Lam.) Decne. with distinctive arrow-shaped (sagittate) segments, and *J. sphaeroramosa* Twist, J.E.Sutherl. & W.A.Nelson, so named to reflect its distinctive growth form as rounded balls (an epiphytic species, formerly referred to as *J. micrarthrodia*).

In addition, there are three species falling within the general grouping of *J. 'rosea'*, and two species for which very few collections have been made, one from the far north, referred to as *Jania* 'sp. fine' in Farr et al. (2009), and one from southern New Zealand.

One of the earliest species described from New Zealand was *Jania crassa* J.V.Lamour., collected from Dusky Sound in Fiordland. The name *J. crassa* had been considered to be a synonym of *J. verrucosa* until the recent work of Woelkerling et al. (2015). They examined material of *J. crassa* and established a lectotype. The dimensions of the lectotype material (particularly the dimensions of the intergenicula) differ from any collections available in New Zealand. The identity and distribution of this species in New Zealand waters remains unclear. Recent collections from southern Fiordland did not yield any specimens conforming to the proportions described by Woelkerling et al. (2015). Sequence data from the lectotype material (housed in France) may enable greater clarity about the correct application of this name.

Mastophora Decne.

A single species, *Mastophora pacifica* (Heydr.) Foslie has been reported from the Kermadec Islands where it is found as an epiphyte on species of *Galaxaura*.

Neogoniolithon Setch. & L.R.Mason

A single species in this genus has been collected from northern North Island. Although the material was initially identified as *N. florida-brassica* (Harv.) Setch. L.R.Mason this needs to be confirmed.

Pneophyllum Kütz.

The phylogenetic analyses have revealed 11 species in this genus, some of which were formerly referred to *Pneophyllum* and some to the genus *Spongites*. It is now clear that none of the species names used in earlier treatments are correctly applied to New Zealand species. Research is required to understand the distribution (both ecological and geographic) and diversity within New Zealand members of this genus.

There are 16 additional genera of Corallinales without current names.

Hapalidiales

Choreonema F.Schmitz

Choreonema thuretii (Bornet) F.Schmitz is a tiny parasite found on non-geniculate coralline algae, particularly species of *Jania*.

Lithothamnion Heydr.

Only a single species in this genus is confirmed from New Zealand waters - the rhodolith forming species *L. crispatum* Hauck (referred to as *L. indicum* in Farr et al. 2009).

Synarthrophyton R.A.Towns.

The generitype, *S. patena* (Hook.f. & Harv.) R.A.Towns. was described from collections made on the Wairarapa coast, North Island. The name has been incorrectly applied to several species within the Hapalidiales and confirmation of the correct identity of this species has been enabled with sequence data from the type collection. A second species of *Synarthrophyton* was described from New Zealand specimens, *S. schielianum* Woelk. & M.S.Foster, but the identity of this species remains unclear: sequence data have revealed that this name has been applied on the basis of morphoanatomical features to several different species/genera within the Hapalidiales, none of which appear to belong to the genus *Synarthrophyton*.

The majority of genera in the Hapalidiales in New Zealand (30) do not have current names.

Sporolithales

There are two species of *Sporolithon* distinguished by sequence data within New Zealand, neither of which conforms to the genetic data from *S. durum* in Australia. One of these New Zealand species forms rhodoliths and the other is found growing epilithically. Recent research on the genus has provided sequence data which is enabling the clarification of species identities (Maneveldt et al. 2017; Richards et al. 2017).

Heydrichia R.A.Towns., Y.M.Chamb. & Keats

There is a single confirmed species of *Heydrichia* in New Zealand found in northern New Zealand, *H. homalopasta* R.A.Towns. & Borow.

Although another species has been reported from New Zealand, *H. woelkerlingii*, it has become clear that material from New Zealand does not belong in this species and in fact represents a new undescribed genus within the Sporolithales.

Incertae sedis

The relationships of the genus *Corallinapetra* T.J.Farr, W.A.Nelson & J.E.Sutherl. were initially unclear (Nelson et al. 2015), but work describing a new order and family for this genus is underway (Jeong et al. 2019). At present it is represented by a single northern species, *C. novaezelandiae* T.J.Farr, W.A.Nelson & J.E.Sutherl.