The Biogeography and Trophic Roles of Coastal Marine Sponges (Porifera) from the west coast of the North Island, New Zealand: Influences of Catchments.

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Abstract

Anthropogenic activities are degrading coastal marine ecosystems globally. While the ecological and biodiversity implications of some of these impacts are well understood, for others there is a need for a greater understanding of the effects of these activities on vulnerable sedentary species. For researchers to pragmatically assess impacts on cryptic sponge species in highly productive reef systems, taxonomic assignment of these taxa is essential. With regards to the sponge fauna of Aotearoa, New Zealand, identification of sponge species is crucial for two main reasons. Firstly, these species significantly contribute to the productivity of inshore coastal reef ecosystems. Secondly, the existing literature of New Zealand's sponge species has scarcities in species characterisation and identification for inshore sponge fauna.

The Taranaki region is arguably foremost for consideration, as the coast would likely reflect any shifts in trans-Tasman current systems, and this region has a highly exposed geomorphology making it logistically difficult to conduct dive surveys. Furthermore, little is currently known about shallow water biogeography from this region.

Focusing on temperate rocky reefs in the Taranaki Region of New Zealand, this thesis investigates the biogeography of sponge assemblages across broad spatial scales (hundreds of kms). It examines ecological processes, linked to trophic cascades to further our understanding of factors affecting the distribution and abundance of sponge communities at smaller spatial scales (tens of kms), with particular focus on the effects of land derived catchment discharges.

A combination of Linnean taxonomic classification and operational taxonomic units (OTUs) were used to identify sponge species and highlight locations with unique assemblages of taxa at regional scales. To achieve this a program of taxonomic revision was required, including the redescription of a collection of common sponge species *Aaptos globosa*, *Acanthoclada prostrata*, *Biemna rufescens*, *Halichondria* (*Halichondria*) *moorei*, and *Stylissa haurakii*. These results progress the modern requirements of these species description from those described in early New Zealand literature that lacked adequate and detailed descriptions and *in situ images*.

As a precursor to the Taranaki ecological survey, a revision of sponge species from the Bay of Plenty was conducted. This study examined the family Dysideiidae and describes two novel

sponge species (*Dysidea tuapokere* and *Dysidea teawanui*), from Tauranga Harbour, in the Bay of Plenty, and validated five species within New Zealand's Exclusive Economic Zone, *Dysidea cristagalli, D. hirciniformis, D. navicularis, D. ramsayi, D. spiculivora*. *Dysidea fragilis* is now considered to be invalid, *and D. elegans* is considered unrecognisable. Further taxonomic assignment of Taranaki sponge fauna is required and is ongoing. The set of qualitative, but validated data now provides a baseline survey of spatial heterogeneity in terms of the distribution of sponge taxa across the Taranaki and central west coast North Island region. Biogeographic data showed that the geographic range of sponge species is highly patchy and supports the hypothesis that species assemblages at the Pariokariwa Reef (now part of the Parininihi Marine Reserve) are highly unique. Results from this investigation provide a baseline species diversity estimate within Taranaki and reveal Waitara reefs as biologically significant areas with the second largest number of unique sponge species out of all six locations surveyed. These findings have important implications for developing conservation strategies for marine fauna in Taranaki, highlighting locations of significant biological diversity, abundance, and uniqueness. Potential drivers for this biogeographic patchiness are addressed in subsequent sections of the research program.

Environmental factors influencing the distribution and abundance of marine sponges as described around the Taranaki region (Waitara reefs, Waiwhakaiho reefs, and Hangatahua Reef) over a three-year period were examined. There was a greater diversity and abundance of sponges at rocky reef stations that were in closer proximity to river mouths. This provides evidence that terrestrially derived organic matter from rivers may be supporting a greater assemblage and biomass of marine taxa on coastal rocky reefs, despite the increased sediment input from some of the catchments examined. The size of sponges in terms of volume were greater at coastal stations positioned next to rivers with a relatively large coverage of indigenous forests as opposed to reef systems adjacent to modified and urbanized catchments. An examination of the effects of several physico-chemical factors including turbidity, total phosphorus, total nitrogen, and *Escherichia coli* presence (an indicator of human and agricultural inputs), revealed that sponges appear to be resilient to certain degrees of exposure to these variables. There appears to be a negative correlation between effects of turbidity and nutrient level on sponges generally, with high levels of turbidity associated with decline in sponge characterised reef habitat. In

contrast, some sponge species appear to thrive in turbid conditions that have high levels of nutrients in a form that they can profit from metabolically. Therefore, the quality of the catchment system can directly influence the quality of the nearshore benthic sponge assemblage.

Finally, the critical role of marine sponges in processing terrestrially derived carbon was investigated by examining the proportional contribution of food from various sources to the diet of sponges on temperate rocky reefs. Our isotope analysis revealed that marine food sources including coastal seston (>1.2–400 μm), coastal GFX (combined fine and coarse glass fibre filter samples >0.7–1.2 μm), and coastal bacteria (>0.2–0.7 μm) contributed the largest proportion to the diet of coastal sponges at 60–73% across our three stations. This was followed by a relatively large proportion of terrestrially derived food sources including freshwater seston (>1.2–400 μm), freshwater GFX (>0.7–1.2 μm), and freshwater bacteria (>0.2–0.7 μm) at 27–40%. Sponges are therefore argued to play significant roles in linking terrestrial and marine food webs, and associated carbon cycles, via recycling terrestrially derived carbon and nitrogen. Combining our estimated C retention rate with the isotopically-determined contribution of foods from terrestrial sources to the diet of coastal sponges (27–40%), suggests that sponge meadows may retain approximately 117–173 kg of terrestrially-derived C km^{-2} day

In summary, the biogeographic distribution of sponge fauna that characterise nearshore reef environments around the Taranaki region has been described at large and small scales. This provides a baseline for future surveillance of nearshore ecological condition over ensuing years. This study highlights the importance of undertaking taxonomic precursor studies of regional sponge fauna to allow researchers to gain the taxonomic expertise to conductor wider scale ecological studies of this diverse phylum. The distribution of assemblages in Taranaki is particularly patchy with several highly unique communities being identified. These findings are important to the management of sponge fauna and the systems that support them. Land-based activities and ground cover and use are having direct effects on coastal reef communities, as seen in the distribution, abundance, and sizes of sponge species over large-scale environmental gradients. An important role of sponges in processing terrestrial derived carbon has been identified. The implications of this are that sponges are ingesting terrestrially derived organic matter on temperate reefs and potentially turning it into sources of food in the form of biomass, and cell shedding. This study shows that rivers and their derived food sources are important for

coastal sponge communities. A unique assemblage of sponges was found close to a catchment system that discharges large quantities of sediment from significantly degraded hinterland suggesting that some taxonomic groups can thrive in areas where other species may struggle hence, species specific studies of how certain taxa adapt to multiple environmental stressors is suggested. Future studies should endeavour to further this research and expand our current understanding of sponge fauna as they constitute useful sentinel organisms.

Acknowledgements

Preface

From left, Prof. Christopher Battershill, Samuel Mc Cormack & Rex Fairweather on a field trip one foggy morning in Taranaki.

Chapter contributions and publications

Chapter 1:
Title: General Introduction.
Chapter writing SMC *and editing*: SMC, CB, PR & KP.

Chapter 2:
Title: The Biogeography of Taranaki Sponges.
Study design: Samuel Mc Cormack, with guidance from Prof. Christopher N. Battershill & Dr Michelle Kelly (NIWA).
Data collection: SMC.
Taxonomy: SMC with guidance from Prof. Christopher N. Battershill & Dr Michelle Kelly (NIWA).
Data analyses: SMC. Kim Pritchard assisted with data processing.
Chapter writing SMC and editing: SMC, CB, PR & KP.
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Samuel P. Mc Cormack, Michelle Kelly, Christopher N. Battershill. Description of two new species of *Dysidea* (Porifera, Demospongiae, Dictyoceratida, Dysideidae) from Tauranga Harbour, Bay of Plenty, New Zealand. Zootaxa, 4780 (3) (2020), pp. 523–542. (*Published during PhD timeframe*).

Samuel P. Mc Cormack, Michelle Kelly, Christopher N. Battershill. Redescription of five sponge species. *In prep (advanced stage) for Zootaxa*.

Chapter 3:
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Data analyses: SMC, with assistance from TI, BH & CB.
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Chapter 5:
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Chapter writing SMC *and editing*: SMC, MK & CB. In addition, Kim Pritchard & Daisy Church proofread this chapter.

Appendix 1: *Publication in prep advanced stage for Zootaxa*: Samuel P. Mc Cormack, Michelle Kelly, Christopher N. Battershill. Redescription of five sponge species from Pilot Bay, Tauranga Harbour, Bay of Plenty, New Zealand (*Written during PhD timeframe*).

Appendix 2: *Publication*: Samuel P. Mc Cormack, Michelle Kelly, Christopher N. Battershill. Description of two new species of *Dysidea* (Porifera, Demospongiae, Dictyoceratida, Dysideidae) from Tauranga Harbour, Bay of Plenty, New Zealand. Zootaxa, 4780 (3) (2020), pp. 523–542. (*Published during PhD timeframe*).

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Chapter 1

General introduction

1.1 An investigation into the trophic ecology and biogeography of sponges influenced by rivers

The overall aim of this thesis is to examine the trophic ecology and biogeography of coastal marine sponges. There is a need for a better understanding of trophic ecological interactions at smaller spatial scales in a biogeographic region on the west coast of the North Island of New Zealand. Specifically, there is an urgent need to understand and explore trophically important sedentary reef forming fauna such as sponges to determine the effects of river(s) catchments on these organisms in a fast-changing climate. Furthermore, there is a need to understand the ecological dynamics of nearshore shallow water reef systems to wider coastal ecology and productivity. To achieve this, fundamental research is required to examine the biosystematics of sponge species present in the Taranaki region. Moreover, the trophic cascades and roles of sponges in the Taranaki region is poorly understood in terms of the wider benthic pelagic coupling on rocky reef systems.

1.2 A general overview of sponge biology

Darwin (1859) first proposed the scientific theory that all life on earth has evolved from a single common ancestor. Diversity of life arose by common descent through a pattern of branching termed evolution (Darwin, 1859). It is not known exactly when life on Earth originated. However, fossilized microorganisms that inhabited hydrothermal vents dating between 3.7 and 4.2 billion years ago, are the earliest records of life forms on Earth (Dodd, 2017). These records are nearly as old as the formation of the oceans 4.4 billion years ago and Earth itself 4.5 billion years ago (Manhes *et al.,* 1980; U.S. Geological Survey, 1997; Dalrymple, 2001; Wilde *et al.*, 2001). There is evidence to suggest that the first multicellular animals on earth were simple balls of cells with limited capacity to differentiate (Sogabe, *et al.*, 2019). However, additional authors have stated that sponges may be the first multicellular animals to have evolved on Earth and are the common ancestor of all other animals with numerous phylogenetic analyses revealing that they are the earliest divergent metazoan group in existence (Peterson & Butterfield, 2005; Sperling *et al.*,

2007; Erwin *et al.*, 2011; Mills et al., 2014; Feuda *et al.*, 2017). Sponges are a sedentary, multicellular, heterotrophic group of animals that have a heterogeneous diet across a size range of particles and organisms including, but not limited to: (a) carnivory of invertebrates such as nauplii of brine shrimp in food poor environments (Vacelet & Boury-Esnault, 1995); (b) prokaryotes (heterotrophic bacteria, e.g. *Prochlorococcus* sp., *Synechococcus* sp.), eukaryotes (protozoa, phytoplankton, and ciliates) (Ribes *et al.*, 1999); (c) dissolved organic matter including coral and crustose coralline algae derived organic matter (Van Duyl *et al.*, 2011; Rix *et al.*, 2016); and (d) larger forms of organic matter through direct phagocytosis (Bergquist, 1978). Sponges have been recorded removing suspended bacteria with efficiencies between 75% and 99% (Reiswig, 1971, 1975; Wilkinson, 1978; Wilkinson *et al.*, 1984). Bergquist (1978) concluded that sponges are non-selective particle feeders and can consume any particles capable of entering their ostia. Nevertheless, the hexactinellid sponge *Aphrocallistes vastus* was found to select against *Synechococcus* sp. during the month of July (Yahel *et al.*, 2006, 2007; Maldonado *et al.*, 2012). The filtration rate of sponges is relatively large. For example, two species of sponges namely *Halichondria* (*Halichondria*) *panicea* and *Haliclona* (*Haliclona*) *urceolus* were shown to have near-identical filtration rates, with maximum rates of approximately 60 mL min^1 (gdry weight)$^{-1}$ at 12°C (Riisgård *et al.*, 1993).

At present, there are 9,372 valid sponge species (marine and non-marine) described worldwide (Van Soest *et al.*, 2021). Sponges have adapted to survive in all marine habitats and ecosystems, in addition to freshwater systems including lakes and rivers. Most sponges actively or passively filter feed by filtering water through their pores (ostia), canals and choanocyte chambers using choanocyte cells (Renard *et al.*, 2013). Their aquiferous systems are not only utilised for collecting food but are also involved in physiological functions such as reproduction and excretion of waste matter (Renard *et al.*, 2013). Sponges are divided into four extant classes (Calcarea; Hexactinellida; Demospongiae; Homoscleromorpha).

The calcareous sponges of class Calcarea are characterised by skeletons composed of calcium carbonate spicules in the form of calcite or aragonite. Class Hexactinellida, also known as glass sponges, are characterized by skeletons composed of siliceous spicules with four to six rays (Hooper & Van Soest, 2002). The class Homoscleromopha are the fourth extant class of sponges that are characterized by siliceous spicules, if present, composed of tetractinal-like

calthrop spicules (diods, triods, and lophate spicules) (Gazave *et al.*, 2011). It is often difficult to differentiate some of the classes as identifications frequently require insight from a professional sponge taxonomist. The largest of the four classes in terms of species diversity are the Demosponges (Class Demospongiae), which are characterized as having 'spongin' skeletons that may or may not be accompanied by siliceous spicules.

Sponges are flexible in terms of their ability to reproduce. They can adapt to their environmental conditions and can use three forms of asexual reproduction: fragmentation, budding, and via the production of gemmules (Battershill & Bergquist, 1990). Additionally, sponges possess the capability of performing sexual reproduction due to most sponges being hermaphrodites functioning as both sexes at the same time (Bergquist, 1978).

Currently there are eight larval types known within the phylum Porifera including dispherula, cinctoblastula, clavablastula, parenchymella, hoplitomella, calciblastula, amphiblastula and trichimella. Each of these larval types have and can be used as morphological identifiers of different sponge taxa (Maldonado, 2004). Most sponges belonging to the classes Calcarea and Demospongiae have indirect larval development phases, whereby the embryos become a larval form which may strongly differ from the adult stage morphologically. This may also be the case for the Hexactinellida, but there is a scarcity of information on the larval ecology of this class (Maldonado, 2004). The advantage of larval stages for sessile organisms such as sponges is that they can increase their dispersal capability allowing them to colonise geographically suitable habitats, both near and distant from their progeny (Maldonado, 2004). This study also stated that the dispersal capability provided by different larval stages may enhance population health by favouring gene flux between subpopulations and decreasing population consanguinity, in addition to increasing recruitment success (Maldonado, 2004). Sponge larvae are lecithotrophic and with a relatively short planktonic life cycle (Maldonado, 2004). Sponges range in size from microplankton (50—500 µm) to mesoplankton (0.5—6 mm) (Maldonado, 2004).

In most sponges the embryo develops internally, and once the larvae are ready to be released they begin to swim through the aquiferous system (Bergquist & Sinclair, 1968; Fell 1989; Maldonado & Young, 1996; Maldonado and Uriz, 1999). Nevertheless, in sponges with external development, embryogenesis occurs either in the water column or on the sea-bed as eggs and

early embryos are usually expelled in negatively buoyant envelopes and or mucus strands (Maldonado, 2004). Brooding sponges usually take several weeks or months to develop their larvae compared to external developers which can take 2—3 days after fertilization (Maldonado, 2004). There are a number of signals which can influence the onset of the release of sponge larvae including temperature, photoperiod, lunar cycles, and pheromones (Reiswig, 1970, 1983; Watanabe, 1978; Fell, 1983; Hoppe & Reichert, 1987; and Fromont, 1994).

There is a large variability in the number of sponge larvae released among sponge species in field observations (Maldonado, 2004). For example, North Atlantic individuals of *Ophlitaspongia papilla* have been observed releasing 18 larvae m^{-2} day^{-1} during a release season, compared to the Spanish Mediterranean sublittoral species *Ircinia oros* was observed expelling on average 2350 larvae day^{-1} and 3.3×10^4 larvae throughout the entire two week period studied (Fry, 1971; M. Maldonado, unpublished data). In contrast, there is a dearth of information regarding external larval development. Nevertheless, Fromont and Bergquist (1994) estimated that a female *Xestospongia bergquistia* spawned 1.4 million eggs with fertilization success of about 71.4% which totals approximately 1 million larvae derived from this single individual.

Sponge larvae disperse by becoming merozooplankton and drifting for a relatively short period of time in the water column. In theory Maldonado (2004) argues that the longer a larvae remains in the water column the greater the dispersal potential. However, a greater dispersal period may also increase the likelihood of mortality from predation or larvae being transported to an area that is not suitable for attachment (Maldonado, 2004). Due to the lecithotrophic nature of sponge larvae Maldonado (2004) has postulated three main limiting factors which influence the larval success and dispersal capabilities of sponge larvae: (1) the level of energy reserves in the larvae, (2) the species specific tempo of the developmental program, and (3) the availability of settlement cues in the environment. The majority of data available on sponge larvae suggest that most have a larval duration in the water column ranging from minutes to a few days (Maldonado, 2004). Nevertheless, unciliated hoplitomella is the only sponge larva consistently reported from offshore plankton samples, and they may remain in the plankton for a long time, perhaps months (Trégouboff, 1939, 1942; Vacelet, 1999).

Sponge larvae are for the most part considered to be lechithotrophic and arguably rely on the maternal egg lipids provided to them. However, Bergquist and Green (1977) found that

monociliated cells may incorporate dissolved compounds via phagocytosis in the pinacocytes. Jaeckel (1995) further demonstrated that larvae were able to assimilate the amino acid alanine and the fatty acid palmitic acid from seawater. The alanine was not considered energetically significant; however, the palmitic acid was estimated to account for 21—55% of larval metabolism. This is further complicated by the addition of research which found that ciliated cells of *Halichondria* (*Halichondria*) parenchymella were able to phagocytose and digest bacteria and small (>4 µm) unicellular organisms. Overall, the potential dispersal distance of sponge larvae is dependent on a number of environmental and physiological factors than can influence how far they travel and their survivability.

1.3 Ecological significance of sponges in marine ecosystems

Sponges play an important role in supporting a multitude of life in marine ecosystems. They create three dimensional habitats including bowls, fingers, tubes, and mounded morphologies that are colonized by a variety of mobile invertebrates such as echinoderms, polychaetes, molluscs, and crustaceans (Ribeiro *et al*., 2003; Henkel & Pawlik, 2005; Roberts *et al*., 2008). Biogenic habitats characterized by sponges are primarily utilized by herbivorous, suspension feeders and tube dwelling amphipods (Roberts *et al*., 2008). Furthermore, sponges have been recorded as supporting several additional sessile invertebrates including ascidians and bryozoans (Ribeiro *et al*., 2003). Notably, New Zealand sponges support important nurseries for goatfish *Upeneichthys lineatus* (Froese & Pauly, 2019), and commercially important fisheries species such as snapper *Pagrus auratus* (Battershill, 1987). Bell (2008a) conducted a literature review on some of the most important functional roles sponges perform in marine ecosystems. These included reef creation, substrate stabilization, benthic pelagic coupling, carbon cycling, silicon cycling, oxygen depletion and nitrogen cycling (Bell, 2008a). Therefore, if sponges are lost from benthic ecosystems this may have negative ecosystem effects by limiting the food and habitat availability for sponge associated organisms.

Sponges act as ecological indicators because they are sedentary, they integrate across prevailing biophysical conditions, hence act to monitor the health of benthic ecosystems, and reflect environmental effects at a localized level (Carballo *et al*., 1996; Vilanova, 2004; Batista *et al*., 2013). Benthic-pelagic coupling is one of the most fundamental properties of sponge biogenic habitats (Bell, 2008a; Maldonado *et al*., 2012). Recent evidence suggests that sponges can be

useful as natural environmental DNA (eDNA) samplers for examining marine biodiversity within a geographic location (Mariani *et al*., 2019). Environmental DNA metabarcoding has surged in its use over the past five years as an alternative method of biodiversity monitoring. Sponges are highly efficient filter feeders that are capable of sifting through 10,000 litres a day, and they can trap and concentrate eDNA from surrounding water which makes them ideal bioindicators (Mariani *et al*., 2019; Kahn *et al*., 2015). Furthermore, unlike other motile organisms, sponges remain fixed to the substrate and are thus useful for monitoring the biodiversity in the surrounding location they are sampled from.

1.4 Carbon cycling and the sponge loop hypothesis

One of the most important roles sponges play in cycling nutrients is their ability to collect organic matter and recycle it to higher trophic levels (Rix *et al*., 2018). The role of sponges in cycling nutrients is particularly important in food-poor oligotrophic environments such as coral reefs and the deep sea where other organisms may rely on food produced by sponges in the form of biomass or particulate organic matter. Sponges on coral reefs facilitate the transfer of coral-derived organic matter to detritivores by producing detrital matter as sponge cells (Fig. 1.1) (Rix *et al*., 2016; Rix *et al*., 2017). However, the importance of the sponge loop hypothesis in temperate marine systems is poorly understood.
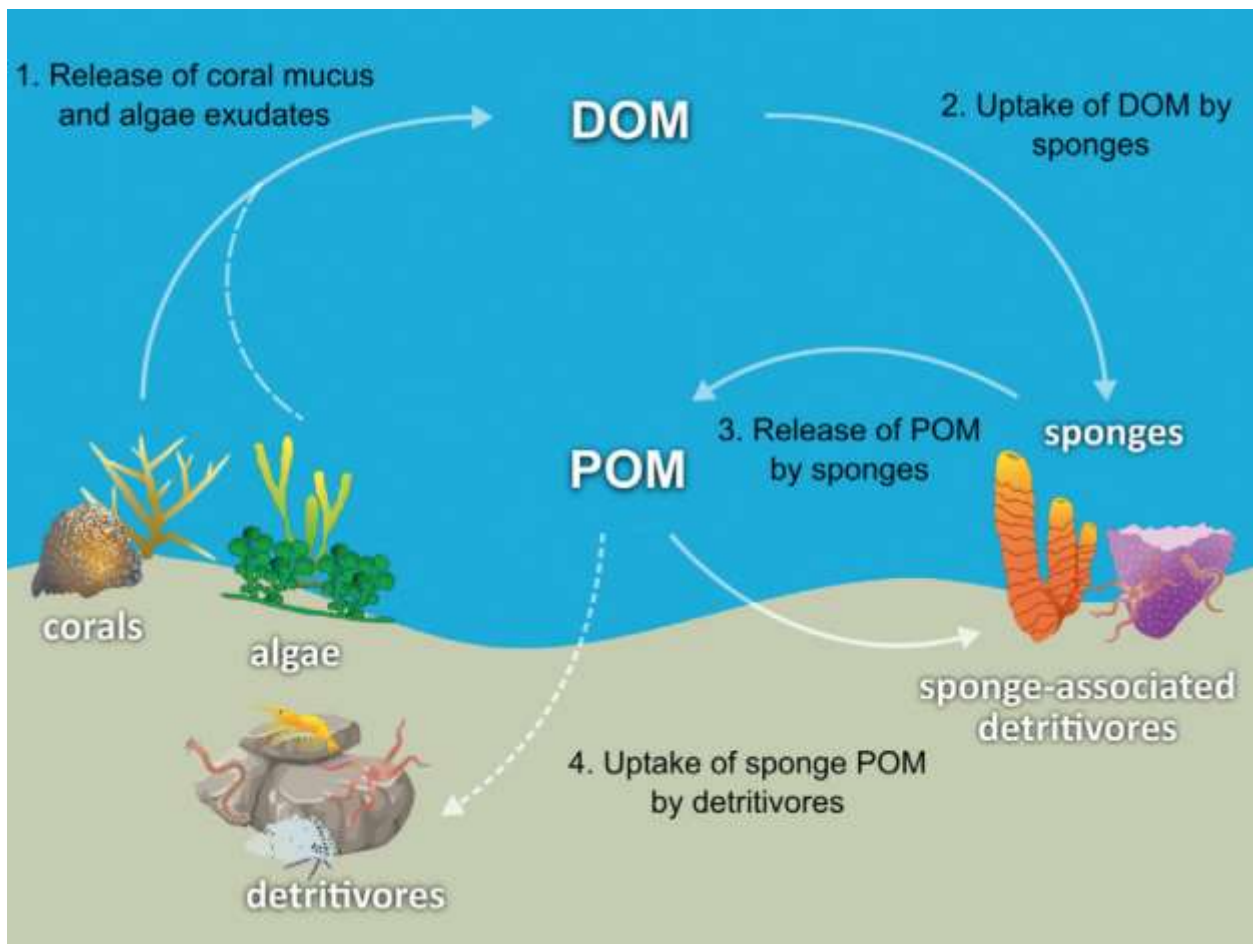
Figure 1.1 Steps of the sponge loop pathway: (1) corals and algae release exudates as dissolved organic matter (DOM), (2) sponges take up DOM, (3) sponges release particulate organic matter usually in the form of sponge cells (POM), (4) sponge detritus (POM) is taken up by sponge-associated and free-living detritivores (modified from Rix *et al.*, 2018).

A carbon balance of sponges is described in its simplest form by Maldonado *et al.* (2012), with the following equation:

$$I = P + R + E,$$

where I = carbon ingestion, P = its use for biomass production, R = respiration, and E = ingestion and excretion of material from sponges.

Both P and R are collectively represented as assimilation (A). Maldonado *et al.* (2012) defined ingestion in sponges as the incorporation of carbon into the tissue of the sponge and not the total amount of organic matter entering the sponge. After ingestion, carbon is utilized for growth, and production of energy (Maldonado *et al.*, 2012). Moreover, sponge waste is often

recorded in the form of detrital material (DOC and POC), composed of digested and undigested material, and an often-overlooked component of sponge excretion is faecal pellets which sink to the ocean floor becoming unavailable for suspension feeders (Witte *et al*., 1997; Maldonado *et al*., 2012).

Growth rates of sponges range from very slow growing specimens in cold waters 0.003% to 0.07% y^{-1} in volume, to 5–60% y^{-1} *in situ* for temperate and tropical individuals (Reiswig, 1973; Dayton, 1979; Hoppe, 1988; Leys & Lauzon, 1998; Koopmans & Wijffels, 2008; ; McMurray *et al*., 2008; Van Duyl *et al*., 2008; Maldonado *et al*., 2012). However, Duckworth and Battershill (2003) recorded much larger growth rates of *Latrunculia* (*Biannulata*) *wellingtonensis* (see also, Alvarez *et al*., 2002), and *Polymastia crocea* which grew 960% and 730% respectively over a six-month period from explants indicating that fast growth is possible and that a size plateau may well be reached. A number of researchers have also reported a large growth rate of the Antarctic sponge *Anoxycalyx joubini* which had increased in size by 30% over a two year period, compared to 1974–77 when several Antarctic species had measurable but very slow growth (Dayton *et al*., 2013; Dayton *et al*., 2016). Moreover, Wulff (2017) recorded the mean specific growth rates of 12 sponge species *in-situ* over a 12 month period and found that growth rates differed among species but ranged from 0.9 to 4.7%: and after 20 months from 1.2 to 9.7% with some species remaining the slowest (*Ectyoplasia ferox*) and fastest growing (*Desmapsamma anchorata*) respectively.

1.5 Impacts and threats to sponges

Rising atmospheric CO_2 and associated acidification of seawater together with other climate change related shifts in temperature, oceanic circulation, stratification, nutrient input, and oxygen content will have potentially devastating impacts on marine ecosystems worldwide (Doney *et al*., 2012). A primary concern of climate change related impacts are the effects on cryptic biota, including sponges, which are increasingly argued to play important roles in marine ecosystems. A review conducted by Webster (2007) stated that marine diseases are significantly impacting sponge populations globally. One of the most severe examples of a sponge disease epidemic occurred in the Caribbean in 1938 causing the mortality of 70–95% of sponge individuals (Galstoff, 1942; Webster, 2007). Wulff (2013) conducted a study examining the

devastating effects of cyanobacterial blooms on the Belize Barrier Reef in 2011 and provided a better understanding on the non-mass mortality dynamics as well as an exact measure of biomass lost for 54 species at the site. Although there has been a general failure to identify causative agents for sponge disease, general causes are potentially correlated to environmental factors including climate change in addition to urban and agricultural runoff (Cervino *et al*., 2006; Webster, 2007). Bell *et al*. (2015a) examined the impacts of sedimentation on marine sponges including pumping rates, feeding, respiration, reproductive output, growth, impacts of sediment on sponge symbionts, and the consequences of altered larval recruitment success and mortality of established sponges on demography and diversity patterns (biogeography). Sediment impacts on sponges are dependent on the quantity, particle size and mineralogy of the material inundating reefs (Bannister *et al*., 2012; Bell *et al*., 2015a). Sedimentation has clear harmful effects on sponges; however, most studies suggest that sponges have developed adaptations to tolerate or sometimes thrive in highly sedimented environments (Bell *et al.,* 2015a).

Despite an increase in the number of sponges reported at some locations, there is a clear decline in other populations. For example, within the tropical Atlantic cyanobacterial blooms reduced the abundance of six sponge species with a mortality rate of 23–80% (Butler *et al*., 1995; Bell *et al*., 2015b). Introduction of non-indigenous taxa may also have a negative impact on sponge fauna. For example, the introduction of a non-indigenous species of algae *Caulerpa scalpelliformis* resulted in the decline in the abundance of sponges on a deep-reef habitat (Davis *et al*., 1997; Bell *et al*., 2015b).

Bell *et al*., (2015b) found that based on all the literature published on the impacts to sponges, there were many stressors that can cumulatively impact sponge populations including change in temperature, increased suspended sediments, substratum loss, introduction to microbial pathogens, abrasion, hydrocarbon contamination, introduction of non-indigenous species, hypoxia, physical damage, changes in salinity, increased turbidity, and changes in pH (Bell *et al*., 2015b). What has not been considered in any detail is how environmental change affects what sponges consume, i.e., the source of sponge food being produced in future climate scenarios, and the response of sponges including potentially increased metabolisms related to temperature and other biophysical conditions. Overall, sponges face a plethora of anthropogenically and environmentally driven impacts globally. It may be difficult to tease apart

exact modes of sponge mortality given the complexity of marine systems; however, sponges have a large diversity of physiological adaptations to combat certain levels of impacts. Some sponge species appear to be well suited to certain levels of stressors including sedimentation and changes in temperature, but it is important to determine how cumulative stressors will affect sponge populations in a changing world.

1.6 Taxonomy of sponges in New Zealand

As with any ecosystem study, it is important to know and identify the species components, particularly those of central interest. For research on sponges and sponge ecology, reliable identifications are frequently lacking, especially if new geographic locations are the focus of the investigation. Therefore, an essential element of this work has been to identify the species of interest. The study herein has led to the discovery and description of new species and improved descriptions of species that have been historically described. However, the current area of interest in the Taranaki region is a relatively new area in terms of the characterization of its sponge fauna and ecology due to the logistical difficulties of conducting diving activities on uncharted reefs. Furthermore, there are often low visibility conditions and prevailing westerly winds making it difficult to work in this region.

Kelly *et al*., (2009) reported on the history of sponge taxonomy in New Zealand, including the earliest work conducted by Gray (1843) who listed three sponge species in his chapter 'Fauna of New Zealand' in Ernst Dieffenbach's *Travels in New Zealand*. Kelly *et al*. (2009) reported on the work of Hutton (1904) who created a list of all the 354 sponge species found in New Zealand at that time. An additional 92 species and 'varieties' of sponge species, and five unnamed sponges were recorded by Kirk (1904) in a book chapter written by Hutton (1904). Later, sponges from the Kermadec Islands were reported by Kirk in 1911 (Kelly *et al*., 2009). Subsequent investigations were conducted by Dendy (1924), and Brøndsted (1923; 1924; 1926) who described a total of 166 sponge species, of which 106 were considered new to science (Kelly *et al*., 2009).

A new era of sponge taxonomic research occurred in the 1960s with the work of Bergquist (1961a; 1961b; 1961c) describing 26 new sponge species (Kelly *et al*., 2009). Dawson (1993) provided a list of all marine Porifera recorded from New Zealand listing 354 sponge species (Kelly *et al*., 2009). Further prominent taxonomic contributions around this period included: Bergquist,

1968, 1970, 1972, 1980, 1996; Ayling, 1979; Bergquist & Warne, 1980; Pritchard *et al*., 1984; Bergquist & Fromont, 1988; Bergquist & Kelly-Borges, 1991, 1995; Kelly-Borges & Bergquist, 1994, 1997; Cook & Bergquist, 1996, 1998, 1999, 2000, 2001, 2002; Bergquist *et al*., 1998; Cryer *et al*., 2000; Kelly, 2000, 2003, 2007; Kelly & Buckeridge, 2005; Kelly *et al*., 2009; and Battershill *et al*., 2010. There were also a significantly large number of taxonomic publications describing the New Zealand sponge fauna in the following decade (Kelly & Vacelet, 2011; Reiswig & Kelly, 2011; Sim-Smith & Kelly, 2011, 2015, 2019; Kelly & Sim-Smith, 2012; Kelly *et al.,* 2015a, 2015b; Sim-Smith & Kelly, 2015, 2019; Hestetun *et al*., 2016; Kelly *et al*., 2016; Kelly & Cárdenas, 2016; Kelly, 2018; Kelly & Rowden, 2019; Zeng *et al*., 2019; and Mc Cormack *et al.,* 2020). There is current work underway to revise the species list for valid sponges found throughout New Zealand over the past decade (M. Kelly, 2021, pers. comm.). However, most of the earlier taxonomic work conducted from 1843 to 2000 have not been reviewed, revisited, or updated to include modern morphological descriptions such as *in situ* photographs. Moreover, there is an urgent need to classify and describe regional fauna, especially in areas where anthropogenic activities are having potential impacts on sponge communities. This is a difficult task given the scarcity of sponge taxonomists working in New Zealand. Suffice it to say, any new marine study focusing on sponges will invariably invoke a need for biosystematics and the identification of new species (Mc Cormack *et al*., 2020; Appendix 1 & 2).

1.7   Aims and organisation of thesis

Sponges face cumulative threats to their survival, and they are ecologically important as they support of diversity of other taxa that are functionally beneficial to marine ecosystems worldwide. Information permitting a more comprehensive understanding of the role sponges play in trophic cascades is difficult, especially for temperate regions. In addition, the influence of coastal processes, especially those associated with catchment discharges of sediments and nutrients on sponge characterised communities is scarce.

Given the potentially devastating effects of CO_2 rise and associated climate change related environmental shifts (Doney *et al*., 2012), in addition to the numerous additional anthropogenic threats facing sponges; the baseline health and physiology of marine sponges and the consequences of altered population's structure, biogeography and trophic exchanges requires urgent attention. There is a need for information regarding the general health including

distribution and abundance of sponges and other taxa in poorly studied regions of New Zealand. What is not clear is the effects that land use and coverage from terrestrial ecosystems are having on sedentary benthic invertebrates such as sponges. Terrestrially derived matter, including pollutants and nutrients, are carried to the oceans by river systems along with sediments. The combined impacts these riverine inputs (positive and negative) are having on sponge communities is poorly understood.

This thesis focuses on four key areas:

Chapter Two: The biogeography of New Zealand Sponges with a Focus on Taranaki.

Chapter Two describes the biogeography of Taranaki from a sponge systematics perspective, providing the backdrop for the remaining thesis. The biogeography of New Zealand benthic encrusting fauna is not well understood at medium geographic scales. Recent reviews by Biosecurity New Zealand cast Aotearoa New Zealand into several large geographic and biogeographic zones (Beaumont *et al*., 2010). There are many gaps in knowledge, especially in areas where research is difficult due to unfavourable weather and sea conditions. These areas also happen to be important areas for monitoring as they are in locations likely to be influenced by changes in oceanic circulation. The Taranaki region is one such high priority location in New Zealand with little detailed information on the ecology and biogeography of shallow water coastal ecosystems. This research focuses predominantly on North Taranaki, which has different bathymetry to South Taranaki. Therefore, the ecology of South Taranaki requires further research to increase our understanding of the whole of the Taranaki region.

Chapter Three: Environmental factors influencing the distribution and abundance of marine sponges around the Taranaki region of New Zealand.

A baseline description of sponge species and associated benthic taxa was created over a three-year period. This was designed to permit ecological focus on sponge characterized communities at moderate spatial scales, to examine the effects of coastal dynamics on trophic cascades. Decadal data on physiochemical conditions of three major Taranaki Rivers were supplied by Taranaki Regional Council to assess potential effects of riverine water quality and their catchments on nearby marine coastal reef communities. Here, I hypothesize that there would be a larger diversity and abundance of sponges in coastal rocky reef communities that were subject

to rivers with 'good' ecological health. Therefore, rivers were chosen to represent a gradient of water quality and catchment land cover types. Environmental factors potentially influencing the distribution and abundance of marine sponges around the Taranaki region of New Zealand were investigated.

Chapter Four: Land-sea connectivity: using stable isotopes (δ^{13}C and δ^{15}N) to understand the role of marine sponges in processing terrestrially derived carbon.

Carbon and nitrogen stable isotopes were analysed to understand the role marine sponges play in processing terrestrially derived carbon. A Bayesian Mixing model (MixSIAR) was used to investigate the food web structure of coastal temperate rocky reef sponges and determine which food sources (terrestrial or marine) contributed the highest proportion of food to their diet. The hypothesis is that there would be a larger availability of food coming from rivers with good water quality and ecological health, and that coastal rocky reef sponges were deriving a large proportion of their food from terrestrial systems.

Chapter Five: General Discussion:

The overall goals of this thesis were to provide a greater insight into the taxonomy, biogeography and ecology of sponges (Porifera) from west coast, North Island, New Zealand. This thesis presents a number of key findings: (1) that the biogeography of the Taranaki region is complex over medium spatial scales and reflects a combination of geological profile and effects of ocean currents, (2) the ecology of Taranaki sponge characterised communities reflects nearshore dynamics of adjacent catchment systems, (3) trophic cascades are occurring via the cycling of terrestrially derived organic matter from rivers into coastal reef communities, (4) a cross section of biophysical dynamics influencing the nature of sponge characterized communities is provided. These dynamics play an important role in nearshore productivity and trophic cascades. Land-sea connectivity and the health of coastal catchments is paramount in supporting nearshore coastal productivity.

Chapter 2

The biogeography of Taranaki sponges

2.1 Abstract

The biogeography of Taranaki sponges is unique over small spatial scales. A high level of endemism in the Taranaki sponge fauna is confirmed, the diversity in some areas so unique that the Department of Conservation established a marine reserve in 2006 to protect the exceptional sponge assemblages (from lost gill net entanglements) - Parininihi Marine Reserve. Apart from surveys in the late 1990s associated with protection of the Parininihi reef system, little was known about the biodiversity of sponges (or benthos in general) at larger spatial scales in this region.

This study has shown that the geographic range of sponge species is patchy, and that species assemblages in places like Parininihi Marine Reserve are highly unique. Results from this investigation provide a baseline species diversity estimate with a total of 127 sponge species recorded from all shallow water stations in Taranaki surveyed herein, with an index estimation of 2.4 sponge species per m^2 of rocky reefs surveyed. Pariokariwa Reef had the largest number of sponge species unique to that area (44 unique species). Surprisingly, Waitara reefs, arguably the most sediment impacted, had the second largest number of unique sponge species among all locations in Taranaki (36 unique species), followed by Patea reef (12 unique species), Hangatahua (9 unique species), and Waiwhakaiho (6 unique species). Overall, these findings have important implications for developing conservation strategies for marine fauna on this coastline, highlighting locations of significant biological diversity, abundance, and uniqueness.

2.2 Introduction

A fundamental property of ecological investigations conducted within any poorly studied region will always be good baseline taxonomic assignments involving the characterization, naming and identification of species. Lack of taxonomic expertise and poorly identified taxa is a major constraint to marine ecological studies, especially those involving sponges. In recent years there has been an increasing interest in potential anthropogenic impacts to sponges, which includes broad scale climate change related stressors such as land derived sedimentation because of accelerated hydrological cycles. Furthermore, recent studies have

heightened the need to understand the health and conservation status of sponge communities facing compounding anthropogenic threats. However, very little research has been conducted on the biogeography, ecology, and taxonomy of marine sponges in the Taranaki region of New Zealand. Sturgess (2015) stated that the distribution of marine invertebrates along the west coast of the North Island of New Zealand has been poorly studied because of the surf conditions which limits the ability to survey these areas. There remain many unanswered questions concerning the significance of the reef system to the wider Taranaki region and west coast New Zealand coastal biogeography, not to mention potential opportunity in hosting future biodiscovery research.

This is seen as a major gap in knowledge as the Taranaki coastline is likely to be one of the regions affected by climate change induced shifts in oceanic currents, and alterations in Tasman Sea oceanography as evidenced recently along the eastern seaboard of Australia (Johnson & Holbrook, 2014; Oliver *et al.*, 2018). As such, the Taranaki coast could be viewed as a sentinel location for any changes likely to be experienced in Aotearoa.

In addition to potential shifts in the ocean climate, rapid changes in riverine inputs from terrestrial sources may also be impacting coastal reef communities in this region. Several researchers have reported on the evolutionary and ecological importance of sponges, yet sponges are not as well studied as corals and other benthic taxa that form structural habitats, and their significance within the global marine ecosystem is far less widely appreciated (Becerro, 2008; Przeslawski *et al.*, 2008; Schönberg & Fromont, 2011; Van Soest *et al.*, 2012; Fromont *et al.*, 2016). There is a general lack of management for sponge communities to the point where they are now considered a 'neglected group' (Saleuddin & Fenton, 2006; Bell *et al.*, 2015b; Fromont *et al.*, 2016).

Fromont *et al.* (2016) noted that knowledge of sponge species distributions is often impeded by significant numbers of undescribed species, making it difficult to characterize all taxa. Biogeographic studies are limited by the number of taxonomic experts available, and the number of taxa required to be identified, especially in poorly studied regions. Therefore, restricting identifications to Linnaean taxa can significantly underestimate the true biodiversity of a region, and the use of OTUs (operational taxonomic units, or morphological concepts) can significantly improve estimates of undescribed or cryptic sponge fauna (Fromont *et al.*, 2016).

There are three key factors that influence the magnitude of dispersal patterns of sedentary marine invertebrate larvae. These include (1) the length of their larval life, (2) the swimming behaviour or ability of their larvae, and (3) the hydrographic regimes that the larvae encounter during the planktonic phase (Young & Chia, 1987; Graham & Sebens, 1996; Paris & Cowen, 2004; Mariani et al., 2006). Timing of larval release is also a factor that influences the magnitude of dispersal patterns as sponges as outgoing tidal cycles could draw sponges away from settlement habitats and nearshore reefs. Although factors affecting larval dispersal of sponge species cannot explain the exact distribution of populations (Mariani et al., 2006) this information may act as a guide for potential modes of distribution. For example, long-lived (typically dispersing for months) sponge larvae may remain close to localized parental populations via specialist behavioural adaptations that limit their horizontal movement in the water column, thus limiting their dispersal (tens of kilometres) (Paris & Cowen, 2004; Mariani et al., 2006). Mariani et al. (2006) also argued that it is likewise possible that even short-lived larvae (typically short dispersing, for several days) that are incapable of efficient swimming can be transported and dispersed by currents over relatively large distances (hundreds of kilometres) after being transported to a mainstream oceanic flow. Interestingly, Mariani et al. (2006) found that pelagic larvae with efficient swimming and cue responses (light intensity) can actively counteract hydrodynamic forces to some degree. However, short-lived, non-feeding larvae of some Order Dictyoceratida species may favour retention near parental habitats, thus enhancing self-seeding and self-recruitment (Mariani et al., 2006). Therefore, in the current study attention is placed on the possibility of spatial selection of localized sponge communities with specialized behavioural adaptations or preference for parental habitats by reproductive propagules, contrasted with species that may have reproductive strategies that are less 'selective' for localized habitats, against the prevailing biophysical conditions of the different locations examined. However, sponge species that can accommodate wide scale distribution patterns should be commonly found at all localities examined. In addressing these theories, the extent that major oceanic current systems can influence the coastal benthos around New Zealand as correlated to the distribution patterns of sponge fauna, can be ascertained.

There have been few ecological studies on sponge populations in Taranaki, which is likely attributed to the logistical difficulties of conducting surveys in this isolated region, in addition to dynamic weather conditions and generally poor water visibility for diving (average subtidal visibility <4 m). Furthermore, a large proportion of the rocky reefs within the Taranaki

region are uncharted. Therefore, local expertise and experienced skippers are required to explore this coastline to locate sponge rocky reef habitats. This study will focus on sponge populations living on shallow coastal rocky reefs at large regional scales (over hundreds of kilometres) and at local scales over tens of meters in the Taranaki region and draw upon information from surveys conducted from Kapiti Island in the Wellington region. Apart from Battershill and Page (1996), and Kelly *et al*. (2017), there is a general lack of research on sponge communities both from a taxonomic and ecological perspective in the Taranaki region.

Regional endemism is substantially higher in sponges than other marine invertebrate phyla across the globe's oceans (Wilson & Allen, 1987; Van Soest, 1989;Kelly *et al*., 2009). Remarkably, for New Zealand Porifera, endemism is reported to be as high as 95%. This is likely due to the isolated nature of New Zealand's land mass and relatively early departure from Gondwanaland (85 mya) (Suggate, 1990). Thornton, 1997). Kelly *et al*. (2009) noted the historical tendency of sponge researchers to give New Zealand sponge species incorrect species names (mostly European), giving the false impression that many sponges are cosmopolitan. Kelly *et al*. (2009) also highlighted the need for documentation of regional sponge fauna in New Zealand, specifically those from the west coasts of both main islands and the South Island. There is continued need here to renew interest in expanding sponge biodiversity initiatives at both regional and national scales.

There have been regional studies that focus specifically on marine sponges, in combination with other phyla while also examining the anthropogenic threats these organisms are facing in a changing world. Battershill and Page (1996) conducted the first ecological study of sponges in the Taranaki Region with a preliminary survey of Pariokariwa Reef in North Taranaki, which now forms part of the 18 km^2 of Parininihi Marine Reserve. This study found dense assemblages of sponges at depths from 5–25 m, covering areas of greater than 75% of available boulder space (Battershill & Page, 1996). Pariokariwa reef is subject to extremely high-energy areas and large-scale erosion and therefore it was surprising for the authors to find such a diverse assemblage of sponge fauna at this location (Battershill & Page, 1996). Further identification work has been conducted by Kelly *et al*. (2017) for sponges at Patea Reef located in South Taranaki as part of a citizen science project involving the identification of organisms at Patea Reef (Project Reef South Taranaki, 2021).

This chapter will focus on qualitatively examining the hypothesis that the biogeography of sponge taxa in the Taranaki region is complex over medium spatial scales

and reflects a combination of geographic aspect, geological profiles, land derived river inputs (sediments), and effects of oceanic currents. It is designed to set the backdrop for the following chapters that examine the drivers for observed distribution and abundance of sponges around Taranaki.

2.3 Methods

A taxonomic biogeographic characterization of sponge species from the Taranaki region was undertaken. Sponge specimens were collected for analysis using SCUBA by Samuel Mc Cormack (SMcC) over three years and two southern hemisphere seasons (autumn, April 4–5, 2019; summer, January 14–17, 2020; and summer, January 15–20, 2021), along three transects from Taranaki in the North Island of New Zealand (Fig. 2.1). Transects were coastally positioned adjacent to three rivers discharging from increasingly 'pristine' catchments: Waitara reefs (Waitara coastal near and distant stations), Waiwhakaiho reefs (Waiwhakaiho coastal near and distant stations), and Hangatahua Reef (Fig. 2.1). Transects were characterized by differences in terrestrial, freshwater, and marine organic inputs from diverse land uses and coverage, and water quality and were selected to provide a representative cross section of anthropogenic impact on the land (Taranaki Regional Council, 2018). We sampled 2–3 stations along each transect (WAI, WAIW and HAN): 1–2 coastal rocky reef stations about 1–2 km offshore (from the three rivers — Waitara, Waiwhakaiho and Hangatahua). At each station, sponges were collected at depths between 12–19 m from rocky reefs using a sharp dive knife and placed in containers for storage.

The survey protocol resulted in a fast plateau of new species 'finds' within each dive and station suggesting that the method effectively permitted collection of most species present at each station.

Data from this project was combined with previous taxonomic information conducted by Battershill and Page (1996), Kelly *et al*. (2017), together with records of sponge taxa recorded from Kapiti Island (also by the author for the Department of Conservation), to determine the biogeography of sponges along the central west coast of the North Island of New Zealand. Previous taxonomic work conducted on sponges from the Tauranga Harbour was used as a precursor study as part of this PhD, to develop the capacity and taxonomic expertise to undertake broad-scale ecological studies of sponges from the remote Taranaki region (see Appendices 1 & 2). The previous taxonomic work conducted on Bay of Plenty

sponges found in Appendices 1 & 2 is an example of the diligence that is required to undertake such a study, and both manuscripts are in preparation for publication as part of this overall study as some of the species overlap the Taranaki fauna. For example, to provide a comprehensive update of five common New Zealand sponge species all sponge specimens for each species stored at the NIWA Invertebrate Collection (NIC) and the Museum of New Zealand Te Papa Tongarewa Wellington (NMNZ) were examined. Institutional records, combined with collections from the current study extend our understanding of the morphological boundaries of each species within New Zealand. The research conducted in appendices one and two sets a precedent for the appropriate method to conducting modern day redescriptions of sponge species in critical need of revision from New Zealand.
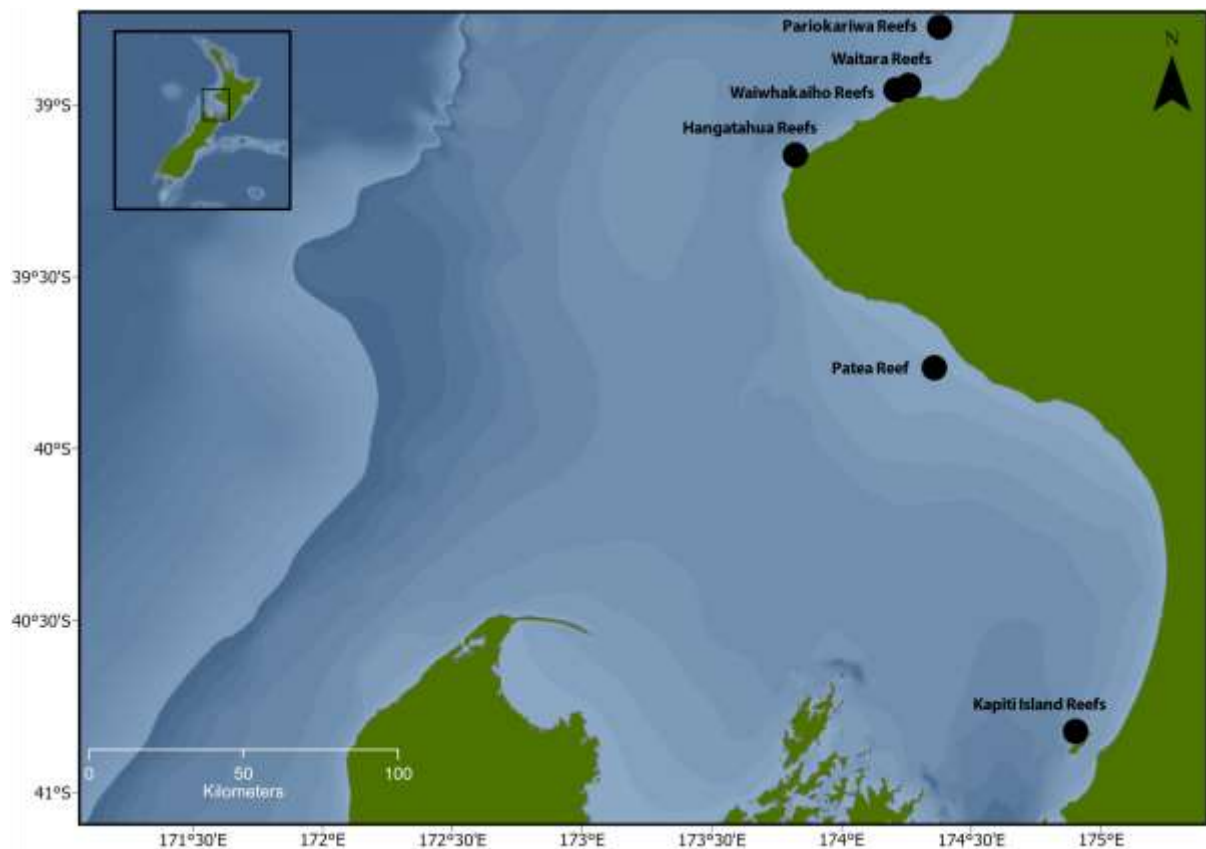
Figure 2.1 Coastal locations surveyed within the current study (black dots), Waitara reefs (Waitara coastal near and distant reefs), Waiwhakaiho reefs (coastal near and distant reefs), and Hangatahua reefs. Additional black dots represent locations not surveyed in the current study but analysed as part of the wider biogeographic study from Patea Reef and Kapiti Island reefs.

2.3.1 Study region oceanography and current systems
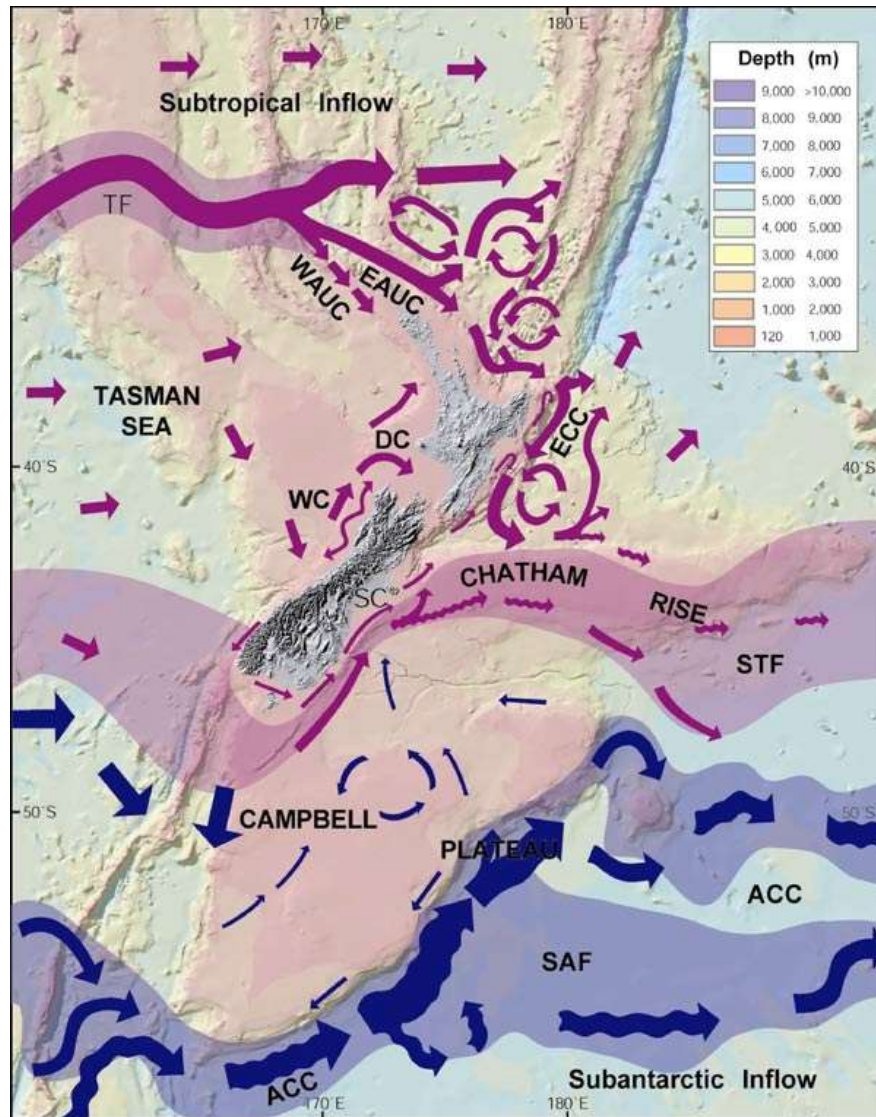
Figure 2.2 The land mass of New Zealand is surrounded by three major water masses, and the boundaries of these masses are called fronts. The diagram above shows the fronts of these water masses including the Tasman Front (TF), Subtropical Front (STF) and Subantarctic Front (SAF). Warmer masses including the Tasman Front has relatively warm waters and surface currents. Eastward flows of warm water split around New Zealand, and currents flow south-eastwards around the North Island's east coast, and north-westward around the South Island's east coast. A cooler Sub-Antarctic Front is found at the bottom of New Zealand's Exclusive Economic Zone. In southern New Zealand Sub-Antarctic and cold Antarctic Circumpolar Current (ACC) flow near the deep ocean floor to the east of Campbell Plateau and Chatham Rise. The D'Urville Current (DC) is an important current system that influences the Taranaki Region and Fauna within the current study area (modified from Te Ara Encyclopedia of New Zealand, 2021).

The current systems around New Zealand's Economic Exclusion Zone (EEZ) likely play important roles in distributing sponge species given the poor swimming abilities of the larvae of certain species. The west coast of New Zealand's North Island is influenced by three major currents including the West Auckland Current flowing south from the top of New Zealand's

North Island, the Westland Current flowing north from the west of the South Island. Finally, the D'Urville Current, flowing southeast through Cook Straight, is the most influential current systems in the Taranaki region and may provide insight into the organisation of some sponge taxa that rely on hydrodynamic systems for dispersal (Salinas-de-León *et al*., 2012; Fig. 2.2). Chiswell and Stevens (2010) used Lagrangian and Eulerian measures to estimate current flow around Kapiti Island and reported that the mean flow was to the south-west, towards the Cook Strait. Nevertheless, current flow and direction is likely heavily influenced by the exposure to wind conditions along most parts of the west coast of the North Island of New Zealand. A study conducted on the sponge larvae of an intertidal gastropod species *Austrolittorina cincta* on the southeast coast of New Zealand's North Island found that most of the positively identified larvae dispersed over a distance of <5 km, low numbers were fund at distant locations (15–50 km), and very few larvae travelled over 100 km (Salinas-de-León *et al*., 2012). Therefore, this study highlights the likelihood of some gastropods having mostly localised <5 km dispersal distances along this coastline, likely attributed to longshore tidal flow. Consequently, this may provide insights into the potentially limited dispersal of other taxa including sponge larvae along the west coast of the North Island of New Zealand.

Although these are different taxa to sponges larvae and sponge larvae may have different swimming, or buoyancy capabilities, these sorts of studies provide insights into potential dispersal distances. Although the wider coastal geomorphology of the sea floor may also potentially influence the biogeographic distribution of sponge populations an examination of these effects is beyond the scope of the current study.

2.3.2 Species assemblages around Taranaki

Datasets were compiled from four sources from around Taranaki and Kapiti Island on the western coast of the North Island (Data from Kapiti is provided for comparison, mindful that it is an offshore island compared to otherwise coastal locations). The first dataset analysed was from work conducted by Battershill and Page (1996) who conducted a preliminary survey of Pariokariwa Reef in north Taranaki. Commissioned by the Department of Conservation (DOC) Battershill and Page (National Institute of Water and Atmospheric Research, NIWA) surveyed the reef and collected specimens of benthic invertebrates for identification. The impetus for the work was based on local iwi reports of a rich and varied sponge-characterised community that was under threat from lost gill nets fouling the reef. NIWA (Battershill, Bergquist, Gordon as taxonomists) was commissioned to identify sponges and brachiopods

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on Pariokariwa Reef, which at the time was being proposed as a new marine reserve (now titled Parininihi Marine Reserve). The survey also had a secondary aim of providing advice on the status of the reef and its occupants (rare, common, undescribed species) (Battershill & Page, 1996). Five dives were completed by the team and visited by NIWA with support from the Department of Conservation with the aim of covering as much different habitat forms as possible (Battershill & Page, 1996). Communities were qualitatively characterized, and collections of as wide a range of diversity of marine fauna and flora as possible were undertaken. Sponge species were then stored for laboratory taxonomic identification to at least genus level by Battershill and Bergquist. This survey highlighted the extreme exposure of the Taranaki region and finer sediments covering slat areas in the subtidal benthos (Battershill & Page, 1996). The Pariokariwa Reef in north Taranaki was found to have exceptionally unique sponge communities in terms of area covered and endemism. For example, one reef was covered by over 70% bright orange sponge *Polymastia crassa* interspersed by *Polymastia* sp., *Tethya aurantium*, and *Aaptos globosa* between 10–15 m (Battershill & Page, 1996). Finger sponges (species not specified) occupied the deeper rocky reefs 10–25 m of Pariokariwa Reef with an inverse relationship between *Ecklonia radiata* coverage and finger sponge abundance (Battershill & Page, 1996). The summary of findings from this report suggested that there were many novel undescribed sponge species with two distinctive communities of *Polymastia crassa* and *Axinella* gardens at Pariokariwa Reef supporting a rich assemblage of associated taxa (Battershill & Page, 1996). A full species list from this survey has been compiled and was used as part of the larger scale biodiversity analysis of sponges in the Taranaki region, reported below, in addition to species from Kapiti Island in the Wellington Region further south (Appendix 3, A3.1).

An additional survey conducted by Samuel Mc Cormack (SMcC), researchers from the University of Waikato Coastal Marine Field Station, and Department of Conservation examined the biodiversity and ecology of marine taxa surrounding Kapiti Island. Ecological surveys conducted inside and outside of the reserve were conducted to determine if there was a greater diversity and abundance of taxa within the Kapiti Island Marine Reserve. Data from the Kapiti Island marine survey was compiled and utilized as part of the current wider geographic study herein.

An additional field identification guide for sponges and other taxa was created by taxonomists for Patea Reef, south Taranaki (Kelly *et al*., 2017). This sponge identification

guide was created to assist citizen science researchers who are part of South Taranaki Reef Life Project, which was developed to raise awareness for this unique offshore reef environment. This ongoing project is co-funded Curious Minds PSP, Ministry of Business Innovation and Employment (MBIE) and capital funds from Toi Foundation. The Reef Life Project is also supported by the voluntary resources of the South Taranaki Underwater Club and aims to obtain baseline ecological and biodiversity data of Patea Reef through regular sub-tidal monitoring. Kelly *et al*. (2017) provides a rough guide and list of sponge species commonly found on Patea Reef. This Patea Reef sponge species dataset was also utilised here to help understand patterns of sponge diversity in Taranaki.

2.3.3 New species descriptions

A comprehensive update of five common New Zealand sponge species was required to permit diligence in sponge taxonomic assignments. This work is a precursor to assignment of the many putative new species collected during this PhD study. A collaboration with researchers from the National Institute of Water and Atmospheric Research (NIWA), and the NIWA Invertebrate Collection (NIC) team allowed for a comprehensive review of all the literature and descriptions of these species from New Zealand. Appendix 1 describes two new species of *Dysidea* (Porifera, Demospongiae, Dictyoceratida, Dysideidae) from Tauranga Harbour, Bay of Plenty, New Zealand as an example of the approach taken to describe sponge taxa herein (Mc Cormack *et al*., 2020).

2.4 Results
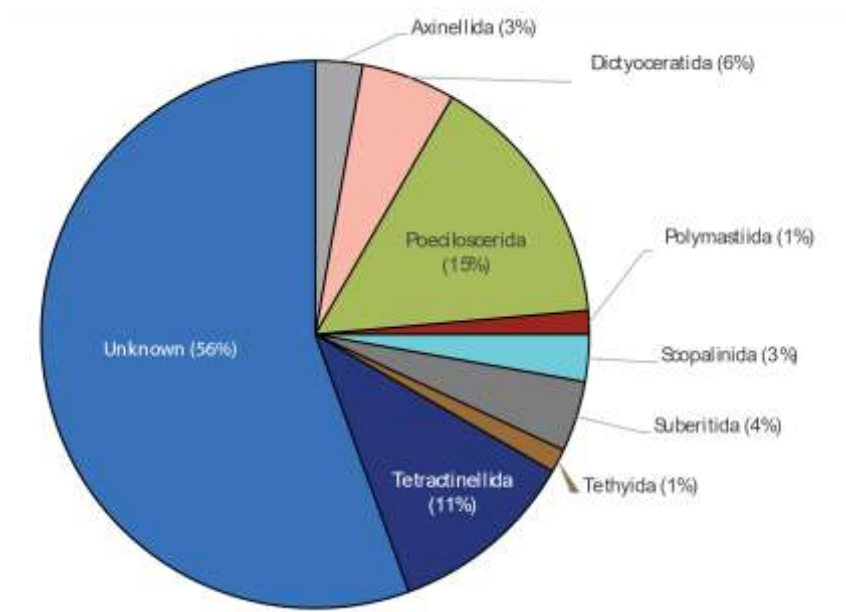
Figure 2.3 Proportion of higher taxa (ordinal classification) across 73 species and OTUs distinguished in this biodiversity survey from five combined coastal rocky reef stations in Taranaki (Waiwhakaiho coastal near, Waiwhakaiho coastal distant, Waitara coastal near, Waitara coastal distant, and Hangatahua coastal near). Values were rounded to the nearest percentage.

Based on taxonomic analysis of sponge specimens and non-destructive sub-tidal visual surveys it is apparent that the order Poecilosclerida Topsent, 1928, had the greatest percentage of individual sponges present at all stations at 15% (Fig. 2.3). The second most common order recorded from all stations was Tetractinellida Marshall, 1876, (11%), followed by Dictyoceratida Minchin, 1900, (6%), Suberitida Chombard and Boury-Esnault, 1999, (4%), Axinellida Lévi, 1953, (3%), Scopalinida Morrow and Cárdenas, 2015, (3%), and Tethyidae Gray, 1848, (1%) (Fig. 2.3). It should be noted that although there was a large proportion of unidentified sponge species across all stations (56%), it is difficult to visually characterize different sponge species sub-tidally without examination of their skeletal and spicule morphology (in progress for full taxonomic assignments).

There were 35 sponge species that only occurred at the northernmost and southernmost locations at Pariokariwa Reef in northern Taranaki and Kapiti Island in the Wellington region to the south (Appendix 3: A3.1). The index estimation for sponges in the Taranaki region was approximately 9.6 sponge species 1 m^{-2} of rocky reef. The black pillow sponge *Ecionemia alata* was the most widely distributed species, and the only taxon recorded at all six locations (Appendix 3: A3.1). Data related to sponge populations from Kapiti Island reefs and Pariokariwa reefs are being used in the current study as general comparisons for the data collected herein.

2.4.1 Species presence by taxonomic class

Heteroscleromorpha Cárdenas, Pérez & Boury-Esnault, 2012, was the most abundant sub class found at all locations (Table 2.1). Species and OTU level diversity were most abundant at Pariokariwa Reef (56 species) and Kapiti Island (86 species) (Fig. 2.4; Appendix 3: A3.3).

Table 2.1 Species presence and total number of species separated into taxonomic subclasses from combined surveyed and taxonomic collection data at each location: Pariokariwa reefs, Waitara reefs, Waiwhakaiho reefs, Hangatahua reefs, Patea Reef, and Kapiti Island reefs.

Class	Subclass	Number of species							
		Pariokariwa	Waitara	Waiwhakaiho	Hangatahua	Patea	Kapiti	Taranaki	All locations
Calcarea	Calcaronea	3	0	0	0	0	1	3	4
Calcarea	Calcinea	0	0	0	0	0	1	0	1
Demospongiae	Unknown	0	2	0	0	0	0	2	2
Demospongiae	Heteroscleromorpha	44	20	11	9	21	71	105	176
Demospongiae	Keratosa	9	4	2	1	2	13	18	31
Total		56	26	13	10	23	86	128	214

There were 242 apparently different sponge species present among all locations surveyed (Table 2.2). Waitara had the highest number of different sponge species at 47, and a percentage of different sponge species at 19% among all stations sampled in the current study (Table 2.2). However, Pariokariwa had the largest number of different sponge species among all Taranaki stations when previous studies are included in the analysis at 56 different species, and 24% of all sponges were different species (Table 2.2). Kapiti Island was the most biodiverse in terms of its number of different species at 89, and 37% of individuals from this station were different species (Table 2.2).

Table 2.2 Number of different species, and percentage of different sponge species that occurred in quadrats at surveyed reefs from each location.

Species	Pariokariwa	Waitara	Waiwhakaiho	Hangatahua	Patea	Kapiti	Taranaki total	ALL
Number of different species	56	47	13	14	23	89	153	242
Percentage of different species (%)	24	19	5	6	9	37	63	
Taranaki percentage of different species (%)	37	31	8	9	15	-		
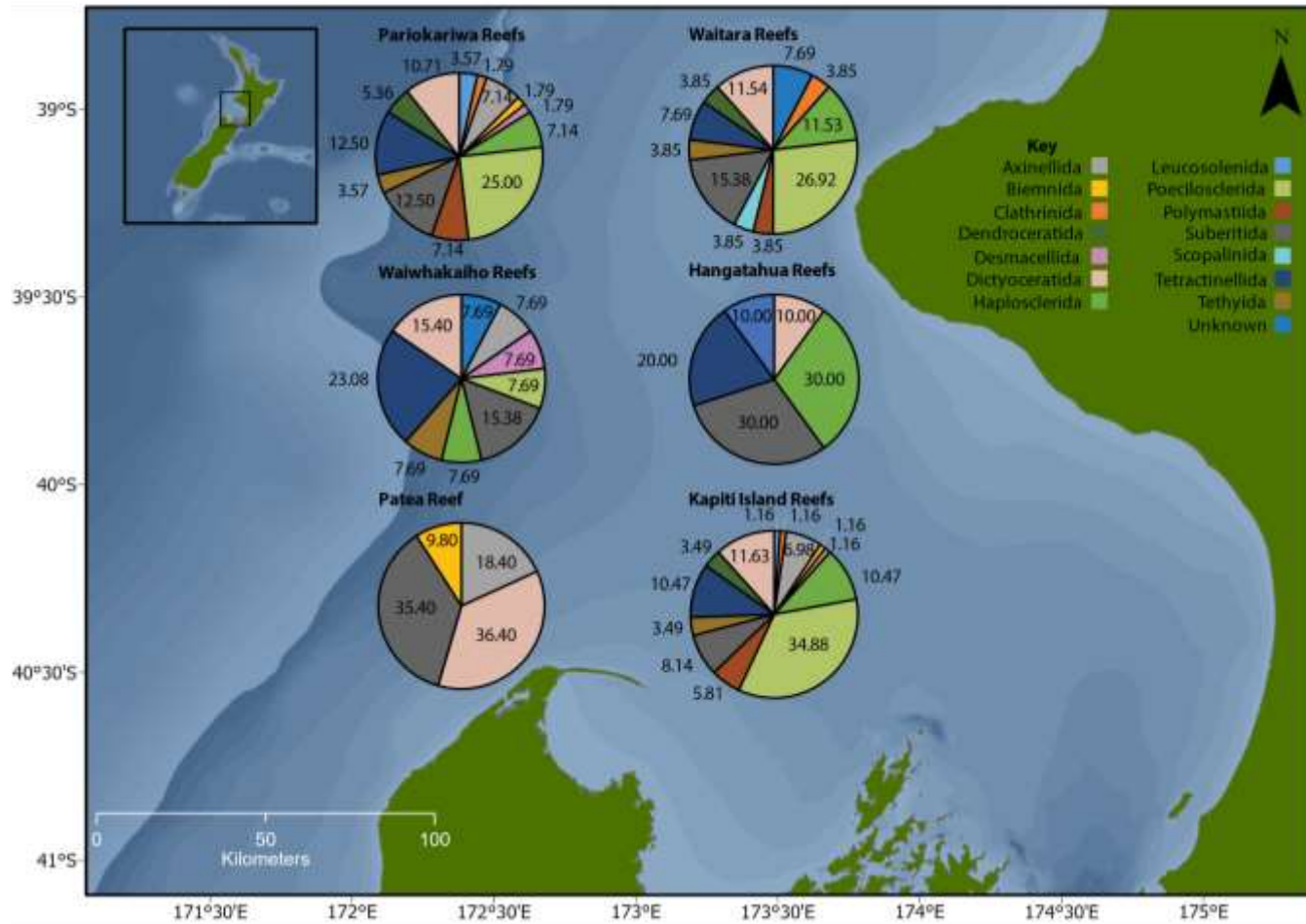
Figure 2.4 Pie charts representing percentage of sponge taxa found within each taxonomic order at six locations in Taranaki and Wellington regions including Pariokariwa reefs, Waitara reefs, Waiwhakaiho reefs, Hangatahua reefs, Patea Reef, and Kapiti Island reefs.

There was a clear trend found within the ordinal level biogeographic distribution of sponges within Poecilosclerida with the largest abundance of this group occurring at Kapiti Island (35%), Waitara reefs (27%), Pariokariwa reefs (25%), and a smaller abundance occurring at Waiwhakaiho reefs (8%) (Fig. 2.4). There were clear spatial affinities and distributions seen among sponge taxonomic families across all locations. For example, some families such as Ancorinidae, Axinellidae and Halichondriidae were recorded at all locations studied and are clearly a commonly distributed taxa on this coastline (Appendix 3: A3.3). Moreover, there was large scale spatial patchiness for some taxonomic families such as Latrunculiidae, Microcionidae, Mycalidae, and Tedaniidae that were found at Pariokariwa reefs and Kapiti Island reefs but were not found near any of the rivers at all coastal stations sampled herein including Waitara reefs, Waiwhakaiho reefs and Hangatahua reefs (Appendix 3: A3.3). A table displaying percentage of sponge taxa found within each taxonomic order at the six locations within the current study can be found in Appendix 3: A3.4.

Table 2.3 Number of unique species at each location (in other words, the number of species that are only found at that location), and the percentage of species that are unique to that location (in other words, the percentage of species that are only found at that location) from Pariokariwa reefs, Waitara reefs, Waiwhakaiho reefs, Hangatahua reefs, Patea Reef, and Kapiti Island reefs.

Species	Pariokariwa	Waitara	Waiwhakaiho	Hangatahua	Patea	Kapiti
Unique to site—including Kapiti	7	36	6	9	11	42
Unique to site—including Kapiti (%)	13	77	46	64	48	47
Unique to site—Taranaki only	44	36	6	9	12	-
Unique to site—Taranaki only (%)	79	77	46	64	52	-
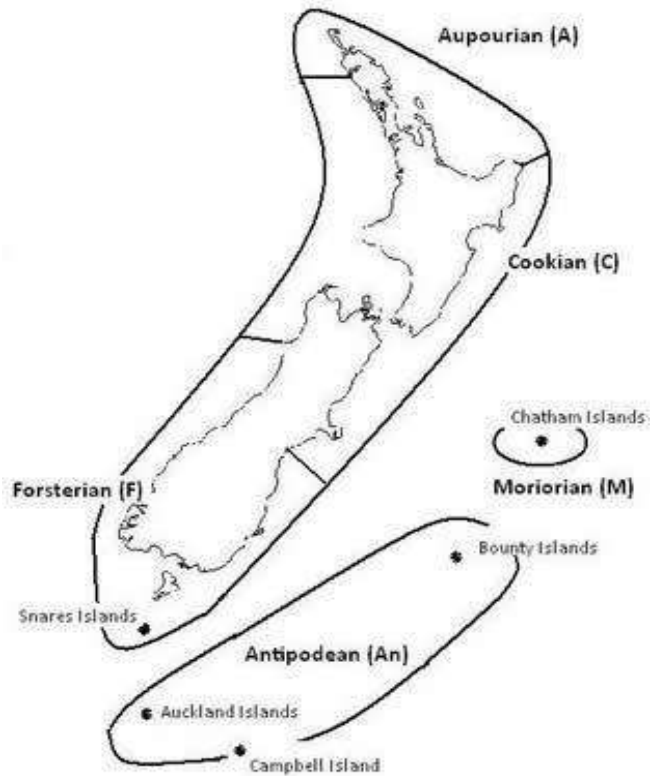
Figure 2.5 Tentative geographic range of Powell (1955) Mollusca species around New Zealand. The geographic range of each marine taxon is indicated by codes (K=Kermadec Islands, A=Aupourian: from the Kaipara Harbour, north around North Cape, encompassing the Three Kings Islands and south to East Cape, C= Cookian: the remainder of the North Island and the northern part of the South Island, F=Forsterian: Otago, Fiordland and Stewart Island, M=Moriorian: Chatham Islands, and An = Antipodean: subantarctic islands of New Zealand (after Powell, 1955). Each of these biogeographic zones also tentatively correlate to the biogeographic distribution of sponge taxa (M. Kelly, pers. comm., 2020).

2.5   Discussion

As mentioned in the literature review, biogeographic studies are reliant on taxonomic species' descriptions. This study utilized classical Linnaean classification based on morphology (skeletal architecture, spicules, colour, and shape), combined with the use of OTUs to significantly improve species estimates of biodiversity in Taranaki. An initial objective of this project was to explore the hypothesis that the biogeography in Taranaki is complex over medium spatial scales, reflecting a combination of geological profiles and potential effects of ocean currents.

This investigation provides novel biogeographic insight into the biodiversity of Taranaki sponge fauna at two spatial scales from tens to hundreds of kilometres, providing both a regional overview and a local understanding of sponge community composition. The current study set out with the aim of qualitatively assessing the diversity of subtidal sponge fauna from this region and provides a list of 127 sponge species or OTUs of marine sponges collected along the Taranaki region based on taxonomic morphological characters (Appendix 3: f).

The results of this study show that Poecilosclerida was the most recorded taxonomic order of sponges represented across all locations surveyed from Waitara, Waiwhakaiho and Hangatahua reefs (Fig. 2.3). The second most common order recorded from all station was Tetractinellida (11%), followed by Dictyoceratida (6%), Suberitida (4%), Axinellida (3%), Scopalinida (3%), and Tethyidae (1%) (Fig. 2.3). An important finding from this study was that there were 35 sponge species that only occurred at the northernmost and southernmost locations at Pariokariwa reefs in North Taranaki and Kapiti Island reefs to the south in the Wellington region (Appendix 3: A3.1). The reasons for patchy distribution of species at both locations are unknown, but possibly reflects the fact that at both locations, there are extensive areas of rocky reef as opposed to small patch reefs and cobble or boulder areas found elsewhere. Hence these are arguably 'preferred' locations with specific habitat features for these taxa in terms of potentially larger abundances of food resources, suitable physical structure, possibly an absence of predators, and less sedimentation. *Ecionemia alata* was the most commonly distributed sponge found at all locations examined and the only species that was recorded from all six locations (Appendix 3: A3.1). This is unsurprising given how commonly distributed this species is around the North and South Islands of New Zealand, with

distributions stretching from the Three Kings Islands down to Mernoo Bank and Chatham Rise (Kelly & Sim-Smith, 2012).

Order Tetractinellida was the most abundant group of sponges from all stations combined, followed by Suberitida and Axinellida (Fig. 2.4). However, the abundance of individuals within orders differed among stations. For example, the largest abundance of Poecilosclerida occurred at Kapiti Island (35%), Waitara reefs (27%), Pariokariwa reefs (25%), and a smaller abundance occurring at Waiwhakaiho reefs (8%) (Fig. 2.4). In comparison these results differ slightly from the abundances of orders found on rocky intertidal zones from the mostly temperate Illawarra region of New South Wales, Australia, where the orders Haplosclerida (36%), Heteroscleromorpha (14%), and Poecilosclerida (18%) were the most abundant orders found in that region (Borges da Silva, 2019). However, much like the current study, there are likely geographical affinities of sponges sound at different locations within the Illawarra region. A further study of ordinal level diversity conducted by Fromont *et al*. (2016) on rocky reef sponges from the Pilbara region in tropical Western Australia found that Haplosclerida (23%, Dictyoceratida (16%), and Poecilosclerida (15%), were the most abundant orders found. These changes in diversity within different parts of the world suggest that the abundance of sponge orders change not only within geographic regions but also among different ecosystems throughout the world.

Ordinal level diversity was most abundant at Pariokariwa Reef (56 orders) and Kapiti Island (86 orders) (Fig. 2.4; Appendix 3: A3.3). There was a clear trend found within the ordinal level biogeographic distribution of sponges within Poecilosclerida with the largest abundance of this group occurring at Kapiti Island (34%), Waitara reefs (26%), Pariokariwa Reef (25%), and a smaller abundance occurring at Waiwhakaiho reefs (7%) (Fig. 2.4). This may be due to the higher loading of sediments at these locations, an issue for usually thinly encrusting species (Chapter 2). However, it should be noted that the sampling efforts at both locations were less intensive than at other locations. It should be noted that there is a critical need to conduct a comprehensive ecological study of Patea Reef to gain a better understanding of the sponge communities on that reef. Nevertheless, there were clear spatial affinities and distributions seen among sponge taxonomic families across all locations. For example, families such as Ancorinidae, Axinellidae, and Halichondriidae were recorded at all locations studied, and are clearly a commonly distributed taxonomic group in this region (Appendix 3: A3.3). Moreover, there was large scale spatial patchiness for some taxonomic families such

as Latrunculiidae, Microcionidae, Mycalidae, and Tedaniidae that were recorded at Pariokariwa reefs and Kapiti Island reefs but were not recorded near any of the locations positioned adjacent to river mouths, including Waitara reefs, Waiwhakaiho reefs, and Hangatahua reefs (Appendix 3: A3.3). Some taxonomic groups have not adapted either physiologically or behaviourally to survive within some of these microhabitats. As mentioned above, the absence of specific taxonomic groups over small spatial scales is also likely attributed to the influence of the nearby rivers that may influence the structure and function of these sponge communities, particularly those communities adjacent to high sedimentary discharges. For example, there was an absence of some families (Latrunculiidae, Microcionidae, Mycalidae, and Tedaniidae) at locations positioned adjacent to river mouths. This is supported by data in the literature which examined the functioning (survival, respiration and morphology) of the New Zealand species *Crella incrustans* after exposure to sediments within a four week experiment and found that the survival rates of individuals were high, and that oxygen consumption of the sponges were not affected (Cummings *et al.*, 2020). These sponges did, however, experience changes in their morphology, with the development of apical fistules, suggesting that it is completely plausible that different sponge species are predisposed to having the ability to cope with large amounts of sedimentation compared to others. Therefore, selective mortality may occur following passive dispersal or lack of dispersal capabilities via oceanic currents, in contrast to taxa that thrive in habitats located near river mouths (see Chapters Two and Three where these relationships are explained in further detail).

Another important finding was the large number of different sponge species at every location examined. Approximately 37% of sponge species at Kapiti Island were different when compared to all locations examined (Table. 2.2), perhaps not surprising for an offshore island. These results support the findings by Mariani *et al.* (2006) that some sponge species with short-lived larvae favour retention near parental habitats, thus enhancing self-seeding and self-recruitment of these populations. There were 242 apparently different sponge species present among all locations surveyed (Table. 2.2), with a total of 170 sponge species recorded among all locations (Appendix 3: A3.1). Within the Taranaki region alone there were 153 sponge individuals recorded and a total of 127 species recorded from all surveys conducted in this region including all the combined data in literature from Battershill and Page (1996), and Kelly *et al.* (2017) (Appendix 3: A3.1).

Of all Taranaki locations surveyed Pariokariwa Reef had the largest number of species that were unique to that area (44 unique species) and found at none of the other locations examined (Table 2.3). This supports research conducted by Battershill and Page (1996) that stated that the sponge populations at Pariokariwa reef have an exceptionally large number of unique sponge species for the Taranaki region. Surprisingly, Waitara reefs had the second largest number of unique sponge species of all locations in Taranaki (36 unique species), followed by Patea reef (12 unique species), Hangatahua (9 unique species), and Waiwhakaiho (6 unique species) (Table. 2.3). This was an unexpected outcome as the Waitara reefs are positioned adjacent to the largest river and river catchment in the Taranaki region (Waitara River), also the most modified catchment with high sedimentary discharges. The suggestion is that the species present at the Waitara location, represent a sediment tolerant specialist group of sponges. Indeed, they have not been identified even at a generic level. These sponges have not been seen elsewhere in New Zealand and await more detailed taxonomic assignment (in progress). Overall, Kapiti Island and Waitara reefs had the largest number of unique species among all locations examined (Pariokariwa, Waitara reefs, Waiwhakaiho reefs, Hangatahua Reef, Patea Reef, and Kapiti Island reefs). These locations represent extremes in habitat biophysical character.

There are several possible explanations for the spatial patchiness of some of the taxonomic groups of sponges recorded including but not limited to favourable substrate for attachment, random distribution caused by ocean currents, predation, competition, adaptation to the effects of riverine sedimentation or lack thereof, presence for dispersal of larvae near parent sponges, and food availability from the rivers (see Chapter Four for an explanation for riverine sources of food for sponges). Wulff (2012) conducted a comprehensive review of factors influencing sponge faunas in all marine habitats and found that there were a large number of ecological factors that can play substantial roles in shaping the distribution and abundance of sponge species. Experiments have revealed that opportunistic predation is one of the primary drivers for distribution boundaries that coincide with habitat boundaries in several systems (Wulff, 2012). Moreover, within habitat influences of predation can be dramatic as a result of unusually high recruitment rates and unusually low mortality rates of predators which often specialise on predating on sponge species (Wulff, 2012). Competitive interactions have been shown to diminish sponge populations in only a few cases. On the contrary competitive interactions often turned out to be neutral or even beneficial relationships among sponge species (Wulff, 2012).

In predominantly tropical systems sponges can form mutualistic symbiosis with other plants or animals which has been shown to increase the abundance, diversity, and habitat distribution of all organisms involved (Wulff, 2012). However, although symbionts may boost the diversity and abundance of sponges it also makes them more susceptible to impacts of environmental changes. Examples of factors that influence the distribution and survivability of sponge fauna in all marine habitats include temperature and salinity (Wulff, 2012).

At 47 sponge species, the Waitara reefs location had the highest diversity of sponge species from all locations surveyed in the current study. These results are congruent with results from Beaumont *et al*. (2010) that found a larger diversity of molluscs, echinoderms, polychaetes, bryozoans, arthropods, sponges, wading birds, diadromous fishes, rocky reef fishes, and macroalgae with a mean rank score of 3.6–4.0 at this location compared to the surrounding areas. Moreover, there is also a likely link between the larger organismal diversity at this location and a larger spatial distribution and habitat complexity at this site with a rank of (2.1–2.5), and a larger diversity of organisms including sponges (Appendix 3: A3.A1–A3.1). Three dimensional physical structures likely provide a greater surface area for benthic encrusting organisms and other taxa to live, in addition to the provision of structure that allows organisms to hide and escape predators.

Although the biogeographic range of sponge species in New Zealand do not match perfectly with estimated biogeographic boundaries proposed by Powell (1955) found in Figure 2.5, there are clear positive correlations between molluscan and sponge biogeographic boundaries, especially in the Cookian biogeographic region, as there are many sponge species which occur on both sides of the North Island that are inexplicable if not for explanations of biogeographic ranges suggested in Powell (1955) (M. Kelly pers, comm., 2020). Nonetheless, Spencer *et al*. (2021) noted that although there are severe limitations with concepts of zoogeographical provinces (especially when applied to deep water species), they do give some approximation of the range of species. The biogeographical range of taxa may not have clear cut distinctions in their exact geographic distribution of sponge species and overlap between biogeographic provinces are likely to occur. Sponge taxa examined within this study all fall within the Cookian Biogeographic Province regardless of whether they were recorded from the Taranaki or Wellington regions (Pariokariwa reefs, Waitara reefs, Waiwhakaiho reefs, Hangatahua Reef, Patea Reef, and Kapiti Island reefs). Beaumont *et al*. (2010) found higher numbers of organismal diversity within the areas containing Pariokariwa and Waitara, which

is similar to results found here with a larger diversity of sponge species at both locations (Appendix 3: A3.1).

Overall, these findings have important implications for developing conservation strategies for marine fauna on this coastline. These results highlight locations of significant biological diversity, abundance, and uniqueness. Sponges are a good indicator taxa for coastal rocky reefs because after the first day of larval settlement they are sedentary for the most of their lifecycle, therefore, any localized impacts can be seen in sponge communities. Furthermore, potential restoration strategies for sponges should consider the genetic diversity of populations that are being restored to determine if they are native to the area being restored or are genetically (minimize genetic pollution) suited to that area to determine 'how local is local' in terms of sponge favoured habitat and biogeographic preference. Further work is required to bulk up the survey efforts from other poorly surveyed habitats in this region, and further regions throughout New Zealand's EEZ that are in critical need of attention for taxonomic, biogeographic, and ecological investigations.

Taxonomic Note:

The appendices for this thesis also include a precursor manuscript which describes two new species of *Dysidea* Johnson, 1842, (Porifera Grant, 1836, Demospongiae Sollas, 1885, Dictyoceratida Minchin, 1900, Dysideidae Gray, 1867) from Tauranga Harbour, Bay of Plenty, New Zealand. Identifying sponge species within the genus *Dysidea* is extremely difficult as they lack spicules which are diagnostic for identifying most sponges. Within this study I examined the skeletal architecture of *Dysidea* species and reviewed the *Dysidea* of New Zealand validating five species. Taxonomic research on species within the genus *Dysidea* was undertaken to gain expertise in the identification of difficult sponge fauna to permit further identification of sponge fauna within the Taranaki region. Overall, the knowledge gained from the taxonomic characterization of sponge species from the Bay of Plenty region found in Appendices 1 & 2 were utilised to differentiate species within the wider biogeographic study conducted herein.

Chapter 3

Environmental factors influencing the distribution and abundance of marine sponges around the Taranaki region, New Zealand

3.1 Abstract

Human-mediated modifications to terrestrial ecosystems have changed the structure and functioning of coastal ecosystems, including loss of diversity, ecological function, and resilience. Discharges of sediments, nutrients and contaminants from land will invariably affect nearshore coastal habitats, with shallow biogenic reefs one of the most impacted. To better understand the influence of terrestrial land use on coastal reef systems a range of environmental factors were examined. Environmental parameters were studied to determine effects on the distribution and abundance of marine sponges and other phyla associated with different riverine and catchment discharges. There was a greater diversity and abundance of sponges at rocky reef stations that were in closer proximity to river mouths. This suggests that terrestrially derived organic matter from rivers may be supporting a greater assemblage and biomass of marine taxa on coastal rocky reefs. We also found that the size of sponges in terms of volume were greater at coastal stations positioned next to rivers with a relatively large coverage of indigenous terrestrial forests as opposed to reef systems adjacent to modified and urbanized catchments. An examination of the effects of several physico-chemical factors including turbidity, total phosphates, total nitrogen, and *Escherichia coli* presence, revealed that sponges appear to be resilient to certain degrees of exposure to these features of inferior water quality. There appears to be a negative correlation between effects of turbidity and nutrient levels on sponges generally, with high levels of turbidity associated with decline in sponge characterised reef habitat. In contrast, some sponge species appear to thrive in turbid conditions that provide high levels of nutrients in a form that they can profit from metabolically. The relationship of sponge diversity and abundance with water quality from catchments is complex with species specific responses. I conclude that marine biodiversity

loss associated with land-derived sedimentation and turbidity is of increasing concern and that there are clear linkages between terrestrial and coastal marine ecosystems.

3.2 Introduction

Anthropogenic impacts on marine ecosystems are of continued concern globally. Previous studies have reported that marine biodiversity loss is increasingly impairing the oceans capacity to provide food, maintain water quality and recover from perturbations (Worm *et al*., 2006). Recent evidence suggests that marine diversity loss may have a significant impact on ecosystem function as global climate change stressors became more prevalent (Cardinale *et al*., 2012; Meredith *et al*., 2019; Cavanagh *et al*., 2021). A meta-analysis of literature conducted by Hooper *et al*. (2012) shows that impacts of species loss are comparable to the extent of impacts from drought, ultraviolet radiation, climate warming, ozone, acidification, elevated CO_2, herbivory, fire, and certain types of nutrient pollution. These rapid changes are having a serious effect on marine ecosystems worldwide, leading to a loss of diversity and ability of ecosystems to provide services. Specifically, resource availability, reef assemblage resilience, and water quality were all shown to be negatively impacted by marine species diversity loss in ocean ecosystems (Worm *et al*., 2006).

Marine sponges are important for maintaining ecosystem function and integrity in benthic communities (Bell *et al*., 2015a). According to Bell *et al*. (2015a), less than 30 species of sponges are listed as threatened, and all are from the Atlantic and Mediterranean. However, a major problem with trying to understand the number of sponge species that are under threat is the taxonomic capacity to be able to describe and identify sponges in the first instance, especially in isolated and difficult to reach regions such as Taranaki in New Zealand (Chapter 2). Work presented in the previous chapter identified that the sponge fauna of Taranaki presented a high degree of endemism and biogeographic patchiness. There was a cline from north to south in terms of assemblage affinity (sub-tropical to cold temperate), but smaller scale patchiness appeared to be associated with coastal biophysical dynamics. This chapter is focused on identifying the possible causes for this.

Sponges perform several important functional roles in marine ecosystems including benthic-pelagic coupling, silicon cycling, nitrogen cycling, facilitation of primary production, settlement substrate and habitat creation (Bell, 2008a). Their relationship with other

components of shallow coastal rocky reef systems is important to understand in the context of what drives their distribution, abundance, and trophic function. The presence of certain taxa may drive the distribution and abundance of some sponge communities. For example, many sponge species are associated with algal forests, and in New Zealand these are characterized by the kelp *Ecklonia radiata*. A recent investigation by Crofskey (2007) on the distribution of *E. radiata* around the North Taranaki Headland and its relationship with key physical characteristics found that water turbidity was the primary factor defining the distribution of *E. radiata* distribution, although wave energy and habitat complexity of the reef were also suggested as further environmental influences affecting distribution of these populations. The direct effects of fine terrigenous fluvial sediments were hypothesised to be the main limiting factor for *E. radiata* distribution on the north-eastern reefs of Taranaki, especially near the Waitara River (Crofskey, 2007). These findings are congruent with findings from research recognizing terrigenous sediments as influential disturbance agents, as fine-grained sediments are prone to smothering and killing small marine infauna and settling propagules (Lohrer *et al.*, 2006). However, it should be noted that although sponges are clearly impacted to some degree by sediments, current evidence suggests that most species have the potential to adapt to and tolerate certain amounts of suspended and settled sediments (Bell *et al.*, 2015b). For example, *Crella incrustans* was found to have the physiological capabilities to withstand varying degrees of sedimentation under experimental conditions (Cummings *et al.*, 2020). This sponge was found to have the capability to remove much of the sediment from its body over a four week period and was capable of changing it morphology and quickly adapt to environmental change (Cummings *et al.*, 2020). Pineda *et al.*, (2015) found that cup shaped sponges including *Callyspongia confoederata* and other species were more susceptible to mortality or tissue necrosis. Therefore, it is possible that cup shaped sponges would be less likely to be found in areas with high sedimentation. Maldonado *et al.*, (2008) conducted a study on 660 asexual explants of the sponge *Scopalina lophyropoda* and found that sponges exposed to silt exposure lived shorter in natural habitats than sponges that were not exposed to silt, suggesting that harbour silt was deleterious to sponge communities. Furthermore, this study found that these impacts of sediments cause reductions in sponge species abundance, in addition to the genetic makeup of sponge populations, favouring sponges that are 'genetic' components involved in the ability of sponges to cope with sediments (Maldonado *et al.*, 2008).

Interestingly, Cárdenas *et al.* (2012) found a negative correlation between algal abundance and several environmental variables on the distribution of sponges on New Zealand rocky reefs. Therefore, we should expect that in areas of high algal abundance in Taranaki such as those presented in Crofskey (2007) there should be a decrease in abundance of sponge species.

Boring clionid sponges studied on West Indian reefs were shown to increase in abundance on reefs with increased levels of eutrophication (Holmes, 2000). Sponges subject to experimental analysis have also been shown to selectively remove pathogenic microbes from the water column including harmful *Escherichia coli* (Maldonado *et al*. 2012). However, these results should be considered with caution as sponges used for bioremediation of microbial pollution may selectively ingest certain bacteria that may end up fuelling growth of harmful bacteria that are less grazed, such as *Vibrio* spp. (Maldonado *et al.*, 2012).

The capacity to taxonomically identify marine organisms is a prelude to conservation efforts. Taxonomic identification linked to knowledge of the drivers of sponge distribution and abundance, are essential to restoration efforts of these taxa if deemed to be under threat. Furthermore, a quantification of the presence (or absence) of different sponge species, together with assessment of their relative health in relation to biomass and morphology, may be important indicators for general rocky reef ecosystem health for an area or region. The research reported in this chapter will review a decade of environmental investigation conducted on rivers in the Taranaki Region and examine potential influences riverine pollution (poor water quality and ecological health) to sponge species distribution and abundance (Taranaki Regional Council, 2016; 2017; 2018; 2019; 2020; 2021).

This is the first study to examine the effects of catchment health on nearshore coastal biogenic health. The data presented here not only fills gaps in biodiversity analysis for this region, but they are also valuable in terms of the ecological knowledge regarding the impacts of terrigenous discharges to coastal ecosystems and specifically on the ecology of marine sponges in this area. These data provide a baseline for further ecological studies and potential habitat degradation of this region caused by anthropogenic stressors.

3.3 Materials and methods

3.3.1 Study region geology and coastal morphology

The Taranaki region is a temperature, mostly sunny, windswept area with a large supply of evenly distributed rainfall and moderate temperatures. This region covers a land area of 9877 km^2, reaching as far north as the Mohakatino catchment, south to include the Waitōtara catchment and inland to the boundary of, but not including the Whanganui catchment. The region extends 12 nautical miles offshore to include waters of the territorial sea (Thompson *et al.*, 2003). The terrestrial landscape is known for its fertile and free-draining volcanic soils centred on the ring plain of Mount Taranaki. The ring plain supports intensive pastoral farming, with the most intensive dairy farming occurring mainly on the flatter land in south Taranaki. There is an abundance of rivers and streams which originate from Mount Taranaki and are extensively utilized by the agricultural sector (Taranaki Regional Council, 2021).

The Taranaki coast is exposed to swells generated in the Tasman Sea and Southern Ocean (Pickrill & Mitchell, 1979). Prior to 1998, this high wave energy coastline was composed of narrow cobble and boulder beaches surrounding a wave-cut shore platform curved from lahar deposits (Cowie *et al.*, 2009). In 1998 there was a massive injection of sand and gravel into the ocean from the collapse of several scarps and volcanic detritus from the headwaters of the Hangatahua (Stony) River (Cowie, 2009). Black sand and scoriaceous gravel were transported into the coastal system and this travelled 22 km to the northeast, which fundamentally altered the characteristics of this coastline (Cowie *et al.*, 2009). Taranaki coast has irregular physical characters composed of sandy floats and rocky reefs (McComb, 2001). Sediment transport has not been quantified along this coastline, but offshore surveys conducted by McComb *et al.* (2003) suggest that the nearshore regions (20–30 m depth) are dominated by rocky reefs, and sandy sediments persisting only within bathymetric depressions.

3.3.2 Land cover in Taranaki

Roughly half (49%) the total land area of the Taranaki Region is covered by indigenous forest and scrub (Fig. 3.1; Table 3.1). Pastures cover the second largest area (35%), followed by exotic forest and scrub 10%. Further land is covered by urban areas 3%, wetland, mangroves, and water 1%, other 1%, and horticulture <1% (Fig. 3.1; Table 3.1).
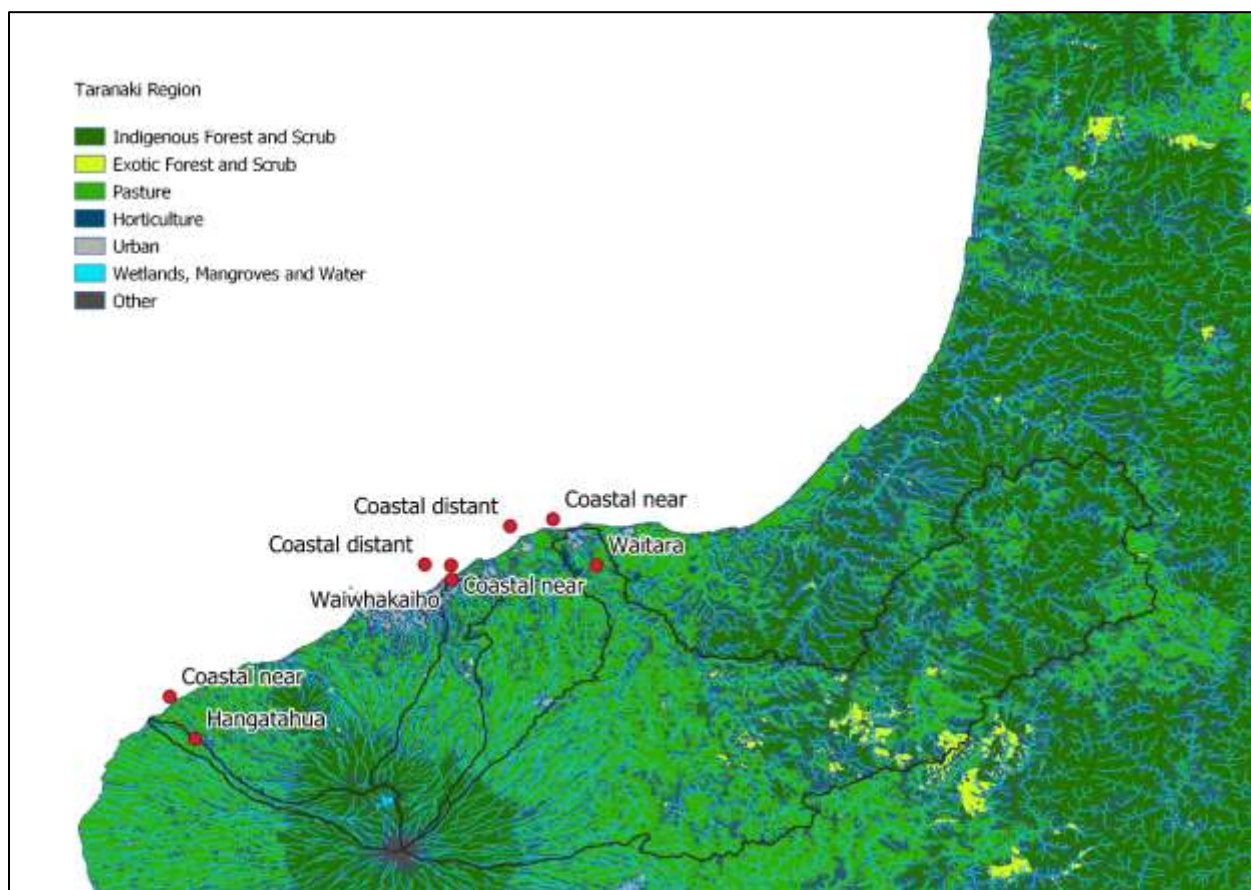
Figure 3.1 Land cover for Taranaki in 2020. Data is taken from the Land Cover Data Base. Inside of the black outlines are the catchments for the three rivers in this study (Waitara, Waiwhakaiho and Hangatahua (Stony) rivers). Red dots represent geographic coastal locations sampled locations of rivers.

Table 3.1 Proportion of land cover categories displayed in square kilometres and percentage values in the Taranaki Region from 2012. Source: Land Cover Database (Thompson *et al.*, 2003).

Land cover type	Area in square kilometres (km²)	Proportion of total (%)
Indigenous forest and scrub	4867	49
Exotic forest and scrub	943	10
Pasture	3505	35
Horticulture	60	<1
Urban	265	3
Wetlands, mangroves, and water	113	1
Other	121	1

3.3.3 State of the environment for river catchments and land-cover in Taranaki

Waitara River:

Waitara River is Taranaki's largest river and has a relatively large catchment of 3102 km^2, and flows south-west and north-west, travelling through both eastern hill country and the eastern side of the Taranaki ring plain. The river passes through the settlement of Waitara (population size 7,040 Jun 2020). Slightly less than half (47.7%) of the Waitara River catchment is covered by indigenous forest and scrub (Fig. 3.1). The second largest coverage of Waitara River catchment is pasture (42.6%), followed by exotic forest and scrub (6.8%). Around 1.1% of the catchment is covered by wetlands, mangroves, and water (Fig 3.1). The remainder of the catchment is covered by urban (1.0%), horticulture (0.6%), and other (0.2%) (Fig. 3.1).

Waitara River is monitored for water quality and ecological health by the Taranaki Regional Council at Autawa Road and Bertrand Road, and environmental data regarding the Waitara River used in the current study was compiled from freshwater ecological monitoring reports conducted by the Taranaki Regional Council (2016; 2017; 2018; 2019; 2020; 2021). The Bertrand Road site is also monitored as part of the NIWA (NZ) rivers survey network and is an existing hydrological station (Taranaki Regional Council, 2016). Waitara River has a different character from other steep ring plain rivers in the region and carries a high silt load (Taranaki Regional Council, 2020).

Waiwhakaiho River:

The Waiwhakaiho River has a catchment area of 489 km^2, and its source is in the Egmont National Park. The river flows in an easterly direction through the city of New Plymouth (Fig. 3.1). A large proportion (64.5%) of the Waiwhakaiho River catchment is covered by indigenous forest and scrub (Fig. 3.1). Roughly a quarter 25.8% is covered by urban areas. The remaining coverage includes areas covered by significantly smaller areas including exotic forest and scrub (5.5%), pasture (1.7%), wetlands, mangroves, and water (1.2%), other (0.8%), and horticulture (0.7%) (Fig. 3.1).

There are four sites throughout the upper and lower reaches of the river that are monitored for the 2002–2003 SEM programme, and environmental data regarding the Waiwhakaiho River used in the current study was compiled from freshwater ecological

monitoring reports conducted by the Taranaki Regional Council (2016; 2017; 2018; 2019; 2020; 2021). The lower Waiwhakaiho River is markedly influenced by industrial impacts and is further monitored by way of site-specific monitoring (Taranaki Regional Council, 2016). Natural headwater erosion including iron-oxide release from tributary systems occasionally happens in the headwaters which may affect the water quality within the Waiwhakaiho River (Taranaki Regional Council, 2016).

Hangatahua River

The Hangatahua (Stony) River has a relatively small catchment covering an area of 347 km^2, and the river itself originates in the Taranaki ring plain within the Egmont National Park (Fig. 3.1). Most of the Hangatahua River catchment (93.9%) is covered by indigenous forest and scrub (Fig. 3.1). The second largest coverage of the Hangatahua River catchment is other (2.8%), followed by wetlands, mangroves, and water (2.0%). Remaining coverage of this catchment includes urban (0.7%), pasture (0.3%), and exotic forest and scrub (0.2%) (Fig. 3.1).

The lower catchment of the Hangatahua River has relatively good water quality and a very narrow catchment area, and environmental data regarding the Hangatahua River used in the current study was compiled from freshwater ecological monitoring reports conducted by the Taranaki Regional Council (2020). The river itself is protected by a local conservation order. Hangatahua River has been affected by significant natural erosion events in the headwaters from 2006–2017 (Taranaki Regional Council, 2020).

3.3.4 Survey design

Ecological data and sponge specimens were collected using SCUBA over two southern hemisphere seasons and three years (autumn, April 4–5, 2019; summer, January 14–17, 2020; and summer, January 15–20, 2021), along three transects from Taranaki in the North Island of New Zealand (Fig. 3.1). Transects were coastally positioned adjacent to three rivers discharging from increasingly 'pristine' catchments (respectively—Waitara (WAI), Waiwhakaiho (WAIW) and Hangatahua (HAN)) and running from rivers to the open ocean (Fig. 3.2). Transects were characterized by differences in terrestrial, freshwater, and marine organic inputs from diverse land uses and coverage, and water quality and were selected to provide a representative cross section of anthropogenic impact on the land (Taranaki Regional Council, 2018). We sampled 1–2

rocky reef stations at each location along latitudinal transects at Waitara (WAI), Waiwhakaiho (WAIW), and Hangatahua (HAN) about 1–2 km offshore from the three rivers — Waitara, Waiwhakaiho and Hangatahua (Fig. 31). We also collected sponge specimens from two additional stations (WAI pilot and WAIW pilot). 'Pilot' stations were used as initial collection sites to determine the best stations for ecological analysis based on consistent physical characteristics of the reef and were not included in subsequent ecological analysis which adopted an optimized survey and sampling design. River systems sampled were chosen based on the availability of ecological data available for them from the Taranaki Regional council, and rivers were of varying sizes in terms of river flow and catchment sizes (Fig. 3.3). At each station, sponges were collected at depths between 12–19 m from each rocky reef using a sharp dive knife and placed in containers for storage.

Due to poor visibility (<4 m) during SCUBA diving at coastal stations (n = 5), a ten-meter circular-search-pattern (360°) was used to collect as many sponge species tissue samples as possible. Five × 0.25 m^2 quadrats were haphazardly placed in the 10 m circular search area. The percentage cover of all phyla was recorded within each quadrat using visual approximations of the area covered by each organism, in addition to volume (height × width × length of every sponge individual, and additional taxa such as algae and other invertebrates). Number of taxa within each phyla, number of different sponge species and number of sponge individuals were also recorded in each quadrat. Where possible, species names of all taxa were recorded. Habitat substratum including percentage cover of substrate (sand, shell hash, and boulders) and height × width × length of every boulder within each quadrate were recorded. Furthermore, general underwater habitat notes were recorded for each station. All sponges were stored in 70% ethanol and transported to the University of Waikato Coastal Marine Field Station laboratory for further analysis. Sponge specimens were individually identified to operational taxonomic units (OTUs) using skeletal sections and spicule morphology. This system ensured that 'like' habitat was sampled evenly in an otherwise very patchy reef dynamic. Also, the survey protocol resulted in a species accumulation curve within each dive and station suggesting that the method effectively permitted collection of most species present at each station.
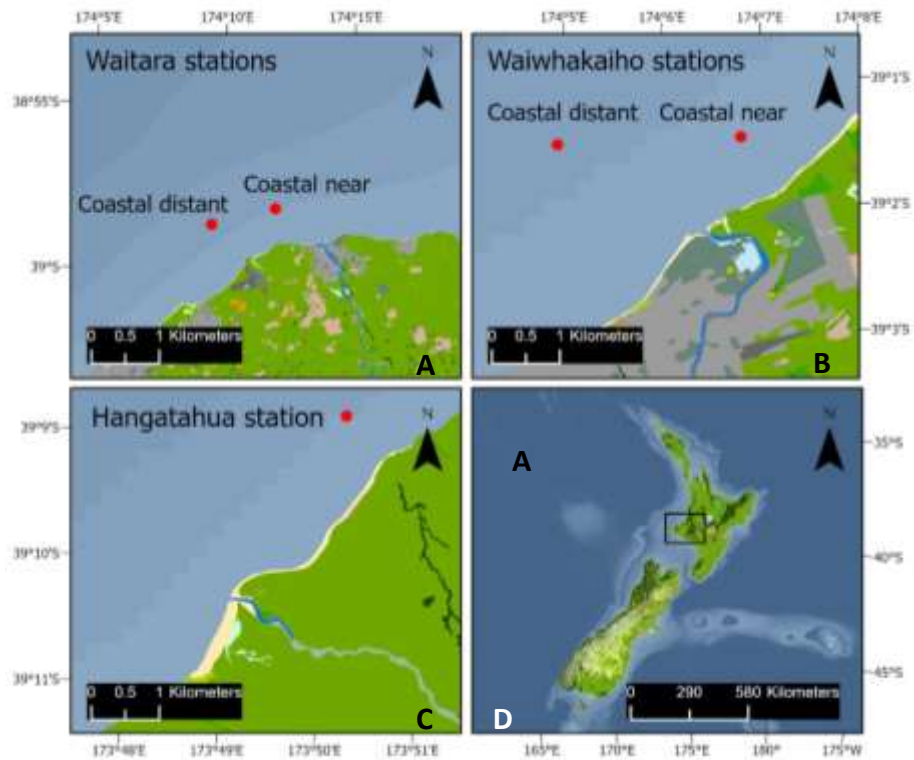
Figure 3.2 Close up of sampling stations along the west coast of Taranaki. Red dots represent geographic stations sampled including freshwater and marine environments: **A.** Waitara (WAI), **B.** Waiwhakaiho (WAIW), **C.** Hangatahua (HAN), and **D.** outline of Taranaki area sampled in New Zealand.

Figure 3.3 Chosen freshwater rivers from left to right: **A.** Hangatahua (Stony) River, **B.** Waiwhakaiho River, and **C.** Waitara River.

3.3.5 Coastal rocky reef stations

Waitara near and distant coastal stations:

Both dive stations (Fig. 3.1) were largely exposed to westerly winds. Sponges from this area were found on rocky reefs down to 18–28 m. Both reef stations sampled were between 12–19 m, respectively. See Table 3.1 for further information regarding Waitara near and distant coastal stations.

Waiwhakaiho near and distant coastal stations:

Diving conditions at both Waiwhakaiho coastal near and distant stations (Fig. 3.1) have relatively good sub-tidal visibility for the Taranaki region (>4 m). Rocky reefs are located on either side of the Waiwhakaiho River. The seawater at both Waiwhakaiho dive stations becomes murky after periods of rain due to sediments and other terrestrially derived matter being ejected by the Waiwhakaiho River. Both reef stations sampled were at depths of 18 m. See Table 3.1 for further information regarding Waiwhakaiho near and distant dive stations.

Hangatahua near coastal station:

The Hangatahua dive station is located near a 1 km long beach that experiences large surf, and sediments become suspended sediments and terrestrially derived matter on rough days leading to poor visibility at this location (Fig. 3.1). The Hangatahua rocky reef station sampled here was located at a depth of 17 m. See Table 3.1 for further information regarding Hangatahua near coastal station.

3.4 Results

3.4.1 Benthic community structure

Assessment of the total area covered by various encrusting algae and invertebrate taxa (Fig. 3.4) showed large proportions of encrusting coralline algae (above 35% cover at all stations), and relatively large proportions of bare substrate (6–23% coverage among all stations). Overall, the benthic assemblage of the coastal zone at the survey stations was relatively sparse with significant proportions of unoccupied space and large areas of turfing species (Fig 3.4). Crustose coralline algae were the most dominant encrusting organisms recorded at all stations. Waitara

coastal distant station had the largest percentage cover of crustose coralline algae (83%), followed by Waiwhakaiho coastal distant (56%), Hangatahua coastal near (51%), Waitara coastal near (51%), and Waiwhakaiho coastal near (35%). It is apparent from Figure 3.4 that the largest coverage of sponges was at the Waitara coastal near station (22%). Waiwhakaiho coastal near station had the second largest percentage cover of sponges at 16%, followed by Hangatahua coastal near (11%), Waiwhakaiho coastal distant (4%), and Waitara coastal distant (4%). These results show that percentage cover of sponges decreased with distance from river mouths as coastal stations had less coverage than stations located closer to rivers (Fig. 3.4). See appendix 3:A3.1 for further information of species patchiness among stations.
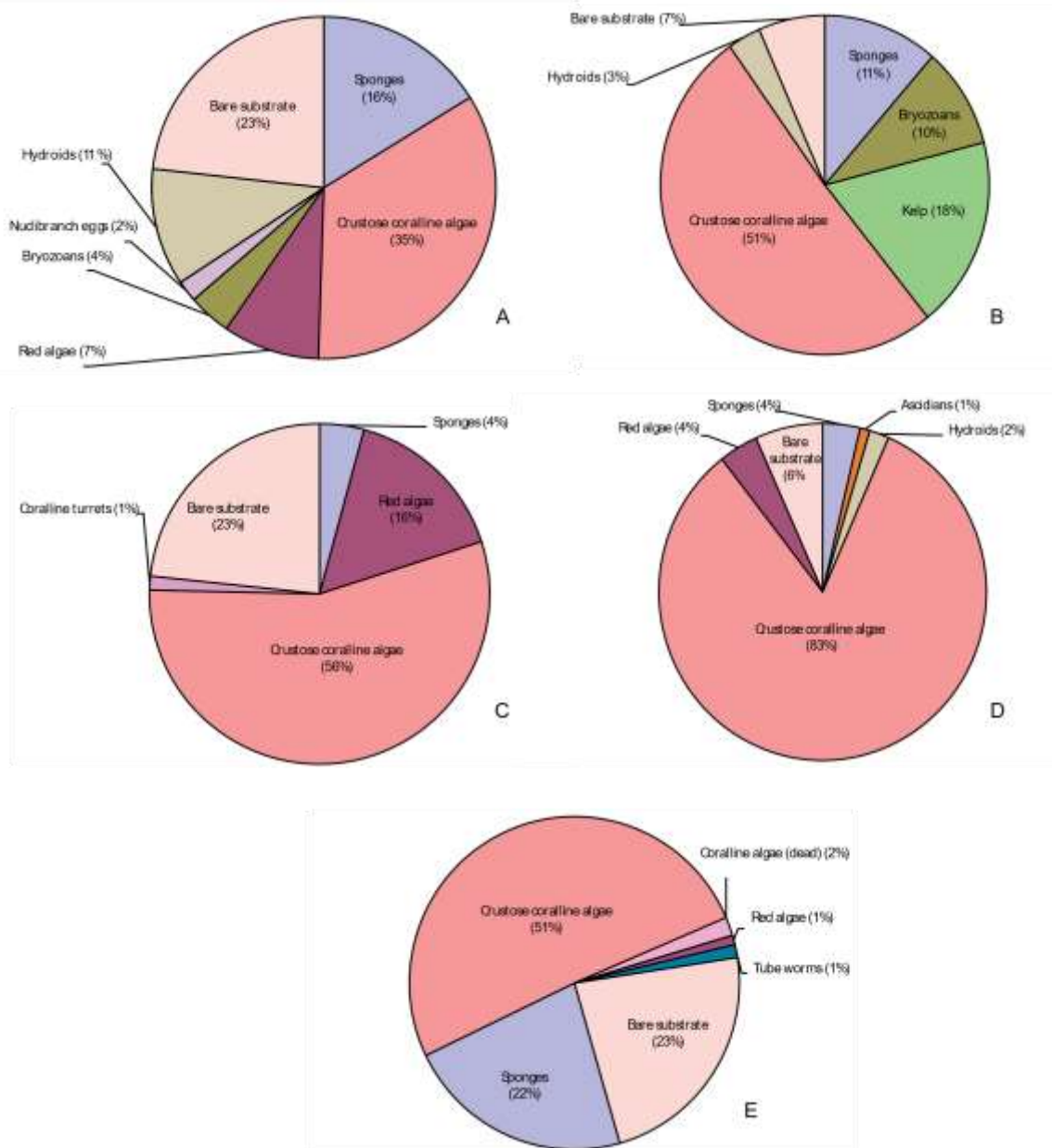
Figure 3.4 Total area covered (%) by taxa represented by species and OTUs (nsp=) distinguished in the study at each station; (A) Waiwhakaiho coastal near (nsp=109), (B) Hangatahua coastal near (nsp=58), (C) Waiwhakaiho coastal distant (nsp=28), (D) Waitara coastal distant (nsp=16), and (E) Waitara coastal near (nsp=75).

3.4.2 Sponge distribution and abundance patterns

To assess sponge species abundance and diversity in the Taranaki Region sponges were identified to species or species descriptors (operational taxonomic units – OTUs) from each sampling station and counted accordingly with their size or and volumes estimated across seven coastal rocky reef stations. *Ecionemia* was the genus with the largest proportion of individuals (n = 13)

found at coastal pilot station WAI pilot (Table 3.2). *Ecionemia alata* was the most common sponge species among all stations studied in the Taranaki region. A summary of the physical nature of five subtidal habitats was recorded for five rocky reef stations to determine if the three-dimensional landscape and substrate types influenced the diversity and abundance of sponges inhabiting each station (Table 3.1). Hangatahua coastal station had the largest boulders, with 84% of boulders larger than 30 cm in diameter, followed by Waiwhakaiho coastal distant with 34% of habitat covered by boulders larger than 30 cm in diameter (Table 3.1). Hangatahua coastal station had boulders ranging in size from 1–1.5 m, which provide large surface areas for sponges to attach to (Table 3.1). Results show that sponges are most common at Waitara coastal near station (Fig. 3.4). Moreover, biomass volume correlates with larger boulders >30 cm (Fig. 3.5; Fig. 3.7B—C, F; Fig. 3.8). Generally, stations sampled closer to shore and river entrances had more sponge diversity and abundance, and sponge biomass volumes were generally larger than the biomass of sponges at stations located more distantly to river systems (Fig. 3.6B—C; Fig. 3.7B—C, F; Fig. 3.8). Waitara had the largest total number of taxa across all phyla, in addition to the second largest number of sponge individuals and species (Fig. 3.6A—C) and was also positioned adjacent to the largest river in terms of volume and land catchment area (Fig. 3.1; Table. 3.1).

Table 3.2 Representation of 21 most common species at generic level across seven coastal rocky reef stations in the Taranaki Region. Dot diameters represent frequencies of individuals within genera and species. Numbers within parentheses where they appear next to a dot represent total number of individuals (n =) within each generic identifier across each coastal rocky reef station (total individuals for each station is shown underneath abbreviated station names) WAI near (Waitara near coastal), WAI distant (Waitara coastal distant), WAI pilot (Waitara pilot), WAIW near (Waiwhakaiho coastal near), WAIW distant (Waiwhakaiho coastal distant), WAIW pilot (Waiwhakaiho pilot) and HAN near (Hangatahua coastal near).

Genera	WAI near (n = 17)	WAI distant (n = 4)	WAI pilot (n = 26)	WAIW near (n = 8)	WAIW distant (n = 4)	WAIW pilot (n = 7)	HAN near (n = 4)
Pararhaphoxya	●(2)			●(2)	●(3)		●(1)
Dysidea			●(1)			●(1)	
Psammocinia				●(1)			
Thorecta			●(1)				
Tedania (*Tedania*)	●(1)					●(1)	
Chondropsis	●(2)		●(2)				
Crella	●(2)	●2					
Clathria				●(1)		●(1)	
Stylissa		●2	●(1)				
Ciocalypta			●(1)			●(2)	
Aaptos			●(1)	●(1)			
Tethya	●(1)		●(2)			●(1)	
Ecionemia	●(5)		●(13)	●(3)			●(3)
Stelletta						●(1)	
Haliclona			●(1)				
Adocia	●(5)						
Thorecta			●(1)				

Frequency of individuals in genera: 1 ● 5 ● 15 ●

Table 3.3 Summary of subtidal habitats surveyed at five coastal rocky reef stations along the Taranaki coastline.

Site	Coordinates	Sponges as percentage of total species found on reef (%)	Wave exposure	Natural habitat features	Percentage (%) of area containing boulders
Waitara coastal near	S38°58.761, E174°12.610	85	North facing reef (Highly exposed)	Predominantly large boulders (flat not regular), and sand. Small to medium boulders are less common. A large quantity of suspended sediments.	>30 cm boulders = 36%, 10–30 cm boulders = 21%, < 10 cm boulders = 21%.
Waitara coastal distant	S38°59.162, E174° 10.118	81	North facing reef (Highly exposed)	Predominantly large and medium boulders, in addition to a variety of smaller boulders. Approximately 5 % of this habitat is gravelly shell-hash.	>30 cm boulders = 40%, 10–30 cm boulders = 37%, < 10 cm boulders = 14%.
Waiwhakaiho coastal near	S39°01.434, E174°6.700	79	North facing reef (Highly exposed)	Has the second largest sized boulders of any site: some are a meter in diameter. Boulders are large enough to create tiny caves and overhangs (caves were 40 cm × 30 cm × 20 cm). Large proportion of medium and small boulders packed together (medium 10–30 cm), (small 0–10 cm). Limited sand, and it is differentiated from sand at other stations with a white to cream yellow colouration. Abundance of tiny broken shells in the sand. Adjacent to this reef is a large area of rippled sand. There is a greater amount of three-dimensional reef structure at this site for organisms to grow inhabit.	>30 cm boulders = 34%, 10–30 cm boulders = 37%, < 10 cm boulders = 19%.
Waiwhakaiho coastal distant	S39°01.378, E174°05.164	29	North facing reef (Highly exposed)	Habitat characterised by large boulders. with a low number of medium boulders, and 30–50% small boulders, sand, gravel, and broken shell. Large and small size ranges of boulders mixed are common.	>30 cm boulders = 35%, 10–30 cm boulders = 25%, < 10 cm boulders = 27%.
Hangatahua coastal near	S39°09.834, E173°48.939	64	Northwest facing reef (highly exposed)	Characterised by 1–1.5-meter-wide boulders sitting on sand and covered most of the quadrats. Smaller boulders covered 15% and sand cover roughly 10% of the habitat. The sand was a white and black colouration. The habitat directly surrounding this reef was comprised of sandy substratum.	>30 cm boulders = 84%, 10–30 cm boulders = 10%, < 10 cm boulders = 1%.

3.4.3 Substrate types of sponge habitats

Ecological surveys examining the percentage composition of substrate types across all five rocky reef stations revealed a wide range in composition of substrates. Hangatahua coastal near had the largest proportion of boulders above 30 cm in diameter at over 80%, followed by Waitara coastal distant with roughly 40%, Waitara coastal near (37%), Waiwhakaiho coastal distant (35%), and Waiwhakaiho coastal near (36%) (Fig. 3.5).
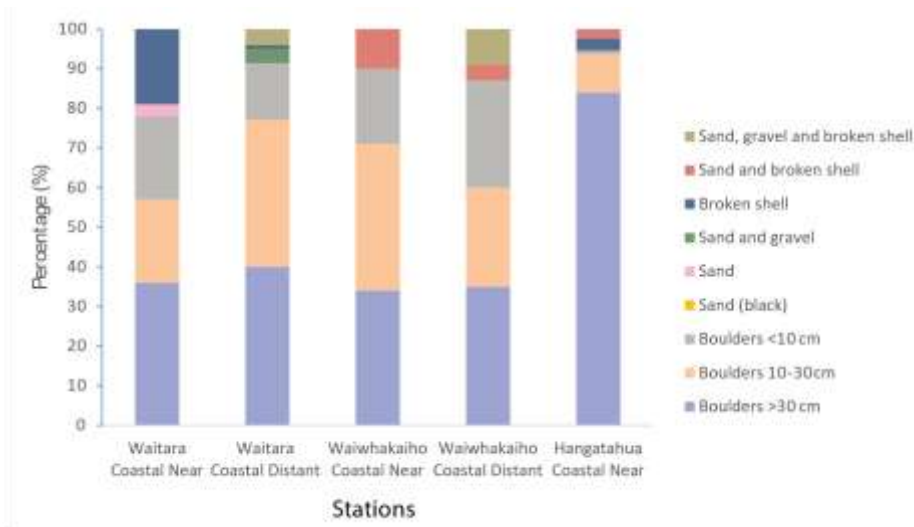
Figure 3.5 Total percent composition of substrate at each of the five study stations (Waitara coastal near, Waitara coastal distant, Waiwhakaiho coastal near, Waiwhakaiho coastal distant, and Hangatahua coastal near).

There is a clear relationship between the boulder profiles in relation to sponge distribution and abundance. For example, 84% of the total reef area at Hangatahua coastal near was covered by boulders >30 cm, and this station also had the largest sized sponges in terms of volume of any station sampled (Fig. 3.5; Fig. 3.7B—C, F; Fig. 3.8). The station with the largest diversity and abundance of sponge taxa was at Waiwhakaiho coastal near, which also had a relatively large percentage coverage of large boulders with the 10—30 cm size category representing 37% coverage, and the >30 cm size category representing 34% coverage (Fig. 3.5; Fig. 3.6A—B).

Waitara coastal near station had the largest number of all taxa across all phyla with over 61 taxa recorded (Fig. 3.6A). This was closely followed by Waiwhakaiho coastal near with more than 53 taxa recorded. The third highest diversity of taxa across all phyla was recorded at

Hangatahua coastal near station with 38 different taxa (Fig. 3.6A). Further stations including Waiwhakaiho coastal distant and Waitara coastal distant had 31 and 20 taxa respectively (Fig. 3.6A). Waiwhakaiho coastal near had the largest diversity of sponge species with 19 (Fig. 3.6B). Waitara coastal near had the second highest diversity of sponges with 17 species recorded (Fig. 3.6B). These were followed by Hangatahua coastal near, Waitara coastal distant, and Waiwhakaiho coastal distant with 11, 9 and 6 sponge species respectively (Fig. 3.6B). Furthermore, Waiwhakaiho coastal near also had the largest total number of sponge individuals at 94 (Fig. 3.6C). Waitara coastal near had the second largest number of sponge individuals at 66, followed by Hangatahua coastal near (31), Waitara coastal distant (13), and Waiwhakaiho coastal distant (8) (Fig. 3.6C).
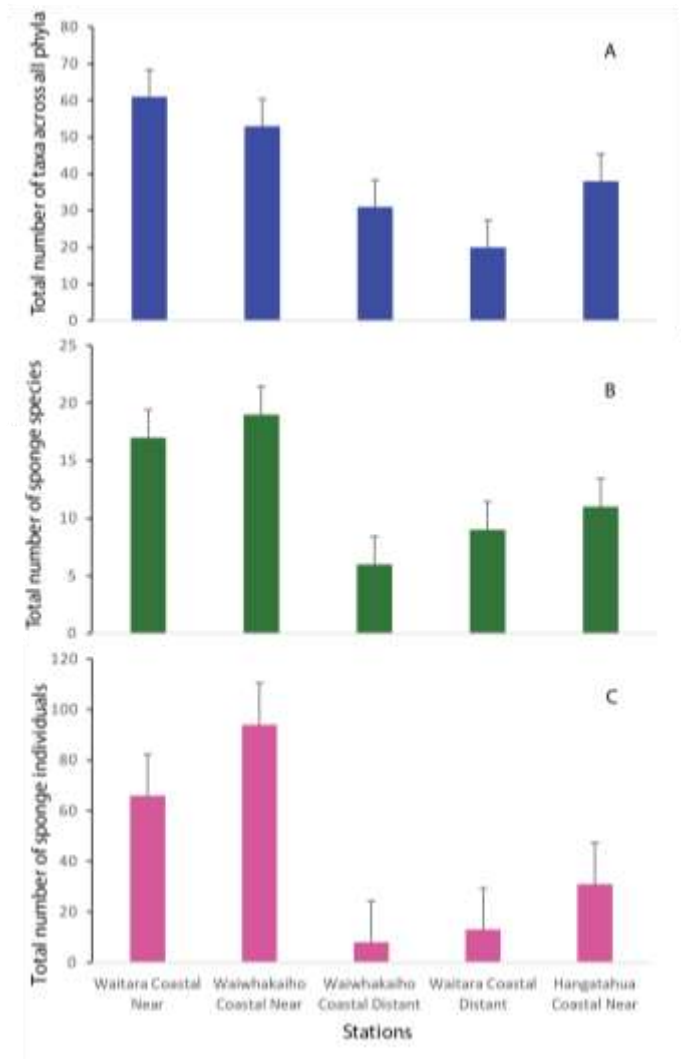
Figure 3.6 Sponge individuals and taxa among each of the coastal stations with standard error bars. **A.** total number of taxa across all phyla including sponges found at each station, **B.** total number of sponge species found at each station, **C.** total number of sponge individuals found at each station.

There were no apparent associations between sponge species diversity and mean turbidity (NTU), mean sponge volume (cm^3), mean total nitrogen (g N m^{-3}), mean total phosphorous (g P m^{-3}), and mean *E. coli* concentrations (cfu 100 mL^{-1}) (Fig.3. 8 A–B, C, E, G). There were associations found between mean sponge volume (cm^3) versus turbidity measured in Nephelometric Turbidity Units (NTU) with sponges appearing to decrease in overall size with an NTU greater than 100 (Fig. 3.7F). Mean sponge volume decrease with an increase in total nitrogen (g N m^{-3}) (Fig. 3.7B). Furthermore, there was an increase in the volumes (cm^3) of sponges at Hangatahua coastal near station with a proportionally large amount of mean total phosphorus at this site (Fig. 3.7C).
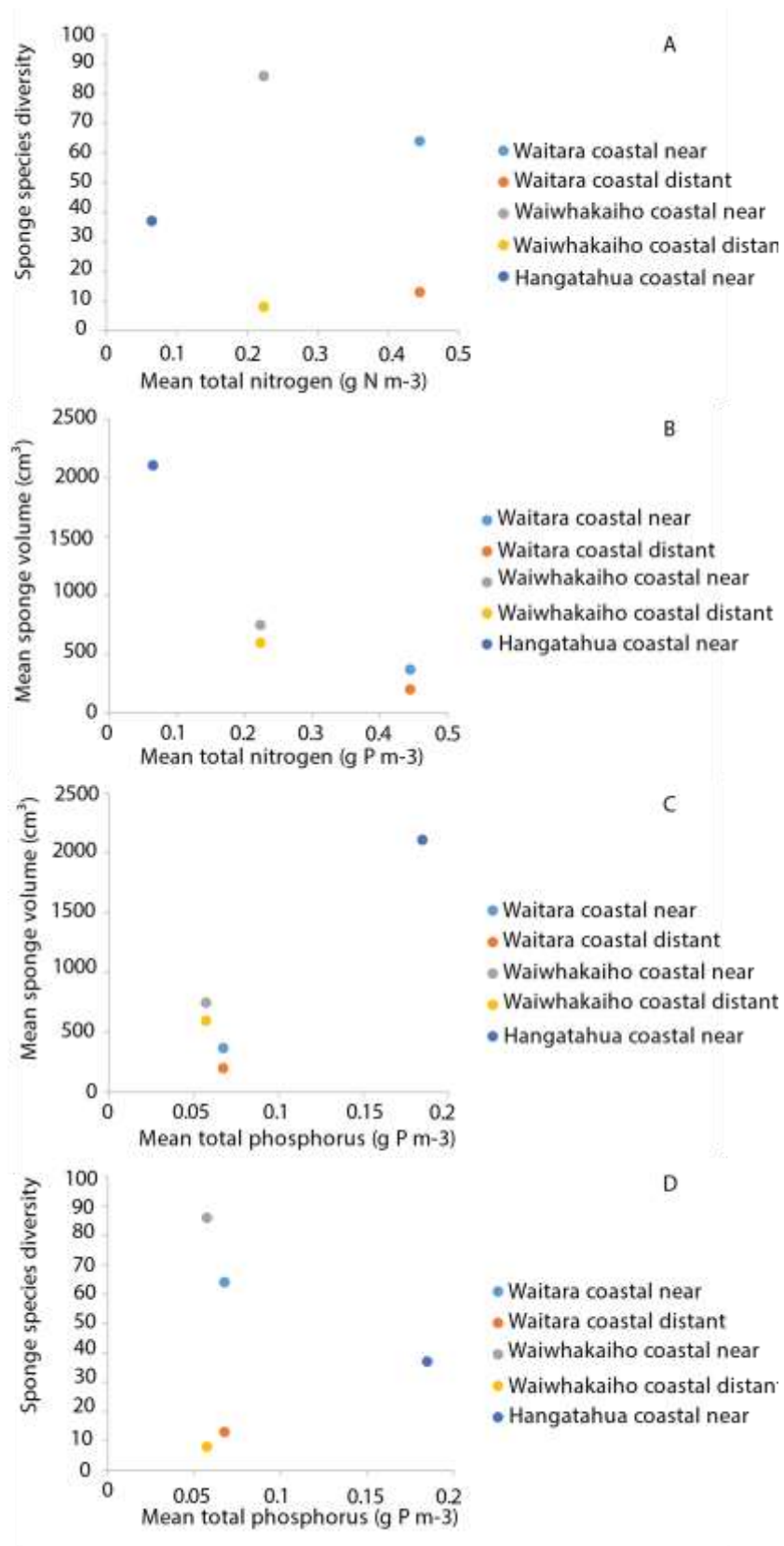
Figure 3.7 Graphical view of combined sponge species data versus environmental parameters including: **A.** Sponge species diversity versus mean total nitrogen (g N m⁻³), **B.** Mean sponge volume (cm³) versus mean total

nitrogen (g N m^{-3}), **C.** Mean sponge volume (cm^3) versus mean total phosphorus (g P m^{-3}), **D.** Sponge species diversity versus mean total phosphorus (g P m^{-3}), **E.** Sponge species diversity versus mean turbidity (NTU), **F.** Mean sponge volume (cm^3) versus mean turbidity, **G.** Sponge species diversity versus mean *E. coli* (*Escherichia coli*) concentrations (cfu 100 mL^{-1}). All environmental parameters measured were from the three rivers (Waitara, Waiwhakaiho and Hangatahua) that flow directly into the waters of the five coastal rocky reef stations studied herein. Data was derived from a decadal monitoring study of riverine environmental parameters collected and supplied by the Taranaki Regional Council (2016; 2017; 2018; 2019; 2020).
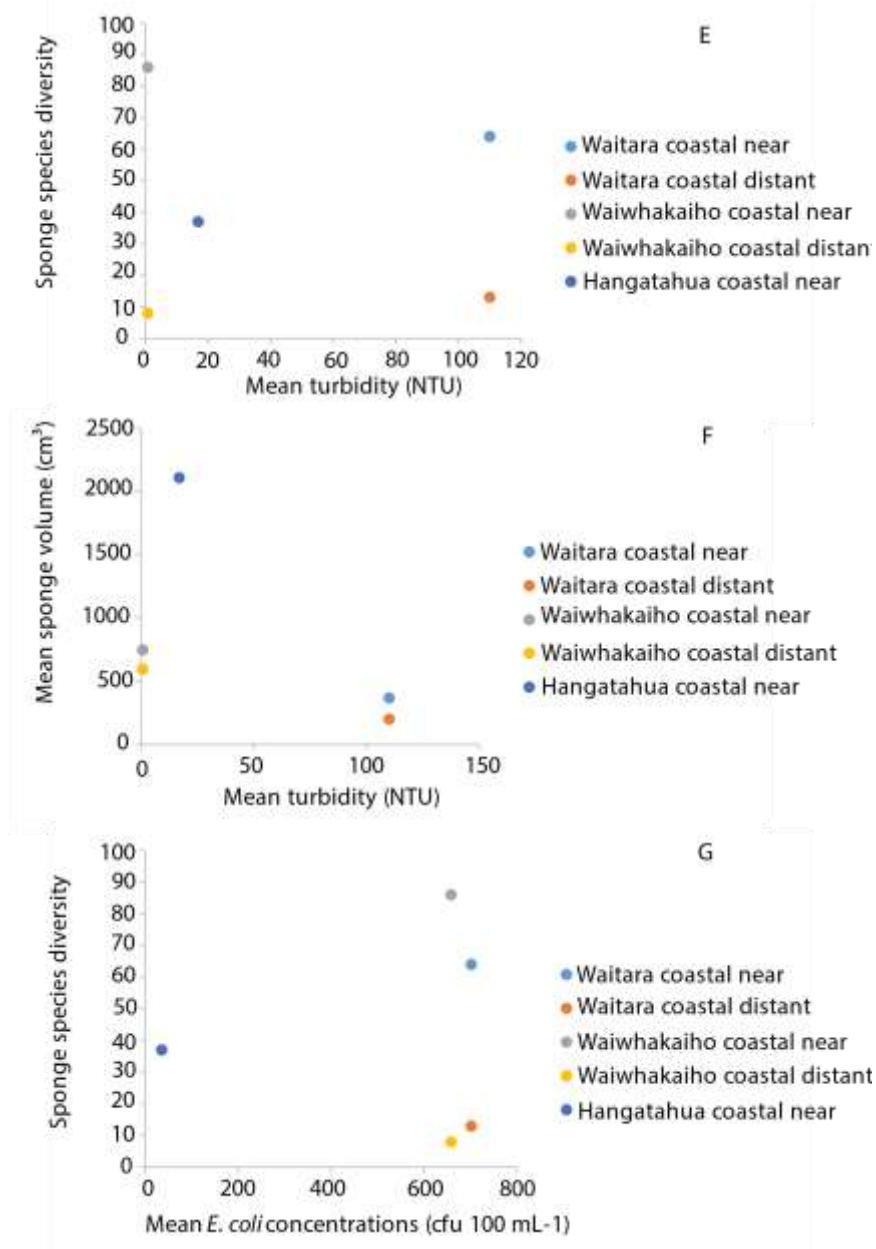
Figure 3.7 (continued).

3.5 Discussion

Contrary to expectations for reefs in a high-sediment environments, the station closest to the Waitara River plume (Waitara coastal near) had 22% coverage of sponge species, the largest percentage for any station (Fig. 3.4E). This station also had the largest diversity of taxa (61) across all phyla among all stations (Fig. 3.6A). Moreover, the Waitara coastal near station had the second highest sponge diversity, with 17 species (Fig. 3.6B), in addition to the second highest number of sponge individuals among all stations at 66 (Fig. 3.6C). These results are interesting because the Waitara River catchment is also the largest river catchment in the Taranaki Region (3102 km^2) and slightly below half of this catchment (47.7%) is covered by indigenous forest and scrub (Fig. 3.1). A similar amount (42.6%) of the Waitara River catchment is covered by pasture (Fig. 3.1). Pasture grasslands are likely to have mostly agricultural grazing land uses including sheep, beef, or dairy farming (Thompson *et al.*, 2003). However, some low producing grasslands may have recreational, or conservation uses. Furthermore, low producing grasslands are predominantly slow growing, and livestock grazing in these areas tend to be grazed over large areas. In comparison, high producing grasslands are usually more intensely grazed with a larger proportion of fertilizers and irrigation commonly used to improve land productivity (Thompson *et al.*, 2003). Therefore, it is surprising to find such a large number and diversity of taxa including sponges across all phyla at the Waitara coastal near station as there may be a larger number of pollutants coming from intensively farmed catchments, and thus riverine sedimentary discharges (Fig. 3.6A–C).

Waitara coastal near station is adjacent to the output of the Waitara River which has the largest turbidity (mean 110 NTU, Fig. 3.7E—F; Fig. 3.8), largest total nitrogen (mean 0.44 TN g N m^{-3}, Fig. 3.7A—B), and largest *E. coli* concentrations (mean 702.39 cfu 100 mL^{-1}, Fig. 3.7G) of all three rivers analysed. Previous studies have reported on the physiological effects of sediments on sponge communities from different geographic locations around the globe. Tjensvoll *et al.* (2013) conducted sedimentation experiments on the deep sea sponge *Geodia barretti* and found that it physiologically shuts down when exposed to sediment concentrations of 100 mg L^{-1} (86% reduction in respiration), with thresholds of responses occurring between 10 to 50 mg L^{-1}. Bannister *et al.* (2012) also found that experimental exposure of the tropical sponge species *Rhopaloides odorabile* to clay and carbonate sediments resulted in an increased metabolic

demand (respiration) of up to 40% in response to fine terrigenous (clay) sediments. Furthermore, this physiological response supports evidence that the load, size, and minerology of sediments are key factors that may affect the distributions and abundance patterns of *R. odorabile* (Bannister *et al*., 2012). Sponges were shown to be influenced in a number of ways to sediment, however, most species are likely to have some ability to tolerate suspended settled sediment (Bell *et al*., 2015a). Moreover, it has been demonstrated in the literature that many New Zealand sponge species have specific adaptations and can thrive in sediment impacted areas (Bell *et al*., 2015a). Bell *et al*. (2015a) found that diversity and abundance of sponges appear to be influenced by patterns of sediment, and generally sponge assemblages are less diverse and abundant in highly sedimented environments. However, these impacts are not seen in all sponges, as some species are more abundant than others. This can be seen in an investigation of the New Zealand sponge *Crella incrustans* where it had a high rate of survival, and no effect of oxygen consumption after four weeks of experimental exposure to a gradient of suspended sediments (Cummings *et al*., 2020). A more natural study was conducted on tropical sponge assemblages and found that the impacts of sedimentation resulted in a reduction of diversity, losses and substitution of species, and shifts from relatively mature and stable communities to more unstable communities dominated by encrusting species better adapted to local environmental conditions (Carballo, 2006). These results are similar to those from the current study in that there was a large dominance of thinly encrusting species at most stations in Taranaki, and all stations were found to have consistent levels of suspended sediments. Therefore, although the diversity of sponges may have been higher at some stations compared to others, this diversity would likely be larger if the sediments were not present. Nonetheless, it is difficult to determine whether this is the case here without further examination of sedimentary impacts along this coastline, and whether many of these sediments are the result of natural or anthropogenic influences.

Further studies highlight the adaptive capabilities of sponges as a result of high levels of sedimentation. For example, it has been reported that the tropical photosymbiotic sponge *Lamellodysidea herbacea* has the ability to clear its tissue of high levels of settled sediment and compensate for metabolic demand by altering its respiration rate (Biggerstaff *et al*., 2017). This species produced large amounts of mucus presumably to attach to and clear settled sediments from its tissue (Biggerstaff *et al*., 2017). This sponge was also found to reduce its pumping rate

to avoid clogging in response to increased levels of sedimentation, therefore, suggesting that some sponges have the capability to tolerate high levels of sediment (Biggerstaff *et al.*, 2017).

Waitara coastal near station had up to 36% of its rocky reef covered in boulders larger than 30 cm in diameter, and boulders less than 30 cm in diameter represented 21% of the reef (Fig. 3.5, Table 3.1). Although not part of the larger ecological survey, a nearby Waitara control (WAI control) station also had the largest number of recorded sponge individuals across all of stations at 26 (Table 3.2). Similar trends were seen at Waiwhakaiho coastal near station which had the second largest percentage cover of sponges at 16%, the second largest diversity of taxa (53) across all phyla at all stations, the largest diversity of sponge species at 19 and the largest recorded number of sponge individuals 94 among all stations (Fig. 3.6A–C). The Waiwhakaiho River has a catchment covering an area of 489 km^2 and has a source originating in the Egmont National Park (Fig. 3.1). What is interesting about the large coverage, diversity, and abundance of sponges at the Waiwhakaiho coastal near station is that a relatively large proportion of the nearby Waiwhakaiho River catchment is covered by indigenous forest (64%) (Fig. 3.1).

Hangatahua coastal near station has the third largest percentage coverage of sponge species at 11% (Fig. 4B), and the third largest diversity of taxa (38) across all phyla among all stations (Fig. 7A). Furthermore, Hangatahua coastal near station had the third largest diversity of sponge species at 11 (Fig. 7B), and the third largest number of sponge individuals among all stations at 31 (Fig. 7C). Although Hangatahua River has the smallest catchment of all three rivers studied (347 km^2), it has by far the largest coverage of indigenous forest (94%) (Fig. 3). While Hangatahua coastal near station had the smallest coverage, diversity, and abundance of sponges, it had the largest sized sponges in terms of volume from all five rocky reef stations (Fig. 8. B, D, F, H). The percentage coverage, diversity, and abundance of sponges were proportionally large relative to the small size of the river and river catchment from nearby Waitara River (Fig. 7B–C). Perhaps this is a function of the proportionally large coverage of indigenous forest (94%) at this coastal station contributing to improved water quality conditions in the Waitara River, and thus also at the adjacent Waitara River coastal station.

The results of this study show that coastal rocky reef stations located closer to river mouths (Waitara coastal near, Waiwhakaiho coastal near, and Hangatahua coastal near) had a larger diversity and number of individual taxa across all benthic encrusting phyla than stations

more distant to rivers (Fig. 3.6A–C). Comparatively, coastal rocky reef stations located more distantly from each of the river mouths had less percentage coverage of benthic invertebrates and a larger dominance of crustose coralline algae (Fig. 3.6A–C).

There were no clear associations between sponge species diversity and turbidity, sponge volume, total nitrogen, total phosphorus, and *E. coli* (Fig. 3.7A, D—E, G; Fig. 3.8). However, the highly turbid waters of Waitara as associated a distinctive assemblage of sponge taxa not seen at the other stations surveyed (Fig. 3.2). Nevertheless, there were significant associations found between sponge volume and turbidity with sponges appearing to decrease in overall size with an NTU greater than 100 (Fig. 3.7F). However, mean sponge volumes appeared to decrease with an increase in total nitrogen (g N m^{-3}) (Fig. 3.7B). Furthermore, there was an increase in the volumes (cm^3) of sponges at Hangatahua coastal near station with a proportionally large amount of mean total phosphorus at this site (Fig. 3.7C). Sponge volumes appeared to be largest at Hangatahua coastal near station, which may suggest that there is a larger availability of food at this station (Fig. 3.7B—C, F; Fig. 3.8). The findings of the current study are consistent with those of Holmes (2000) who found an increase in abundance of clionid sponges with increased levels of eutrophication on west Indian reefs. Specifically, Holmes (2000) examined several indices of water quality including reactive phosphate, nitrate-nitrite-nitrogen, suspended particulate matter, volatile particulate matter, particulate organics in sediments, and chlorophyll a from seven fringing reefs across a eutrophication gradient. Reef comparisons from Holmes (2000) demonstrated that abundance of clionid sponges increased with increasing levels of eutrophication. However, the aforementioned study was specific to clionid sponges, and different species may have species specific results to increased eutrophication.

Here we see similar trends with coastal station located closer to river mouths and thus sources of eutrophication may have a greater abundance of all encrusting taxa across all phyla (including sponges) and a larger number of sponge individuals (Fig. 3.6A–C). There are several potential explanations for these results including a greater food availability on reefs that are closer to rivers. However, the reason why there may be differences in the number of sponge species, individuals and biomass may be entirely different and are the result of a large number of biotic and abiotic factors. Wulff (2001) highlighted that the reasons for differences in numbers of sponge individuals versus differences in biomass are rarely the same. Sponge biomass can

provide a useful way of understanding the functional roles and health of sponges in natural systems (Wulff, 2001). However, some sponge species are more susceptible to fragmentation including branching and encrusting species and, therefore, the number of individuals is highly unstable and does not reflect the number of larval recruitment events (Wulff, 2001). Conversely, counting the number of sponge individuals can be useful to determine if they are in decline, but it has not yet been clearly demonstrated that important functional roles of sponges are related to number of individuals (Wulff, 2001). Furthermore, size-dependant mortality can also cause changes in volume and numbers of individuals. For example, Wulff (2001) found that during a hurricane shallow reef populations of the erect branching species *Amphimedon compressa* decreased by 43% by number of individuals, but only 5% by volume.

An investigation by Wulff (2012) found that although abiotic factors are the primary drivers for indicating which sponge species can thrive at a particular site, ecological interactions can play a substantial roles in influencing distribution, abundance, and diversity. Predation may be the primary enforcer of sponge distributional boundaries in some areas if the number of predators is high and there is a relatively low rate of predator mortality. Mutualistic relationships of sponges with other biota with sponges is generally suggested as a driver for increased abundance, diversity and distribution. However, symbiotic relationships, including those of sponges with symbionts, can make sponges more susceptible to environmental changes given their reliance on other species that may be impacted by these changes such as increased temperature negatively influencing their symbiotic algae (Wulff, 2012). Therefore, not only is further research required to decouple abiotic effects on sponges in Taranaki, but future investigations should aim to investigate ecological interactions within these communities to better understand the drivers for species biomass, diversity and habitat distribution.

Rivers with larger catchments may provide a greater source of food from existing grassland and additional terrestrially produced organic matter. There is evidence that sponges consume freshwater derived seston (refer to Chapter 4 in this thesis). Another possible explanation for these results is that the habitat types at each of the five stations had different physical features which were more suitable for benthic taxa to settle on. However, all five stations had relatively similar three-dimensional boulder structures (Fig. 3.5, Table 3). Hangatahua was the site with the largest boulders, however, the complexity of structure on the

boulders themselves likely influences the settlement and survival behaviour of encrusting taxa. These data must be interpreted with caution because without experimentation on individual factors, it is difficult to tease apart specific reasons for differences in diversity and abundance of taxa among stations.

There were no apparent associations between sponge species diversity and mean turbidity (NTU), mean sponge volume (cm^3), mean total nitrogen (g N m^{-3}), mean total phosphorous (g P m^{-3}), and mean *E. coli* concentrations (cfu 100 mL^{-1}) (Fig.3. 8 A–B, C, E, G). Total nitrogen and total phosphorus were utilised as a proxy for land use and do not offer direct insights into physiological effects on sponges as there were no clear patterns found within these data. These data were analysed in an attempt to understand the levels of potential nutrient enrichment as a result of the land use types ranging from indigenous forest and scrub to pasture.

The three river systems studied here have markedly different sized catchments (Waitara 1139 km^2, Waiwhakaiho 136 km^2, and Hangatahua 54 km^2), and mean annual flows (Waitara 55.74 m^3 s^{-1}, Waiwhakaiho 11.13 m^3 s^{-1}, and Hangatahua 5.87 m^3 s^{-1}) (Jowett, 1998). However, these rivers were selected based on the physiochemical data available for them as other rivers in the Taranaki region were not as well monitored. Although the Hangatahua river catchment is relatively small in comparison to the other two rivers studied, coastal rocky reef sponges living adjacent to this river had a proportionally high diversity of taxa across all phyla including sponge species, in addition to a relatively large number of sponge individuals (Fig. 3.6A– C). This is interesting because although this is a significantly smaller river and catchment, it is also the river with the catchment with the largest proportion of land covered by indigenous forest (94%).

The data presented here suggests that the diversity and abundance of sponges and other benthic encrusting taxa occupying coastal rocky reefs are proportionally larger when they are living near rivers with a large proportion of catchment covered by indigenous forest, as opposed to mainly grasslands found in the Waitara and Waiwhakaiho river catchments. A possible explanation for this is that sponges may prefer feeding on food coming from land covered by indigenous forest, or that there is a greater availability of food coming from indigenous forests that sponges can potentially consume. These results are supported by data provided in the stable isotope analyses that suggest that sponges living at the Hangatahua coastal rocky reef station are

obtaining a large proportion of their diet from food coming from the Hangatahua River (Chapter 4). This finding has implications for land use management and development, as there appears to be a link between land use types and the abundance and diversity of encrusting taxa on rocky reef systems in Taranaki. Perhaps a greater diversity of indigenous plants on land are positively correlated with a greater diversity of coastal benthic encrusting taxa. However, while a greater amount of suitable food could possibly explain a greater volume in the sponge tissue, there are no current mechanisms or explanations which can explain the greater numbers of individuals or species at these stations. The results of this study do not explain the exact occurrence of sponge species diversity and abundance, but it sheds some light on potential correlations that may have large scale repercussions for the management and preservation of biodiversity on this coastline.

Further work is required to establish if there is a direct correlation between marine and terrestrial diversity. Specifically, further investigations are required to determine whether indigenous forests are responsible for supporting a greater diversity and abundance of coastal marine taxa via the output of terrestrially derived riverine organic matter. This could be achieved by conducting an interdisciplinary study with terrestrial, freshwater and marine ecologists to understand whether land and riverine diversity of biota has an influence on coastal reef communities. Such a study would provide some fundamental insights into the dependence and connectivity of marine organisms on land and riverine based ecosystems.

Chapter 4

From rivers to the sea: using stable isotopes of C and N to reveal the critical role of marine sponges in processing terrestrially derived carbon

4.1 Abstract

Sponge meadows play fundamental roles in cycling energy and matter between benthic and pelagic regions. Our knowledge of the origin and types of food consumed by sponges on temperate rocky reefs is poorly understood so our aim was to better understand the critical role sponges play in processing terrestrially derived organic matter. Our isotope analysis revealed that marine food sources including coastal seston (>1.2–400 µm), coastal GFX including combined fine and coarse glass fibre filter samples (>0.7–1.2 µm), and coastal bacteria (>0.2–0.7 µm) contributed the largest proportion to the diet of coastal sponges at 60–73%. This was followed by a relatively large proportion of terrestrially derived food sources including freshwater seston (>1.2–400 µm), freshwater GFX (>0.7–1.2 µm), and freshwater bacteria (>0.2–0.7 µm) at 27–40%. Isotope analyses showed that coastal seston ranging in size from >1.2–400 µm was the largest contributor to the diet of temperate rocky reef sponge species (50–60%), and freshwater bacteria ranging in size from >0.2–0.7 µm was the second highest contributor to the diet of sponges across all reef systems (10–29%). Further, proportional contributions to the diet of sponges included suspended particulate organic matter comprising freshwater seston ranging in size from >1.2–400 µm (6–10%), coastal GFX ranging in size from >0.7–1.2 µm (7–9%), freshwater GFX ranging in size from >0.7–1.2 µm (7–8%), and coastal bacteria ranging in size from >0.2–0.7 µm (6–8%). Combining our estimated C retention rate with the isotopically-determined contribution of foods from terrestrial sources to the diet of coastal sponges (27–40%), suggests that sponge meadows may retain approximately 117–173 kg of terrestrially-derived C km^{-2} day. These results suggest that sponges play a crucial role in linking terrestrial and marine food webs and associated carbon cycles via recycling of terrestrially derived carbon and nitrogen.

4.2 Introduction

Sponges are an opportunistic group of filter feeders with proven adaptability to survive in a diversity of ecological niches. Of significant importance is the ability of sponges to absorb and efficiently recycle organic matter and energy. Sponges are predominantly unselective particulate feeders that are capable of filter feeding on dissolved organic matter (DOM) and particulate matter from ~0.2 μm to 70 μm (Bergquist, 1978; Ribes *et al.*, 1999; Rix *et al.*, 2018). However, selective feeding has been reported in some sponge species, potentially creating a mechanism for niche structure, and allowing for increased species diversity because different species are not competing for the same resources (Banister, 2008). However, feeding experiments measuring exactly what food sources are ingested by particular species would bolster this idea of niche structure, and provide insights into the diversity of functional roles among sponge species. This selective feeding includes coral and algal exudates, picoplankton, and microplankton (Bergquist, 1978; Ribes *et al.*, 1999; Rix *et al.*, 2018). For example, the heterogeneous filter-feeding diet of the temperate sponge *Dysidea avara* includes a broad range of plankton sizes, from heterotrophic bacteria (0.3 μm) to pennate diatoms [70 μm; Ribes *et al.* (1999)]. Furthermore, direct phagocytosis by exo- and endopinacocytes of particles >50 μm can occur (Bergquist, 1978). Although phagocytosis extends the upper limit of size particles sponges consume, there is little known about how much larger plankton (>50 μm) contribute to the diet of sponges via ectosomal phagocytosis. Contributions of different planktonic groups may differ among sponge species because of variation in choanocyte numbers and feeding methods (Maldonado *et al.*, 2012, and references therein).

Despite sponges being an important part of the marine carbon cycle (Rix *et al.*, 2016), it remains unknown as to whether sponges consume terrestrially derived carbon. Approximately 0.25×10^9 t of dissolved (<0.5 mm) organic carbon (DOC) and 0.15×10^9 t of particulate organic carbon (POC, >0.5 mm) are transported from riverine sources into the ocean per year (Hedges *et al.*, 1997). The fate of this riverine organic carbon is an important component of the global carbon budget, and these sources alone are enough to sustain annual turnover of the entire pool of organic carbon dissolved in the ocean. However, one of the largest remaining enigmas within the global carbon cycle budget is that only a small fraction of organic matter dissolved in seawater and preserved in marine sediment is land derived (Hedges *et al.*, 1997). Burdige (2005) estimates

that only 25–30% of terrestrially-derived organic matter that reaches the ocean is efficiently buried in sediments on continental margins. Therefore, perhaps sponges are responsible for cycling some of this 'missing' terrestrial derived organic matter in the marine environment.

Sponges transform DOM to particulate organic matter (POM) which is subsequently consumed by higher trophic levels (De Goeij *et al.*, 2008; De Goeij *et al.*, 2013; Rix *et al.*, 2017; Rix *et al.*, 2018). Neverthless, Rix *et al*. (2018) suggested that additional studies are required to determine the quantitative importance of carbon from sponge detritus to the diet of associated fauna. Although extensive research has been carried out on the diet of sponges, no single study has investigated their importance in linking terrestrial and marine carbon cycles. Therefore, the main aim of this investigation is to determine the origin, and proportion of terrestrially derived organic carbon to the diet of temperate rocky reef sponges. To test this, the stable C and N isotope ratios of rocky-reef sponges and their putative food sources were sampled as δ^{13}C and δ^{15}N ratio's permit tracing of trophic interactions (Van Duyl *et al.*, 2011).

The major objectives of this paper were (1) to examine to what degree coastal temperate marine sponges rely on food coming from: (a) river water-derived, or (b) coastal and open water-derived; to (2) investigate the predominant size fractions of 'food' items sponges are consuming; and finally (3) to determine what proportion of the diet of marine sponges are in the size category (>1.2–400 μm) that largely excludes bacteria, henceforth called seston in this study.

4.3 Materials and methods

4.3.1 Study stations

Samples were collected over two seasons and three years (autumn, 4-5 April 2019; summer, 14-17 January 2020; and summer, 15-20 January 2021), along three transects in the Taranaki Region, on the North Island of New Zealand (Fig. 4.1). Transects were positioned along the coast near three rivers discharging from modified to increasingly 'pristine' catchments (respectively—Waitara (WAI), Waiwhakaiho (WAIW) and Hangatahua (HAN)) and running from rivers to the open ocean (Fig. 4.1). Stations along transects were characterised by differences in terrestrial, freshwater, and marine organic inputs from diverse land uses and water quality (Taranaki Regional Council, 2018). We sampled 2–3 stations along each transect (WAI, WAIW and HAN):

1) a freshwater station on each of the three rivers Waitara River, Waiwhakaiho River, and Hangatahua (Stony), 1–6 km inland, depending on how tidally influenced the rivers were, to avoid marine contamination: water samples were collected near the surface at a depth of 0.5 m.

2) 1–2 coastal rocky reef stations about 1–2 km offshore (from the three rivers Waitara, Waiwhakaiho and Hangatahua). Bottom-water samples were collected approximately 0.5 m above the reef and sponges at depths between 6–21 m.
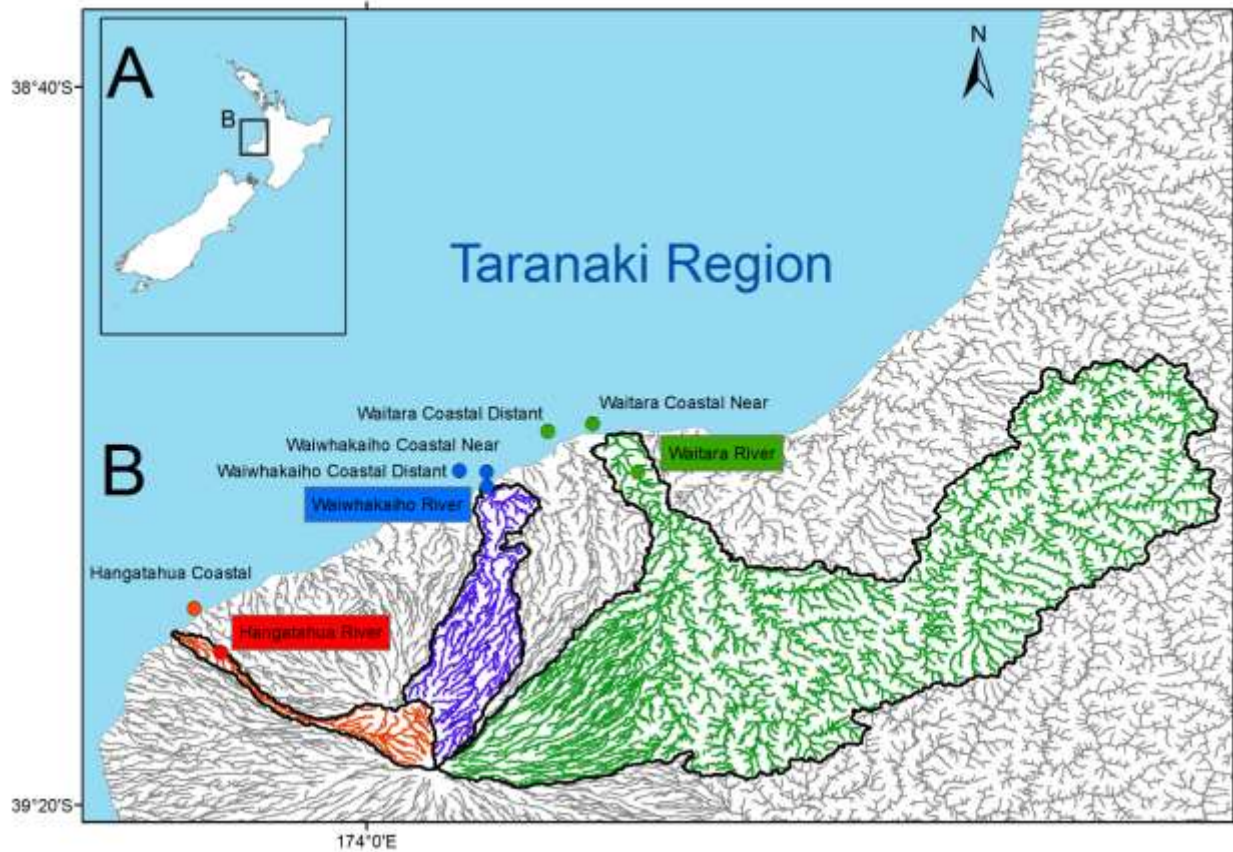
Figure 4.1 Areas inside of thick black outlines represent river catchment areas for three rivers (Waitara, Waiwhakaiho and Hangatahua) accompanied by their respective coastal rocky reef stations. Coloured lines (green, blue and red) represent rivers and their connecting water bodies. Rivers and their coastal stations combined collectively form three transects (Waitara (WAI), Waiwhakaiho (WAIW), and Hangatahua (HAN)).

Table 4.1 Stream order, catchment area, mean flow and mean annual low flow of the three Taranaki rivers adjacent to the marine sampling sites. Source: River Environment Classification layer in Freshwater Fish Database Assistant Version 6.1, Jowett, (1998).

Name	Stream order at the coast	Catchment area (km^2)	Mean flow (m^3 s^{-1})	Mean annual low flow (m^3 s^{-1})
Hangatahua (Stony) River	3	53.54	5.87	2.39
Waiwhakaiho River	5	135.89	11.13	4.04
Waitara River	6	1138.74	55.74	13.32

4.3.2 Sample collection

Water samples were collected from freshwater and marine stations with a deep well submersible pump (12 V and 22 W) attached to a hose and five-stage filtration media (47, 125, 200, 300 and 400 μm) to obtain different seston sizes as potential food sources for sponges. Additional freshwater and marine seston samples were collected using plankton nets from all stations, including: (1) river stations using 40-μm and 150 μm-mesh plankton nets, (2) and coastal stations using 20 and 350-μm plankton nets. Water was pumped through the five stage filtration media for approximately 2 h to obtain seston samples. A portion of this filtrate was collected in clean, sample washed 20-L containers. For each station, these 20-L water samples were collected (*n* = 65) and transported back to the laboratory for further filtration. The 20-L freshwater and seawater samples collected from all stations were filtered over 47-mm-diameter combusted glass microfiber filters (Whatman), then over a glass fibre coarse filter (GFC nominal pore size 1.2 μm), followed by a glass fibre fine filter (GFF nominal pore size 0.7 μm).

After freshwater and seawater filtration, filters were shortly washed with Milli-Q water (MQ) to remove salt (from marine samples only) and were dried at 50°C in an oven and stored in aluminium foil until processing. Freezing filtered samples was avoided to limit potential impacts on nitrogen isotope values (Lorrain *et al*., 2003). The remaining bacterioplankton in the GFF filtrate was concentrated with an ÄKTA flux tangential flow filtration system using a filter cartridge (CFP-1-E-3MA nominal pore size of 0.1 μm). The concentrate was consequently filtered over 0.2 μm pore size 25-mm-diameter Anopore discs (aluminium oxide membrane filters, Whatman). The discs were briefly washed with MQ (excluding freshwater discs) and dried at 50°C in an oven (12 h). Once dry, filters were crumbled in an acid-washed (1 mol L^{-1} hydrochloric acid) glass funnel, the integrated polypropylene support rings of the filters were removed and the filter

fragments were transferred to tin capsules, which were closed with tweezers. Subsequently, folded capsules were placed in coded trays and stored until processing.

Due to poor visibility (<4 m) during SCUBA diving at coastal stations (n = 5), a 10-m circular-search-pattern (360°) was used to collect as many sponge species tissue samples as possible, between depths of 6–21 m. The phylogenetic range was chosen to represent a large trophic cascade. The sponges were brought to the surface in labelled in zip lock bags (27 × 33 cm) and stored in a 35 litre chilly bin with ice for transport. Any biota found living on, or inside sponge samples were removed. Coastal rocky reef sponges were washed with MQ water to remove salt and tissue was removed from substratum, if present, using a knife and scalpel. Sponges were preserved in 70% ethanol for taxonomic identifications. The remainder of samples were collected in aluminium foil cups dried at 50°C for 12 h.

Sponges and tentative food sources were subject to stable isotope analysis. Both C and N isotopic composition of the samples were determined using a Dumas Elemental Analyser (Europa Scientific ANCA-SL) interfaced to an isotope mass spectrometer (Europa Scientific 20–20 Stable Isotope Analyser), at the University of Waikato Stable Isotope Unit. The C and N isotope ratios are expressed as $\delta^{13}C$ and $\delta^{15}N$ relative to an ANU C_4 sucrose standard for carbon and relative to urea for nitrogen, respectively, and the standard error of the instrument measurements is ± 0.5 $\delta^{13}C$ and ± 0.2 $\delta^{15}N$. All carbon isotope samples (except bacteria that were caught on aluminium filters) were acidified in hydrochloric acid (HCl) (sponge biomass was treated directly with acid in a test tube, then processed through glass filters; larger seston portions were treated using HCl acid vapour inside a desiccator with a ceramic base) prior to measurements and corrected for individual sets of blanks (isotope mass balance corrections). The filter paper was rinsed with MQ water at the end of filtration. $\delta^{15}N$ values represent total nitrogen.

Dried sponge samples were first ground up using a ceramic mortar and pestle. For isotope measurements, adequate amounts of sponge material were transferred into glass test tubes by adding 1 mol L^{-1} hydrochloric acid drop-by-drop until no further CO_2 was released. These were oven dried once more at 50°C (12 h) without rinsing to minimize loss of DOM and ground again (Jacob *et al*., 2005; Schlacher & Connolly, 2014). The aforementioned methodology for sample treatment was modified from Van Duyl *et al*. (2011).

4.3.3 Analysis of stable isotope data

The complete collection of stable isotope data was tested for normality using a Shapiro-Wilk test. A Levene's test for homogeneity of variance using $\delta^{13}C$ and $\delta^{15}N$ values was conducted on coastal versus freshwater habitat food sources. A Kruskal-Wallis one-way ANOVA was conducted on coastal versus freshwater food sources with a post-hoc Dunne's test to infer difference in mean rankings of each group.

MixSIAR was used to run a Bayesian mixing model to quantify the contribution of each food source to the diet of sponges (Stock & Semmens, 2016; Stock *et al*., 2018). We assumed trophic enrichment factors (TEFs) for sponge consumers of 3.5 ± 0.5 for $\delta^{15}N$ and 1 ± 1 $\delta^{13}C$ based on presumed stable isotope ratios of animals as there are no measured data on TEFs for sponges in food web studies (Vander Zanden & Rasmussen, 2001; Behringer & Butler, 2006; Van Duyl *et al*., 2011).

Food sources collected on Anopore filters (>0.2–0.7 µm) were characterised as a proxy for bacterial samples in the model input. As there were no significant statistical differences between GFF (nominal pore size 0.7 µm) and GFX (nominal pore size 1.2 µm) food sources, and for the purpose of simplifying model inputs, we grouped these two similar sized food categories into a single GFX category (>0.7–1.2 µm) (Figs. 4.2, 4.3). All larger suspended food sources collected were grouped into a single category characterised as seston (>1.2–400 µm) for model analysis. The rationale for the grouping of these food categories was to capture the large diversity of potential food sources that sponges may be consuming in freshwater and marine environments, including picoplankton (>0.2–2 µm), nanoplankton (>2–20 µm), microplankton (>20–200 µm), and mesoplankton (>0.2–20 mm) as either whole or broken-down organic matter (Omori & Ikeda, 1992).

R Studio v 4.0.3 software was used for analyses (R Core Team, 2020). MixSIAR, a model with a Bayesian framework for constructing stable isotope mixing models was performed on all six sponge food sources (bacterioplankton, GFX fractions of suspended matter and seston from freshwater and marine ecosystems) to determine the relative consumption of each food (Stock & Semmens, 2016).

Before Bayesian mixing models are run, they require prior distributions to be specific for estimated parameters including proportion of each food source to diet. These priors reflect knowledge of the system before models are run, and then updated with data to obtain a result, called a posterior distribution (DeVries *et al*., 2016). We ran the model using uninformed Dirichlet priors where sponges consumed all *n* food sources in equal proportions, $1/n$, (α = 1,1,1,1,1,1) which gives weight to the model of a generalist diet (DeVries *et al*., 2016). Three Markov chain Monte Carlo (MCMC) chains were utilised to fix the mixing model and assessed the convergence with the coda package (Plummer *et al*., 2006), the Gelman-Rubin diagnostic (Gelman *et al*., 2003). We ran the model with the 'long' MCMC setting in MixSIAR, with a chain length of 300,000, a burn in of 200,000, and a thin of 100.

4.4 Results

Freshwater food sources generally had lower $\delta^{13}C$ and $\delta^{15}N$ values than their coastal equivalents (Fig. 4.2; Table 4.2). For example, there was no overlap in $\delta^{13}C$ and $\delta^{15}N$ values between freshwater and marine seston sources (Fig. 4.2). The significance of these results was important because it allowed for the examination of the degree to which coastal sponges relied on food coming from riverine versus marine sources.
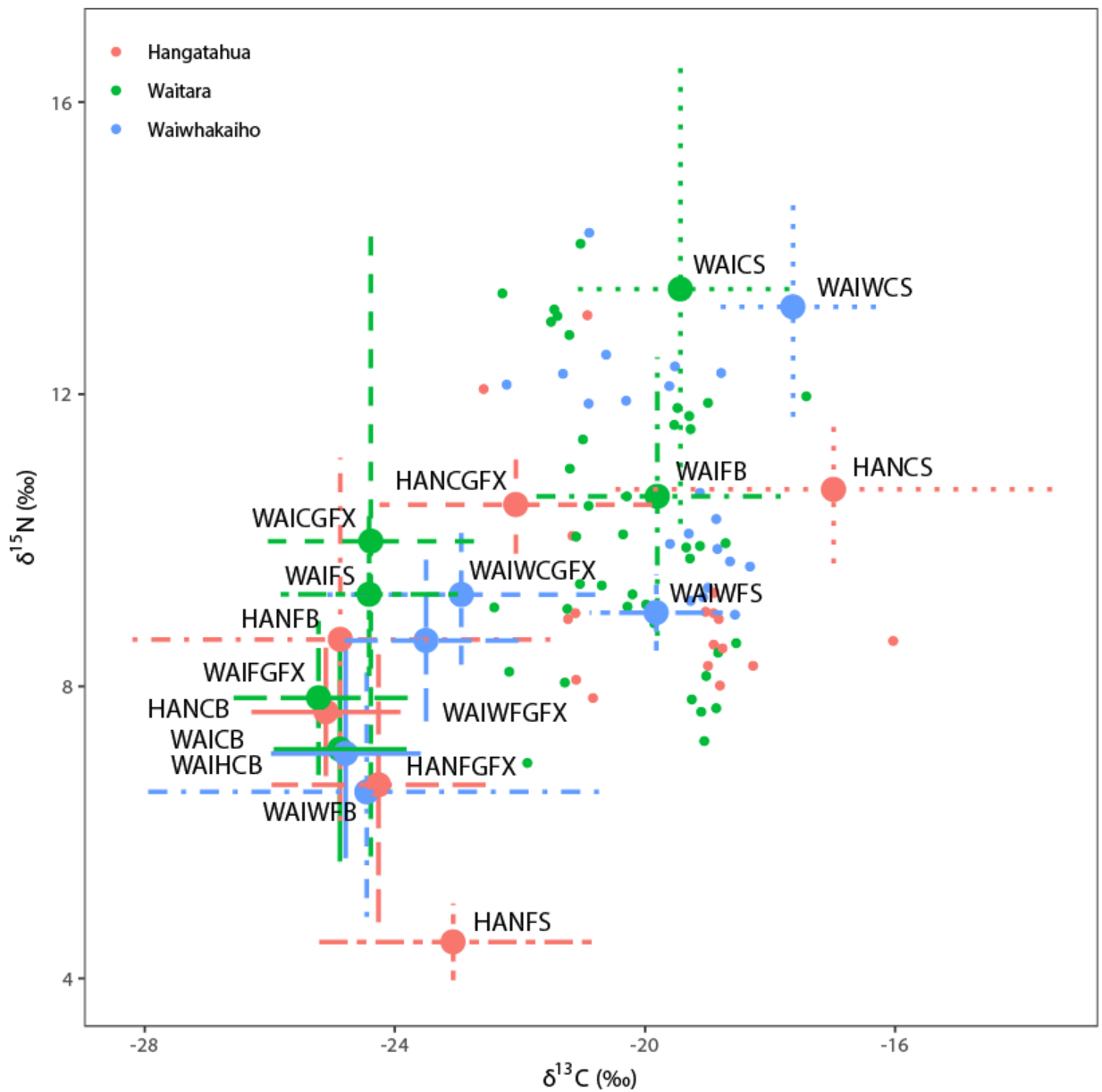
Figure 4.2 Dual isotope plot of sponges (smaller circles: red (Hangatahua (HAN), red; Waitara (WAI), green; Waiwhakaiho (WAIH), blue) relative to means of their potential food items (larger circles) corrected for trophic enrichment factors (raw $\delta^{13}C$ + 1‰, raw $\delta^{15}N$ + 3.5‰). For point labels, the first three or four letters are the river, and then CS = coastal seston, CGFX = coastal GFX, CB = coastal bacteria, FS = freshwater seston, FGFX = freshwater GFX, and FB = freshwater bacteria. For sample sizes of sponge taxa and food sources, see Table 4.1.

Table 4.2 Means ± 1 SD for δ^{13}C and δ^{15}N isotope values measured in parts per thousand (‰) of putative food sources and sponge consumers, including suspended particulate matter. Glass fibre coarse (GFC), glass fibre fine (GFF), bacteria, and seston collected from reef stations Waiwhakaiho (WAIW), Waitara (WAI) and Hangatahua (HAN) (stations, n = 1–8).

Substrate sources	WAIW Waiwhakaiho			WAI Waitara			HAN Hangatahua		
	n	δ^{13}C	δ^{15}N	n	δ^{13}C	δ^{15}N	n	δ^{13}C	δ^{15}N
Bacteria (>0.2–0.7 μm)									
Coastal water	5	−25.8 ± 0.7	3.6 ± 1.3	3	−25.9 ± 0.4	3.6 ± 1.5	5	−26.1 ± 0.6	4.2 ± 0.7
Freshwater	7	−25.4 ± 3.6	3.1 ± 1.6	2	−20.8 ± 1.7	7.1 ± 1.8	5	−25.9 ± 3.2	5.1 ± 2.4
SPM-GFX (>0.7–1.2 μm)									
Coastal water	12	−23.9 ± 1.9	5.8 ± 0.8	4	−25.4 ± 1.3	6.5 ± 4.3	4	−23.1 ± 1.9	7.0 ± 0.4
Freshwater	13	−24.5 ± 1.1	5.1 ± 1.0	7	−26.2 ± 1.0	4.3 ± 0.9	7	−25.3 ± 1.4	3.2 ± 1.8
Seston (>1.2–400 μm)									
Coastal water *(h)	3	−18.6 ± 0.9	9.7 ± 1.4	6	−20.4 ± 1.4	9.9 ± 3.2	4	−18.0 ± 3.3	7.2 ± 0.9
Freshwater *(h)	2	−20.8 ± 0.4	5.5 ± 0.1	1	−25.4 ± 0	5.8 ± 0	4	−24.1 ± 2.0	1.0 ± 0.2
Sponges	21	−19.7 ± 1.1	11.0 ± 1.5	39	−20.3 ± 1.1	10.1 ± 1.9	17	−19.7 ± 1.6	9.2 ± 1.4

All sponges were morphologically identified to species or operational taxonomic units (OTUs) using tissue and skeletal characteristics. Seventy-seven different sponges representing 54 species and OTUs were identified and sampled. Sponge values ranged from a mean δ^{13}C of −16.0‰ (*Stelletta arenaria*) to −22.5‰ (Haplosclerida sp. 1), and a mean δ^{15}N of 7.0‰ (*Darwinella oxeata*) to 14.2‰ (*Hymeniacidon sphaerodigitata*) (Figs. 4.3, 4.4). However, there were no significant differences in δ^{13}C and δ^{15}N species values among sponge populations at each reef station (ANOVA, *F* = 2.17, *P* = > 0.12). For a full individual breakdown of mean isotope signatures of sponge individual species and OTUs collected from each reef (see Appendix 4). Putative food source values are uncorrected for isotopic discrimination. Significant differences in δ^{13}C or δ^{15}N for food sources only (ANOVA significance value of *p* < 0.05, 8 comparisons) are indicated by a superscript: *(*h*) = significant difference between habitats (freshwater and coastal). *n* = number of individuals analysed for δ^{13}C and δ^{15}N values.
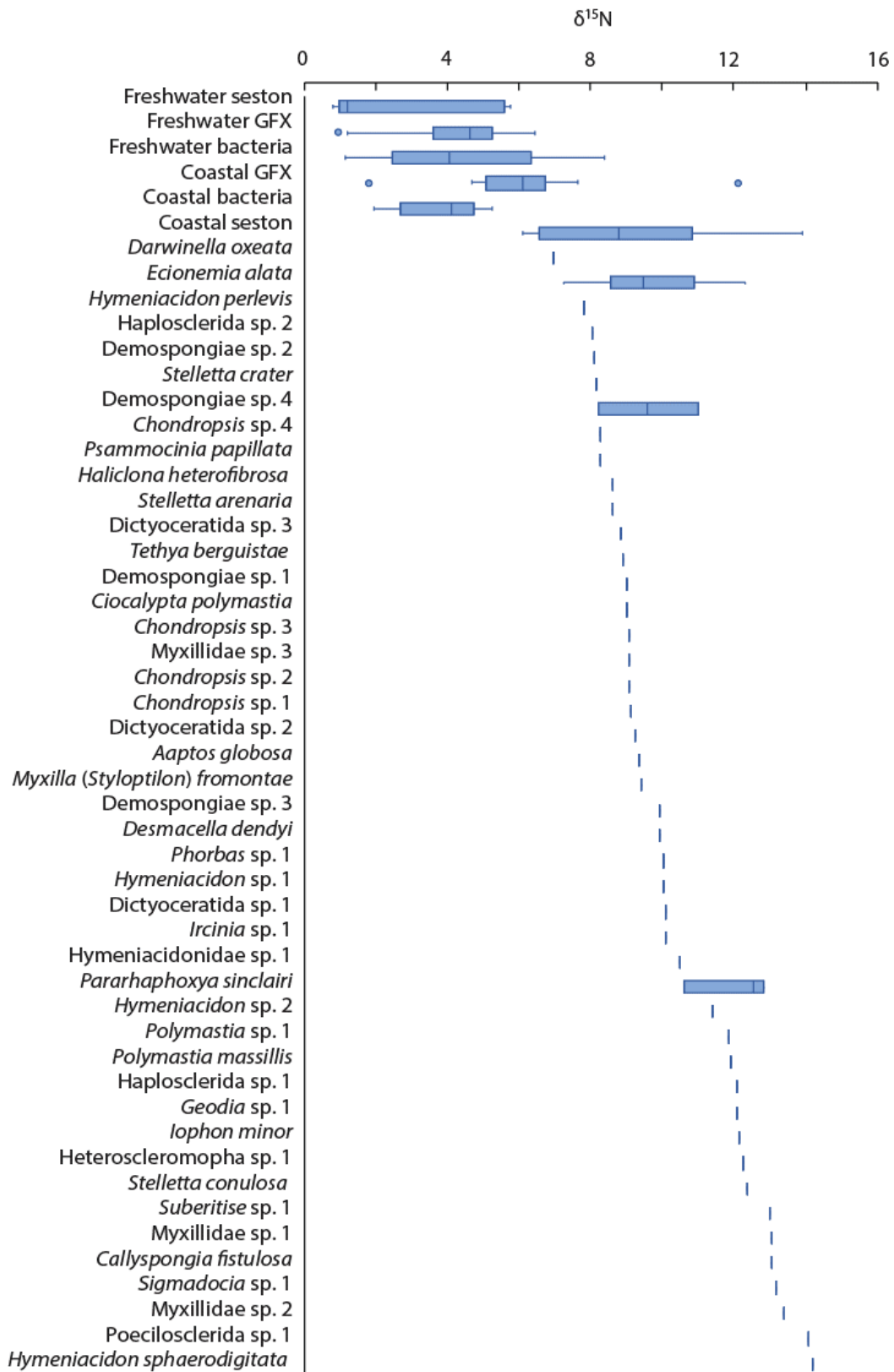
Figure 4.3 Mean ± SD for freshwater and coastal seston and sponge δ15N values for individual taxa from all stations.
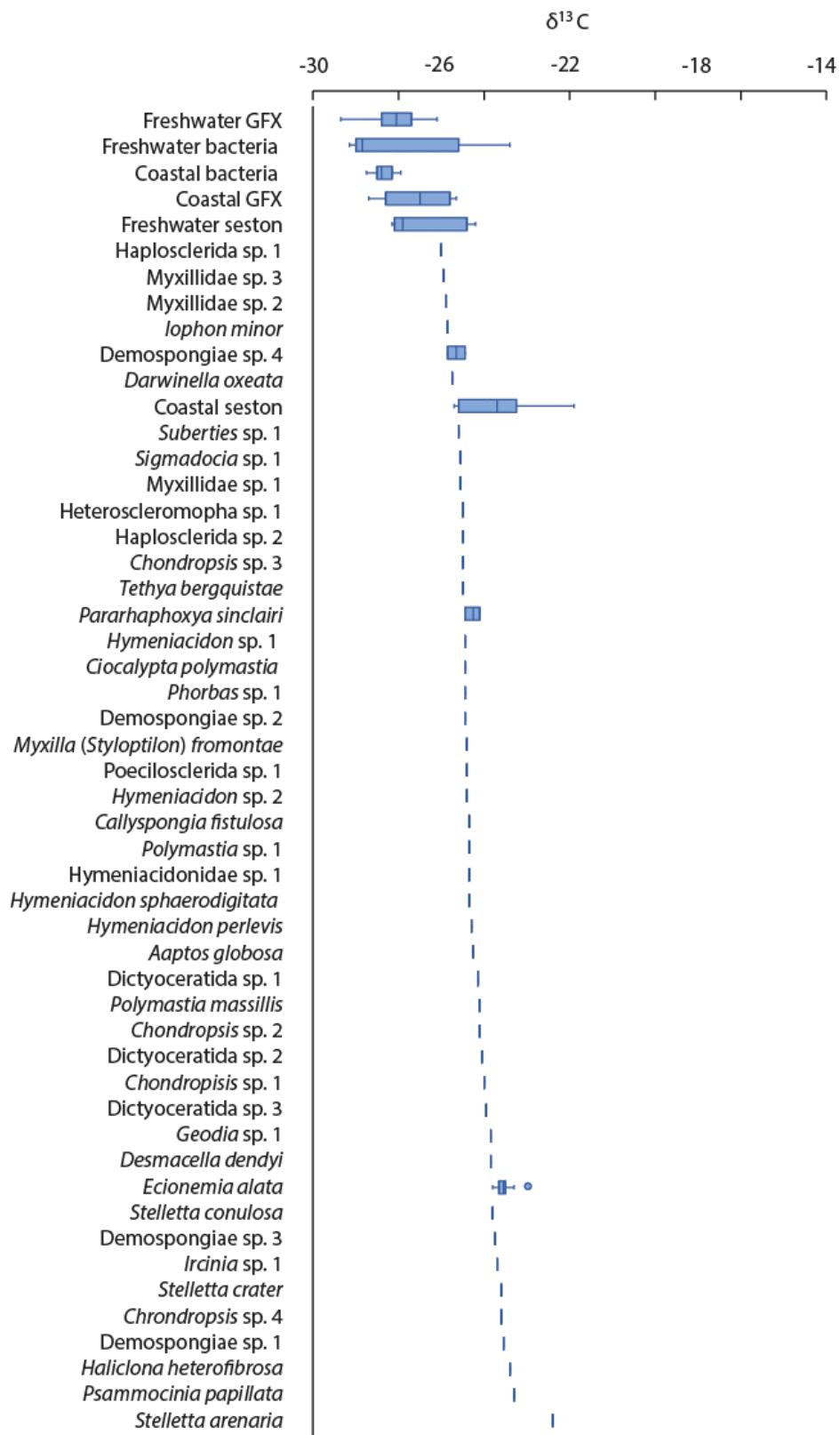
Figure 4.4 Mean ± SD for freshwater and coastal seston and sponge δ¹³C values for individual taxa from all stations.

Mean ± SD coastal bacteria δ^{13}C and δ^{15}N values were not within trophic reach of sponges (TEFs of ~3.5 ± 0.5 for δ^{15}N and ~1 ± 1 for δ^{13}C) at any of the stations (Fig. 4.5). Freshwater bacteria δ^{13}C values were in trophic reach of sponges at Waitara station, and freshwater bacteria δ^{15}N values were in trophic reach of sponges at Hangatahua and Waitara stations (Fig. 4.5). GFX δ^{13}C values were in trophic reach of sponges at the Hangatahua station, but did not overlap with sponges at Waitara or Waiwhakaiho stations, and coastal GFX δ^{15}N values were also in trophic reach of sponges at Hangatahua and Waitara stations, but did not overlap with δ^{15}N values at the Waiwhakaiho station (Fig. 4.5). Freshwater GFX δ^{13}C and δ^{15}N values were not in trophic reach of sponge values at any of the stations sampled (Fig. 4.5). Means ± SD δ^{13}C and δ^{15}N values for coastal seston were in trophic reach of sponges at all stations (Fig. 4.5). Freshwater seston values were in trophic reach of sponges at Waiwhakaiho, but freshwater seston δ^{15}N values did not overlap with sponges at any of the stations (Fig. 4.5).
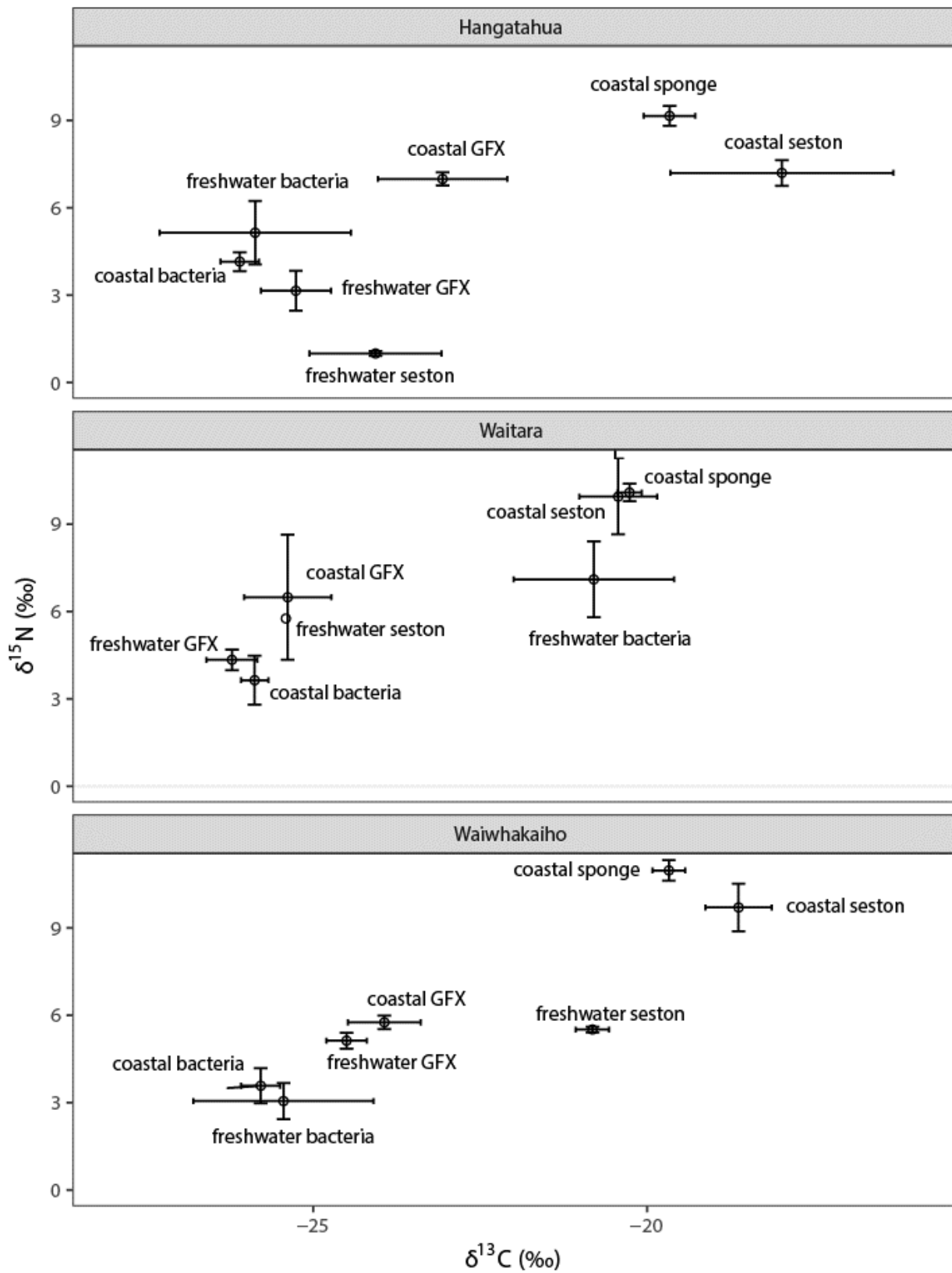
Figure 4.5 Mean ± SE $\delta^{13}C$ and $\delta^{15}N$ for all sponges, freshwater and coastal seston from three transects, Waiwhakaiho, Hangatahua, and Waitara.

Mixing models indicated that when combined food sources from all stations are separated into freshwater and coastal categories, combined marine sources (coastal seston, coastal GFX and coastal bacteria) contributed means of 60–73%, and combined freshwater sources (freshwater seston, freshwater GFX, and freshwater bacteria) contributed means of 27–40% (Table 4.3). Therefore, terrestrial sources represented a significant proportion of the diet of sponges at all coastal stations. Across all stations, a substantial fraction of the diet of sponges was coastal seston (50–60%) and freshwater bacteria (10–29%), followed by freshwater seston (6–10%), coastal GFX (7–9%), freshwater GFX (7–8%), and coastal bacteria (6–8%). The proportional contributions of each food source varied among stations (Table 4.3). These results suggests that the sponges were feeding predominantly on marine derived food, but also obtained a significant portion of their food from terrestrially derived sources. However, the amount of terrestrially derived organic matter that sponges were consuming was likely dependent on the amounts of terrestrial inputs at different coastal locations.

Table 4.3 Bayesian mixing model mean estimates (± standard deviation, SD), of the percentage (%) proportional contribution of each food type to the diet of sponges at each rocky reef station. SPM-GFX is suspended particulate matter collected on fine and coarse glass-fibre filters.

Food source	Proportional contribution to diet					
	Waiwhakaiho (WAIW)		Waitara (WAI)		Hangatahua (HAN)	
	Mean	SD	Mean	SD	Mean	SD
Bacteria (>0.2–0.7 µm)						
Coastal water	0.060 ±	0.061	0.053 ±	0.053	0.078 ±	0.067
Freshwater	0.101 ±	0.080	0.293 ±	0.252	0.150 ±	0.098
SPM-GFX (>0.7–1.2 µm)						
Coastal water	0.070 ±	0.078	0.051 ±	0.056	0.085 ±	0.077
Freshwater	0.070 ±	0.074	0.052 ±	0.051	0.081 ±	0.066
Seston (>1.2–400 µm)						
Coastal water	0.599 ±	0.091	0.496 ±	0.25	0.521 ±	0.083
Freshwater	0.100 ±	0.115	0.055 ±	0.057	0.085 ±	0.066

For example, sponges at the Waiwhakaiho River station (WAIW) had the largest amount of coastal seston in their diet of (60 ± 9%, mean ± SD) followed by freshwater seston (10 ± 12%), and the least dietary contribution from freshwater bacteria at all stations with 10 ± 8% (Table 4.3). Coastal seston was also the largest contributor to the diet of sponges at HAN station with at 52 ± 8%, followed by freshwater seston (9 ± 7%), freshwater bacteria (15 ± 10%), and minor contributions from other sources (Table 4.3). Moreover, sponges at WAI station had the lowest proportional contribution of coastal seston of all the river stations in their diet with 50 ± 25%, followed by freshwater bacteria (29 ± 25%), and minor contributions from other size fractions (Table 4.3). Coastal seston was also the largest contributor to the diet of sponges at HAN station with at 52 ± 8%, followed by freshwater seston (9 ± 7%), freshwater bacteria (15 ± 10%), coastal GFX (9 ± 8%), freshwater GFX (8 ± 7%), and coastal bacteria (8 ± 7%) (Table 4.3). Moreover, sponges at WAI station had the lowest proportional contribution of coastal seston in their diet with at 50 ± 25%, followed by freshwater bacteria (29 ± 25%), freshwater seston (6 ± 6%), coastal GFX (5 ± 6%), freshwater GFX (5 ± 5%), and coastal bacteria (5 ± 5%) (Table 4.3). Coastal seston contributed by far the greatest contribution of food to the diet of coastal sponges among all stations (Fig. 4.6). This was followed by the second largest contribution from freshwater bacteria which was highest at Waitara station (Fig. 4.6). In comparison coastal bacteria, coastal GFX, freshwater seston and freshwater GFX contributed relatively low amounts of food to the diet of all sponges (Fig. 4.6).
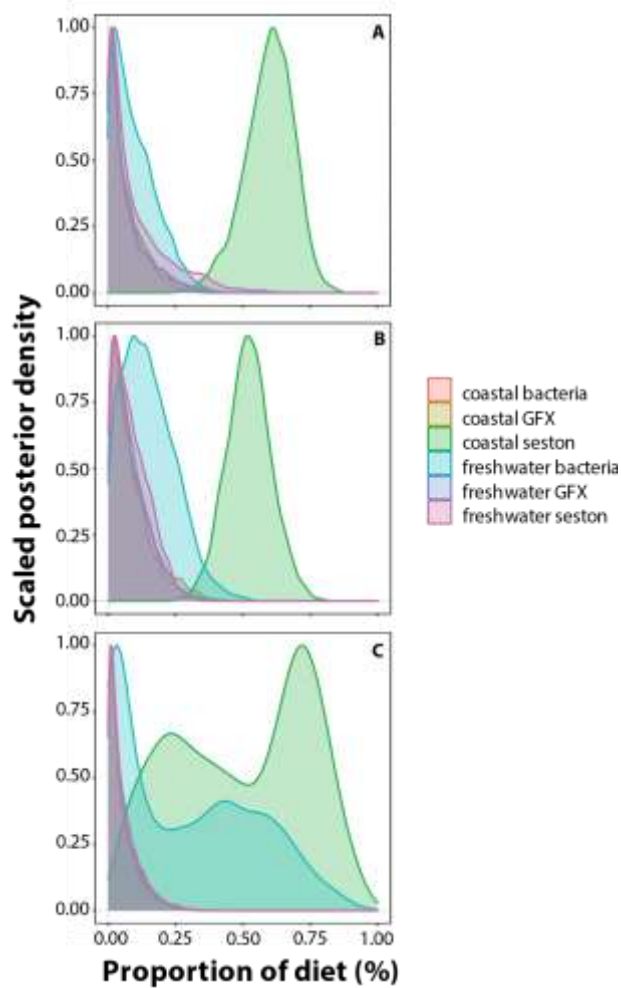
Figure 4.6 Posterior density plots from the best fit Bayesian Mixing Model displaying proportional contributions of coastal bacteria (pink, n = 13), coastal GFX (mustard, n = 20), coastal seston (green, n = 13), freshwater bacteria (light blue, n = 14), freshwater GFX (violet, n = 27), and freshwater seston (light purple, n = 7) in the diet of coastal rocky reef sponges along three transects **A.** Waiwhakaiho, **B.** Hangatahua, and **C.** Waitara. Results show that the largest contributors to sponge diet were coastal seston at 50–60%, and freshwater bacteria at 10–29% (peak values).

When the proportional contribution of coastal GFX was high, the contribution from coastal seston was low with a negative correlation of –0.45 (Fig. 4.7). The inverse was also true for coastal seston. There was also a negative correlation shown between the contribution of coastal seston and freshwater bacteria at –0.38 (Fig. 4.7).
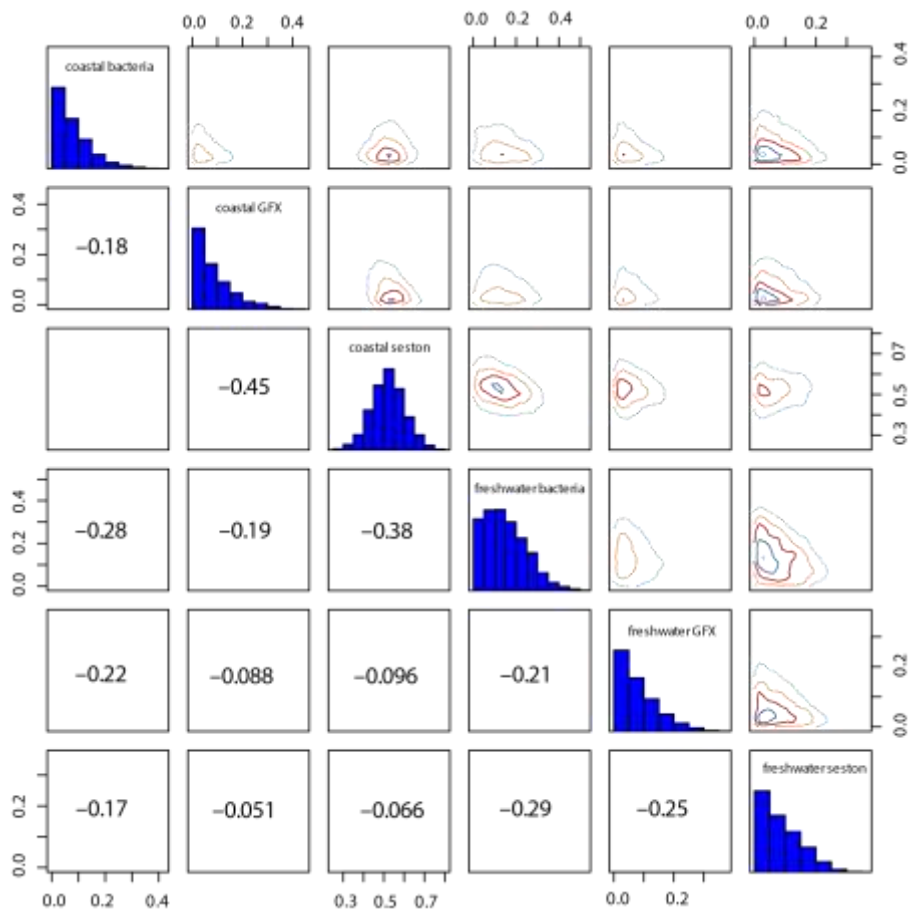
Figure 4.7 Pairs plot of the posterior diet proportions of the total sponge population. The cell above the diagonal displays contour plots with distribution of proportional contributions, and the cells below the diagonal show the correlations between the contributions from different dietary sources.

4.5 Discussion

Bentho-pelagic coupling via the transfer of food and nutrients including carbon, oxygen, silicon, and nitrogen are one of the most significant influences sponges have on pelagic ecosystems (Bell, 2008a). The pelagic microbial food web has been reported as the main food source for sponges throughout their entire bathymetric and latitudinal range (Yahel *et al*., 2005; Pile & Young, 2006; Bell, 2008b, Maldonado *et al*., 2012). In contrast, we found that larger size fractions of food (>1.2– 400 µm) contributed most of the diet (mean 60–73%). However, based on stable carbon and nitrogen isotope and fatty acid biomarkers, the main sources of food for sponges on a tropical coral reef in the Caribbean was not phytoplankton or bacterioplankton, but coral mucus and organic matter from crustose coralline algae (Van Duyl *et al*., 2011). There were no coral species recorded at any station in the current study, and therefore coral mucus was not included as

potential of food sources for sponges herein. Mixing model analysis revealed that marine food sources including coastal seston (>1.2–400 μm), coastal GFX (>0.7–1.2 μm), and coastal bacteria (>0.2–0.7 μm) contributed the largest proportion of combined food to the diet of coastal sponges at 67%, followed by a relatively large proportion of freshwater food sources including freshwater seston (>1.2–400 μm), freshwater GFX (>0.7–1.2 μm), and freshwater bacteria (>0.2–0.7 μm) at 40%. This provides novel information on the utilisation of terrestrial carbon and nitrogen as sources of food for marine sponges, thus filling this gap in the literature. The probable main source of food for sponges in our study were seston that were larger than bacteria ranging from >1.2–400 μm. Coastal seston (>1.2–400 μm) contributed up to (50–60%), to the diet of sponges based on our dual stable isotope (C and N) analysis. These results were relatively similar to those found by Ribes *et al*. (1999) who found the largest proportion contribution to the diet (74%) of the temperate sponge *Dysidea avara* was prokaryotes ranging in size from 0.5–70 μm. Therefore, when combined with the results from this study, temperate sponges appear to be obtaining the majority of their food from sources ranging in size from 0.5–400 μm. However, these results are different to those presented in Van Duyl *et al*. (2011) stating that coral mucus-derived dissolved organic matter may contribute up to 60% to the diet of examined sponges in that tropical environment.

The different niche structures found in sponges from temperate versus tropical reefs appears to be related to the most abundant sources of food available within each respective system. This further highlights the opportunistic nature of sponges throughout the world's oceans. Moreover, the current study has revealed that freshwater bacteria ranging in size from >0.2–0.7 μm was the second highest contributor to the diet of sponges across all reef systems (10–29%). Further, proportional contributions to the diet of sponges included suspended particulate organic matter comprising freshwater seston ranging in size from >1.2–400 μm (6–10%), coastal GFX ranging in size from >0.7–1.2 μm (7–9%), freshwater GFX ranging in size from >0.7–1.2 μm (7–8%), and coastal bacteria ranging in size from >0.2–0.7 μm (6–8%). However, it should be noted that the contributions of terrestrial organic matter to the diet of marine sponges may vary depending on several factors including proximity of sponges to freshwater sources, amount of terrestrial organic matter input in that area, and the bioavailability of organic matter.

The coastal sponges with the largest proportional contribution of freshwater bacteria to their diet (29%) were from Waitara (Fig. 6). Coastal sponges with the second largest contribution of freshwater bacteria were found at Hangatahua (15%), which was surprising because the Hangatahua River and therefore freshwater input was the smallest of the three rivers sampled (mean annual flow 5.83 m^3 s^{-1}; Table 4.1). This may also be because the Hangatahua River has the best water quality out of the three rivers (Taranaki Regional Council, 2020). Furthermore, rivers with catchments containing a larger coverage of forested areas may potentially yield more organic matter from leaf material, therefore, providing a source of food for sponges living on nearby rocky reefs. This is supported by Pawlik *et al*. (2016) who suggested that dissolved organic carbon coming from rivers may be partially responsible for the large abundance of sponges on Caribbean coral reefs.

Trophic enrichment factors (TEFs) are a fundamental part of mixing models (Stock & Semmens, 2016) and proxy taxa including benthic invertebrates and animals have been used in the past to obtain TEFs for sponges in marine ecosystem mixing models (Vander Zanden & Rasmussen, 2001 cited in Van Duyl *et al*., 2011; and Peterson & Fry, 1987 cited in Van Duyl *et al*., 2018). However, TEF data are obtained largely via a combination of field and artificial experimentation, and do not necessarily reflect contributions of sponge individuals or species (Vander Zanden & Rasmussen, 2001). Assumed trophic enrichment factors, therefore, are the weakest part of most applications of stable isotope mixing models for food web studies. Nevertheless, no single study exists that investigates TEFs based on sponge taxa. Therefore, general TEFs applied for animals were utilized here to allow for consistent comparison between other sponge stable isotope mixing model studies such as (Van Duyl *et al*., 2011; Van Duyl *et al*., 2018). Until a TEF estimation for sponges is produced, researchers should aim to consistently utilise the same TEF estimation values for sponges to make it easier to compare results across relative studies. It is worth noting, however, that the C and N isotopic composition of sponges recorded here had significant variation in isotopic values among species (Figs. 4.3, 4.4), which suggests that sponge TEFs are likely to be subject to interspecies variation. Large isotopic ranges among species data in the current study suggest that the diet of each sponge species is highly varied (Figs. 4.3, 4.4).

We assumed TEFs for sponge consumers of 3.5 ± 0.5 for $\delta^{15}N$ and 1 ± 1 $\delta^{13}C$ based on presumed stable isotope ratios of animals as there is no data on exact trophic enrichment factors for sponges in food web studies (Vander Zanden & Rasmussen, 2001; Behringer & Butler, 2006; Van Duyl *et al*. 2011). The basis for choosing these TEFs for sponge consumers is that they are plausible based on previous food-web studies and were used by other authors such as Van Duyl *et al*., (2011). Using TEFs consistent with other sponge studies allows comparisons to be made between similar sponge stable isotope data.

One important component of the global carbon cycle is the modern global fluviatile discharge and burial rates of organic carbon into the coastal ocean. Schlünz *et al*. (1999) estimates that approximately 430×10^6 t of terrestrial organic carbon per year are transported to the ocean from rivers in modern times. Only 43×10^6 t C year^{-1} (10%) of terrestrial carbon input is likely buried in marine sediments, although it is not known exactly what happens to the remaining carbon, or how much terrestrial organic matter is bioavailable to sponges and other marine organisms. However, given the relatively high proportion of freshwater carbon to the diet of sponges proposed herein, there is evidence to suggest that coastal temperate sponges are potentially processing large quantities of terrestrially-derived organic carbon in Taranaki.

Feeding efficiency and metabolic experiments conducted in New Zealand and Australia suggest that an average retention rate of 500 µg C L^{-1} for water pumped through each sponge (Bannister, 2008; Bannister *et al*., 2007, 2012). Based on an average pumping efficiency of sponges of 100 mL m^{-2} s^{-1} across a typical sponge meadow (Battershill & Bergquist, 1990; Bell, 1998), approximately 432 kg C km^{-2} day^{-1} could be retained. This is an estimate based on conservative estimates for carbon retention and pumping efficiencies, which nevertheless falls within the estimates for carbon retention calculated from other studies. For instance, Gili and Coma (1998) report an ingestion rates of 29–1970 kg C km^{-2} day^{-1} for a range of temperate and tropical sponge species. Combining our estimated C retention rate with the isotopically-determined contribution of foods from terrestrial sources to the diet of coastal sponges (27–40%), suggests that sponge meadows may retain approximately 117–173 kg of terrestrially-derived C km^{-2} day^{-1}.

When all proportional values of freshwater carbon were combined across the river stations, there were significant mean contributions of terrestrial carbon sources to the diet of sponges

(freshwater bacteria, 18%; freshwater seston, 8%; and freshwater GFX, 7%), which suggests that a strong link exists between terrestrial and coastal food webs. Therefore, for the first time we report large-scale benthic processing of terrestrial organic matter by sponges in river-dominated margins. Consequently, revealing an important role sponges have in linking terrestrial-marine food webs. There is abundant room for further progress in determining how much of this terrestrially derived carbon is being processed by marine sponges, and what implications this is having on coastal ecosystems globally.

4.6 Conclusions

We aimed to investigate the role of sponges in processing terrestrial carbon. The main goal of the current study was to determine to what extent coastal temperate sponges consume food coming from river-derived and coastal-derived food sources. We also set out to determine the predominant sources and proportions of each of these putative food sources to the diet of sponges, and what size categories of food sponges consumed the most. This study has shown that coastal seston and freshwater bacteria appear to be the main food sources for sponges on temperate, coastal rocky reefs in Taranaki. Interspecies variation in δ^{13}C and δ^{15}N stable isotope values may be the result of differential feeding mechanisms and dietary preferences among sponge species.

One of the largest remaining enigmas within the global carbon cycle budget is that only a small fraction of organic matter dissolved in seawater and preserved in marine sediment is derived from the land (Burdige, 2005; Hedges *et al.*, 1997). This data indicates for the first time that sponges consume terrestrially derived organic carbon and provides a mechanistic link for incorporation of terrestrial carbon into coastal marine environments (the 'missing' terrestrial carbon; Burdige, 2005; Hedges *et al.*, 1997; Kandasamy & Nagender Nath, 2016). This research shows that sponges can process a wide range of types of organic matter from both freshwater and marine environments. Further work could be undertaken to determine which portion of this land derived organic matter (labile versus refractory) is bioavailable to sponges in marine environments.

Sponges have been shown to transfer DOM, which is the largest resource produced on reefs to higher trophic levels via the rapid expulsion of choanocyte filter cells as detritus

consumed by larger fauna (De Goeij *et al.*, 2013). This suggests that sponges act as ecosystem engineers by potentially channelling terrestrially derived organic carbon towards higher trophic level organisms, and creating sponge based biogenic habitats (Bell, 2008a; De Goeij *et al.*, 2013). This would account for a portion of the 'missing' terrestrial carbon in both continental marine sediments and seawater. The current research extends our knowledge of the roles that sponges play in linking benthic-pelagic zones, but in also linking terrestrial-marine zones.

Chapter 5

General discussion

5.1 Summary of key findings

This thesis investigated aspects of environmental drivers of sponge assemblages over time, and some of the terrestrially derived inputs that may be influencing them. Land-sea connectivity between river and marine ecosystems were investigated. This thesis also set out to understand the critical role of marine sponges in processing terrestrially derived organic matter in marine ecosystems. However, sponge taxonomy which includes the characterisation and identification of species is fundamental to sponge ecology. This thesis had four main aims: (1) Chapter 2 aimed provide a quantitative baseline of sponge species diversity and abundance at a regional level along the Taranaki coastline, and provide a baseline of the biodiversity from this region; (2) Chapter 3 examined environmental factors influencing the distribution and abundance of marine sponges link to land coverage use around the Taranaki region; (3) Chapter 4 examined land-sea connectivity using stable isotopes (δ^{13}C and δ^{15}N) to understand the role of marine sponges in processing terrestrially derived carbon; (4) Chapter 5 provides a synthesis of findings.

Two appendices are provided as some preliminary taxonomic work was required in order to provide a basis for accurate species and operational taxonomic unit identifications in the field. Appendix 1 provides an update to the descriptions of five common sponge species from New Zealand using a combination of locally and nationally collected specimens from around the country; Appendix 2 provides a publication on two species that were described from Pilot Bay, Tauranga Harbour, New Zealand. This paper also constitutes a review of the Dictyoceratida also necessary for investigation in Taranaki (on-going taxonomic writeup for publication).

The key findings of this thesis were: (1) a baseline record of sponge species diversity estimates from Taranaki and greater detail in knowledge of a spatially patchy biogeography around the Taranaki coastline with both warm temperate and cold temperate affinities in addition to some unique species assemblages. These findings have important implications for developing conservation strategies for marine fauna on this coastline, highlighting locations of significant biological diversity, abundance, and uniqueness; (2) there was a greater diversity,

abundance and larger sized sponges in rocky reef communities that were positioned closer to river outputs from three major rivers in the Taranaki Region, likely as a result of increased food from terrestrially derived sources; (3) isotope analyses reveal that that marine food sources including coastal seston (>1.2–400 µm), coastal GFX including combined fine and coarse glass fibre filter samples (>0.7–1.2 µm), and coastal bacteria (>0.2–0.7 µm) contributed the largest proportion to the diet of coastal sponges at 60–73%, followed by a relatively large proportion of terrestrially derived food sources including freshwater seston (>1.2–400 µm), freshwater GFX (>0.7–1.2 µm), and freshwater bacteria (>0.2–0.7 µm) at 27–40%. These results suggest that sponges could play a crucial role in linking terrestrial and marine food webs and associated carbon cycles via recycling of terrestrially derived carbon and nitrogen; (4) an improved characterisation of five common sponge species that extends our knowledge on the geographical range of these species within New Zealand's Exclusive Economic Zone; (5) the characterisation of two novel sponge species which will allow researchers to better understand them, and protect them into the future

In this chapter, I discuss my results in a broader context of sponge taxonomy and biogeography, ecology, important functional roles, while considering the general implications of land cover types and associated catchment runoff on coastal reef communities. This chapter will also discuss the critical role of sponges in cycling carbon from both terrestrial and marine ecosystems. I will explain why sponges may constitute a hitherto unexamined trophic link explaining some of the conundrum of where the "missing' terrestrial organic matter coming from freshwater sources is going. Finally, I summarise the results of this thesis to provide suggestions for future research efforts on sponge ecology and taxonomy.

5.2 Biogeographic patterns

In Chapter 2 I showed that the biogeography of Taranaki sponges is unique over small spatial scales, and the distribution of species is patchy. The results of this study show that Poecilosclerida were the most recorded taxonomic group of sponges represented across all locations surveyed in the current study from Waitara, Waiwhakaiho and Hangatahua reefs. The second most common order recorded from all station was Tetractinellida (11%), followed by Dictyoceratida (6%), Suberitida (4%), Axinellida (3%), Scopalinida (3%), and Tethyidae (1%). An important finding from this study was that there were 35 sponge species that only occurred at

the northernmost and southernmost locations at Pariokariwa reefs in North Taranaki and Kapiti Island reefs to the south in the Wellington region.

This study also highlights areas with particularly high biodiversity including Waitara and Pariokariwa reefs. Results from this investigation provide a baseline species diversity estimate with a total of 127 sponge species recorded from all shallow water stations in Taranaki surveyed herein, with an index estimation of 2.4 sponge species per m^2 of rocky reefs surveyed. Pariokariwa Reef had the largest number of sponge species unique to that area (44 unique species). Surprisingly, Waitara reefs, arguably the most sediment impacted, had the second largest number of unique sponge species among all locations in Taranaki (36 unique species), followed by Patea reef (12 unique species), Hangatahua (9 unique species), and Waiwhakaiho (6 unique species). Biodiversity estimates from Taranaki are difficult to compare to other regions of New Zealand because of differentiated sampling methods, varying degrees of sampling effort, and the differences in habitats sampled among sponge biodiversity surveys. Nevertheless, sixty-five different sponge species from 27 families and eleven orders of Demospongiae, and four families and three orders of calcareous sponges were reported from the Wellington Region of New Zealand (Berman & Bell, 2010). There are a small number of additional regional surveys of sponge biodiversity in the grey literature from between North Cape and Cape Reinga at the very tip of the North Island (Cryer *et al*., 2000); and a sponge species survey recorded from Cape Rodney to Okari Point Marine Reserve located approximately 90 km from Auckland (Ayling, 1979; Pritchard *et al*., 1994).

There are several possible explanations for the spatial patchiness of some of the taxonomic groups of sponges recorded including, but not limited to, favourable substrate for attachment, random distribution caused by ocean currents, predation, competition, adaptation to the effects of riverine sedimentation or lack thereof, presence for dispersal of larvae near parent sponges, and food availability from the rivers (see Chapter 4 for an explanation for riverine sources of food for sponges). At 47 sponge species, the Waitara location had the highest diversity of sponge species from all stations surveyed herein. These results are congruent with results from Beaumont *et al*. (2010) that found a larger diversity of molluscs, echinoderms, polychaetes, bryozoans, arthropods, sponges, wading birds, diadromous fishes, rocky reef fishes, and macroalgae with a mean rank score of 3.6–4.0 at this location compared to the surrounding areas.

Overall, these findings have important implications for developing conservation strategies for marine fauna on this coastline, highlighting locations of significant biological diversity, abundance, and uniqueness.

Two taxonomic reviews of sponge taxa were used to develop the taxonomic expertise to undertake this larger scale biogeographic study (see Appendix 1 & 2). Although these reviews were conducted in the Bay of Plenty region, they are relevant to the current study because many of the described and reviewed species are also found in the Taranaki region, and delineated the techniques used in delineating differences between species. Therefore, this taxonomic work is important and relevant to the major aims of this thesis, which uses taxonomic and operational assignments of sponge taxa to better understand their biogeographic patterns, ecological interactions, and important roles in marine systems.

Prior studies that have noted the importance of consulting local iwi, the importance of naming Māori language communities and language experts to understand the rules of naming species using Māori names within the Linnaean characterization system (Whaanga *et al*., 2013). Furthermore, with the aim of preserving cultural heritage and with respect for Māori authors consulted local Tauranga Iwi and consulted Caine Taiapa and Reon Tuanau from Manaaki Te Awanui for approval and blessing to use meaningful te reo Māori names of the two species names described in Appendix 2 (*Dysidea tuapokere* Kelly, Mc Cormack & Battershill, 2020 and *D. teawanui* Kelly, Mc Cormack & Battershill, 2020). Named for the beautiful, translucent, pale lilac colouration of this species in life (*tuapokere*, violet; te reo Māori). This species name was accepted and approved by local Tauranga Moana iwi, Ngāti Ranginui, Ngāi Te Rangi and Ngāti Pūkenga. *Dysidea teawanui* was named for Tauranga Moana, Te Awanui, a spiritual symbol of identity for all whanau, hapu and iwi living in the harbour catchment area (*Te Awanui*, Tauranga Moana; te reo Māori). This species name was accepted and approved by local Tauranga Moana iwi, Ngāti Ranginui, Ngāi Te Rangi and Ngāti Pūkenga.

Improved taxonomic descriptions of sponge including individuals from difficult groups to characterize are important because they help us understand the diversity of sponge species worldwide. Some of the issues relating to sponge taxonomic work are inadequate historical descriptions that require updating. Some issues emerging from this finding relate specifically to a dearth of biologists working on the ecology of the phylum Porifera in New Zealand. If sponges

were easier to differentiate and recognize in the field it would make it easier to study and understand some of the potential threats they are facing in changing ecosystems. Accurate measures of sponge biodiversity are difficult but would allow us to detect changes in their abundance and diversity over time and allow resource managers to implement specific conservation strategies to protect ecologically important communities.

Overall, sponges have affinities with both cool and temperate regions but also have a high level of uniqueness in key places (Paraninihi and Waitara) where there are species that are not found anywhere else in the country. This is especially the case at Waitara reefs which had the second largest number of sponge species of all the stations in Taranaki (36 unique species to that area), followed by followed by Patea reef (12 unique species), Hangatahua (9 unique species), and Waiwhakaiho (6 unique species). These results are congruent with results from a study by Beaumont *et al*. (2010) who found a large diversity of marine taxa from all of the phyla they examined from around the Waitara area.

5.3 Importance of land cover for distribution and abundance of sponge communities

In chapter three I showed that sponge abundance, diversity, percentage cover and volumes were greatest at coastal stations positioned near river mouths. I also showed that sponge volumes were highest at the coastal site that was adjacent to the most ecologically healthy river (Hangatahua River), which also had the largest catchment coverage of indigenous forest (93%). This suggests that sponges grow larger in areas where freshwater sources are more 'pristine', which may be the results of potentially greater abundance of food coming from indigenous forests compared to land covered by pastures or urban area. However, it should be noted that these influences require further investigation to determine if catchment and land use type were the underlying reasons for these ecological patterns in abundance, diversity, percentage cover and volumes of sponges, and are statistically tested. Based on the literature it has been suggested that some clionid sponges thrive in areas with increased eutrophication (Holmes, 2000). The findings from the current study support research of Pawlik *et al*. (2016) who suggested that a large abundance of sponges on Caribbean coral reefs may be partially the result of large inputs of dissolved organic carbon from riverine sources. However, many of these studies are species

specific and do not support the broad influence of eutrophication on different sponge species. The influence of water quality including eutrophication and sedimentation has been shown to influence the reproductive output of a sponge species *Rhopaloeides odorabile* on the Great Barrier Reef (Whalan *et al.*, 2007). The levels of female reproduction increased with increasing distance from the coastline with oocytes from offshore sponges found to be significantly larger than oocytes from coastal sponges and sponges from offshore reefs had a reproductive index approximately 15 times greater than coastal reef sponges (Whalan *et al.*, 2007). Moreover, an investigation by Polónia *et al.* (2015) found that although the composition of sponges was primarily related to habitat variables, satellite imagery revealed that water quality parameters including coloured dissolved organic matter index, and remote sensing reflectance at 645 nm proved significant predictors in variation of the composition for sponges. Therefore, differences in water quality or increased eutrophication may influences the community structure of sponges along the Taranaki coastline. However, further studies using remote sensing data may provide additional supporting information to bolster these claims.

Land cover types appear to be affecting the diversity and abundance of coastal marine sponge communities. However, further research is required to ascertain whether these land cover attribution patterns are affecting the diversity of sponge fauna as there are many physical and biological variables that were not measured in the current study. For example, further study could determine the effects of sediments, temperature, salinity, and chlorophyll on the abundance and diversity of sponge populations among stations. Nevertheless, Waiwhakaiho 'coastal near' rocky reef station positioned near Waiwhakaiho River which has a river catchment with a relatively large coverage of indigenous forest (64%) Waiwhakaiho coastal reef station had the largest diversity and abundance of sponge species. Dudley *et al*. (2020) conducted a national-scale investigation in New Zealand examining the effects of land cover effects on coastal water quality from rivers while controlling for marine dilution. Dudley *et al*. (2020) found that sites with greater freshwater influence had higher nutrient and faecal indicator bacteria concentrations and turbidity, indicating that open coast and estuarine water quality is reduced predominantly via flows from land. Concentrations of nitrate, ammonium, total and dissolved reactive phosphorus, and water column chlorophyll-a concentrations were greater in estuaries with higher urban land cover and total phosphorus concentrations were greater with higher agricultural land cover

(Dudley *et al*., 2020). Therefore, not surprisingly the largest diversity and abundance of sponges was seen at more eutrophic coastal near stations that were positioned near the Waitara and Waiwhakaiho river mouths. What is surprising is that the largest sponges in terms of volume occurred at the smallest river with the smallest river catchment (Hangatahua River), this may be attributed to the greater quality of food coming from the river catchment with a greater proportion of indigenous forest (94%). The next steps for studying this would be to conduct a study that clearly distinguishes influences of indigenous forests versus other land cover types on the food quality of coastal filter feeders like sponges and other benthic biota.

This chapter also aimed to examine potential environmental factors influencing the diversity and abundance of benthic marine taxa along the Taranaki coastal zone. The outcome was that there were no correlations observed between sponge species diversity versus mean turbidity (NTU), mean sponge volume (cm^3), mean total nitrogen (g N m^{-3}), mean total phosphorous (g P m^{-3}), and mean *E. coli* concentrations (cfu 100 mL^{-1}). The adaptability of sponges to survive in water with large amounts of *E. coli* are not surprising, however, as sponges have been recorded selectively feeding on pathogenic microbes including harmful *E. coli* in experimental conditions (Maldonado *et al*., 2012). However, those results should be considered with caution as sponges used for bioremediation of microbial pollution may selectively ingest certain bacteria that may end up fuelling growth of harmful bacteria that are less grazed, such as *Vibrio* spp. (Maldonado *et al*., 2012). There were associations found here between mean sponge volume (cm^3) versus turbidity (NTU) with sponges appearing to decrease in overall size with a turbidity NTU greater than 100. These results support research conducted by Bell *et al*. (2015a) which found that sedimentation has several effects on sponges including pumping rates, feeding, respiration, reproductive output, growth, impacts of sediment on sponge symbionts, larval success and mortality and abundance and diversity patterns. However, sediment impacts on sponges are dependent on the quantity, particle size and mineralogy (Bannister *et al*., 2012; Bell *et al*., 2015a). The results from the current study must be treated with caution as there is no universal relationship between turbidity and sediment, but a good correlation can be established for individual rivers, and therefore this data can be supported by future work examining this correlation the rivers studied here. Nevertheless, for the purpose of this work, and given the limited time and resources for this study turbidity was utilized as a proxy for sedimentation.

Mean sizes of sponge individuals (volume) appeared to decrease with an increase in total nitrogen (g N m^{-3}), and there was also an increase in volumes of sponges at Hangatahua coastal near station with a proportionally large amount of mean total phosphorus at this site. However, the exact reasons for both the decrease and increase of sponge volumes with total nitrogen and phosphorus respectively are not known, and one cannot assume that these correlations are the cause for changes in sponge volumes without experimentally understanding these relationships.

Hangatahua River is the river with the best ecological health of all three rivers studied (Taranaki Regional Council, 2020). Waitara coastal near station had the largest percentage coverage of sponge species at 22%, and the largest diversity of taxa (61) across all phyla among all stations. Moreover, the Waitara coastal near station had the second highest diversity of sponge species at 17 in addition to the second highest number of sponge individuals among all stations at 66. These results are interesting because the Waitara River catchment is also the largest river catchment in the Taranaki region and is largely covered by a combination of indigenous forest (48%), and pasture (43%). Pastures are likely to have mostly agricultural grazing land uses including sheep, beef, or dairy farming.

The evidence from this study suggests that sponges are a resilience group of animals that have adapted to survive in eutrophic environments with large amounts of turbidity, total nitrogen, phosphorus, and *E. coli*. There is also evidence that sponge diversity and abundance increase closer to river mouths. Although correlation does not imply causation, there was also a correlation between a decrease in the volume of sponges with an increase in total nitrogen coming from rivers.

This research extends our knowledge of sponge species diversity and abundance in Taranaki. It also extends our knowledge of potential environmental factors affecting the distribution of benthic taxa on this coastline. Despite its exploratory nature, this study offers some insight into the influence of rivers and river catchment coverage on populations of marine organisms. Finally, several important limitations need to be considered: (1) It is difficult to determine exact reasons why the diversity, abundance and volume of taxa change from station to station without performing individual experiments on each of the potential factors that may be affecting these taxa; (2) This study was limited to available data collected by the Taranaki Regional Council, and there is scope to examine other potential factors that may be influences

coastal taxa including sedimentation from rivers. However, due to limited time and resources we could only examine the aforementioned factors; (3) All three rivers were different in terms of their mean annual flow, catchment size and catchment land cover, and therefore it is difficult to make definitive statements that draw comparisons between rivers.

Additionally, general trends can be drawn from individual rivers, especially between sites near and distant to rivers. It would be preferable to also increase the sample size of rivers and conduct a larger scale study examining the effects of river catchments with a larger proportion of indigenous forests on the diversity and abundance of coastal marine taxa. What is now needed is a cross-national study involving large scale geographical information of land coverage types and studies of benthic fauna to determine if specific land use types can increase our coastal biodiversity and abundance of taxa, and thus the resilience of these systems into the future. Another important practical implication is that although some of the river catchments including Waitara had a relatively large proportion of grasslands, they had a larger diversity of coastal taxa located closer to river mouths than distant stations. Therefore, rivers are clearly important for benthic fauna, and sponges may thrive near river mouths with a larger proportion of indigenous forest. Management to enhance sponge populations might involve setting up terrestrial reserves on land that have a large coverage of indigenous forest to protect coastal marine communities.

5.4 Role of sponges in processing terrestrially derived carbon

In Chapter 3, the MixSIAR model found a high proportional content of terrestrially derived organic matter in the diet of coastal marine sponges. This outcome has significant implications for the functional role of sponges in processing terrestrial carbon entering marine systems throughout the world. However, the exact amounts of terrestrial carbon sponges are consuming is still unknown. The benefits of sponges processing carbon, including dissolved organic carbon on coral reefs has been found to provide significant benefits to higher trophic levels (Rix *et al.*, 2016). Therefore, if sponges are consuming potentially large amounts of terrestrially derived carbon this may also have a knock-on effect to other taxa by sponges either creating food via the production of sponge cell detritus or via the direct consumption of sponge biomass by other invertebrates such as nudibranchs. Results from chapter four reveal that sponges were mainly consuming larger seston (>1.2–400 μm) from both marine and freshwater sources.

Prior studies have noted that not all sponges are created equal and that sponge expansion on coral reefs in the future may be limited by nutrient availability, including higher concentrations of particulate, and dissolved organic matter (McMurray *et al.*, 2018; Rovellini, 2019). Previous authors suggested that sponges on some coral reefs may be food limited and rely on food coming from rivers and from wind-borne dust (Pawlik *et al.*, 2018; Rovellini, 2019). However, sponges living on temperate coastal reefs are usually not as food limited as tropical oligotrophic environments. Sponges living on temperate rocky reefs are also obtaining large portions of dual sources of food from both terrestrial and marine sources. Although the results of chapter 3 show that sponges on these temperate reefs obtained most of their food from marine sources, there is also a clear reliance in some cases on food coming from terrestrially derived sources (up to 40% of diet) and therefore the connectivity between freshwater sources providing food for coastal marine ecosystems is highlighted.

5.5 Future research

Analysis of the abundance and diversity of sponges in chapter two allowed an in-depth assessment of the state of five coastal rocky reef stations along the Taranaki coastline. For the first time, a species list including taxa from all phyla examined here provided a baseline for rocky reef fauna on this coastline. However, further experimental work on environmental factors is required to better understand why there were a greater diversity and abundance of sponge taxa at some of the stations studied. For example, diversity and abundance of sponges was largest at the Waitara coastal near station, which has the largest river and river catchment, but it remains unclear if this is related to the larger food availability at these stations that may sustain larger populations of sponges. Therefore, further experimentation is required to understand specific and cumulative effects of each of the environmental factors investigated here on the physiology and populations structure of sponge populations. For example, the literature states that sedimentation has clear physiological effects on sponges, but the degree to which is affects sponges is dependent on the characteristics of the sediment and the volumes of sedimentation that the sponge is experiencing. However, if a river transporting large amounts of sediments that were having a negative physiological effect on sponges in that area, but the river was also providing large amount of food in the form of terrestrially derived organic matter that was benefiting the sponges it may be difficult to tease apart whether this river system was beneficial

overall to the coastal sponge communities. Therefore, understanding the tolerances of sediments specific to each river and or the tolerance to other pollutants is important as these need to be monitored in terms of their effects on sedentary coastal taxa including sponges. Nevertheless, it is clear from the research conducted in chapter two that there is a larger diversity and abundance of sponges located closer to river systems. Therefore, understanding exact interactions between freshwater ecological health, land coverage types and river pollutants on coastal marine communities requires further investigation.

Research described in Chapter 3 highlights the importance of sponges for cycling terrestrially derived organic matter. However, there is further work required to quantitatively assess how much terrestrially derived organic matter sponges are processing. Previous studies have shown that sponges are important to coral reefs because they are cycling energy and matter providing food to higher trophic levels via the production of particulate organic matter via the sponge loop. However, it is not clear what functional roles marine sponges play in terms of nutrient cycling in food rich temperate waters where higher trophic levels may not be as reliant on sponges producing particulate organic matter. Therefore, sponges may fill a different ecological niche in temperate systems. Future research should focus on what effects sponges are having in food-rich environments by cycling terrestrial and marine organic matter and determine how much land derived organic matter sponges are consuming in these systems.

5.6 Concluding remarks

In summary, the results presented in this thesis suggests that sponge meadows and other coastal taxa are supported by freshwater systems. Sponge communities are relatively resilient to environmental change and have proven adaptability within their environment. Increased abundances of sponges in coastal areas will likely depend on the influence of lard-derived anthropogenic activities including land cover and land use. However, the current study highlights the importance of terrestrially derived carbon to the diet of sponges on temperate rocky reefs in the Taranaki region. Ecological interactions between sponges and terrestrially derived matter will largely shape coastal communities in the future, thus determining the biogenic complexity of sponge habitats that provide significant benefits to diversity of taxa including commercially important fisheries species. The exact amounts of terrestrially derived carbon that sponges are consuming in globally is not yet known. Sponge terrestrial organic processing is likely having

ecological benefits through the direct production of sponge tissue for fishes and invertebrates, to the production of particulate organic matter for other detritivores. The specific ecological health of sponge communities along the Taranaki coastal zone is not known, however, this work provides a baseline to measure future impacts to this area and provides a reference for a before-after-control-impact assessment (BACI) for potential future environmental disasters, including sedimentation from climate change induced flooding.

The taxonomic tools provided from this study are important for both descriptions of taxonomically difficult groups to classify and groups that require taxonomic redescriptions. Given the logistical difficulties of assessing the sponge diversity on the Taranaki coastline this study provides a critical baseline for understanding the taxonomic, functional, and ecological significance of these sponge communities. This research extends our knowledge of land-sea connectivity, and specifically the role of sponges in linking these two systems. A key policy priority therefore should be to plan for long-term care of sponge communities by gaining an increased understanding of their health at local, national, and international scales and research the key anthropogenic activities and land use practices that are influencing them either negatively or positively. Perhaps a combination of terrestrial reserves grouped with adjacent marine reserves would improve the overall health and wellbeing of coastal marine ecosystems and would offer ecologically unique and highly biodiverse coastal locations improved protection.

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Appendix 1

Redescription of five sponge species from Pilot Bay, Tauranga Harbour, Bay of Plenty, New Zealand

Authors: Mc Cormack, Kelly, & Battershill, 2021.

Redescription of five sponge species from Pilot Bay, Tauranga Harbour, Bay of Plenty, New Zealand

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Abstract

A collection of sponges (Porifera, Demospongiae) from Pilot Bay, Tauranga Harbour, Bay of Plenty, New Zealand, has facilitated the re-examination and redescription of five common New Zealand sponge species: *Aaptos globosa* Kelly-Borges and Bergquist, 1994 (Subertida, Subertidae), *Acanthoclada prostrata* Bergquist, 1970 (Axinellida, Stelligeridae), *Biemna rufescens* Bergquist & Fromont, 1988 (Biemnida, Biemnidae), *Halichondria* (*Halichondria*) *moorei* Bergquist, 1961 (Suberitida, Halichondriidae), and *Stylissa haurakii* Brøndsted, 1924 (Scopalinida, Scopalinidae). The results progress the modern requirements of description from those described in early New Zealand literature which lack adequate and detailed descriptions of species and images of these sponges in life.

Key words:

Porifera, Demospongiae, taxonomy, New Zealand EEZ

Introduction

Sponges (Porifera Grant, 1836, Demospongiae Sollas, 1885) collected from Pilot Bay in Tauranga Harbour, Bay of Plenty, have facilitated redescription of five common New Zealand species: *Aaptos globosa* Kelly-Borges and Bergquist, 1994 (Subertida Chombard & Boury-Esnault, 1999, Suberitidae Schmidt, 1870), *Acanthoclada prostrata* Bergquist, 1970 (Axinellida Lévi, 1953, Stelligeridae Lendenfeld, 1898, *Biemna rufescens* Bergquist & Fromont, 1988 (Biemnida Morrow *et al*., 2013, Biemnidae Hentschel, 1923), *Halichondria* (*Halichondria*) *moorei* Bergquist, 1961 (Subertida Chombard & Boury-Esnault, 1999,

Halichondriidae Gray, 1867), and *Stylissa haurakii* (Scopalinida Morrow & Cárdenas, 2015, Scopalinidae Morrow *et al.* 2012). Fresh material from Pilot Bay and examination of preserved material from the National Institute of Water & Atmosphere (NIWA) Invertebrate collection (NIC), and the Museum of New Zealand Te Papa Tongarewa, Wellington (NMNZ) has helped extend our understanding of the morphological boundaries of each species within the Bay of Plenty region. We have focussed on spicule analysis, skeletal characteristics and the use of *in-situ* photographs that enhance our knowledge of their morphology and ecology in life.

There is a dearth of information regarding the biodiversity and systematics of sponges from Tauranga Harbour, and indeed, many shallow coastal seas around New Zealand. Recently, Mc Cormack *et al.* (2020) addressed this through describing two new species of *Dysidea* Johnston, 1842 (Demospongiae, Dictyoceratida Minchin, 1900, Dysideidae Gray, 1867) from Tauranga Harbour: *Dysidea tuapokere* Kelly, Mc Cormack and Battershill, 2020 and *D. teawanui* Kelly, Mc Cormack and Battershill, 2020, both in Mc Cormack *et al.* (2020) (see thesis appendix).

Species redescriptions here extend our knowledge on the general morphology, and diagnostic characters of these species. Collated information from NIWA, NMNZ and specimens collected from Tauranga Harbour expands our knowledge on the geographical distribution and depth ranges of these species. Original or subsequent descriptions of species such as *H.* (*H.*) *moorei* have poor information on general morphological characters. Furthermore, many early species descriptions such as those found in Bergquist (1970) lack photographs of external morphology (and/or they are monochromatic), spicules, and skeletal characters, making them challenging to identify. Therefore, there is a critical need for clear descriptions of these species that emphasise diagnostic characters and include photographs of morphology, skeletal architecture, and spicules.

Kelly *et al.,* (2009) provided a thorough review of the history of sponge studies, estimates of species diversity and a list of valid sponge species recorded from New Zealand to the year 2000. Kelly *et al.,* (2009) found there were 724 extant marine sponge species known in the New Zealand Exclusive Economic Zone (EEZ), including 76 hexactinellid or glass sponges (class Hexactinellida Schmidt, 1870), 54 calcareous sponges (class Calcarea Bowerbank, 1862), and 594 demosponges (Class Demospongiae).

Kelly & Sim-Smith (in prep) are revising the sponge species list for the New Zealand EEZ. Preliminary indications suggest the number of known species has doubled. However, a serious deterrent to obtaining accurate estimates of sponge species remains and that is the poor

state of early and original descriptions, confirming the need for work such as provided in this study.

Materials and methods

Specimens were collected using SCUBA by Samuel Mc Cormack (SMcC) from Tauranga Harbour, Bay of Plenty, between January and October 2014, September and October 2017, and in August 2020 (Fig. X). Photographs of specimens *in-situ*, *ex-situ*, and after preservation in 70% ethanol, were taken using a Canon EOS 60D camera. Specimens were deposited at the National Institute of Water and Atmospheric Research Invertebrate collection. Histological sections were prepared by embedding a small cutting of sponge in paraffin wax followed by sectioning with a microtome at 50 and 100 μm. Spicules and skeletons were photographed and measured on slides in Canada Balsam dissolved in xylene using an Olympus CX41RF compound microscope fitted with a Pixelink M15C-PRO-CYL camera using uScope-PRO imaging software (Pixelink®, a Navitar Company, Ottawa, Canada). Spicule dimensions and skeletal characters were measured at 40–400× magnification. Spicule measurements in the species descriptions are given as the mean length (range) × mean width (range) of twenty spicule measurements per specimen unless stated otherwise and are based on measurements from the holotype or paratypes and confirmed through examination of all other specimens.

Abbreviations used in text. NIC, NIWA Invertebrate Collection, Evans Bay, Wellington; NIWA, National Institute of Water & Atmospheric Research, Evans Bay, Wellington; NMNZ, The Museum of New Zealand Te Papa Tongarewa, Wellington.

Systematics

General classification and the names of the class, subclass, order, and suborders follow the classification proposal by Morrow & Cardenas (2015).

Class Demospongiae Sollas, 1885

Subclass Heteroscleromorpha Cárdenas, Pérez & Boury-Esnault, 2012

Order Suberitida Chombard & Boury-Esnault, 1999

Family Suberitidae Schmidt, 1870

Genus *Aaptos* Gray, 1867

Type species. *Aaptos adriatica* Gray, 1867

Diagnosis. Lobate or spherical sponges with a radial skeleton, often consisting of confluent globular or lobate units. Surface smooth or tuberculate-papillate, usually rough to touch. Some species show a distinct colour change when taken out of the water. In cross section, the outer region is often fibrous and may be considered as a cortex which grades into the choanosome. Skeleton strictly radiate, with tracts and single spicules issuing from the centre of the lobe or globular body. At the surface the tracts fan out and form a dense palisade consisting of smaller spicules intermingled between the ends of the larger spicules. Spicules are strongyloxeas, in three overlapping size categories; the intermediate and smaller spicules are occasionally oxeas, styles or tylostyles. The genus is cosmopolitan. Several species produce a distinctive compound aaptamine (Soest & Braekman, 1999), which appears to be a good marker of the genus (modified from Soest, 2002).

Aaptos globosa Kelly-Borges & Bergquist, 1994
Figs. 1–3, table 1

Aaptos aaptos, Ayling 1979: 47; Pritchard *et al.* 1984: 80–81, 135.
Aaptos globosa Kelly-Borges & Bergquist, 1994: 305, 309–310; Fig. 4, pl.C on p. 305.
Aaptos globosa (as *A. globosum*), Cryer *et al*. 2000: 86, 96, 152; Battershill *et al*. 2010: 114; Kelly *et al*. 2009: 43; Kelly 2018: 11, 45.

Material examined. Holotype—NMNZ PO.000133, Cornwallis Beach, Manukau Harbour, Auckland, New Zealand, 37.016° S, 174.6° E, 1 m, 14 Dec 1989.

    Pilot Bay, Tauranga Harbour, Bay of Plenty: NIWA 92972, 37.637° S, 176.171° E, 10 m, 27 Sep 2017.

    Other material. *Spirits Bay, North Cape, Northland*: NIWA 51121, NIWA Stn KAH9901/24, 34.364° S, 172.841° E, 57 m, 25 Jan 1999; NIWA 51133, NIWA Stn KAH9901/25, 34.369° S, 172.825° E, 55 m, 25 Jan 1999; NIWA 51281, NIWA Stn KAH9901/47, 34.374° S, 172.701° E, 53 m, 27 Jan 1999; NIWA 51408, NIWA Stn KAH9901/61, 34.324° S, 172.749° E, 69 m, 28 Jan 1999; NIWA 51649, NIWA Stn Z9096,

34.370° S, 172.768° E, 44 m, 5 May 1998; NIWA 51654, RV *Benn Gunn* Stn BG9701/64, 34.368° S, 172.768° E, 44 m, 28 Feb 1997; NIWA 62301, NIWA Stn Z18247 (SDCC/NZ496), 34.422° S, 172.846° E, 17 m, 23 Mar 2007; NIWA 101826, NIWA Stn KAH9901/24, 34.364° S, 172.841° E, 57 m, 25 Feb 1999; NIWA 101842, NIWA Stn KAH9901/25, 34.369° S, 172.825° E, 55 m, 25 Feb 1999; NIWA 101962, NIWA Stn KAH9901/47, 34.375° S, 172.701° E, 53 m, 27 Jan 1999; NIWA 101995, NIWA Stn KAH9901/61, 34.324° S, 172.749° E, 69 m, 28 Jan 1999.

Kahuwhera Bay, Bay of Islands, Northland: NIWA 62171, 62176 NIWA Stn KWB_Feb, 35.263° S, 174.182° E, 6 m, 9 Feb 2010.

Home Point, Bream Bay, Northland: NIWA 86755, NIWA Stn Z16096, 35.850° S, 174.525° E, 8 m, 17 Feb 2007.

Great Barrier Island, Hauraki Gulf: NIWA 101219, NIWA Stn Z15892, 36.203° S, 175.337° E, 20 m, 27 Apr 1999.

Goat Island Bay, Leigh, Hauraki Gulf: NMNZ PO.000430, 36.266° S, 174.791° E, 16 m, 8 Mar 1991.

Rakino Island, Hauraki Gulf: NIWA 62353, NIWA Stn Z18568, 36.428° S, 175.188° E, 8 Jun 2009.

Motuketekete Island, Kawau, Hauraki Gulf: NIWA 52281, NIWA 52282, NIWA Stn WREB03, 36.471°S, 174.807°E, 6–10 m, identified 19 June 2007.

Cornwallis Beach, Manukau Harbour, Auckland: NMNZ PO.000428, 37.016° S, 174.6° E, 1 m, 14 Dec 1989.

South Taranaki Bight, Taranaki:; NIWA 86707, NIWA Stn Z18389, 2 Mar 2013

Tatapouri Bay, Gisborne: NIWA 100821, NZOI Stn X724, 38.660° S, 178.394° E, 72 m, 13 Mar 1998.

Distribution. Northland, Hauraki Gulf, Auckland, Bay of Plenty, Taranaki, Gisborne and Nelson; 1–70 m.

Diagnosis. Spherical, solitary sponge ranging from 3–10 cm diameter × 2–8 cm in high (Fig. 1A). Sponge may produce large buds during February and April from basal stolons which remain attached to parent individual for extended periods. A large basal skirt attaches the sponge to the substratum (Fig. 1C). When inflated, the surface is irregular to lumpy with blunt conules 1–5 mm high and 1–2 mm in diameter (Fig. 1A). When visible, oscules are compound in mature specimens, occuring in surface depressions around 1 cm in diameter, that may be surrounded by an elevated rim (Fig. 1A). Surface is slightly compressible when inflated in life, and incompressible and hard when contracted in preservation. Texture is smooth and rubbery

to touch. Colour ranges from deep red-brown, red-pink (Fig. 1A–B), to yellow-brown in life, and mustard to yellow brown internally. Sponge turns mustard in air (Fig. 1C), and chocolate brown to grey after preservation.

Choanosomal skeleton (Fig. 2A–B) composed of dense radiating tracts tracts 500–700 µm wide comprised of large primary megascleres radiating through choanosome and branching into bouquets near surface (Fig. 2A). These ectosomal branching tracts are comprised of intermediate sized megascleres. Small tylostyles and slightly larger subtylostyles form an erect superficial palisade; spicules do not penetrate surface (Fig. 2A). Collagen is found throughout ectosome as small diffuse tracts around 1200 µm wide, and collagen is found in a much greater abundance throughout choanosome.

Megascleres (Table. 5, Fig. 2C–H) large strongyloxeas finely tapered to a fusiform distal end, 1689 (1021–2337) × 21 (5–39) µm, n=160 (Fig. 2G–H). Intermediate sized strongyloxeas finely tapered with a fusiform distal end, 947 (481–1500) × 14 (4–30) µm, n=160 (Fig. 2E–F). Tylostyles, with a pin-like morphology and hastate oxeote ends, occasionally slightly curved, 344 (106–1215) × 9 (3–30) (Fig. 2D). Subtylostyles, faint subterminal expansion with a slender curved shaft, 401 (110–1444) × 10 (4–36) µm, n=160 (Fig. 2C).

Remarks. *Aaptos globosa* has a highly characteristic spherical to subspherical morphology with compound, apical oscules and bright orange red colouration. It differs from other spherical sponges such as *S. perfectus* Ridley and Dendy, 1886, due to lack of solitary raised oscules, a perfectly spherical morphology and smooth surface (Kelly, 2018). Note that this species was originally described as *A. globosum* by Kelly-Borges & Bergquist (1994) but this was corrected to *A. globosa* to match the gender of the genus name, in 2015, by Kelly in the World Porifera Database (http://www.marinespecies.org/porifera/).

Kelly-Borges and Bergquist (1994) found a similarity in the dimensions of spicules among *Aaptos globosa* and *Aaptos tenta* Kelly-Borges and Bergquist, 1994, but noted that primary and intermidiate megascleres of the latter species were slightly longer and thicker than those of *A. globosa*. Kelly-Borges and Bergquist (1994) further differentiated *A. globosa* from *A. tenta* by spicule morphology, with the second category of superficial megascleres of *A. globosa* being either styles or weak subtylostyles, as opposed to the equivilant spciules in *A. tenta* representing subtylostyles only. Spicule tracts between each species can also be differentiated with tracts of *A. globosa* branching several times in the ectosomal region (Fig. 2A–B), compared to fanned unbranched spcicule tracts found in the ectosome of *A. tenta*

(Kelly-Borges and Bergquist, 1994, Fig. 3). Furthermore, the spicules in the ectosomal region of *A. globosa* are more dense than those found in *A. tenta*, with no brushes or bouquets forming in the latter species (Kelly-Borges and Bergquist, 1994). Ectosomal collagen scattered below the surface of *A. globosa* is characterised by random formations of collagen wisps, compared to *A. tenta* that has two marked bands of parallel collagen tracts seperated by a region relatively devoid of collagen (Kelly-Borges and Bergquist, 1994). A final point of morphological difference between *A. gobosa* and *A. tenta* is that *A. globosa* appears as almost perfectly spherical solitary individuals with incompressible texture in life and low flattened mounds, compared to *A. tenta* which is commonly found as an irregular mass of basally confluent individuals (Kelly-Borges and Bergquist, 1994).

We note here that the length and thickness of tylostyles [692 (184–1215) × 20 (5–30)] and subtylostyles [905 (121–1444) × 22 (4–36)] within the holotype (PO.000133) were larger on average than those from other specimens around the North Island (Table 1). However, large [1620 (1229–2091) × 25 (15–36)] and intermediate sized strongyloxeas [915 (593–1159) × 19 (11–30)] found in PO.000133 were more consistently similar to those from the other North Island specimens (Table 1). These differences are in part due to the difficulty of being able to strictly differentiate the three size categories of megascleres in this genus.

Key diagnostic characters
- spherical morphology
- basal skirt
- irregularly lumpy with blunt conules
- oscules occuring in depressions
- slightly compressible in life and incompresible in preservation
- plumose choanosome with ectosomal bouquets

Class Demospongiae Sollas, 1885

Subclass Heteroscleromorpha Cárdenas, Pérez & Boury-Esnault, 2012

Order Axinellida Lévi, 1953

Family Stelligeridae Lendenfeld, 1889

Genus *Acanthoclada* Bergquist, 1970

Type species. *Acanthoclada prostrata* Bergquist, 1970: 22–23 (by original designation).

Diagnosis. Thickly encrusting; choanosomal skeleton lax, fibrous, consisting of ascending fibres and tracts reinforced with small quantities of collagen, without distinctive axis; basal skeleton composed of tangled bundles of spicules containing rhabdostyles in plumose or 'hymedesmioid' tracts erect on a substrate base of larger choanosomal styles embedded in these bundles, with abundant microscleres lying on the basal spongin; ascending fibres cored by smooth styles forming multispicular tracts, with smooth rhabdostyles scattered within and protruding fibres. Long styles also protrude through fibres and abundant microscleres are scattered throughout the mesohyl producing a lax halichondrioid skeleton. Subectosomal fibres terminate in brushes of long centragulate oxeas which form conulose surface projections. Ectosome is also packed with acanthose microscleres. Megascleres include smooth styles, rhabdostyles and oxeas which are usually centrangulate or toxiform. Microscleres acanthose cladotoxas and birotules are present (after Hooper 2002).

Acanthoclada prostrata **Bergquist, 1970**
Figs. 4–5, table 2

Acanthoclada prostrata Bergquist, 1970: 22–23; pl. 5B, 10A, F, 16A–B; table 2.

Acanthoclada prostrata, Gordon & Ballantine 1976: 99; Ayling 1979: 70; Pritchard *et al.* 1984: 135; Dawson 1993: 21, 87; Cryer *et al.* 2000: 92, 100, 103, 152; Hooper 2002: 756–758; fig. 1; Kelly *et al.* 2009: 28, 34, 44; Battershill *et al.* 2010: 107–108, 605; Morrow *et al.* 2019: 9, 34.

Material examined. Holotype—NMNZ PO.000027, North (Takatu) Channel, between Tāwharanui Peninsula and Kawau Island, Hauraki Gulf, Auckland, New Zealand, 36.383° S, 174.85° E, 18 m.

Other material. *Spirits Bay*, *North Cape*, *Northland*: NIWA 51699, RV *Benn Gunn* Stn BG9701/64, 34.368° S, 172.768° E, 44 m, 28 Feb 1997; NIWA 51168, 101862, NIWA Stn KAH9901/27, 34.360° S, 172.720° E, 48 m, 26 Jan 1999; NIWA 62213, NIWA Stn KAH1005/33, 34.359° S, 172.756° E, 51 m, 14 May 2010; NIWA 51108, 101850, NIWA Stn KAH9901/24, 34.364° S, 172.841° E, 57 m, 25 Jan 1999.

Leigh, Rodney Coast, Hauraki Gulf: NIWA 52789.

North (Takatu) Channel, between Tāwharanui Peninsula and Kawau Island, Hauraki Gulf, Auckland: NMNZ PO.000145, 36.383° S, 174.85° E, 11 m, Nov 1960.

Takatu Point, east of Warkworth, Auckland, Hauraki Gulf: NMNZ PO.000148, 36.366° S, 174.883° E.

Pilot Bay, Tauranga Harbour, Bay of Plenty: NIWA 113639, 37.637° S, 176.171° E, 12 m, 27 Sep 2017.

Distribution. Northland; Hauraki Gulf; Bay of Plenty; 3–57 m.

Diagnosis. Morphology thickly encrusting with a low mounded surface, typically up to 10 cm diameter × 4 cm wide × 2.5 cm thick (Fig. 4A–B). Surface has abundant conules up to 1–2 mm in height giving it a shaggy appearance (Fig. 14A–B), the ectosome appears translucent. Oscules are 1–2 mm in diameter, inconspicuous, flush with ectosome. Texture granular, slightly compressible, and easily torn. Colour in life orange to yellow externally with slight purple surface tinges (Fig. 4A–B), cream throughout after preservation. Sponge exudes mucus upon being damaged and removal from substrate.

Choanosomal skeleton (Fig. 4C–D) composed of ascending fibres, cored by styles and echinated by rhabdostyles (Fig. 4H). Spongin can be found in small amounts around spicule tracts. Ectosomal membrane is filled with birotules and cladotoxas. Fibres terminate with bundles of oxeas, which elevate the dermal membrane into conules, and penetrate surface (Fig. 4C). Sponge encrusts bivalves, subtidal reef slopes and sponge gardens, and is typically found between 3–57 m.

Megascleres (Table 2, Fig. 4) are centrangulate oxeas of varying widths, fine forms resemble large toxas, 525 (61–1509) × 8 (1–35) µm, n=400 (Fig. 4G). Rhabdostyles (Fig. 4H), shorter, more slender than styles, smooth, curved sharply near the anterior end, with prominent basal rhabd, 293 (178–602) × 9 (4–18) µm, n=400; Styles (Fig. 4E–F), straight, curved, or slightly curved with evenly rounded, slightly subtylote or occasionally subterminal tylote swellings, 1119 (162–2655) × 12 (4–23) µm, n=400.

Microscleres (Table 2, Fig. 4), birotules (Fig. 4J), small, curved or slightly curved, with small spines distributed evenly over the shaft with nail-like apical heads, encircled by a ring of backwardly directed spines, 52 (37–86) × 5 (2–11) µm, n=400, clad width 7 (3–12) µm, n=200. Cladotoxas (Fig. 4I), curved, smooth shaft, with spines on one or both sides of shaft, spines may be reduced to only one. Apical clads are curved with 3–8 sharp spines and no constant disposition, 89 (62–119) × µm n=400, clad width 6 (2–13), n=200.

Remarks. *Acanthoclada* is a monospecific genus characterised by the possession of unique cladotoxa microscleres. Using 28S gene sequences, Morrow *et al*., (2019) found *A. prostrata* clustered with family Stelligeridae, resulting in transfer of the genus *Acanthoclada* to that family. Tauranga and Spirits Bay specimens examined here conform to Bergquist's (1970) original and Hooper's (2002) descriptions of the holotype, in terms of their thickly encrusting morphology, shaggy surface, conulose formation and granular texture.

We note considerable variability in the size ranges of spicules in all specimens examined (Table 2) and the smaller size of the centrangulate oxeas in four specimens from Spirits Bay (NIWA 51168, 51699, 52789, 101862). These spicules are much smaller [334 (61–1191) $\times$ 8 (4–14) µm, n=60] than the lengths of the same spicules in other specimens recorded from the North Island [607 (130–1509) $\times$ 7 (1–35) µm, n=140]. Remaining Spirits Bay specimens (NIWA 51108, 62213, 101850) have centrangulate oxeas that fall within the range of those in other North Island specimens and are simply noted at this time.

Key diagnostic characters

- thickly encrusting
- low mounded surface
- abundance of surface conules (1–2 mm high)
- granular slightly compressible texture
- surface orange to yellow, with slight tinges of purple in life
- exudes mucus after damage or removal
- ascending choanosomal fibres cored by styles and echinated by rhabdostyles
- globally unique cladotoxa microscleres

Class Demospongiae Sollas, 1885

Subclass Heteroscleromorpha Cárdenas, Pérez & Boury-Esnault, 2012

Order Biemnida Morrow *et al*., 2013

Family Biemnidae Hentschel, 1923

Genus *Biemna* Gray, 1867

Type species. *Halichondria variantia* represented as *Biemna variantia* Bowerbank, 1858: 286; Fig. 39 (by original designation).

Diagnosis. Massive, cup-shaped, or tubular sponges, with uneven surface. Plumose or plumoreticulate choanosomal skeleton, with variable development of spongin fibres cored by (subtylo-) styles of a single size, occasionally replaced by oxeote spicules; ectosomal skeleton made of brushes of megascleres making the surface often shaggy; microscleres include sigmas, raphides, microxeas, commata, microstrongyles and spheres. Most species cause a dermatitis-like reaction when in touch with bare skin (after Hadju & Soest, 2002).

Biemna rufescens Bergquist & Fromont, 1988
Figs. 6–8, table 3
Biemna rufescens Bergquist & Fromont, 1988: 32–33; Pl. 9D–F; 10A; Table. 13.
Biemna rufescens, Cryer *et al*. 2000: 94, 103; Kelly *et al*. 2009: 43; Battershill *et al*. 2010: 59, 89, 608; Kelly 2018: 11, 68.
Biemna sp. Ayling 1979: 71; Pritchard *et al.* 1984: 40–41.

Material examined. Holotype— NMNZ PO.000087, *Middle Arch, Poor Knights Islands, Northland, New Zealand*: 35.458° S, 174.731° E, 15 m.

 Other material. *Spirits Bay, North Cape, Northland*: NIWA 51025, NIWA Stn KAH9901/3, 34.405° S, 172.832° E, 29 m, 24 Jan 1999; NIWA 51340, NIWA Stn KAH9901/57, 34.398° S, 172.923° E, 34 m, 27 Jan 1999; NIWA 62272, NIWA Stn Z18253 (SDCC/NZ435), 34.417° S, 172.954° E, 20 m, 22 Mar 2007; NIWA 62295, NIWA Stn Z18287 (SDCC/NZ488), 34.430° S, 172.730° E, 23 m, 24 Mar 2007; NIWA 101813, NIWA Stn KAH9901/3, 34.405° S, 172.833° E, 29 m, 24 Jan 1999.

 Houhora Harbour, Northland: NIWA 101308, NIWA Stn Z15913, 34.822° S, 173.151° E, 3 m, 30 Nov 2002.

 Home Point, Bream Bay, Northland: NIWA 62387, NIWA Stn Z18386, 35.849° S, 174.523° E, 12 m, 20 Sep 2011.

 Man of War Passage (*Governor Pass*) *north side, Great Barrier Island, Hauraki Gulf*: NIWA 101032, NIWA Stn Z15852, 36.184° S, 175.315° E, 10 m, 9 Jun 2006.

 Sponge Garden, Goat Island, Leigh: NMNZ PO.000258, 36.266° S, 174.8° E, 16 m; NMNZ 000214, 36.266° S, 174.8° E, 18 m.

Kawau Bay, *Hauraki Gulf*: NIWA 52297, 28 May 2007, no additional data.

Rakino Island, *Auckland, Hauraki Gulf*: NIWA 62356, NIWA Stn Z18243, 36.720° S, 174.940° E, 08 June 1999.

Pilot Bay, *Tauranga Harbour*, *Bay of Plenty*: NIWA 92967, 37.637° S, 176.171° E, 11 m, 27 Sep 2017; NIWA 113659 (Spon00262), 37.380° S, 176.102° E, 10 m, 25 Aug 2020.

Patea, *South Taranaki Bight*, *Taranaki*: NIWA 81612, NIWA Stn TQI1201/71, 39.802° S, 174.296° E, 27 m, 12 Mar 2012.

Sugar Loaf Islands, *New Plymouth*, *Taranaki*: NIWA 101176, NIWA Stn Z15882, 39.057° S, 174.03° E, 20 m, 1999.

Distribution. Endemic to New Zealand. Found in coastal waters of the North Island: Northland, Hauraki Gulf, Bay of Plenty, Taranaki, living at depths of 3–34 m.

Diagnosis. Spherical, hemispherical to massive or thickly encrusting sponge with shaggy oscular turrets, 4–10 mm high, on the upper surface of the sponge. Turrets have apical oscules, 2–5 mm wide, that are slightly tattered around the edges (Fig. 6A–C). Encrusting specimens can cover areas up to 1 m^2. Texture soft, velvety, microscopically hispid, with a compressible and easily torn body. Specimens with foreign debris incorporated into their superficial layers have a grainier texture. *In situ* sponge is a purple maroon to red-brown external colour and dirty yellow to dull-gold internally (Fig. 6A–B). In preservation sponge is coloured cream to light brown both internally and externally. Irritating to the skin when touched.

Choanosomal skeleton (Fig. 7A) composed of plumose tracts of styles about 50 μm wide that run perpendicular to the surface (Fig. 7A). Styles are predominantly positioned with the distal end facing outwards and to the surface. Skeleton is confused between tracts, and styles are predominantly found loose in choanosome at right angles to the primary tracts (Fig, 7A). These columns can be traced to the ectosome where they form bouquets which penetrate the surface (Fig. 7B). Trichodragmata form short tracts within choanosome. Oxeas and raphides are also interspersed haphazardly within choanosome.

Ectosomal skeleton composed of styles in bouquets with distal ends facing outwards and echinating through ectosome (Fig. 7B). Trichodragmas or lax bundles of raphides and sigmas are positioned transversely along ectosome. Ectosomal layer may also incorporate foreign material. A thin, dark ectosomal layer of collagen can be found along ectosome (Fig. 7B), but its quantity varies in different sections of dermal tissue. Subdermal chambers are sometimes found directly below surface, lined by sigmas.

Megascleres (Fig. 7C–H; Table 3) are styles, long, slender with bent or wavy and occasional oxeote forms, 449 (282–629) × 11 (2–25) µm, n=640 (Fig. 7C).

Microscleres are fusiform microxeas with two size classes; the smaller size class of microxeas is shorter and thicker [58 (42–80) × 3 (1–5) µm, n=640] than the larger size class [111 (64–194) × 2 (1–3) µm, n=640] (Fig. 7D–F). Sigmas, morphologically variable, predominantly C-shaped, or hooks, in three size classes: small, 14 (10–20) × 2 (1–3) µm, n=640; medium, 24 (16–44) × 2 (1–4) µm, n=640; large 42 (27–59) × 3 (1–5) µm, n=640, of which the largest size is thicker than both smaller classes (Fig. 7F–H).

Remarks. *Biemna rufescens* is a well-known endemic to New Zealand, with an easily recognisable purple colouration and turreted surface structure. It is commonly found off the east coast between Northland and the Bay of Plenty but has also been recorded in Taranaki on the west coast of the North Island. This species can be differentiated from other *Biemna* in New Zealand by its hemispherical morphology, oscular fistules, and three size classes of sigma microscleres. *Biemna rufescens* is easily distinguished from the two other known New Zealand species of *Biemna*: *B. rhabderemioides* Bergquist, 1961 (Fig. 10A–B), has an encrusting or cushion-like morphology; *B. flabellata* Bergquist, 1970 (Pl. 5C, 17A) has an erect and lamellate form.

The length and thickness of all spicules in all categories within the holotype are average for specimens around the North Island which vary with different latitudes and degrees of exposure; those from sheltered harbour environment of Pilot Bay (NIWA 92967, 113659) consistently have the longest and thickest of all spicules in all categories, possibly reflecting the greater amount of food availability.

Key diagnostic characters
- Spherical to hemispherical or thickly encrusting
- Surface covered in prominent oscular fistules tattered around edges
- purple to maroon externally in life
- velvety texture and irritating to the touch
- three size classes of sigma microscleres
- choanosome composed of plumose tracts of spicules
- ectosome composed of projecting bouquets of styles

Heteroscleromorpha Cárdenas, Pérez & Boury-Esnault, 2012

Order Subertida Chombard & Boury-Esnault, 1999

Family Halichondriidae Gray, 1867

Genus *Halichondria* Fleming, 1828

Type species. *Spongia panicea* Pallas, 1766: 388 (by original designation).

Diagnosis. Encrusting, massive, occasionally irregularly branching, or digitate sponges with smooth or papillate surface. Oscules often on conical elevations. Surface skeleton well-developed with tangential bundles of spicules and single spicules intercrossing to form a lighter or heavier built surface crust. Subectosomal spaces usually well-developed causing the surface crust to be often rather independent of the main skeleton and easily peeled off. Choanosomal skeleton of rather ill-defined bundles of spicules, which at the surface become orientated perpendicular to the surface crust. They often fan out and carry the surface crust. Many single spicules distributed randomly. Spongin not visibly present. Spicules oxeas with gradually tapering sharp points, in a wide size range, often seemingly divisible into smaller and a larger category but overlap is extensive. Occasionally style-like modifications occur at a low frequency (after Erpenbeck & Soest, 2002).

Subgenus *Halichondria* (*Halichondria*) Fleming, 1828

Type species. *Spongia panicea* Pallas, 1766: 388 (by original designation).

Diagnosis. *Halichondria* with smooth or digitate surface (after Erpenbeck & Soest, 2002).

ingitate surface (after Erpenbeck & Soest, 2002).

***Halichondria* (*Halichondria*) *moorei* Bergquist, 1961**
Figs. 9–11, table 4

Halichondria moorei Bergquist, 1961: 40–41: Fig. 11A–B.

Halichondria moorei, Battershill *et al.* 2010: 105–106; Bergquist 1970: 12, 32–34; Bergquist 1978: 106; Bergquist & Bedford 1978: 217–218, table 1, table. 3; Bergquist & Glasgow 1986, 113–116, 118–119, figs. 1–3, 5, 8; Bergquist & Green 1977: 85–86; Bergquist & Hogg 1969: 212; Bergquist & Sinclair 1968: 426–427, 429, 430–431, 434, 436, fig.1, table 1; Bergquist *et al.* 1970: 248, 254, 258, table. 1; Bergquist *et al.* 1980: 424–425, 427, Tables 1, 2 & 4; Bradstock 1985: 105; Dawson 1993: 47–48, 91; Evans 1977: 427, 432, Pl. I–III; Evans & Bergquist 1977: 197; Gordon & Ballantine 1977: 97; Green & Bergquist

1980: 153; Gregson *et al*. 1979: 1108; Hogg 1966: 58; Kelly 2018: 10, 54; Kelly *et al.* 2009: 44; Lawson *et al*. 1986: 19, 21–24, fig. 1, table 1–2; Morton & Miller 1973: 66, 97, 112, 389, Pl. 5; Pritchard *et al.* 1984: 134.

Material examined. Holotype—NMNZ PO.000008, Te Tokaroa Reef, Point Chevalier, Auckland, New Zealand, 36.841° S, 174.711° E, May 1958.

Other material. NIWA 51669, no additional data available.

Te Tokaroa Reef, Point Chevalier, Hauraki Gulf, Auckland: NMNZ PO.000144, 36.841° S, 174.711° E.

Pilot Bay, *Tauranga Harbour*, *Bay of Plenty*: NIWA 113671, 37.637° S, 176.171° E, 10 m, 31 Aug 2020; NIWA 113672, 37.380° S, 176.102° E, 11 m, 31 Aug 2020; NIWA 113673, 37.380° S, 176.102° E, 10 m, 31 Aug 2020.

Distribution. North Island, including Northland, Auckland, Bay of Plenty, 1–12 m.

Diagnosis. Massive, thickly encrusting to globular sponge, with a smooth to irregularly mounded, verrucose surface resulting from projecting spicule tracts, typically up to 1.2 m diameter × 80 cm wide × 11 cm thick (Fig. 9). Oscules are prominent with a translucent membrane surrounding them, 2–5 mm diameter. Texture, relatively firm, easy to tear, fleshy to the touch, and compressible. Colour in life salmon pink, dull orange to light brown internally and externally, in spirit orange-light brown to almost white. The body is often infested by polychaete worms visible as black dots at the surface and as sandy canals throughout choanosome.

Choanosomal skeleton confused with occasional radially disposed loose tracts of oxeas which may raise the surface. Dark pigmented cells are abundant throughout entire body.

Ectosome a tangential reticulation of oxeas.

Megascleres (Fig. 10, table 4) are smooth, straight, or curved oxeas with fusiform tips, 370 (242–739) × 10 (4–21) µm, n=140. Oxeas are the same size in both the ectosome and choanosome.

Remarks. Bergquist (1961) originally noted an abundance of opaque darkly pigmented cells in *H*. (*H.*) *moorei*, also noted in the specimens examined here. Bergquist (1970) considered (*H.*) *moorei* to be extremely common in the mid-intertidal, especially in crevices, under stones, and most abundantly around the edges of rock pools. Bergquist (1970) also found that *H*. (*H.*) *moorei* was commonly associated with red-pink turfing coralline algae, *Corallina officinalis* Linnaeus, 1758, and the sponge *Hymeniacidon perlevis* Montague, 1814 species.

Halichondria (*H.*) *moorei* can also be found in the shallow subtidal., such as in Pilot Bay. The species is known to be highly abundant on the intertidal Meola Reef in Waitematā Harbour (Fenn, 1982).

Key diagnostic characters
- Irregularly mounded external morphology
- slightly transparent dermal membrane
- visible surface fibre reticulation
- easy to tear, delicate, soft and fleshy
- salmon pink, dull orange to light brown in life
- ectosome a tangential reticulation of oxeas
- choanosome confused or radially disposed mass of oxeas
- straight or curved oxeas

Class Demospongiae Sollas, 1885

Heteroscleromorpha Cárdenas, Pérez & Boury-Esnault, 2012

Order Scopalinida Morrow & Cárdenas, 2015

Family Scopalinidae Morrow *et al*., 2012

Genus *Stylissa* Hallman, 1914

Type species. *Stylotella flabelliformis* Hentschel, 1912: 298, 355–356 (by original designation).

Diagnosis. Erect, flabellate, or compressed-lobate sponges with irregularly conulose and/or ridged surface. Conules blunt. Surface smooth between conules often with a slight colour difference between smooth and conulose parts. Colours usually red, orange or yellowish. Skeleton confused, but some plumose reticulation usually recognizable. In the interior and in the stem of erect forms there is axial condensation. Styles curved, usually stout, relatively short and of a single size category. Several species are common in the Indo-West Pacific, one is recorded from the Caribbean (after Soest *et al*. 2002).

Stylissa haurakii **Brøndsted, 1924**

Fig. 12–14, table 5

Hymeniacidon haurakii Brøndsted, 1924: 477, fig. 30.

Hymeniacidon haurakii, Bergquist 1970: 12, 35–36, pl. 8C–D, pl. 17B; Ayling, 1979: 38; Dawson 1993: 49, 92; Gordon & Ballantine 1976: 97; Bergquist *et al.* 1980: 424–425, tables 1–2; Pritchard *et al.* 1984: 54–55, 149, fig. on p. 55; Kelly *et al.* 2009: 34, 44; Battershill *et al.* 2010: 106; Kelly 2018: 10, 37.

Axiamon erecta, Bergquist 1961: 41, fig. 12.

Stylissa haurakii, Kelly *et al.* 2009: 44.

Material examined. NIWA 92920, Pilot Bay, Tauranga Harbour, Bay of Plenty, New Zealand, 37.637° S, 176.171° E, 11 m, 4 Aug 2014.

Other material. *Spirits Bay, North Cape, Northland*: NIWA 101445, NIWA Stn Z15929, 34.397° S, 172.863° E, 33 m, 23 Jul 2003.

North Cape, Northland: NIWA 100995, NIWA Stn Z15758, 34.400° S, 173.034° E, 3 m, 19 Apr 1999.

Kahuwhera Bay, Bay of Islands, Northland: NIWA 62175, NIWA Stn KWB_Feb, 35.263° S, 174.182° E, 5 m, 9 Feb 2010.

Sponge Gardens, Leigh Marine Reserve, Cape Rodney, Hauraki Gulf: NIWA 94721, 94723, 94793, 94794 NIWA Stn Z9033, 36.267° S, 174.800° E, 18 m, 6 Jul 1997; NIWA 94803, NIWA Stn Z9035, 35.589° S, 174.541° E, 18 m, 12 Jul 1997.

Tryphena Harbour, Great Barrier Island, Hauraki Gulf: NIWA 101194, NIWA Stn Z15889, 36.333° S, 175.474° E, 6 m, 28 Apr 1999.

North (Takatu) Channel, between Tawharanui Peninsula & Kawau Island, Hauraki Gulf: NMNZ PO.000330, 36.383° S, 174.85° E, 11 m.

South Taranaki Bight: NIWA 81583, NIWA NZOI Stn KAH1206/26, 39.929° S, 174.238° E, 31 m, 20 Apr 2012; NIWA 81592, NIWA Stn KAH1206/15, 39.960° S, 174.152° E, 36 m, 19 Apr 2012; NIWA 81599, NIWA Stn KAH1206/12, 39.982° S, 174.110° E, 43 m, 19 Apr 2012; NIWA 81609, NIWA 81618, NIWA Stn TQI1201/73, 39.789° S, 174.283° E, 27 m, 12 Mar 2012.

Manawatū-Whanganui coast, North Island: NIWA 82408, NIWA Stn TAN1202/29, 40.14° S, 174.716° E, 80 m, 2 Feb 2012.

Distribution. Three Kings Islands, Northland, Hauraki Gulf, Bay of Plenty, Taranaki, Manawatū-Whanganui; 3–80 m.

Diagnosis. Generally spherical to hemispherical sponge, with a shaggy surface of conulose digitate projections (Fig. 12A–C) that may be quite elongate (Fig. 12A), or short and stubby (Fig. 12B). Sponge ranges from 4–15 cm diameter and 3–10 cm high. Surface composed of conulose, digitate projections, 2–6 cm high, and oscules are not visible (Fig. 12A–C). Each conule is formed by brushes of dermal styles that stop short of the ectodermal membrane (Fig. 13B). Dermal membrane is translucent. Texture soft and fleshy. Colour in life bright orange to dull orange-gold internally (Fig. 12A–C). Colour becomes dull orange after preservation. Produces large amounts of mucus after removal from substratum. This species is commonly found in areas of broken shell or sand 5–30 cm deep.

Skeleton. Choanosome composed of a confused mass of styles that form loose, semi-plumose tracts, that ascend towards the ectosome (Fig. 13A). Ectosomal skeleton composed of tufts of styles emerging towards a translucent membrane, about 0.1 mm thick (Fig. 13B). Subectosome slightly cavernous (Fig. 13B).

Megascleres (Fig. 13C–D; table 5) are a single size class of curved, to slightly curved styles, 737 (541–935) × 17 (6–29) µm, n=160.

Remarks. *Stylissa haurakii* is a relatively common endemic New Zealand species with a distinctive shaggy surface and characteristic bright orange colour in life. The specimens examined here are morphologically similar to other specimens recorded from New Zealand in Bergquist (1970).

Key diagnostic characters

- shaggy conulose surface tufts
- bright orange colouration in life
- large amounts of exudates after removal

Discussion

This study set out to provide comprehensive redescriptions of species commonly found in Tauranga Harbour. Prior studies including Mc Cormack *et al*. (2020) have noted the importance of key morphological characters such as gross morphology, *in-situ* colouration, and skeletal architecture to identify sponge taxa. The current study provides updated descriptions of five common species found in Tauranga Harbour and elsewhere (e.g. Taranaki) as new ecological work examines previously less well explored coastlines, in partnership with NIWA, extending

our knowledge on their depth and geographic distribution around the North Island of New Zealand.

Considerable variability was seen in the size ranges of spicules in the specimens of all species; the more specimens examined the better we approach the true ranges of spicule dimensions in the species. One of the characters we noted was the increase in length and thickness of all spicule categories in *B. rufescens* from harbour environments including Tauranga Harbour and the Taranaki coast.

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TABLE 1. Spicule dimensions (μm) of *Aaptos globosa* Kelly-Borges & Bergquist, 1994, given as length [mean (min–max)] × width [mean (min–max)], n=20 unless stated otherwise.

Specimen No.	Location	Megascleres			
		Large Strongyloxeas	Intermediate Strongyloxeas	Tylostyles	Subtylostyles
NR* (Kelly-Borges and Bergquist, 1994: 305, 309–310; Fig. 4, pl.C on p. 305)	Combined locations cited in Kelly-Borges and Bergquist, 1994	1793 (980–2401) × 27 (18–33)	695 (332–1029) × 11 (8–16)	161 (104–198) × 5 (4–5)	317 (208–458) × 7 (5–8)
NMNZ P0.000133 (Holotype)	Cornwallis Beach, Manukau Harbour, Auckland	1620 (1229–2091) × 25 (15–36)	915 (593–1159) × 19 (11–30)	692 (184–1215) × 20 (5–30)	905 (121–1444) × 22 (4–36)
NIWA 51281	Spirits Bay, North Cape, Northland	1754 (1406–2290) × 16 (10–26)	1038 (499–1500) × 10 (6–17)	183 (112–344) × 5 (3–8)	299 (125–449) 6 × 6 (4–7)
NIWA 62353	Rakino Island, Hauraki Gulf, Auckland	1727 (1298–1967) × 25 (15–34)	870 (481–1119) × 19 (11–29)	150 (106–488) × 5 (3–7)	185 (110–394) × 6 (4–7)
NIWA 92972	Pilot Bay, Tauranga Harbour, Bay of Plenty	1655 (1021–2337) × 18 (5–39)	964 (551–1170) × 8 (4–18)	352 (140–948) × 7 (4–13)	214 (121–433) × 6 (4–8)

NR*= No registered number for specimen.

TABLE 2. Spicule dimensions (μm) of *Acanthoclada prostrata* Bergquist, 1970, given as length [mean (min–max)] × width [mean (min–max)], n=20 unless stated otherwise.

Specimen No.	Location	Megascleres			Microscleres	
		Centrangulate oxeas	Styles	Rhabdostyles	Cladotoxas	Birotules
Holotype NMNZ PO.000027	North Channel, between	1206 (960–1320) × 7 (1–9)	1420 (677–1850) × 7 (1–9)	420 (213–600) × 7 (6–8)	90 (80–96) × 5 (5–6) spines up to 12 long cladome 28–34 wide	66 (52–72) × (3–4) clad width 8–10
NMNZ PO.000145	Tāwharanui Peninsula and	589 (130–914) × 6 (4–10)	865 (204–1967) × 11 (4–18)	281 (201–460) × 8 (5–15)	92 (76–107) × 7 (6–7) spines 13 (7–18) long	53 (44–65) × 5 (3–7) clad width 6 (2–12)

	Kawau Island, Hauraki Gulf, Auckland				cladome 28 (21–32)	
NMNZ PO.000148		545 (223–1060) × 6 (1–9)	948 (392–1924) × 14 (5–23)	294 (188–419) × 8 (5–15)	98 (77–119) × 6 (3–8) spines 12 (6–15) long cladome 26 (15–38)	53 (37–66) × 5 (2–7) clad width 7 (3–10)
NIWA 113639	Pilot Bay, Tauranga Harbour, Bay of Plenty	893 (629–1178) × 5 (4–7)	1246 (660–1773) × 11 (4–22)	267 (178–512) × 8 (5–15)	85 (73–95) × 7 (6–8) spines 10 (7–12) long cladome 25 (17–28) wide	47 (41–55) × 6 (4–11) clad width 7 (5–12)
NIWA 51108		681 (244–1417) × 7 (4–10)	618 (244–1793) × 9 (5–16)	268 (211–327) × 7 (4–9)	86 (72–103) × 6 (5–9) spines 14 (10–21) long cladome 29 (21–36) wide	52 (39–68) × 5 (4–6) clad width 6 (4–9)
NIWA 51168		420 (198–1190) × 8 (4–14)	948 (392–1924) × 14 (8–22)	339 (231–457) × 11 (6–18)	92 (83–102) × 6 (5–8) spines 12 (7–20) cladome width 29 (21–35)	52 (45–61) × 5 (3–6) clad width 7 (4–9)
NIWA 51699	Spirits Bay, North Cape, Northland	274 (185–321) × 7 (4–6)	956 (162–1833) × 12 (6–16)	285 (201–367) × 9 (4–15)	78 (62–89) × 7 (5–9) spines 13 (9–17) long cladome width 28 (24–33)	53 (41–65) × 6 (4–8) clad width 8 (5–12)
NIWA 62213		648 (193–1509) × 15 (5–35)	1563 (357–2283) × 12 (7–19)	305 (224–436) × 10 (5–15)	89 (70–114) × 5 (2–8) spines 14 (6–19) long cladome width 27 (19–38)	53 (37–63) × 4 (2–7) clad width 6 (4–9)
NIWA 101862		306 (61–794) × 9 (4–14)	1505 (377–2139) × 14 (9–19)	335 (247–602) × 12 (8–16)	96 (81–112) × 7 (4–13) spines 13 (9–17) long cladome width 28 (22–36)	58 (48–86) × 7 (4–8) clad width 8 (4–10)
NIWA 101850		558 (181–1494) × 7 (4–10)	1588 (310–2655) × 11 (7–18)	297 (205–350) × 8 (5–12)	83 (80–91) × 7 (6–7) spines 11 (8–12) long cladome width 26 (25–28)	54 (42–82) × 5 (2–8) clad width 6 (3–8)
NIWA 52789	Leigh, Auckland	334 (205–730) × 7 (5–16)	923 (278–1899) × 10 (5–17)	276 (204–365) × 7 (5–10)	87 (68–100) × 6 (3– 8) spines 13 (5–19) long cladome width 27 (12–43)	50 (39–64) × 5 (3–7) clad width 7 (3–11)

TABLE 3. Spicule dimensions (μm) of *Biemna rufescens* Bergquist & Fromont, 1988, given as length [mean (min–max)] × width [mean (min–max)], n=20 unless stated otherwise.

Specimen No.	Location	Megascleres	Microscleres				
		Styles	Small microxeas	Large microxeas	Small sigmas	Medium sigmas	Large sigmas
Holotype (remeasured) NMNZ PO.000087	Middle Arch, Poor Knights Islands	454 (380–582) × 7 (4–11)	54 (46–62) × 2 (2–3)	108 (95–120) × 2 (1–3)	15 (13–20) × 2 (1–3)	23 (17–27) × 2 (1–3)	40 (35–45) × 2 (1–3)
NMNZ PO.000214	Goat Island, Leigh, Cape Rodney	427 (376–467) × 10 (3–12)	53 (45–61) × 2 (2–3)	106 (89–123) × 2 (2–3)	14 (12–15) × 2 (1–3)	25 (21–31) × 2 (1–3)	40 (34–51) × 3 (2–3)
NR* (Bergquist & Fromont, 1988: 32–33, Table 13)	Middle Arch, Poor Knights Islands	430 (390–470) × 6 (5–8)	53 (50–58)	111 (103–115)	16 (13–17)	23 (21–25)	37 (30–45)
	Waterfall Reef, Leigh, Cape Rodney	421 (360–465) × 6 (6–7)	54 (48–60)	117 (100–125)	16 (14–20)	26 (23–31)	42 (33–48)
	Sponge Garden, Leigh, Cape Rodney	465 (410–480) × 9 (8–12)	60 (55–73)	119 (103–130)	15 (14–19)	25 (21–40)	43 (33–50)
	Sponge Garden, Leigh, Cape Rodney	403 (370–440) × 8 (6–9)	65 (45–63)	103 (90–113)	15 (14–17)	24 (20–30)	44 (38–50)
	Māori Island, Leigh, Cape Rodney	412 (350–440) × 8 (6–9)	54 (48–59)	106 (95–118)	15 (13–16)	25 (22–32)	42 (37–46)
NIWA 51025	Spirits Bay, Northland	457 (352–512) × 9 (3–12)	56 (46–63) × 3 (2–4)	118 (106–133) × 2 (1–3)	14 (12–15) × 2 (1–2)	23 (20–28) × 2 (1–3)	42 (29–48) × 3 (2–4)
NIWA 51340		413 (363–475) × 7 (4–11)	56 (42–71) × 2 (2–3)	90 (78–101) × 2 (1–3)	14 (11–16) × 2 (1–2)	23 (18–29) × 2 (1–3)	39 (34–46) × 2 (2–4)
NIWA 62272		427 (361–491) × 10 (6–14)	63 (54–71) × 2 (2–4)	116 (104–194) × 2 (2–3)	15 (12–19) × 2 (1–3)	25 (20–27) × 2 (1–3)	42 (36–49) × 2 (2–4)
NIWA 62295		425 (359–484) × 6 (4–7)	52 (43–58) × 3 (2–4)	105 (88–115) × 2 (1–3)	14 (12–16) × 2 (1–3)	24 (19–31) × 2 (1–3)	40 (30–47) × 3 (2–5)
NIWA 101813		467 (417–515) × 9 (3–13)	58 (50–68) × 2 (2–3)	119 (106–133) × 2 (1–2)	15 (12–16) × 2 (1–3)	24 (21–28) × 2 (1–4)	43 (37–48) × 3 (2–4)
NIWA 101308	Houhora Harbour, Northland	495 (335–565) × 8 (4–12)	64 (53–73) × 2 (2–3)	115 (99–127) × 2 (1–3)	15 (13–17) × 2 (1–3)	23 (18–28) × 2 (1–3)	43 (35–51) × 3 (2–3)
NIWA 62387	Home Point, Bream Bay, Northland	464 (290–549) × 10 (7–14)	63 (58–79) × 2 (1–3)	106 (79–119) × 2 (1–3)	14 (10–16) × 2 (1–2)	22 (16–28) × 2 (1–3)	48 (44–52) × 2 (1–3)

NIWA 62356	Rakino Island, Hauraki Gulf	431 (282–489) × 7 (2–11)	54 (49–66) × 3 (2–4)	112 (101–127) × 2 (1–2)	13 (11–16) × 1 (1–2)	21 (18–28) × 2 (1–2)	40 (31–49) × 2 (1–3)
NIWA 101032	Great Barrier Island, Hauraki Gulf	468 (405–520) × 9 (4–13)	61 (47–73) × 3 (2–4)	119 (106–127) × 2 (1–3)	15 (14–17) × 2 (1–2)	23 (19–25) × 2 (1–3)	41 (31–46) × 2 (2–3)
NIWA 52297	Kawau Bay, Hauraki Gulf	424 (308–472) × 10 (5–17)	66 (56–72) × 3 (2–4)	110 (64–127) × 2 (1–3)	15 (13–17) × 1 (1–2)	26 (21–30) × 2 (1–2)	45 (40–59) × 3 (2–5)
NIWA 92967	Pilot Bay, Tauranga Harbour	462 (425–520) × 15 (8–25)	57 (49–65) × 4 (3–5)	115 (103–127) × 2 (1–3)	15 (12–18) × 2 (1–2)	23 (20–28) × 2 (1–3)	42 (31–46) × 4 (2–6)
NIWA 113659		497 (433–629) × 15 (7–21)	62 (49–69) × 4 (3–5)	119 (104–147) × 2 (2–3)	16 (13–18) × 2 (1–2)	26 (21–37) × 2 (2–3)	46 (39–53) × 3 (1–4)
NIWA 81612	Patea, South Taranaki Bight	406 (333–505) × 9 (3–13)	51 (44–58) × 2 (1–3)	105 (84–171) × 2 (1–3)	15 (12–17) × 1 (1–2)	22 (17–27) × 2 (1–2)	37 (28–44) × 2 (1–3)
NIWA 101176	Sugar Loaf Islands, Taranaki	466 (377–527) × 8 (4–13)	58 (52–70) × 3 (2–5)	115 (99–126) × 2 (1–3)	14 (12–17) × 2 (1–2)	23 (19–27) × 2 (1–3)	41 (36–47) × 3 (2–5)

NR*= No registered number for specimen.

TABLE 4. Spicule dimensions (µm) of *Halichondria* (*Halichondria*) *moorei* Bergquist, 1961, given as length [mean (min–max)] × width [mean (min–max)], n=20 unless stated otherwise.

Specimen No.	Location	Megascleres
		Oxeas
Holotype NMNZ PO.000008	Te Tokaroa Reef, Point Chevalier, Hauraki Gulf, Auckland	300–800 × 5–17
Holotype NMNZ PO.000008 (remeasured)		431 (291–771) × 12 (9–21)
NMNZ PO.000144	Te Tokaroa Reef, Point Chevalier, Hauraki Gulf, Auckland	380 (242–786) × 10 (7–18)
NIWA 113671	Pilot Bay, Tauranga Harbour, Bay of Plenty	390 (298–739) × 12 (9–19)
NIWA 113672		365 (299–735) × 10 (4–21)
NIWA 113673		431 (309–766) × 12 (8–22)
NIWA 92914		352 (304–540) × 10 (6–12)
NIWA 51669	Unknown location	353 (265–681) × 9 (4–12)

TABLE 5. Spicule dimensions (µm) of *Stylissa haurakii* Brøndsted, 1924, given as length [mean (min–max)] × width [mean (min–max)], n=20 unless stated otherwise.

Specimen No.	Location	Megascleres
		Oxeas
Brøndsted, North (type)	Kawau Island, North Channel, Hauraki Gulf	(400–800) × (up to 14)
NMNZ P0.000330, Bergquist 1970	North (Takatu) Channel, between Tawharanui Peninsula & Kawau Island	720 (605–847) × 13 (6–15)
NMNZ P0.000330 (remeasured)	North (Takatu) Channel, between Tawharanui Peninsula & Kawau Island	644 (541–780) × 14 (7–20)
NIWA 113657	Pilot Bay, Tauranga Harbour, Bay of Plenty	746 (617–935) × 19 (13–27)
NIWA 113660		765 (655–926) × 22 (15–29)
NIWA 92920		793 (675–932) × 15 (6–20)

FIGURE 1. *Aaptos globosa* Kelly-Borges & Bergquist, 1994, NIWA 92972: **A.** *In-situ* image showing the conulose surface features in life and distinct clusters of oscules (compound oscules) in depressions; **B.** *In-situ*, showing blunt raised conules; **C.** Out of water, showing the broad basal skirt of attachement.
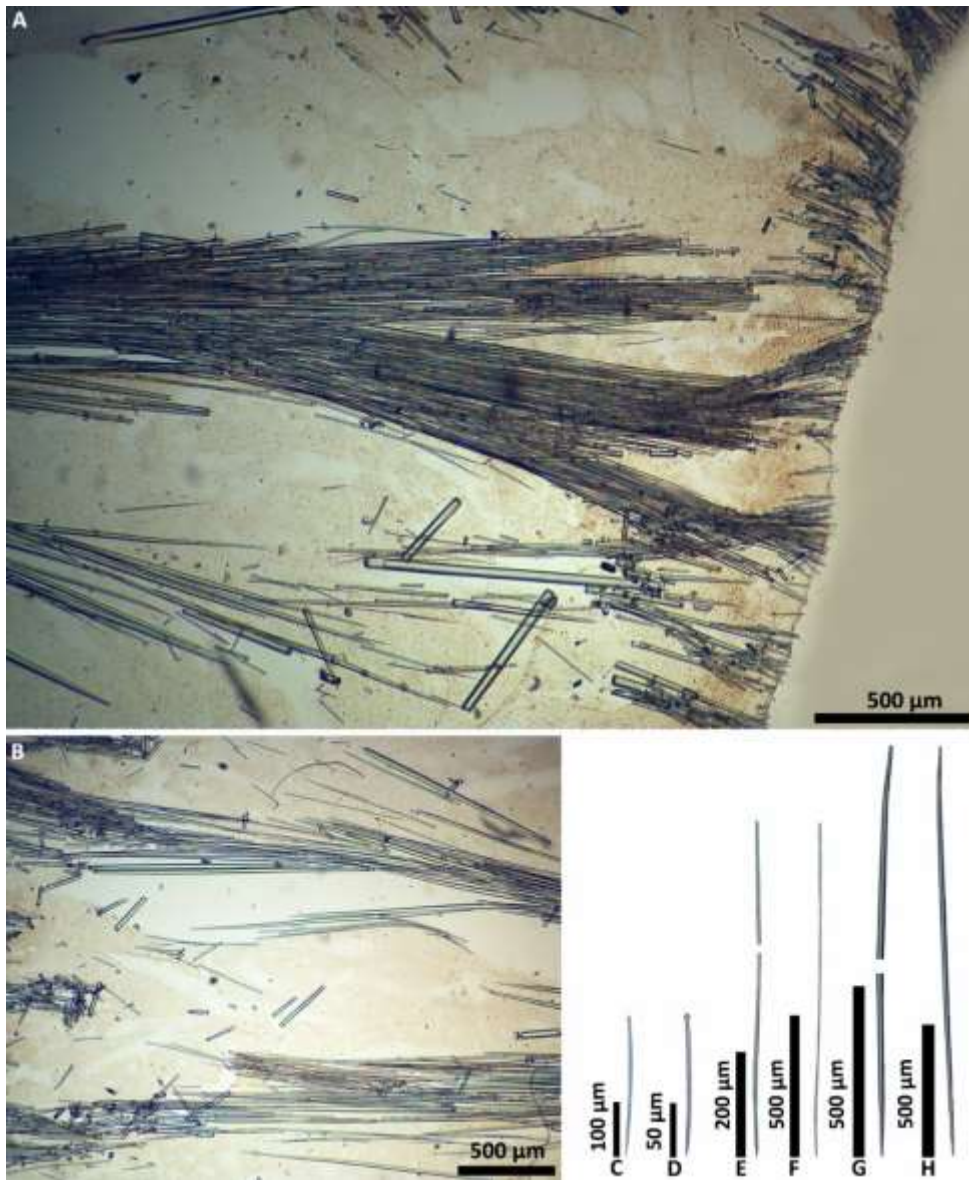
FIGURE 2. *Aaptos globosa* Kelly-Borges & Bergquist, 1994, NIWA92972: **A.** With dense plumose tracts comprised of large primary megascleres radiating through choanosome and branching into bouquets near surface; **B.** Dense choanosonal tracts of megascleres; **C.** Subtylostyle with faint subterminal expansion with a slender curved shaft; **D.** Tylostyle with a pin-like morphology and hastate oxeote end and slight curvature; **E.** Close view of a head and base of intermediate sized strongyloxea; **F.** Intermediate sized strongyloxea that is finely tappered with a fusiform distal end; **G.** Close view of a head and base of large sized strongyloxea; **H.** Large sized strongyloxeas finely tappered with a fusiform distal end.
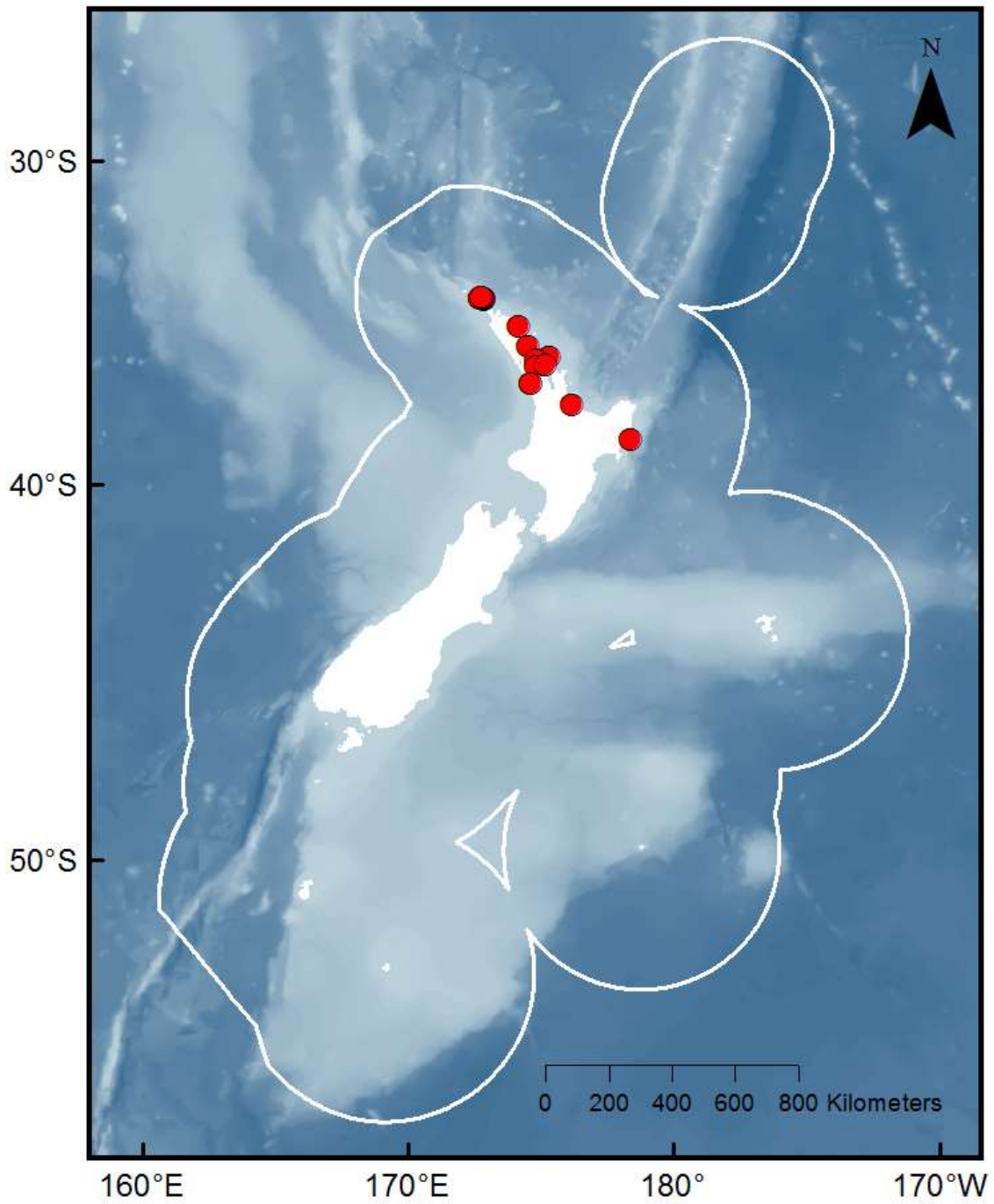
FIGURE 3. Distribution of *Aaptos globosa* Kelly-Borges & Bergquist, 1994, around New Zealand. The white outline shows New Zealand's Exclusive Economic Zone.
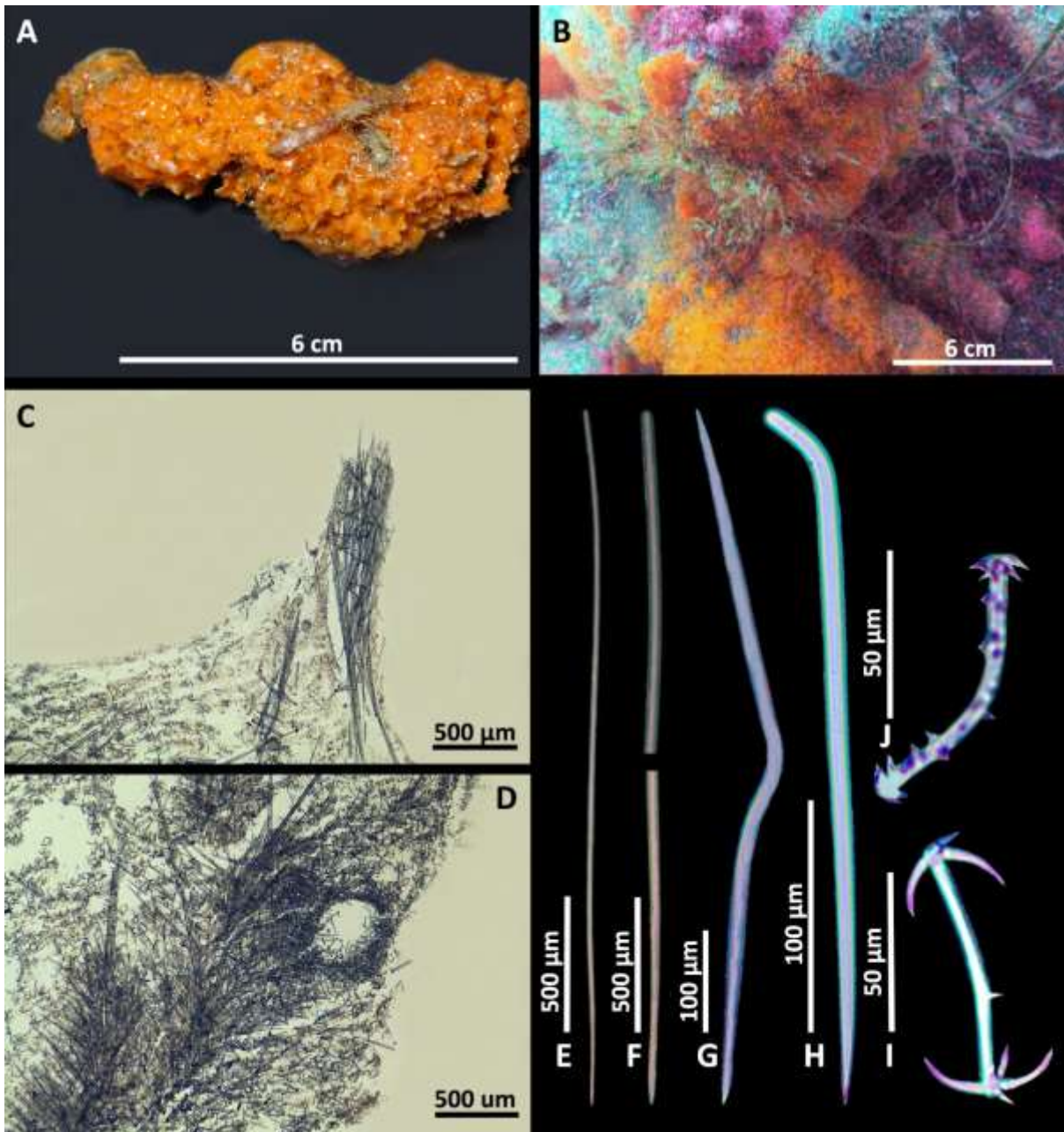
FIGURE 4. *Acanthoclada prostrata* Bergquist, 1970, NIWA 113639: **A.** NIWA 113639, deck photo before preservation; **B.** NIWA 113639, in life; **C.** Spicule tracts protruding through ectosome**; D.** Subectosomal spicule tracts echinating through ectosome; **E.** Complete choanosomal style; **F.** Close view of a head and base of a choanosomal style; **G.** Centrangulate Oxea; **H.** Rhabdostyle; **I.** Cladotoxa; **J.** Birotule.
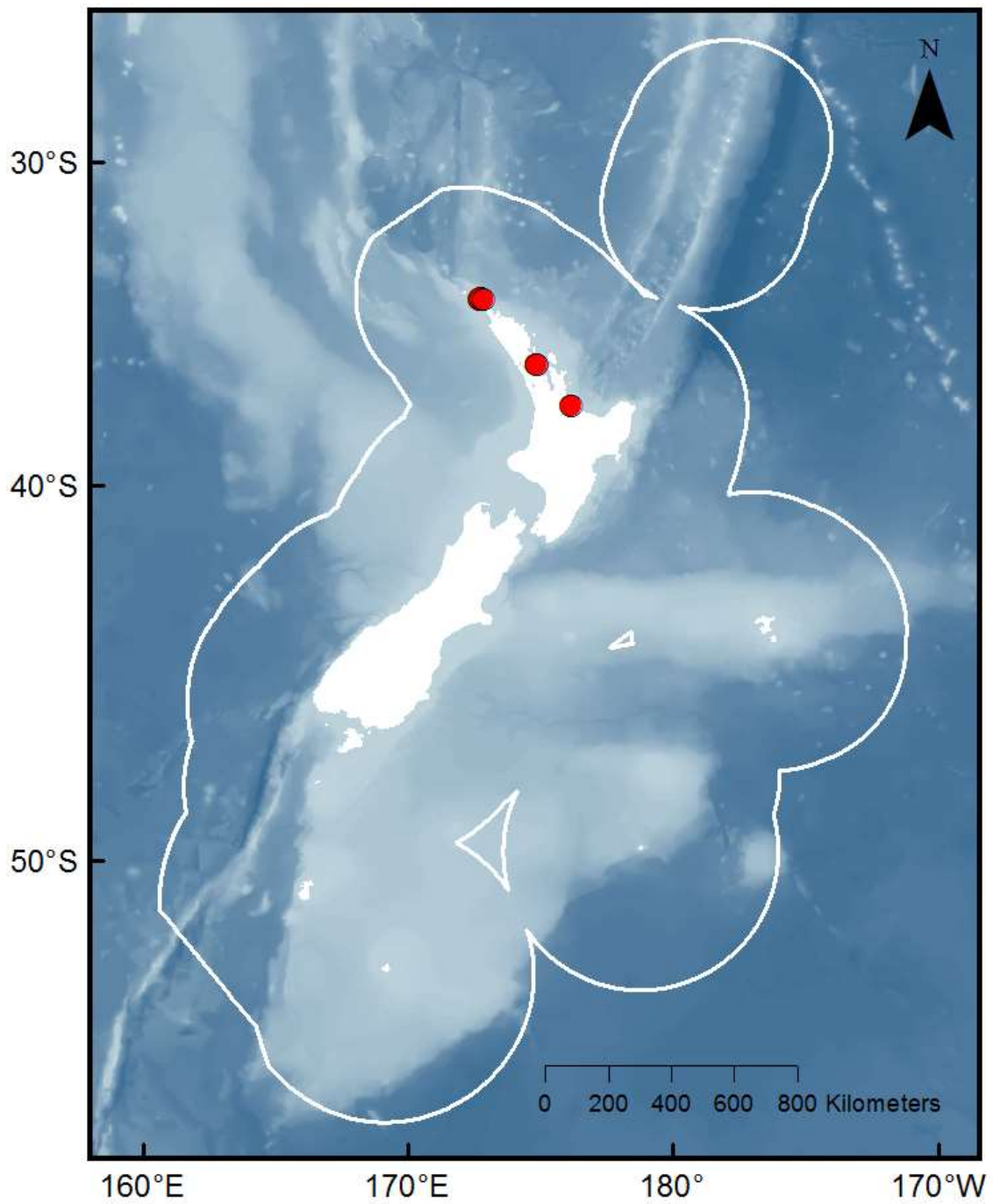
FIGURE 5. Distribution of *Acanthoclada prostrata* Bergquist, 1970, around New Zealand. The white outline shows New Zealand's Exclusive Economic Zone.
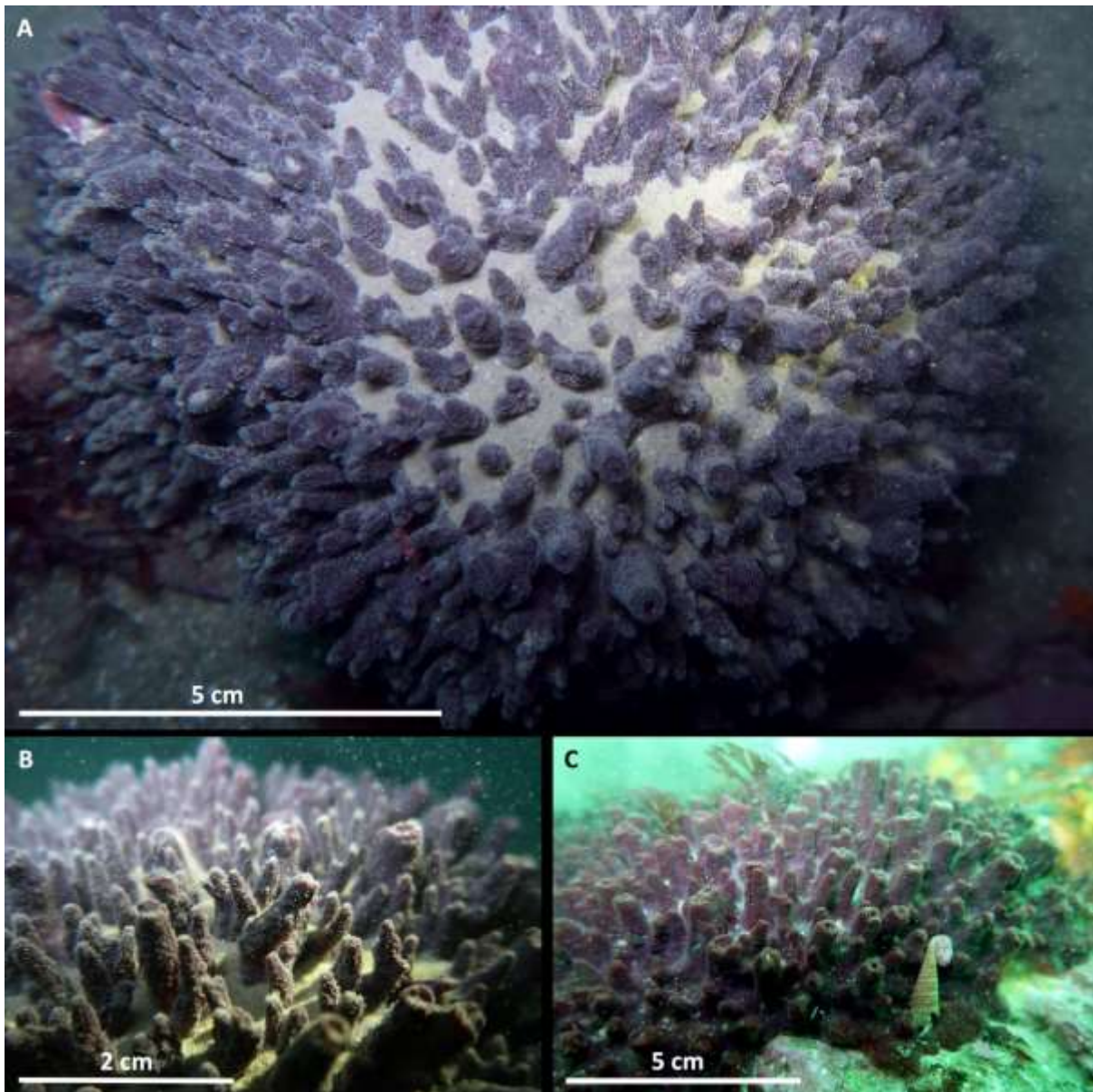
FIGURE 6. *Biemna rufescens* Bergquist & Fromont, 1988, NIWA 113659: **A.** Specimen showing the highly digitate surface typical of this species (NIWA 113659); **B.** NIWA 92967 showing closeup of irregular turrets; **C.** Encrusting growth form shown in NIWA 92967.
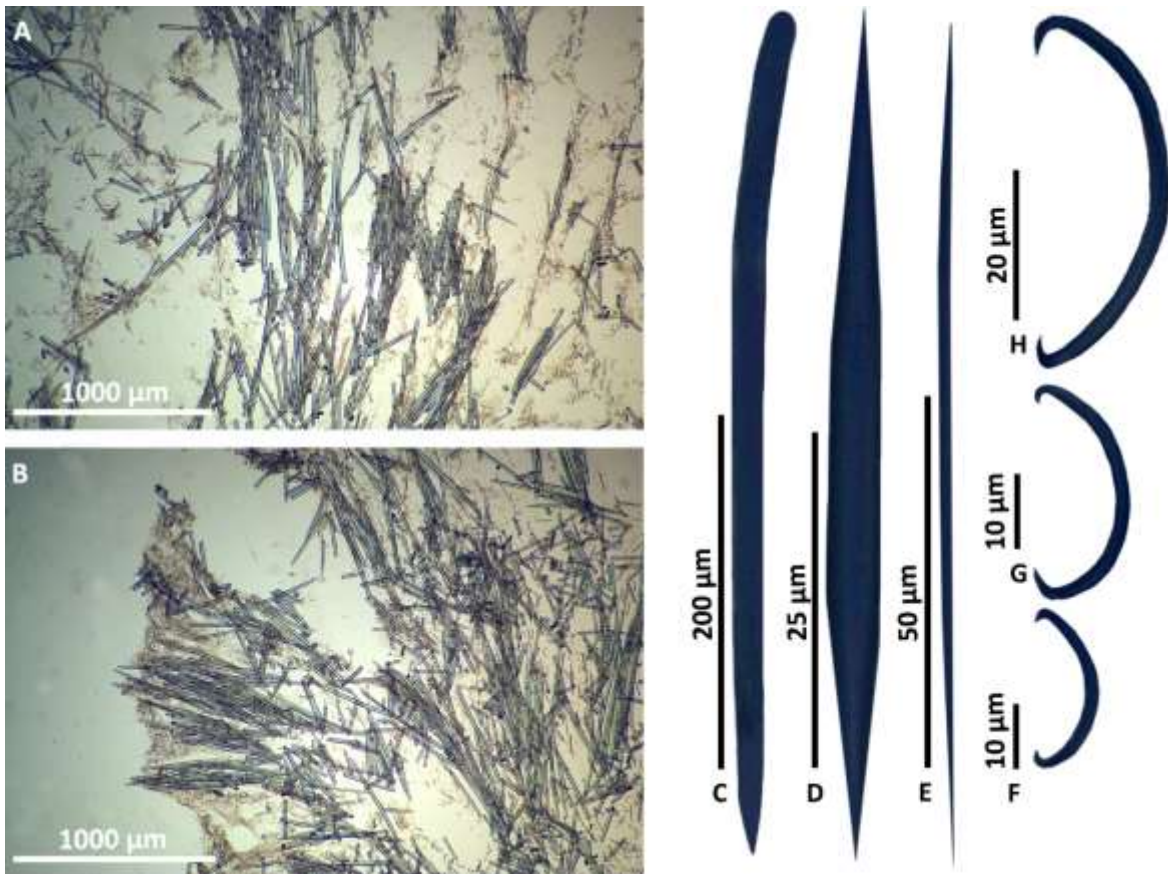
FIGURE 7. *Biemna rufescens* Bergquist & Fromont, 1988, NIWA 92967: **A.** Plumose choanosomal skeleton; **B.** Spicule bouquets protruding through surface of ectosomal skeleton; **C.** Style; **D.** Small microxea; **E.** Large microxea; **F.** Small sigma; **G.** Medium sigma; **H.** Large sigma.
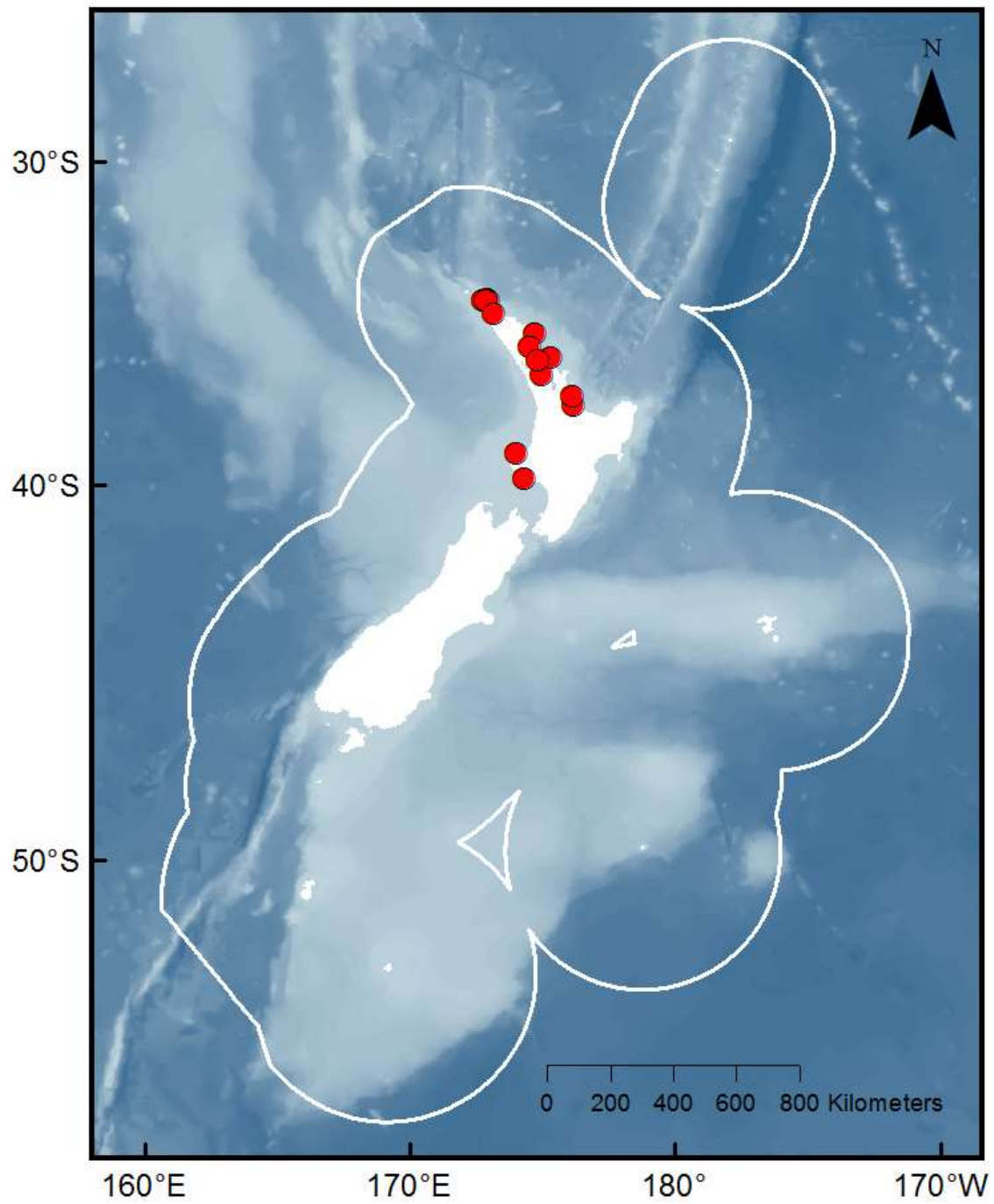
FIGURE 8. Distribution of *Biemna rufescens* Bergquist & Fromont, 1988, around New Zealand. The white outline shows New Zealand's Exclusive Economic Zone.
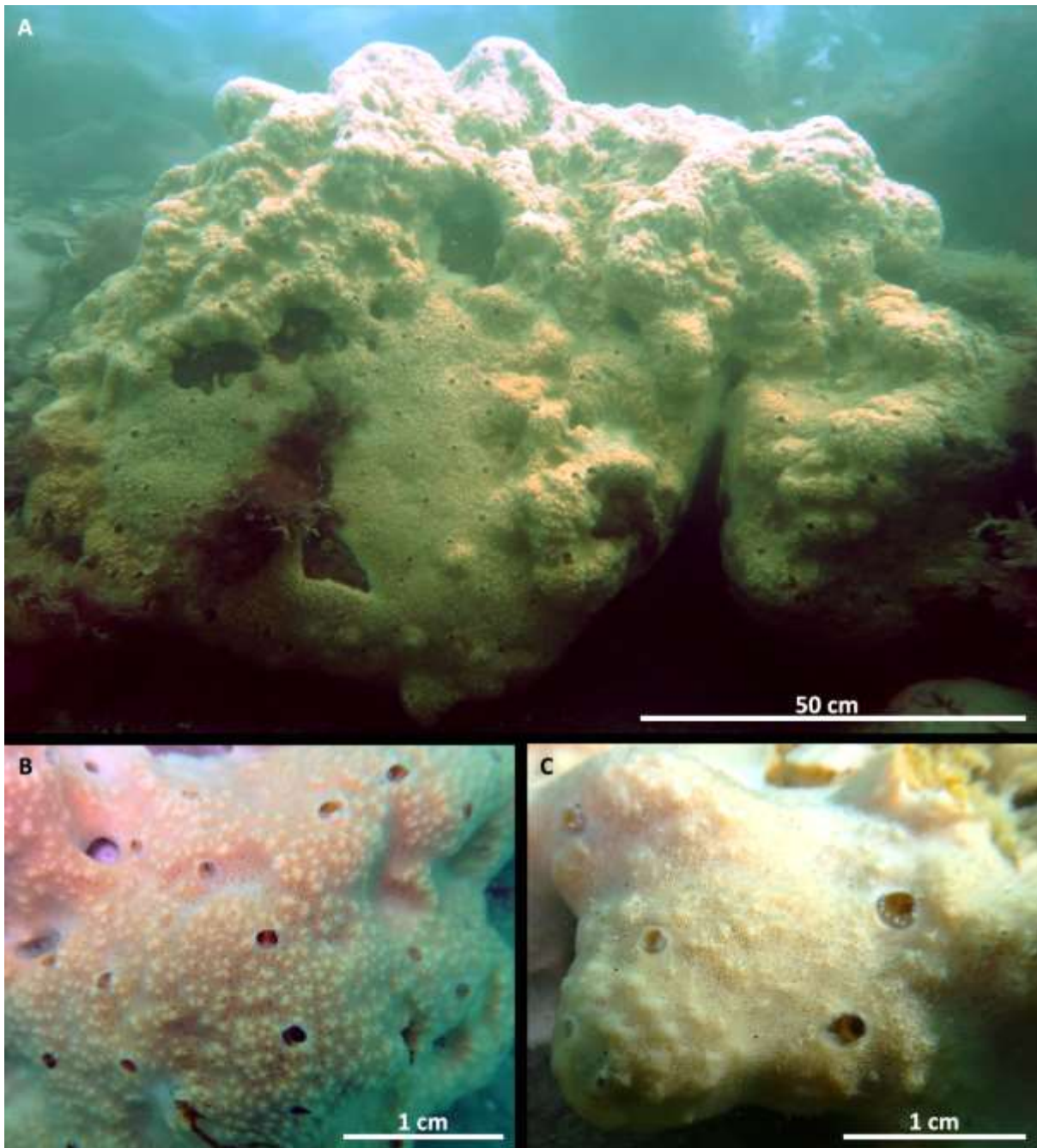
FIGURE 9. *Halichondria* (*Halichondria*) *moorei* Bergquist, 1961: **A.** *In-situ* image of NIWA 113673 when living, showing an irregular surface structure-**B.** *In-situ* image of NIWA 113672 showing the raised surface and large oscules; **C.** *In-situ* image of NIWA 113671 showing the membranous rim around each oscule.
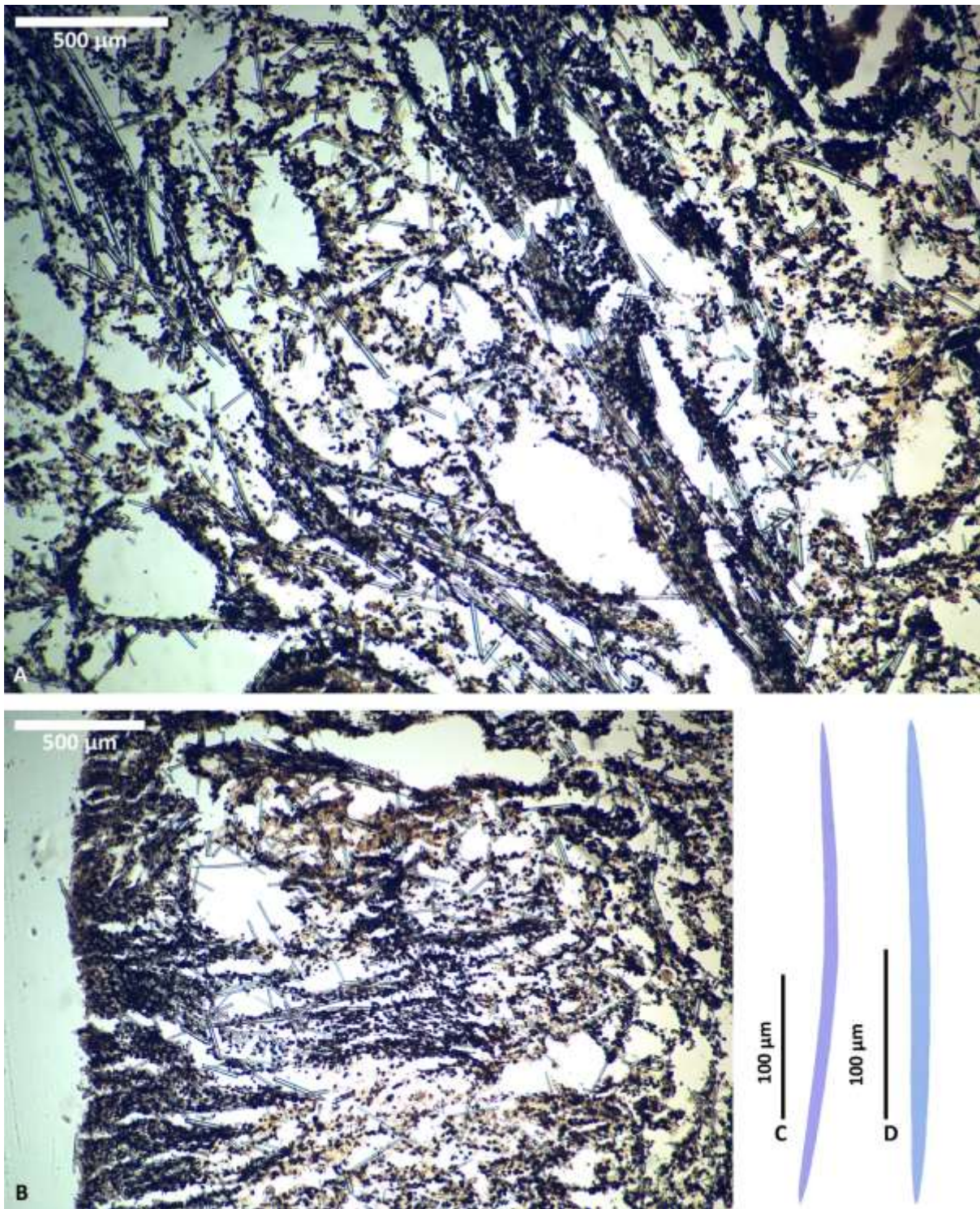
FIGURE 10. *Halichondria* (*Halichondria*) *moorei* Bergquist, 1961, NIWA 92914: **A.** Choanosome showing irregular loose tracts of megascleres with isolated interstitial megascleres in a confused arrangement; **B.** Ectosome (left) showing extreme density of pigmented cells and loose tract of megascleres centrally, with a generally confused arrangement; **C.** curved oxeas; **D.** Less common relatively straight oxeas.
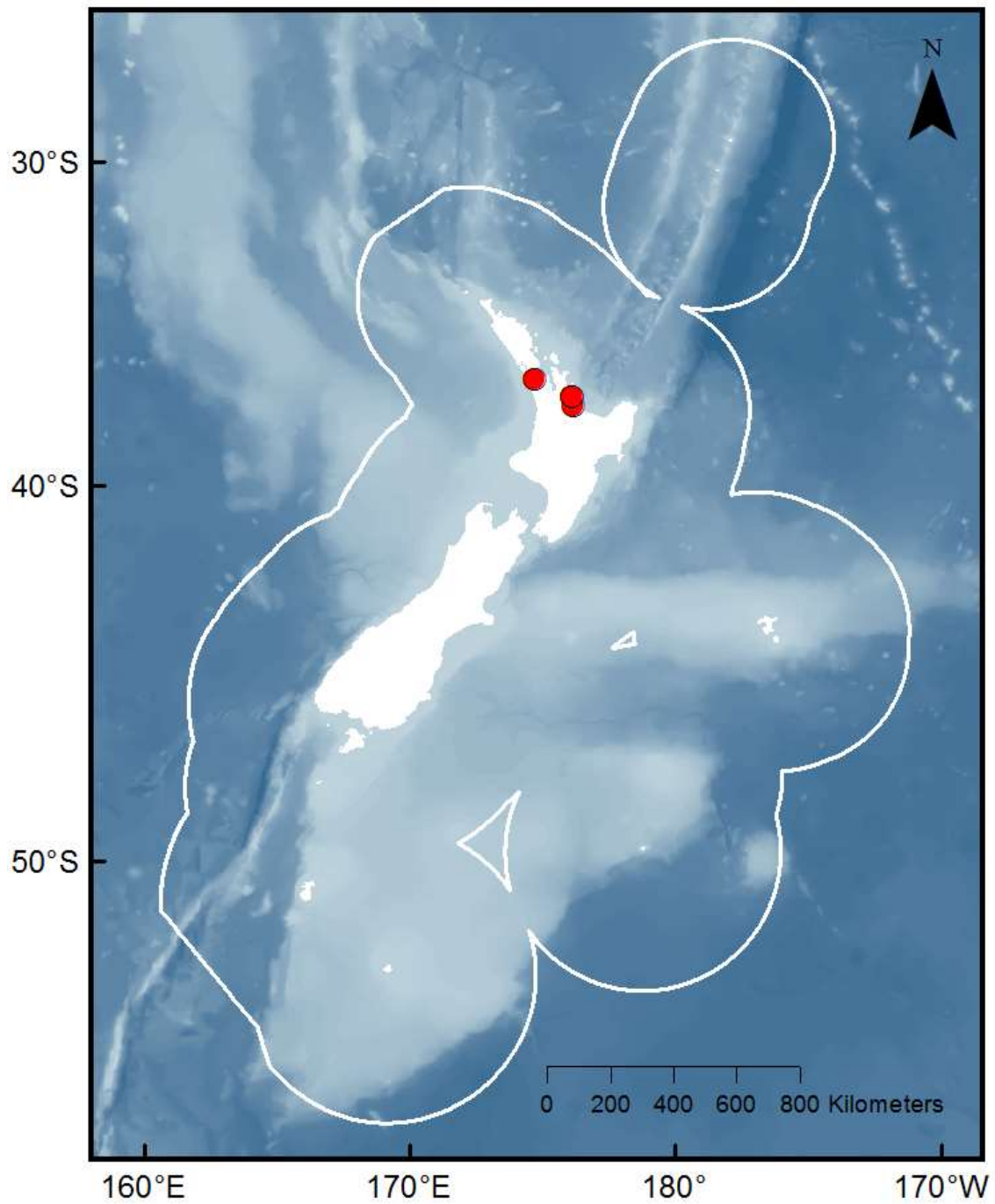
FIGURE 11. Distribution of *Halichondria* (*Halichondria*) *moorei* Bergquist, 1961, around New Zealand. The white outline shows New Zealand's Exclusive Economic Zone.
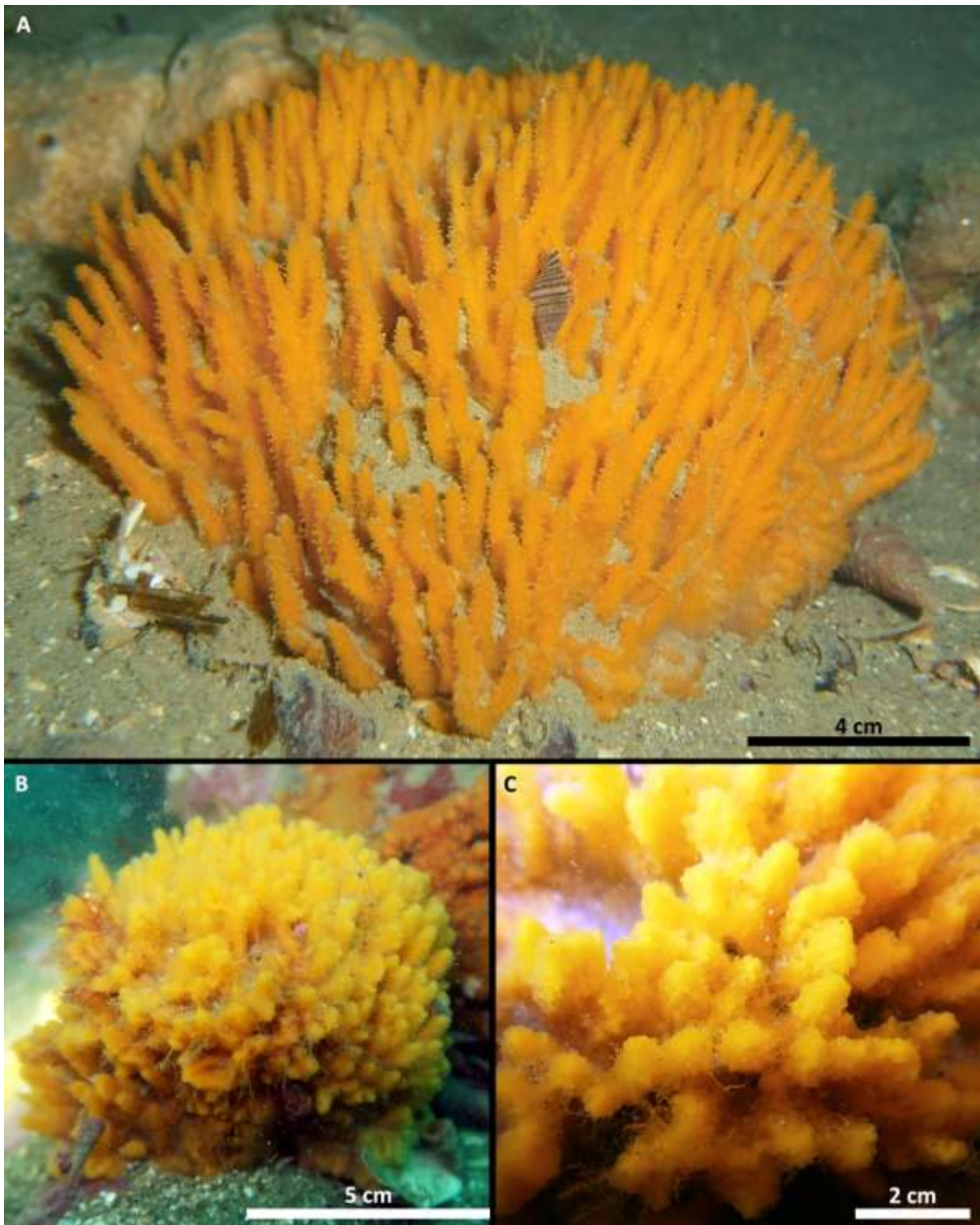
FIGURE 12. *Stylissa haurakii* Brøndsted, 1924: **A.** NIWA 92920 showing shaggy conulose surface projections and bright orange colouration; **B.** NIWA 113660 juvenile specimens with smaller conules and a more spherical morphology; **C.** Close view of shaggy surface conules shown in NIWA 113660.
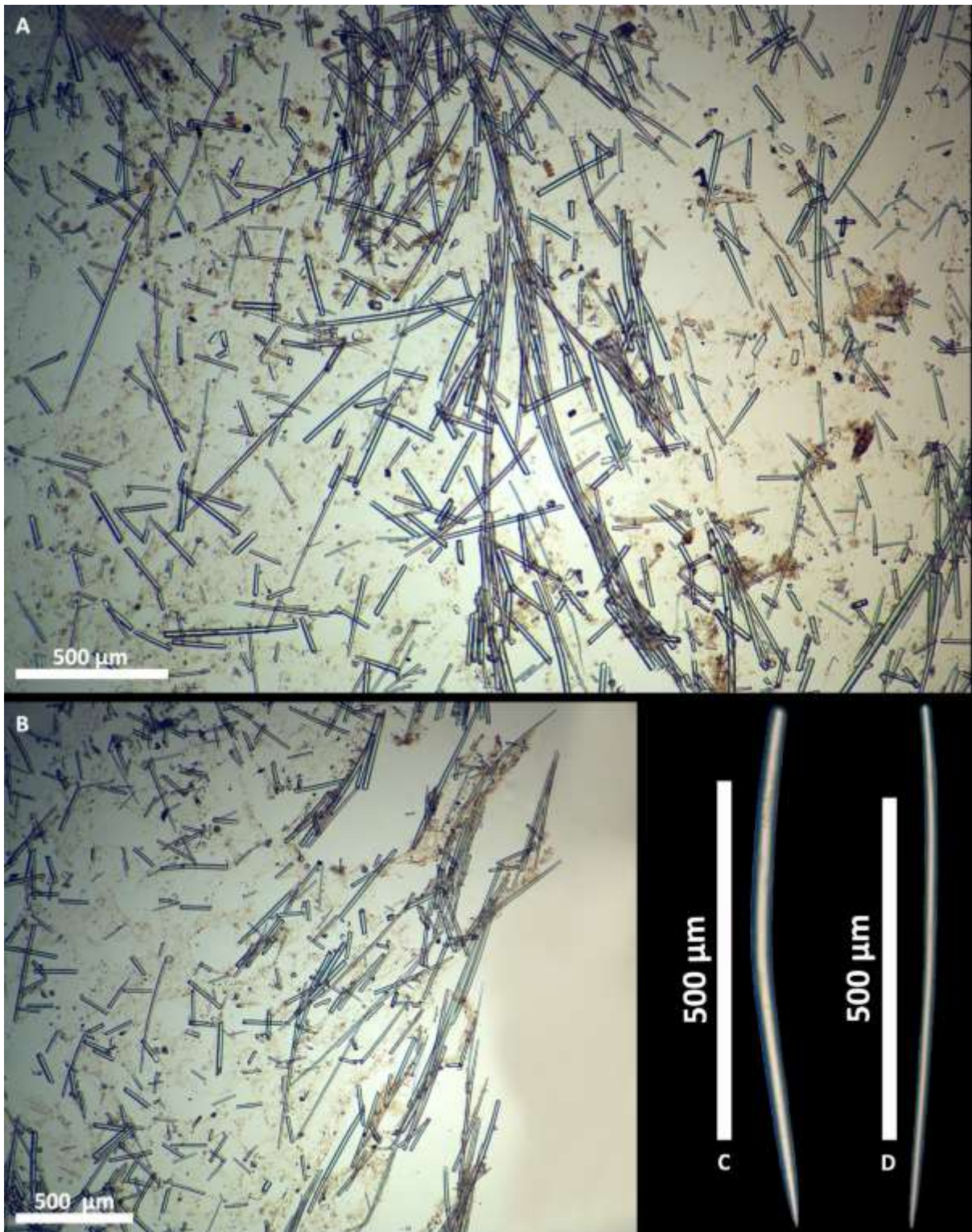
FIGURE 13. *Stylissa haurakii* Brøndsted, 1924, NIWA 92920: **A.** Choanosomal skeleton with a confused mass of spicules forming tracts of styles; **B.** Ectosomal skeleton with thin membrane and styles penetrating through ectosome; **C.** Curved style; **D.** Slightly curved style.
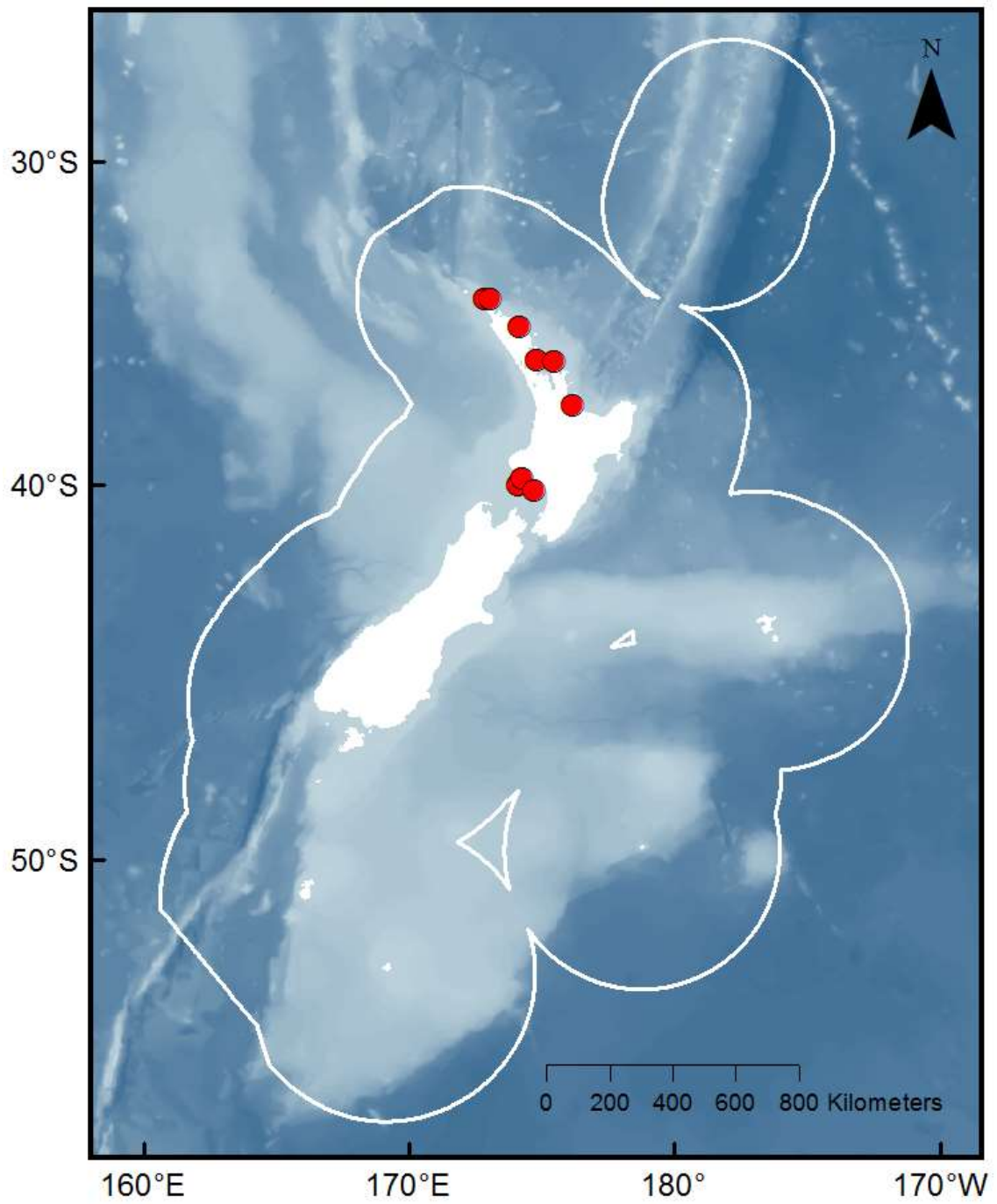
FIGURE 14. Distribution of *Stylissa haurakii* Brøndsted, 1924, around New Zealand. The white outline shows New Zealand's Exclusive Economic Zone.

Appendix 2

Description of two new species of *Dysidea* (Porifera, Demospongiae, Dictyoceratida, Dysideidae) from Tauranga Harbour, Bay of Plenty, New Zealand

Authors: Mc Cormack, Kelly & Battershill, 2020.

Article

Description of two new species of *Dysidea* (Porifera, Demospongiae, Dictyoceratida, Dysideidae) from Tauranga Harbour, Bay of Plenty, New Zealand

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Abstract

Differentiation of species within the genus *Dysidea* Johnston, 1842 (Order Dictyoceratida Minchin, 1900, Family Dysideidae Gray, 1867) is extremely difficult as they lack spicules which are strongly diagnostic in other Demospongiae, and their primary and secondary fibres and the mesh that they form, may be irregular in shape and thickness, thus difficult to measure for comparisons. Here we review species of *Dysidea* known from the New Zealand Exclusive Economic Zone (EEZ), validating five species: *Dysidea cristagalli* Bergquist, 1961a, from the Hauraki Gulf; *D. hirciniformis* (Carter, 1885a) *sensu* Dendy (1924), from North Cape; *D. navicularis* Lendenfeld, 1888, from Port Lyttleton on the east coast of the South Island; *D. ramsayi* (Lendenfeld, 1888) from the Chatham Islands; *D. spiculivora* Dendy, 1924, from Cape Maria Van Diemen and the Three Kings Islands to the north of New Zealand. *Dysidea fragilis* (Montagu, 1818) *sensu* Bergquist (1961b), from Mernoo Bank on Chatham Rise, is now considered to be invalid, and *D. elegans* (Nardo, 1847) *sensu* Brøndsted (1927), from the Coromandel Peninsula, is considered unrecognisable. Several partially characterised species have also been cited in the literature. Two new species from Tauranga Harbour, on the northeast coast of the North Island, *Dysidea tuapokere* **sp. nov**. and *D. teawanui* **sp. nov.**, are described. These descriptions are based on fresh material and *in situ* photography, facilitating clear, informative descriptions, that will enable ease of identification of these species in the future.

Key words: Sponges, morphology, taxonomy, biodiversity, systematics, New Zealand EEZ, Porifera

Introduction

Differentiation of species within the genus *Dysidea* Johnston, 1842 (Order Dictyoceratida Minchin, 1900, Family Dysideidae Gray, 1867) is extremely difficult; the skeletal fibres of most species are irregular in shape, making standard measurements difficult, and they also lack spicules which are strongly diagnostic in other Demospongiae (Cook & Bergquist 2002). Globally, there are 62 species considered to be valid (Van Soest *et al.* 2020).

Species of *Dysidea* are considered to be fairly homogeneous as each possesses a skeleton of pithed and laminated primary and secondary fibres, axially or fully cored to varying degrees with sand and spicule debris, differing only in small dimensional differences and perhaps, the degree of coring. Species can be differentiated, however, if details of external morphology in life are available (when the sponge is fully inflated), and *in-situ* and *ex-situ* colouration is known, but these data are rarely available in earlier New Zealand collections.

Two North Atlantic/Mediterranean species names have been applied to New Zealand material from Coromandel Peninsula on the North Island and Mernoo Bank on the South Island's Chatham Rise: *D. elegans* (Nardo, 1847) *sensu* Brøndsted (1927) and *D. fragilis* (Montagu, 1818) *sensu* Bergquist (1961b), respectively. One South Australian species of *Dysidea* has been attributed to New Zealand material from North Cape [*D. hirciniformis* (Carter, 1885a) *sensu* Dendy (1924)], and a further species attributed to New Zealand material was originally described from Mauritius (*Dysidea ramsayi* Lendenfeld, 1888).

Three species were described *de novo* from the New Zealand region: *Dysidea navicularis* (Lendenfeld, 1888) from Port Lyttleton (as the type species of the now synonymised genus *Haastia*); *Dysidea spiculivora* Dendy, 1924, from Cape Maria Van Diemen and the Three Kings Islands, and *D. cristagalli* Bergquist, 1961a, from the Hauraki Gulf. Several additional, partially characterised species have been cited in the literature: *Dysidea* sp. a and b in Brøndsted (1924) from the Auckland Islands; *Dysidea* sp. nov. (Battershill *et al*. 2010) from Three Kings Islands, Poor Knights Islands and the Hauraki Gulf; *Dysidea* sp. in Perry *et al*. (1987) and a further nine species in Kelly *et al*. (2009) from Spirits Bay, Northland (Table 1). These latter species are in critical need of characterisation and description but are beyond the scope of this work.

TABLE 1. The status of previously described species of *Dysidea*, within the New Zealand EEZ, and proposed changes.

Taxon name	Comment	Status
Dysidea cristagalli Bergquist 1961a		
Bergquist (1961a: 33–34, fig. 1b); Dawson (1993: 24); Kelly *et al*. (2009: 45) Waitemata Harbour: Noises Islands, coll. L. B. Moore, 2 May 1937, intertidal; Rangitoto Island, coll. P. R. Bergquist, 7 Jun 1957, intertidal rock pools in caves	Erect, tubular, or conjoined tubes with common base; oscules apical with deep cloacae; firm, friable; colour ash-grey; skeleton irregular, close-knit reticulation of fibres, 20–200 µm diameter, no obvious distinction between primary and secondary fibres, fibres filled with broken spicules; no special dermal skeleton (from Bergquist 1961a)	Valid
Dysidea cf. *cristagalli*, Kelly in McNamara *et al*. (2005) Supplementary information; Spirits Bay, 33 m, coll. M. Page	Sub-spherical mass of meandering ridges and interconnected, short, blunt, branches; oscules situated on ends of short branches; surface sandy to the touch, distinctly conulose, raised by the sub-surface sandy fibres; texture in life somewhat compressible, reasonably elastic, but is brittle when torn; colour in life greyish white, deep brown with a magenta tinge, in preservative. Skeleton a loose reticulation of large sand-grains cemented into fibres with clearly visible spongin, numerous smaller secondary spongin fibres contain predominantly spicule debris (after McNamara *et al*. 2005)	*Dysidea* sp. indet.
Dysidea elegans Nardo, 1847 *sensu* Brøndsted (1927)		
Brøndsted (1927: 296) Coromandel Peninsula: Slipper Island (Whakahau), off Pauanui, intertidal	Brøndsted (1927) was uncertain about the identification of his "fragments of a lobose or lump-shaped sponge" as *Spongelia elegans* Nardo, 1847, and probably based his identification on Lendenfeld's (1889) description of a sponge from Broken Bay, New South Wales. *Spongelia elegans sensu stricto* is now synonymised with *Dysidea tupha* (Pallas, 1766) and is restricted in distribution to the Mediterranean Sea.	Unrecognisable
Dysidea fragilis (Montagu, 1818) *sensu* Bergquist (1961b)		
Bergquist (1961b: 211–212, fig. 3a, b); Dawson (1993: 25) Mernoo Bank, Chatham Rise, 75 m	Irregular sponge, 5 cm long, 3 cm wide, with cylindrical process arising from a basal mass, oscule apical, 1–1.5 mm diameter; surface conulose, 3 mm high, 1–3 mm apart; fibres densely cored with sand and spicules; primary fibres 150–340 µm; secondary fibres 35–48 µm; colour in life brownish grey (after Bergquist 1961b). The application of the name, *Dysidea fragilis* (Montagu, 1818), to New Zealand material, is doubtful (Battershill *et al*. 2010). The species is restricted to the Northeastern Atlantic and Mediterranean regions.	Invalid *Dysidea* sp. indet.

TABLE 1. (Continued)

Taxon name	Comment	Status
Evans & Bergquist (1977: 191–199; table 2)	A histological study tested the suggestion that the cytological localization of acid mucopolysaccharides (AMPs) within the Class Demospongiae may prove of taxonomic value. It was found that AMPS in dictyoceratid species were generally dispersed throughout the mesohyl although some localization was apparent in the amoebocytes of *Dysidea fragilis* [(after Evans & Bergquist (1977)].	*Dysidea* sp. indet.
Perry *et al*. (1987: 373–376; table 1)	Perry *et al*. (1987) extracted Dictyoceratida for the sesterterpene variabilin, represented by three specimens identified as *Dysidea fragilis*. Variabilin was absent in all Dysideidae.	*Dysidea* sp. indet.
Pritchard *et al*. (1984: 133); Gordon & Ballentine (1976: 98)	Cited in Appendix 1 as being present in the Cape Rodney to Okakari Point Marine Reserve.	*Dysidea* sp. indet.
Dysidea hirciniformis (Carter, 1885a) *sensu* Dendy (1924)		
Carter (1885a: 217); Lendenfeld (1889: 665); Dendy (1924: 383–384) Port Phillip Heads, South Australia, 34.7 m; North Cape, 26–66 m	Originally described from Port Phillip Heads, South Australia, by Carter (1885a) as forming a bunch of cylindrical, digitate, upright branches, arising from a common stem that divides two to three times, ending in pointed extremities. The consistency was soft, delicate, and the colour in life, pale buff with purple tips; oscules scattered on the branches; with vertical and lateral fibres, all sandy. Lendenfeld (1889) added dimensions for the branches (about 15 mm thick, 150 mm long), surface conules (2.5 mm high, 2.5 mm apart), oscules (scarce, 3–4 mm diameter), fibres (packed, arenaceous, primary fibres 180 µm thick, secondary fibres 80–150 µm thick), and meshes (about 80 µm wide). Dendy's (1924) specimens are thin (R.N.XXIII.b: 4–8 mm thick, 120 mm long; R.N.XXIII.a: 10 mm thick, 330 mm long), ramose, with no evidence of branching. Skeleton is axial, formed of laminated, dark-coloured spongin fibres, primaries (up to 340 µm thick), and are abundantly cored with sand and spicules, the secondaries much less so. Choanocyte chambers are eurypylous and 120 µm diameter. Dendy considered the North Cape specimens to be "merely a more robust variety" of Carter's Australian species, with the former having less robust fibres, but greater development of the subectosomal peripheral fibres. Despite the disjunct distribution, the likelihood of conspecificity of North Cape specimens with a South Australian species is moderate as there are several clear precedents.	Valid as *Dysidea* cf. *hirciniformis* (Carter, 1885a) *sensu* Dendy (1924)

TABLE 1. (Continued)

Taxon name	Comment	Status
Dysidea navicularis (Lendenfeld, 1888)		
Lendenfeld (1888: 204). Bergquist (1980: 482); Kelly *et al.* (2009: 45) Lyttleton Harbour, South Island, New Zealand	Lendenfeld (1888) described a sponge consisting of a bunch of erect, cylindrical, digitate processes, about 15 mm thick, growing from an incrusting basal mass, height 150 mm. The surface had uniform conules, 1 mm high, 1.5–2 mm apart; oscules were confined to summits of the digitate processes. Bergquist (1980: 482) stated that the genus *Haastia* Lendenfeld, 1888, erected for *H. navicularis*, from southern New Zealand, is in every respect a typical *Dysidea*, close in surface and skeletal characteristics to *Dysidea fragilis*. Bergquist retained the species name as valid because of the geographical separation of the type material in Lyttleton Harbour.	Valid
Dysidea ramsayi (Lendenfeld, 1888)		
Lendenfeld (1888: 209) Mauritius Chatham Islands	Lendenfeld (1888) described this sponge as a hard, "irregular, meandrically-folded, lamellar sponge, which attains a maximum diameter of 140 mm; oscules, 2 mm diameter, situated on one face of the lamella; main (primary) fibres very knotty, charged with sand-grains, average 250 µm diameter; connecting (secondary) fibres containing scattered foreign bodies, 100 µm diameter.	Valid
Dysidea spiculivora (Dendy, 1924)		
Dendy (1924: 384–385); Kelly *et al.* (2009: 45); Dawson (1993: 25) Near Three Kings Islands, 183 m Near Cape Maria van Diemen, 64–73 m	Dendy (1924) described this species as irregularly massive, sub-digitate, 54 mm long, 20 mm diameter, probably repent; surface coarsely sub-conulose, conules low and far apart; no aquiferous pores visible; interior cavernous; texture in ethanol firm, tough; colour white, with a "curiously translucent appearance". Skeleton an irregular jumble of spicules only; no dermal skeleton.	Valid
Dysidea sp. 'a' of Brøndsted (1924)		
Brøndsted (1924: 164–165) Carnley Harbour, Auckland Islands, 6 Dec 1914, sandy clay, 82.3 m	Brøndsted (1924) admitted a lack of experience with the genus *Dysidea*, considering the Australian species of Lendenfeld to be, "in most places, incompletely described, that I for one cannot recognise them; and besides, it seems to me that the genus *Spongelia* needs a critical monographic revision; I will therefore not further complicate the matter by adding new uncertain species". *Dysidea* sp. a was partially characterised as irregularly shaped, consisting of densely anastomosing, thick, even branches, 40–50 mm long, with a conulose surface, conules 2 mm high, 2–4 mm apart, oscules 1 mm diameter; dermal membrane thin, pellucid; consistency soft, a little elastic, colour fleshy.	Only partially characterised; valid for Auckland Islands

TABLE 1. (Continued)

Taxon name	Comment	Status
Dysidea sp. 'b' of Brøndsted (1924)		
Brøndsted (1924: 165) Coleridge Bay, Carnley Harbour, Auckland Islands, 4 Dec 1914, sandy mud, 45.7 m	*Dysidea* sp. b was partially characterised as variable, oblong, lumpy in shape, 50 mm long, attached to shell; dermal membrane tough, large subdermal cavities; primary fibres about 160 μm thick, packed with foreign matter; secondary fibres are "almost devoid of detritus". Texture soft, elastic; colour pale grey to yellowish grey.	Only partially characterised; valid for Auckland Islands
Dysidea sp. nov. of Battershill *et al*. (2010)		
Cook (2000: 111–112, fig. 6.1F–G); *Dysidea* sp. 'A' Cook & Bergquist in Kelly *et al*. (2009: 45); Battershill *et al*. (2010: 79–80) *Dysidea* n. sp. 2 Kelly & Wilkinson in Cryer *et al*. (2000: 96, 98–99, 105, 107) Three Kings Islands, Poor Knights Islands, Hauraki Gulf, Spirits Bay	Battershill *et al*. (2010) partially characterised a species first recognised in Cook (2000). The sponge has been recorded from the Hauraki Gulf and sheltered areas of offshore islands, 5–30 m. It is delicate, lobate with digitate projections, 2–3 cm high, 2 cm diameter, overall dimensions 6 cm high with an average basal diameter of 5–10 cm; apical oscules 5 mm diameter; texture soft, highly compressible, easily torn; colour in life pastel pink, yellow or blue.	Only partially characterised; valid for Northeastern New Zealand
Dysidea spp. of Perry *et al*. (1987)		
Perry *et al*. (1987: 373–376; table 1)	Perry *et al*. (1987) extracted Dictyoceratida for the sesterterpene variabilin, represented by what were thought to be several species of *Dysidea*. Variabilin was absent in all Dysideidae.	*Dysidea* spp. indet.

Characters of the living sponge such as external morphology and colouration in life, coupled with differences in the dimensions and coring of the fibres, the degree of surface armouring which governs the morphology and distribution of surface conules, and the density and distribution of collagen in the mesohyl, are key to the clear recognition of species of *Dysidea*, globally. Here we describe two new species from Tauranga Harbour, Bay of Plenty: *Dysidea tuapokere* **sp. nov**. and *D. teawanui* **sp. nov.**, the descriptions of which are based on living material and *in situ* imaging to facilitate clear descriptions that will ensure ease of identification, in the field and lab, in the future.

The validity of known, documented species, is considered in the light of this new material, and the morphological characters of living species are highlighted for future ease of identification in the field.

Materials and methods

Specimens were collected using SCUBA by Samuel Mc Cormack (SMcC) from Tauranga Harbour, Bay of Plenty, between January and October 2014, and in October 2017 (Fig. 1). Photographs of specimens *in-situ*, *ex-situ*, and after preservation in 70% ethanol, were taken using a Canon EOS 60D camera. Histological sections of the sponges were prepared by embedding a small piece of sponge in paraffin wax and then sectioning with a microtome at 50 and 100 μm. The overall architecture of the cored fibres was captured by macerating pieces of sponge in 10% sodium hypochlorite (NaOCl) for 2–5 minutes, dropping this solution directly on to the section with a pipette, until the surrounding tissue had dissolved to expose the delicate skeletal structure (see Bergquist & Kelly-Borges 1995). Skeletons were photographed in water with a Nikon SMZ1000 stereomicroscope using a Canon EOS 60D camera. Fibres and other dimensions are presented as the mean length [mean (min–max)] × mean width [mean (min–max)], n = 10, unless stated otherwise. Abbreviations used in the text: NIC, NIWA Invertebrate Collection, Evans Bay, Wellington; NIWA, National Institute of Water & Atmospheric Research, Evans Bay, Wellington. Primary and secondary type materials are accessioned within NIC at NIWA (prefix NIWA). The taxonomic authority is to be cited as Kelly, Mc Cormack & Battershill.

Systematics

The names of class, order, and family follow the classification proposal by Morrow & Cárdenas (2015).

Class Demospongiae Sollas, 1885

Order Dictyoceratida Minchin, 1900

Family Dysideidae Gray, 1867

Genus *Dysidea* Johnston, 1842

Type species. *Spongia fragilis* Montagu, 1814: 78 (by subsequent designation).

Diagnosis. Thickly encrusting, massive or branching growth form, often with a marked conulose surface and a distinct net or web-like surface pattern, interconnecting conules. Species with heavy intra-mesohyl detritus are not conulose. Skeleton consists of a relatively regular, usually rectangular arrangement of concentrically laminated primary and secondary fibres, with primary fibres orientated perpendicular to the surface, but may also be less regular, with divaricating primary fibres and secondary fibres supported by fine auxiliaries. All fibres are axially or fully cored, although this may be in the form of scattered fragments rather than a dense core. Primary fibres are also pithed though this is usually obscured by the coring material. The sponge is soft and compressible, sometimes made fragile by large amounts of sand etc. incorporated into the sponge tissue. There is only light collagen deposition in the mesohyl, and the sponges are histologically simple, with few secretory cell types present (modified from Cook & Bergquist, 2002).

Dysidea tuapokere **sp. nov.**
Figs 1–4
urn:lsid:zoobank.org:act:F79D832D-AD90-44CE-A18C-83DB4E29306C

Material examined. *Pilot Bay, Tauranga Harbour, Bay of Plenty*: **Holotype**—NIWA 92974, 37.380° S, 176.102° E, 5–12 m, 27 Sep 2017. **Paratypes**—NIWA 113646–113649, 37.380° S, 176.102° E, 13 m, 05 Feb 2019.

Type location & distribution. Pilot Bay, Tauranga Harbour, Bay of Plenty, New Zealand, 12–13 m.

Description. Sponge forms a cavernous mass of interconnected lobate digits, sprawling across the substrate, up to 4–23 cm long, 14–15 cm wide, 2–4 cm high, in general dimensions, digits about 1–3 cm thick (Fig. 2A). Surface conulose in life, conules predominantly clustered on the tips of the lobes (Fig. 2B), but scattered irregularly on the surface, about 0.5–1.0 mm high; conule apices resemble hairs in the preserved specimen (Fig. 2C). Dermal membrane thin and translucent in life and after preservation. Cobwebs of fibrillar collagen in the surface membrane are visible, stretching between the tips of primary fibres, between which are set membranous oscules, about 2 mm diameter (Fig. 2A, B). Conules accentuated in the shrunken, preserved condition (Fig. 2C). Texture soft, compressible, slightly elastic and fragile due to the incorporation of large amounts of detritus in the fibres. Colour in life, translucent lilac under natural lighting *in situ* (Fig. 2A, C), and tan in shaded sections (Fig. 2C). Cream to tan in preservative.

Skeleton. Primary fibres heavily cored with sand and foreign spicule fragments, about 308 (200–500) µm thick (Fig. 3A), frequently bifurcating or divaricating further below the surface (Fig. 3B). Secondary fibres are variable in thickness, often flanged where they join the primary fibre, and generally only partially cored, in which case the laminated golden spongin is visible surrounding the inclusions in histological sections (Fig. 4A, B); 69 (50–100) µm thick. The secondary fibres are supported by cored auxiliary fibres that link the secondary and primary fibres; 10–15 µm thick (Fig. 3B).

The overall architecture is extremely irregular and mesh size difficult to provide meaningful dimensions for but range from about 0.5–3 mm wide. The irregularity of the overall skeleton is evident in Figs 2A and B which show the surface conules clustered in groups on the tips of the branches, being evidence of extensive divarication below the surface [compare to the regularity of the surface in *D.* cf. *cristagalli* (Fig. 5) and *D. teawanui* **sp. nov.** (Fig. 6D)].
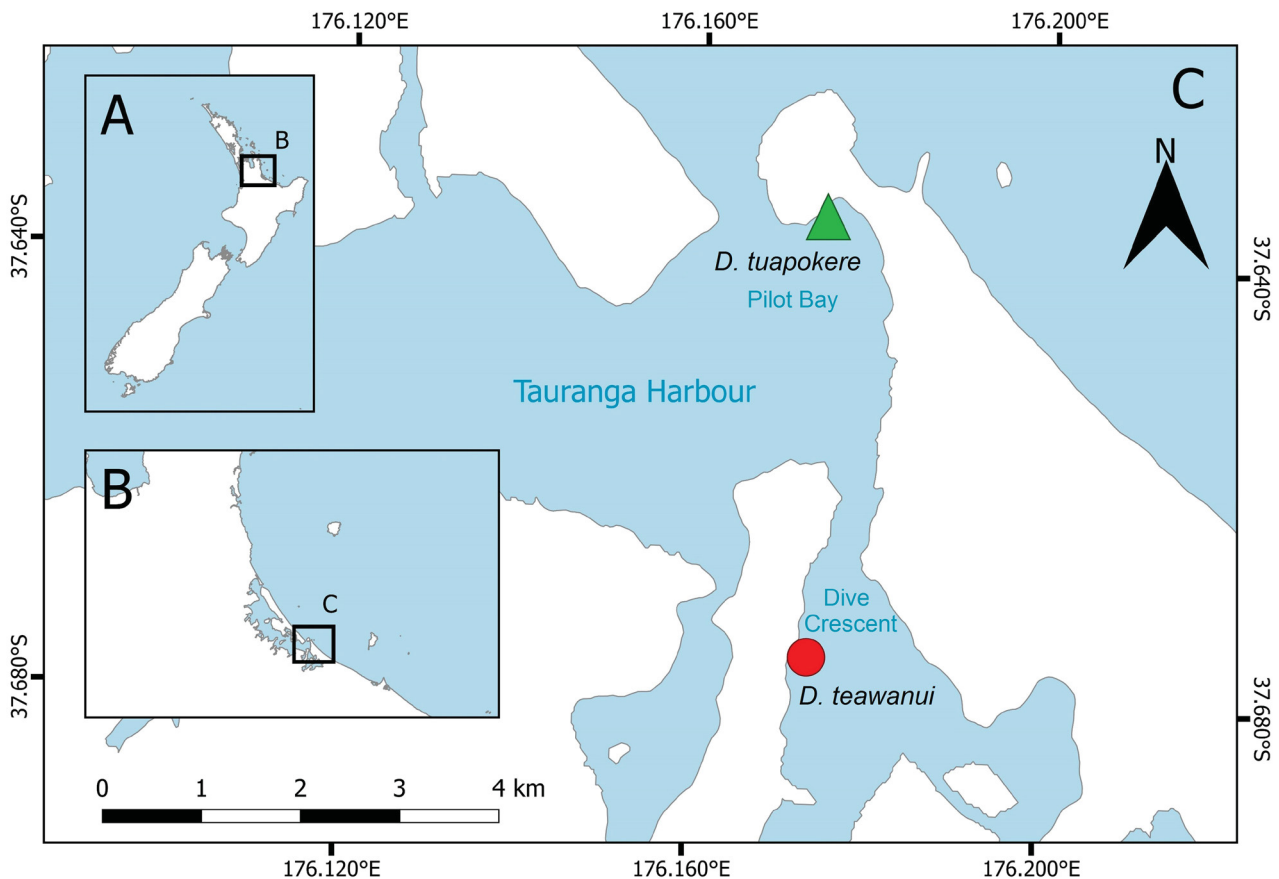
FIGURE 1. Map showing type localities for new species, *Dysidea tuapokere* **sp. nov.** and *D. teawanui* **sp. nov.**, from Tauranga Harbour, Bay of Plenty, New Zealand.

The ectosome consists of a dense band of pigmented collagen fibrils (Fig. 4C) and appears cavernous in sections; about 30–100 μm deep, strands of which stretch between the apex of the primary fibres. A translucent dermal membrane is raised by large primary fibres, rarely with any inclusions of detritus; unarmoured (Fig. 4C). The choanocyte chambers are eurypylous, 30–50 μm diameter, and clearly visible in the choanosome (see Fig. 3A, 4A, B). Detritus is scattered lightly through the choanosome and ectosome.

Substrate, depth range and ecology. Found predominantly on rocky reefs within a relatively sheltered location. Associated with kelp forests or sponge gardens. Depth range is 5–12 m.

Etymology. Named for the beautiful, translucent, pale lilac colouration of this species in life (*tuapokere*, violet; te reo Māori). This species name was accepted and approved by local Tauranga Moana iwi, Ngāti Ranginui, Ngāi Te Rangi and Ngāti Pūkenga.

Remarks. *Dysidea tuapokere* **sp. nov.** is a shallow-water harbour species, with a cavernous lobo-digitate morphology, similar to several species described or noted from New Zealand waters. Most of these species are, however, inadequately described and figured, so only a limited comparison can be made in most cases. The most recently described species, *D. cristagalli* Bergquist, 1961a, was collected from the intertidal zone on Rangitoto Island in the North Island's Waitemata Harbour, and the Noises Islands in the inner Hauraki Gulf (Table 1). *Dysidea cristagalli* differs morphologically from *D. tuapokere* **sp. nov.** in being, "erect, tubular in shape, with several tubes coalescing to give a tubula-flabellate condition" (Bergquist 1961a: Fig. 1b). The oscules were "apical, giving access to deep cloacae", a completely different morphology to the cavernous lobo-digitate form of *D. tuapokere* **sp. nov.** which has small, flush oscules scattered across the sponge. Additional key differences are the colouration in life (*D. cristagalli*: "ash-grey"; *D. tuapokere* **sp. nov.**: translucent lilac) and skeletal architecture: Bergquist (1961a) stated that she could not distinguish between the primary and secondary fibres, which ranged in diameter from 20–200 μm, whereas in *D. tuapokere* **sp. nov.** the secondary fibres are much smaller than the primaries which can be up to 500 μm thick. Bergquist (1961a) also noted that the fibres of *D. cristagalli* are exclusively packed with broken sponge spicules.

Several specimens have been attributed to *D. cristagalli* with hesitation, including one by Kelly in McNamara *et al.* (2005). That sponge (NIWA 101432) was described as forming a "spherical mass of meandering ridges and interconnected short blunt branches", with oscules situated on the ends of branches and along the tops of ridges (Fig. 5). While this arrangement is superficially similar to the "tubula-flabellate" condition of Bergquist's *D. cristagalli*, the oscules in NIWA 101432 do not lead to deep cloacae (Fig. 5). Although the colour of NIWA 101432 was cited as "greyish white", the *in-situ* image was taken in natural lighting and is misleading with red light absorption at depth. The skeleton of NIWA 101432 is comprised of a loose reticulation of large sand-grains cemented into fibres with spongin clearly visible, connected to each other by numerous fibres containing predominantly spicule debris, features not noted by Bergquist (1961a). With the benefit of hindsight, the sponge NIWA 101432 is almost certainly not *Dysidea cristagalli*, most likely representing a new species. *Dysidea tuapokere* **sp. nov.** is distinct from NIWA 101432 in the sandy surface texture of the latter (implying a dermal membrane charged with detritus), and in the extremely regular disposition of the surface conules, compared to that in *D. tuapokere* **sp. nov.** (compare Fig. 2A, B).
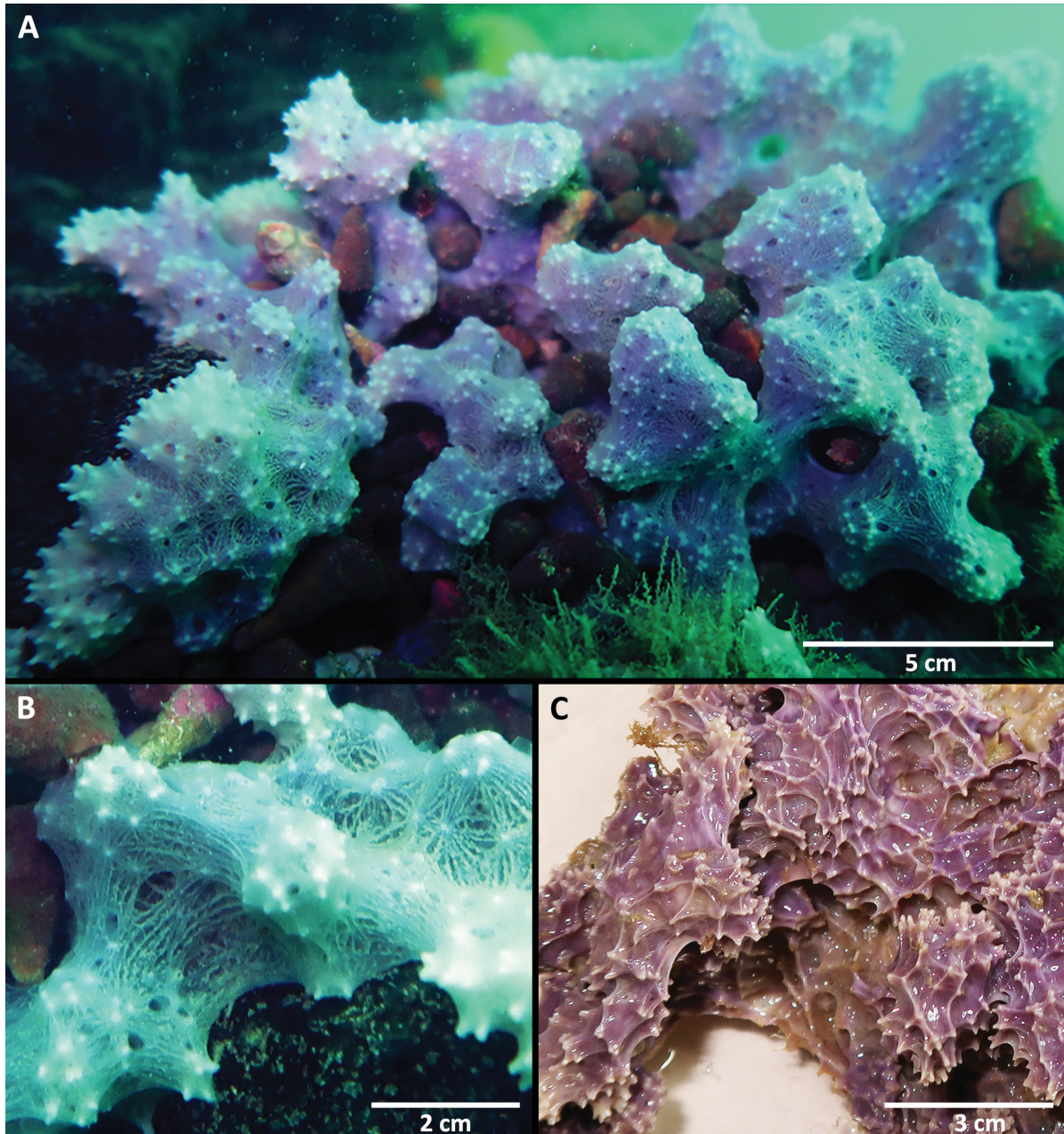
FIGURE 2. *Dysidea tuapokere* **sp. nov.**, holotype NIWA 92974: **A.** Before collection, showing the irregular, bulbous, digitate morphology, and irregularly dispersed conules; **B.** Close-up, showing the irregularly spaced conules that appear opaque, due to the presence of abundant sand, and between which stretch collagenous fibrils giving the surface a tent-like appearance; **C.** *Ex-situ* photograph showing the shrunken, cavernous appearance upon collection, and the lilac colouration.
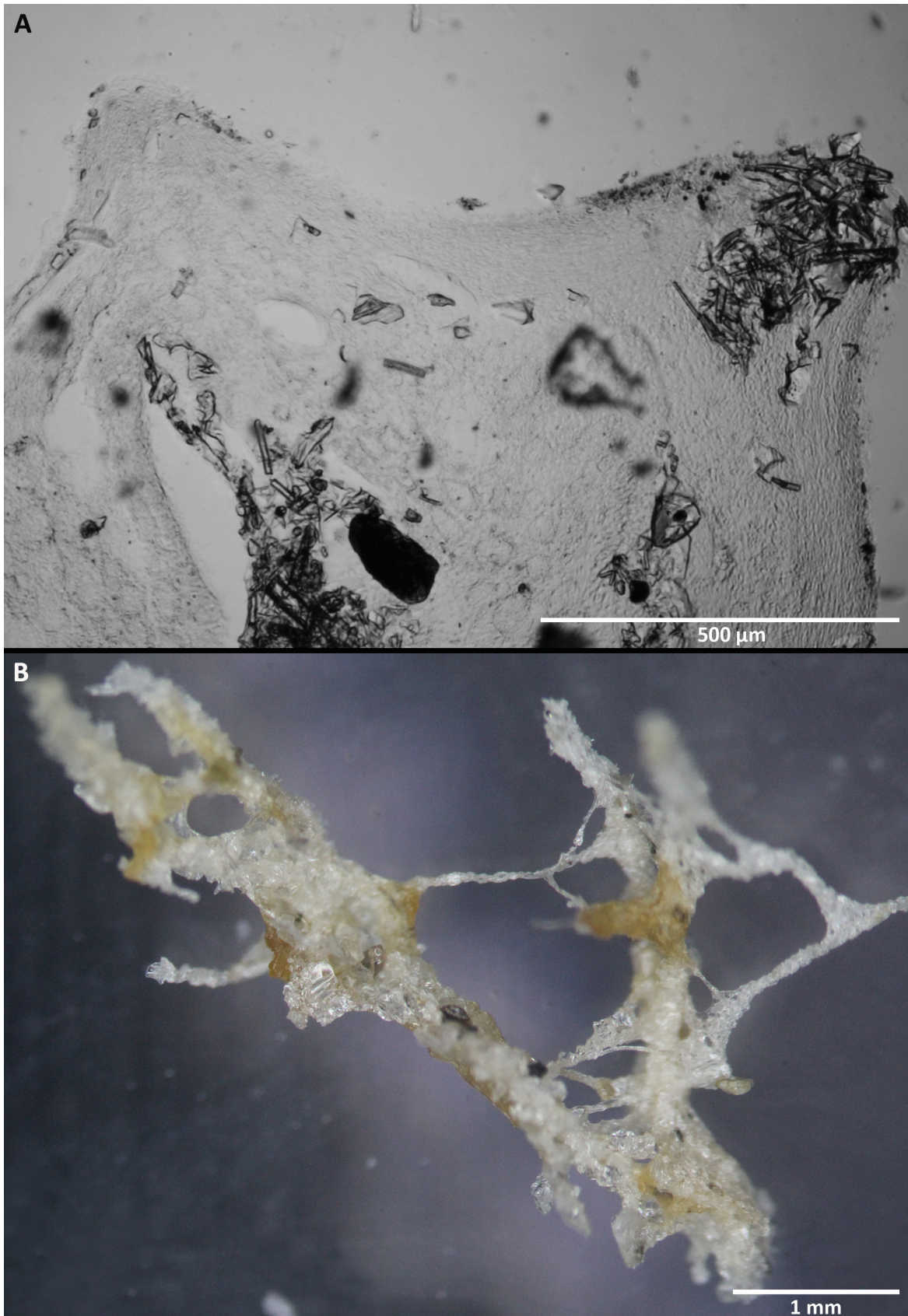
FIGURE 3. *Dysidea tuapokere* **sp. nov.**, holotype NIWA 92974: **A.** Histological section showing a heavily cored primary fibre extending beneath a surface conule, and eurypylous choanocyte chambers in the surrounding mesohyl which is relatively clear of detritus, and unarmoured surface; **B.** Macerated, heavily cored, highly irregular, divaricating primary fibre, connected by slender, cored secondary fibres with fine auxiliary struts attaching the secondary fibre to the primary fibre.
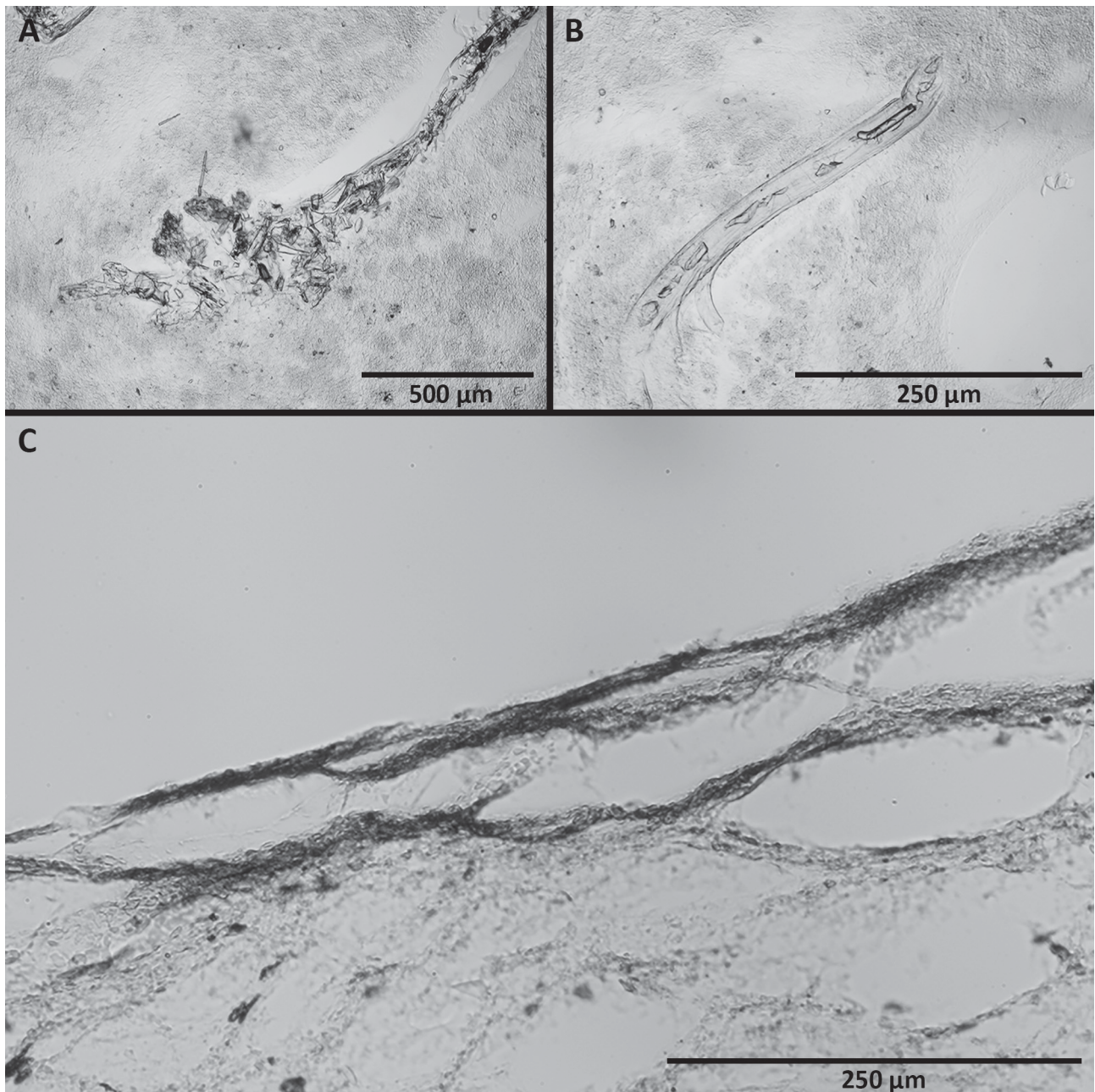
FIGURE 4. *Dysidea tuapokere* **sp. nov.**, holotype NIWA 92974: **A.** Laminated spongin less visible in more heavily cored primary fibres; **B.** Laminated golden spongin visible in lightly cored secondary fibres; **C.** Ectosomal membrane containing fibrillar collagen in the surface. Note only traces of detritus in mesohyl.

Dysidea spiculivora (Dendy, 1924) was described as "irregularly massive, sub-digitate, 54 mm long, 20 mm diameter, probably repent," with a "coarsely sub-conulose surface with conuli low and far apart". The interior was cavernous and no oscules were seen. The colour in life was described as "white, with a curiously translucent appearance". Dendy described the skeleton as an irregular jumble of spicules and a dermal skeleton was not noted by Dendy (Table 1). Two specimens closely comparable to this, NIWA 52374 and NIWA 52390, have been collected since this first description: the defining characteristics are the translucent white colouration in life, the cavernous interior and broadly sub-conulose surface.

Dysidea sp. 'a' Brøndsted, 1924, from the Auckland Islands (Table 1), is closely comparable to *D. tuapokere* **sp. nov.** in morphology, composed of "densely anastomosing, evenly thick branches" about 40–50 mm long, with a regular, abundantly conulose surface and small oscules, a "thin, pellucid dermal membrane", a soft consistency and the colour of flesh. However, no skeletal description was attempted as Brøndsted admitted to unfamiliarity with

the genus; a direct comparison is not possible in this work. The likelihood of conspecificity of *D. tuapokere* **sp. nov.** with this ill-defined, almost unrecognisable Auckland Island specimen, is low: there are only a few precedents of well-characterised, deep subtidal species, existing off both the North Island and Subantarctic New Zealand (see Sim-Smith & Kelly 2019).

Key diagnostic characters:
- mass of interconnected lobate digits
- surface with irregularly disposed conules clustered on lobes, unarmoured
- texture soft, elastic
- oscules flush, membranous
- colour in life, translucent lilac
- skeleton irregular, sparse, with dominating fingers and lobes
- primary fibres divaricate in the subsurface region; 308 (200–500) μm thick
- secondary fibres with clear spongin around core; 69 (50–100) μm thick
- auxiliary secondary fibres that attach secondaries to primaries; 10–15 μm thick
- overall mesh shape highly irregular, 0.5–3 mm wide
- eurypylous choanocyte chambers, 30–50 μm diameter
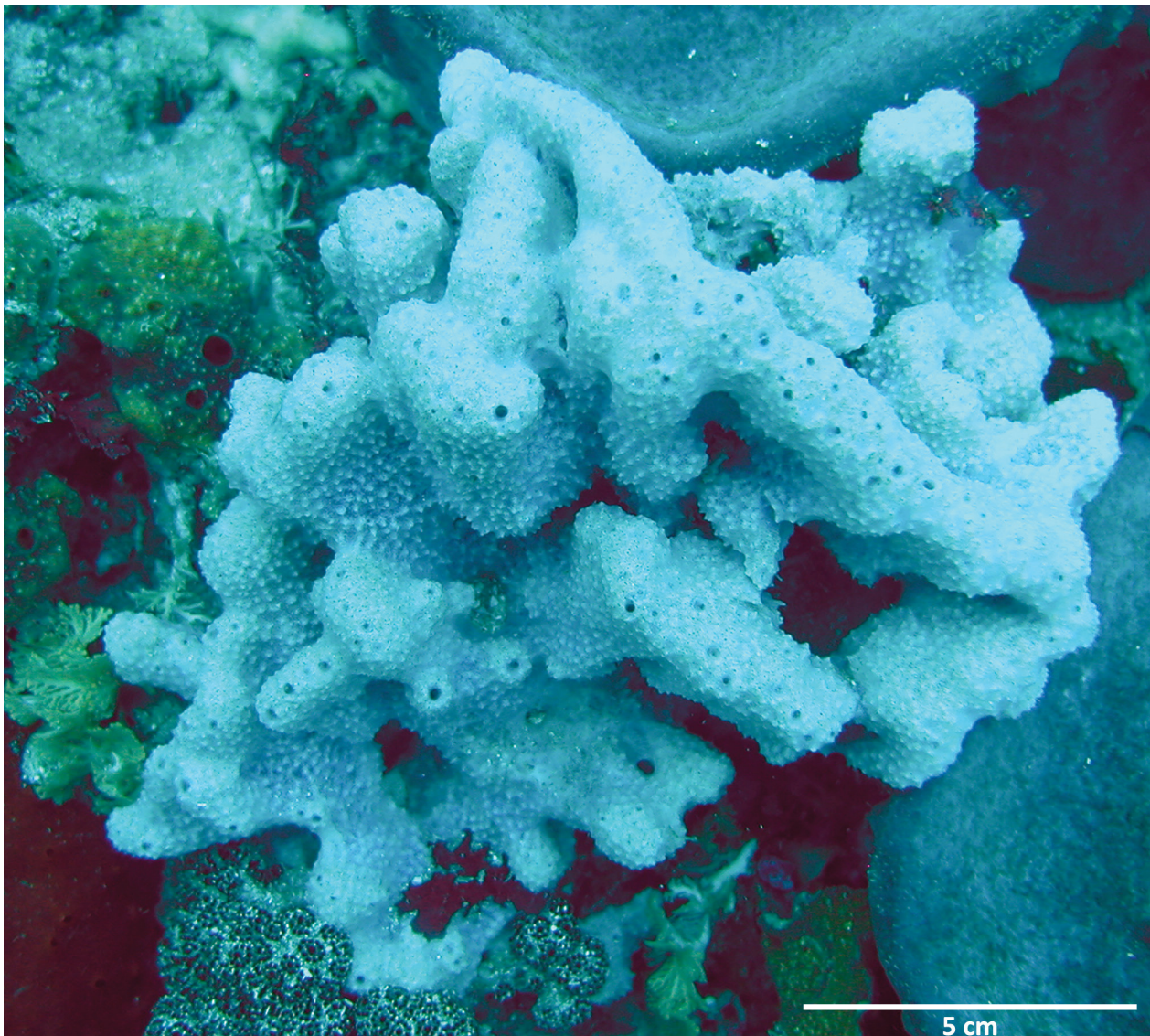
FIGURE 5. A. *Dysidea* cf. *cristagalli* (NIWA 101432, MNP7240, UKNHM 2004.10.5.1) collected from a reef flat at 33 m, in Spirits Bay, North Cape, in 2002.

Dysidea teawanui sp. nov.
Figs 1, 6–8
urn:lsid:zoobank.org:act:6476B247-9085-46A4-B7DE-7D8F97BEFBCA

Material examined. *Tauranga Harbour, Bay of Plenty*: **Holotype**—NIWA 113650, 37.681° S, 176.171° E, 8 m, 27 Nov 2018. **Paratypes**—*Pilot Bay, Tauranga Harbour, Bay of Plenty*: NIWA 113651–113655, 37.681° S, 176.171° E, 12 m, 09 Dec 2018, SCUBA dive.

Distribution. Tauranga Harbour, Bay of Plenty, New Zealand, 8–12 m.

Description. Massive, spherical to hemispherical, multilobed cushions, frequently conjoined, forming broad matts covering up to 2.5 m² (Fig. 6A–E), typically 10–50 cm long, 6–50 cm wide, 7.5–10 cm high; immature specimens spherical with low surface mounds (Fig. 6C), often 3–4 cm long, 1.5–3 cm wide, 1.5–2.5 cm high. Larger specimens frequently only alive in the top 4–5 cm of the sponge; when torn, the base is usually dead with only the ladder-like primary fibres visible (Fig. 7A). Surface with regularly spaced conules, 1–3 mm in height (Fig. 6C–E), granular to the touch. Cobwebs of fibrillar collagen in the surface membrane are clearly visible, stretching between the tips of primary fibres, joining adjacent conules (Fig. 6E). Oscules are relatively large, up to 5 mm diameter, scattered over the surface, with raised translucent collars (Fig. 6C, E). Texture in life, soft, slightly elastic, compressible. In life, the sponge is covered in sediment, appearing as rock substrate. Colour in life beneath surface sediment, powder blue-grey externally (Fig. 6C–E; 7A), cream to tan, sometimes orange-tinged in the non-illuminated base, cream in ethanol. Dermal membrane translucent.

Skeleton. Large, thick, primary fibres, 483 (300–800) μm diameter, relatively uniform in their thickness, dominate the skeleton (Fig. 7A), forming an irregular, laddered reticulation (Fig. 7B) with thin secondary fibres 113 (80–160) μm diameter, flanged where they join the primary fibres (Fig. 8A, B). Thin, clear, auxiliary secondary fibres are visible in places; about 15 μm thick (Fig. 7B). All secondary fibres are solidly cored, spongin along the edges of the fibres is not visible. The secondary fibres directly link the primary fibres or may form a reticulation between the primary fibres (Fig. 8A, B). Primary fibres diverge from the base of the sponge (Fig. 7A), forming meshes about 814–2567 μm long and 800–1500 μm wide. All fibres heavily cored with sand and foreign spicule fragments.

Ectosome cavernous, mesohyl shrinking between the fibres in the preserved specimen (Fig. 7A). Canals filled with detritus and sediment, possibly resultant from worm activity in the aquiferous canals. Ectosome about 108 (105–140) μm deep, reinforced by a thin layer of fibrillar collagen (Fig. 8C), strands of which stretch between the apex of the primary fibres (Fig. 6E). A translucent dermal membrane is raised by large primary fibres, rarely with any inclusions of detritus; unarmoured (Fig. 8C). Choanocyte chambers are obscured by the abundant detritus in the mesohyl.

Substrate, depth range and ecology. Found on sheltered rocky reef substrate, covering rocks and boulders to a depth of 10 cm, and on wharf pilings, 5–8 m deep. The clown nudibranch, *Ceratosoma amoenum* (Cheeseman, 1886) predates on this species, and fan worms are often integrated into the matrix of the sponge.

Etymology. Named for Tauranga Moana, Te Awanui, a spiritual symbol of identity for all whanau, hapu and iwi living in the harbour catchment area (*Te Awanui*, Tauranga Moana; te reo Māori). This species name was accepted and approved by local Tauranga Moana iwi, Ngāti Ranginui, Ngāi Te Rangi and Ngāti Pūkenga.

Remarks. *Dysidea teawanui* **sp. nov.** has a highly characteristic morphology and colouration that separates it clearly, in the field, from *D. tuapokere* **sp. nov.** in the same location; *D. teawanui* **sp. nov.** forms massive, pale blue-grey, multi-lobed cushions or spheres while *D. tuapokere* **sp. nov**. forms a cavernous lilac mass of lobed branches. Only two species noted from New Zealand waters, *Dysidea* sp. 'b' of Brøndsted (1924) and *D. elegans* (Nardo, 1847) *sensu* Brøndsted (1927) (Table 1), vaguely resemble the characteristic cushion-shape of *D. teawanui* **sp. nov.**

Dysidea sp. 'b' Brøndsted, 1924, from a "sandy mud" seabed, at 46 m in Carnley Harbour on the Auckland Islands (see Brøndsted 1924: 165), provides a reasonable description of a sponge attached to shell, with a variable shape, but generally "oblong, lump-shaped". The "greatest extent" was about 50 mm, the colour in life was "pale grey to greyish yellow" and the surface was conulose, conules being 1 mm high and 4 mm apart. The primary fibres formed an irregular network, generally running perpendicular to the surface and were about 160 μm thick. The thinner spongin fibres were "almost devoid of foreign particles", and the primary fibres cored with sand grains and broken spicules. While the general form and colour in life are reminiscent of *D. teawanui* **sp. nov.**, the fibres are much thinner than in the latter. Furthermore, as for *D. tuapokere* **sp. nov.**, the possibility of conspecificity of *D. teawanui*

sp. nov. with a Subantarctic New Zealand sponge, is low. Finally, with relatively clear secondary fibres, the sponge may be more closely comparable to several Chatham Rise species described by Bergquist (1961b) as *Leiosella levis* (Lendenfeld, 1886), *Polyfibrospongia australis* (Lendenfeld, 1888) [now considered to be *Fasciospongia turgida* (Lamarck, 1814) (Van Soest *et al*. 2018a)], or *Euryspongia arenaria* Bergquist, 1961b.
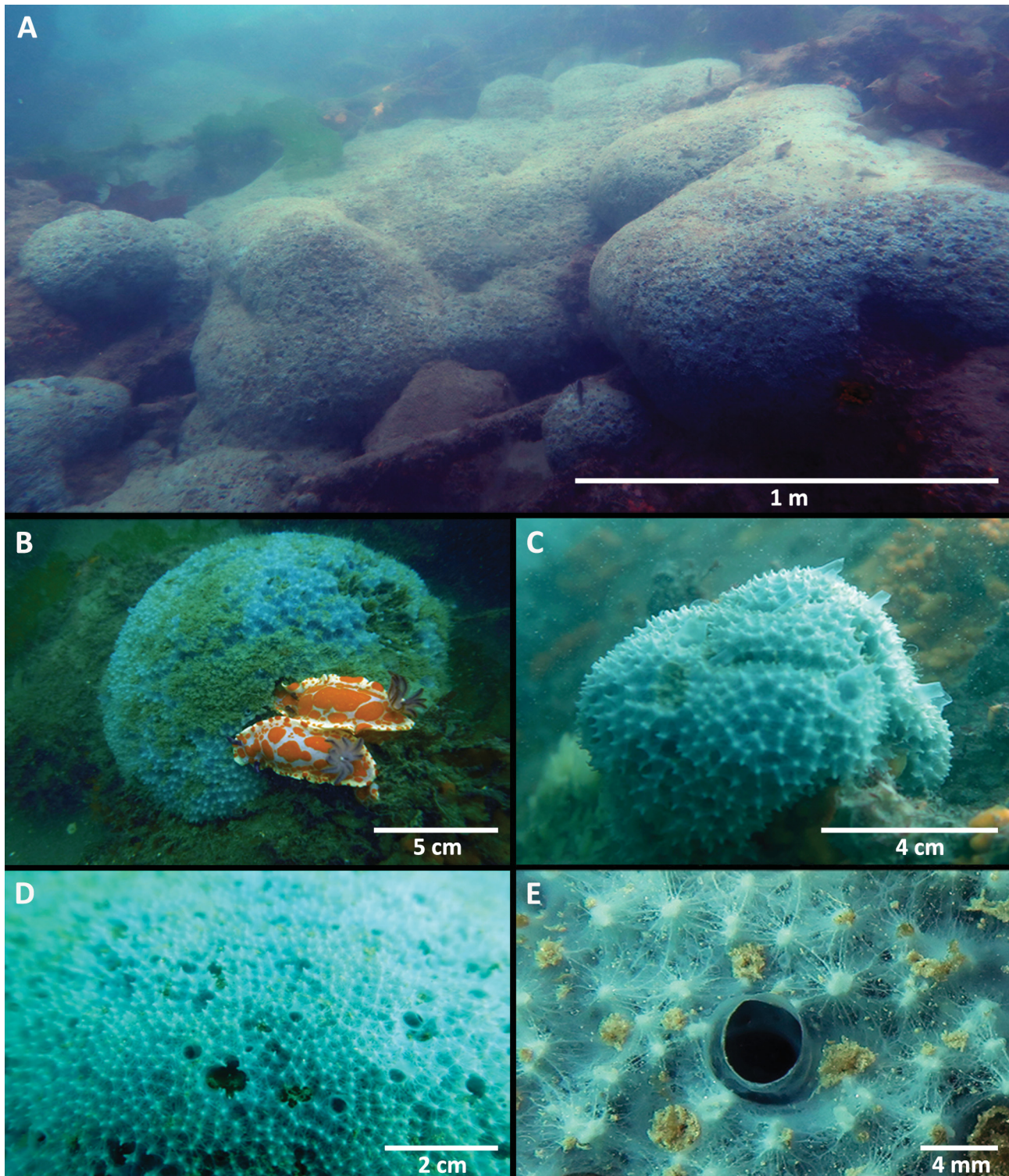
FIGURE 6. *Dysidea teawanui* **sp. nov.**: **A.** Massive, hemispherical, to multilobed specimens covering rocks and boulders at Dive Crescent, Tauranga Harbour at a depth of 5 m; **B.** Spherical specimen with predatory sea slugs *Ceratosoma amoenum*; **C.** Holotype NIWA 113650, showing the almost spherical morphology of smaller specimens, the regular conulose surface with raised, membranous oscules visible in profile on the surface; **D.** Surface of a massive specimen showing large apical oscules with raised membranous collars; **E.** Apical oscule showing regular distribution of conules and collagen fibrils stretching between conules.
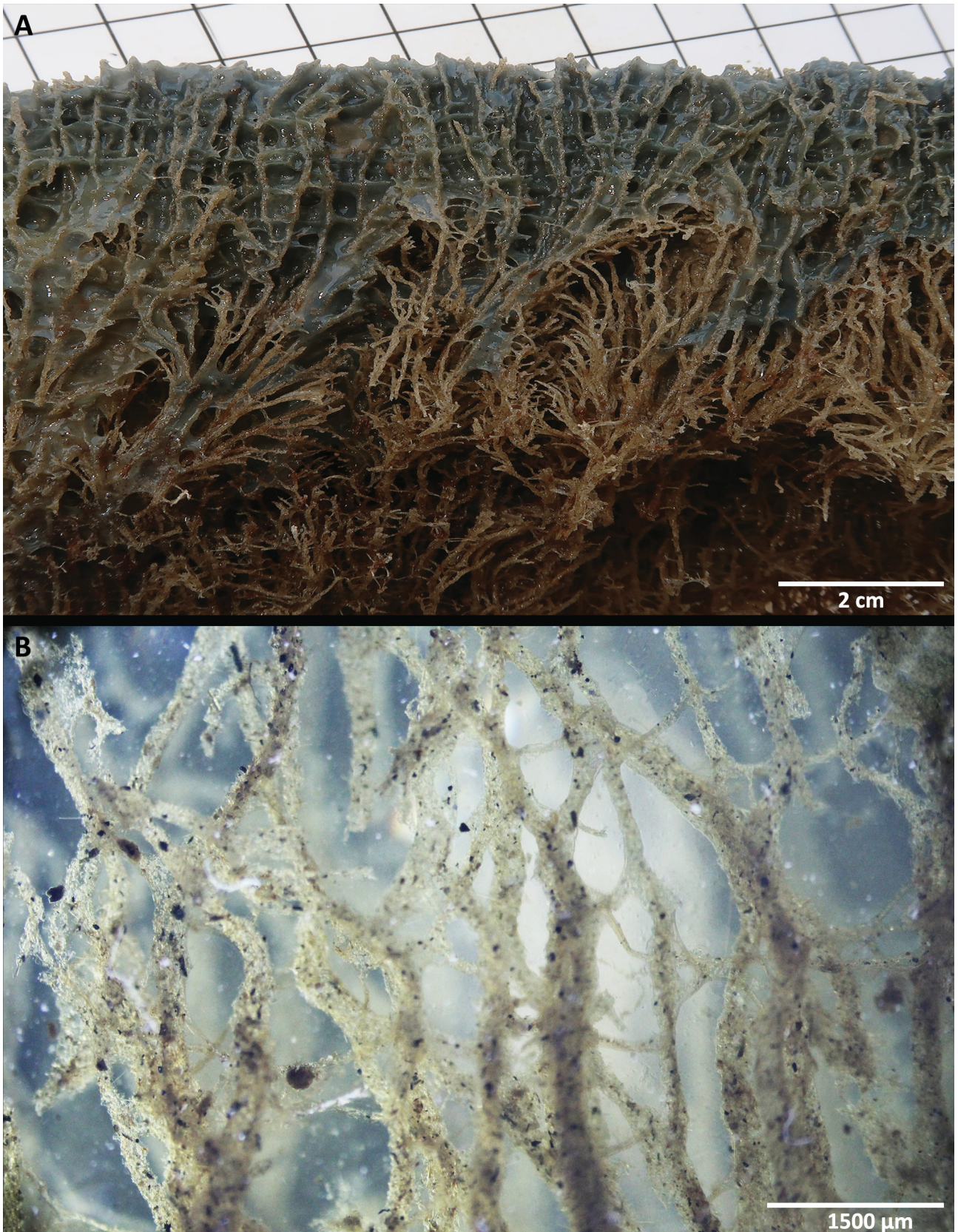
FIGURE 7. *Dysidea teawanui* **sp. nov.**, holotype NIWA 113650: **A.** Dense, ladder-like architecture of the primary and secondary fibres, showing the powder bluey-grey colouration of the freshly collected sponge; **B.** Macerated fibrous skeleton, showing densely aligned and anastomosing primary fibres, connected by slender, cored secondary fibres.

Dysidea laxa (Lendenfeld, 1889: 671), from 30–40 m in Port Philip Bay, Australia, is the only other Southwest Pacific species of *Dysidea* that has a massive, lobose morphology with a light bluish-violet colour in life. However, unlike for *D. teawanui* **sp. nov.**, the surface is tuberculate, sand-armoured and the oscules are arranged in a longitudinal series along the sides of the lobes. The fibres of *D. laxa* are quite large (200–500 mm thick) but they form a highly irregular, angular network in which the primary fibres are not clearly pronounced, differentiating it further from *D. teawanui* **sp. nov.**, which has a highly regular ladder-like architecture. While all fibres in *D. laxa* are charged with small, abundant sand grains, these are more irregularly scattered in the slender fibres (after Lendenfeld 1889).
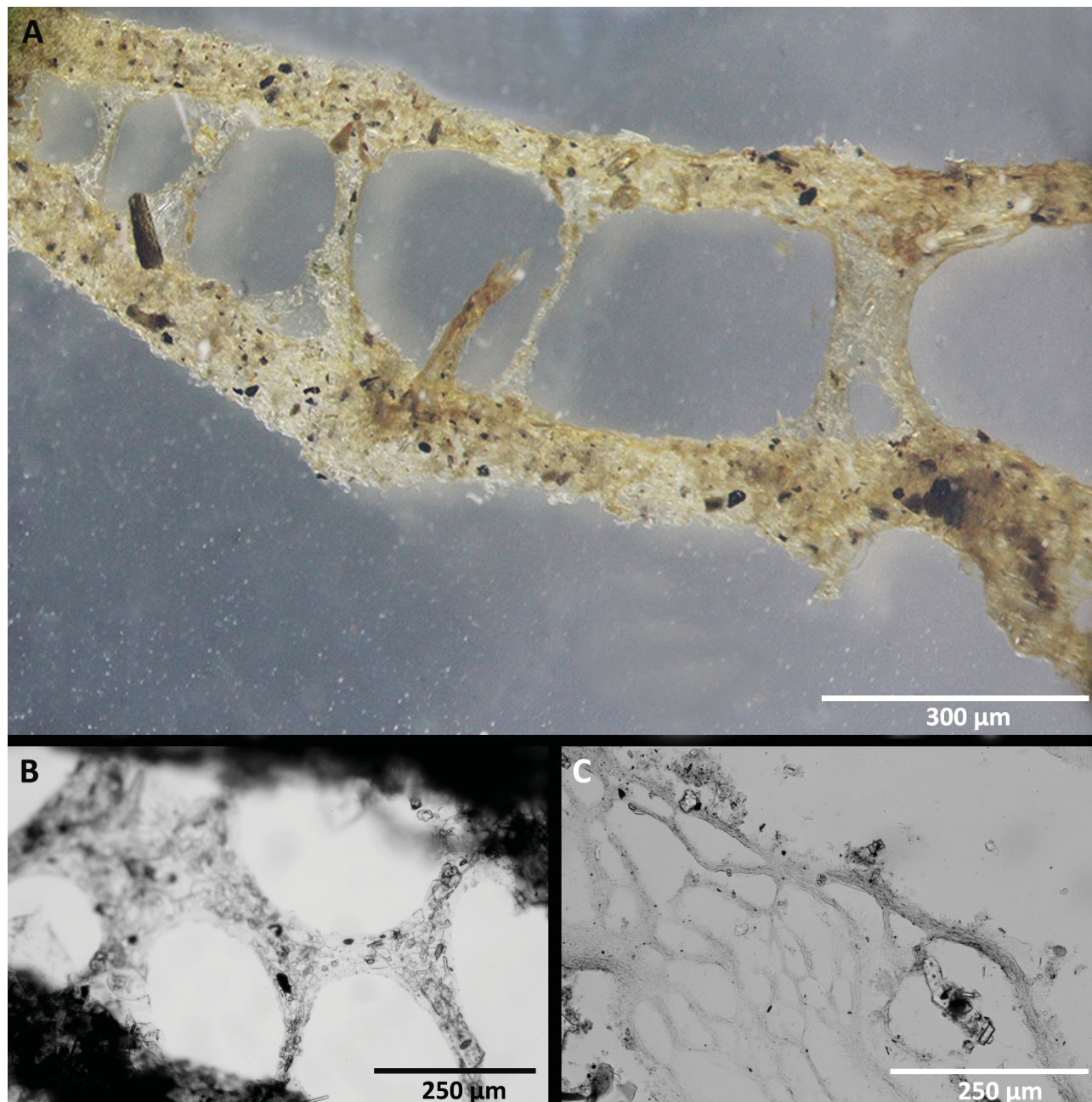
FIGURE 8. *Dysidea teawanui* **sp. nov.**, holotype NIWA 113650: **A.** Two primary fibres joined by slender, fully cored, flanged, secondary fibres; **B.** Branching secondary fibres between two primary fibres; **C.** Ectosomal membrane containing fibrillar collagen in the surface. Note only traces of detritus in mesohyl.

Key diagnostic characters:
- massive cushion up to 2.5 m^2 diameter
- surface with regularly spaced conules, unarmoured

- texture firm
- oscules with raised membranous collars
- colour in life, powder blue-grey
- skeleton a regular, laddered reticulation
- primary fibres uniform, diverging from the base; 483 (300–800) µm diameter
- secondary fibres thin, flanged against primary fibres, forming a reticulation in places; 113 (80–160) µm diameter
- overall mesh shape rectangular, about 814–2567 µm long and 800–1500 µm wide

Additional remarks on New Zealand EEZ *Dysidea*

Of the seven species of *Dysidea* now considered valid for the New Zealand EEZ (Table 1) (*D. cristagalli*, *D. hirciniformis*, *D. navicularis*, *D. ramsayi*, *D. spiculivora*, *D. tuapokere* **sp. nov.**, and *D. teawanui* **sp. nov.**), three have not yet been considered thus far (*Dysidea hirciniformis*, *D. navicularis* and *D. ramsayi*), as they are sufficiently different from either of the new species to be discounted as conspecific. *Dysidea fragilis* (Montagu, 1818) *sensu* Bergquist (1961b), from Mernoo Bank on Chatham Rise, is now considered to be invalid, and *D. elegans* (Nardo, 1847) *sensu* Brøndsted (1927), from the Coromandel Peninsula is unrecognisable.

Dysidea hirciniformis (Carter, 1885a) *sensu* Dendy (1924)
Dendy (1924) considered his highly characteristic, thin, ramose, deep subtidal North Cape specimens, to be similar to *Dysidea hirciniformis*, from Port Phillip Heads, South Australia. Lendenfeld (1889) described them as forming a bunch of cylindrical, digitate, upright branches, about 15 mm thick, 150 mm long, with a conulose surface, conules being 2.5 mm high and the same distance apart, with rare oscules, 3–4 mm diameter. The colour in life was pale buff with purple tips and the fibres were packed with sand-grains, the primary fibres 180 µm thick, secondary fibres 80–150 µm thick, forming a mesh about 80 µm wide (Lendenfeld 1889: 665).

Without histological examination of the original specimens and comparison with Dendy's material, it is impossible to say with certainty whether the name *hirciniformis* is valid for the North Cape specimens: Dendy (1924: 384) indicated that there were differences. Despite the disjunct distribution, the likelihood of conspecificity of North Cape specimens with a South Australian species is moderate, as there are several clear precedents including *Polymastia* cf. *massalis* Carter, 1886 (in Kelly-Borges & Bergquist 1997), *Tethya bergquistae* Hooper in Hooper & Wiedenmayer, 1994 (in Bergquist & Kelly-Borges 1991), and *Chondropsis kirkii* (Bowerbank, 1841), *Crella incrustans* (Carter, 1885b), *Callyspongia ramosa* (Gray, 1843), *Callyspongia* cf. *annulata* (Ridley & Dendy, 1886), and *Dactylia varia* (Gray, 1843) (in Kelly & Herr 2018).

Dysidea navicularis (Lendenfeld, 1888)
Dysidea navicularis is one of only three species described *de novo* from New Zealand waters, and the second species described from a harbour environment (Lyttleton Harbour). Lendenfeld established this species as the type of his new genus *Haastia* Lendenfeld, 1888, named for Lendenfeld's late friend and famous New Zealand explorer, Sir Julius von Haast. This species also forms bunches of long, thin, cylindrical branches, about 15 mm thick, growing from an incrusting basal mass, height 150 mm. The surface has uniform conules, 1 mm high, 1.5–2 mm apart, and oscules are confined to summit of digitate processes. The sponge was described as pinkish-grey in life. Bergquist (1980: 482) considered *Haastia navicularis* to be, in every way, typical of the genus *Dysidea*. She retained the species name as separate because of the geographical separation of the type material in Lyttleton.

Dysidea ramsayi (Lendenfeld, 1888)
Lendenfeld (1888) described *Dysidea ramsayi* from the Chatham Islands as a hard, irregular, meandrically-folded lamellar sponge, diameter 140 mm, with 2 mm diameter oscules situated on one face of the lamella. The primary fibres were very knotty and charged with sand-grains, about 250 µm diameter; connecting fibres contain scattered foreign bodies, 100 µm thick (after Lendenfeld 1888). As there are no illustrations of this species in Lendenfeld (1888) and the species is not treated in detail in Lendenfeld (1889), histological examination of the material is required to determine the integrity of this species. In the meantime, the species is considered recognisable, and thus valid, on the basis of the unique morphology and texture.

'*Dysidea* sp. nov.' of Battershill *et al.* (2010)

Dysidea sp. nov. [=*Dysidea* sp. 'A' Cook & Bergquist in Kelly *et al.* (2009: 45), from the Hauraki Gulf and offshore islands, can be compared to *Dysidea cristagalli* in terms of morphology with a lobo-digitate form and regular surface, but the colouration seems to be distinct, being pastel pink, yellow or blue (Battershill *et al.*, 2010). No material is available for study.

Dysidea fragilis (Montagu, 1818) *sensu* Bergquist (1961b)

Bergquist (1961b) applied the name *fragilis* to poorly described material from Mernoo Bank on the Chatham Rise: the sponge was irregular, about 5 cm long and 3 cm wide, with cylindrical projections arising from a basal mass. The fibres were relatively thick, being 150–340 μm wide with secondary fibres 35–48 μm thick, and the colour, presumably in life, brownish grey (after Bergquist 1961b). Application of the species name *fragilis* to New Zealand material, is doubtful (Battershill *et al.* 2010), as the species is restricted to the Northeastern Atlantic and Mediterranean regions (Van Soest *et al.* 2018b).

In more recent times, the name *fragilis* has been applied widely to *Dysidea* specimens from various environments around New Zealand, in biodiversity inventories (Gordon & Ballantine 1976; Pritchard *et al.* 1984), or marine natural products investigations (Evans & Bergquist 1977; Perry *et al.* 1987), yet none of these publications provide descriptions suitable for evaluation. Examination and redescription of the original Bergquist (1961b) and subsequent specimens is beyond the scope of this contribution and probably impossible due to loss of voucher specimens. We concur with Battershill *et al.* (2010) that use of the name *Dysidea fragilis* in New Zealand waters is invalid.

Dysidea elegans (Nardo, 1847) *sensu* Brøndsted (1927)

Brøndsted (1927: 296) briefly and hesitantly compared a "lump-shaped" sponge from Slipper Island, off Pauanui on the Coromandel Peninsula, with the type of *D. elegans*, a Mediterranean species now recognised as *D. tupha* (Pallas, 1766) (Van Soest *et al.* 2018c). While the external appearance did not conform to the type, Brøndsted considered that the height of the conules and their separation on the surface, and the fibre dimensions and their mode of anastomosing, did conform. No dimensions or illustrations of the New Zealand specimen were given, however. Brøndsted (1927) also cited Lendenfeld's (1889: 655) record of *D. elegans* from Broken Bay, New South Wales, but this is a palmate species, now recognised as a species of *Hyrtios* Duchassaing & Michelotti, 1864 (Van Soest *et al.* 2018d). *Dysidea elegans* (Nardo, 1847) *sensu* Brøndsted (1927) is unrecognisable.

Discussion

This study emphasises key morphological characters for the differentiation of *Dysidea* species in New Zealand waters: gross morphology, *in-situ* colouration, skeletal architecture, and degree of coring of the fibres. The taxonomic difficulty in characterising 'heterogeneous' species within *Dysidea* has been noted in the literature (Cook and Bergquist 2002 and references therein), and historical literature often lacks adequate photographs and little information on the colour in life. Histologically, *Dysidea* species are relatively simple, but can be differentiated on the form of the skeleton (of pithed and laminated primary fibres) and the degree to which the fibres are cored (with sand and spicule debris). The differences are, however, often small, and because the architecture of the skeleton is irregular, the skeleton is difficult to describe systematically.

We have found that *Dysidea* species can be quite clearly differentiated if freshly collected material and histological sections are available. Both new species described here have markedly different, highly distinctive gross morphologies and *in-situ* colouration: *D. tuapokere* **sp. nov.** forms a translucent, lilac, mass of interconnected lobate digits, while *D. teawanui* **sp. nov.** forms a powder blue-grey, massive cushion, up to 2.5 m² diameter. Both also have markedly different skeletal characters: *D. tuapokere* **sp. nov.** has an irregular, sparse skeleton and *D. teawanui* **sp. nov.** has a more regular, laddered skeletal reticulation.

A total of seven species of *Dysidea* are presently considered valid species from the New Zealand EEZ: *D. cristagalli*; *D.* cf. *hirciniformis sensu* Dendy, *D. navicularis*, *D. ramsayi*, *D. spiculivora*, *D. tuapokere* **sp. nov.**, and *D. teawanui* **sp. nov.** (Table 1). *Dysidea fragilis sensu* Bergquist (1961b), is now considered to be invalid, *D. elegans sensu* Brøndsted (1927) is unrecognisable, and *D.* **sp. nov.** *sensu* Battershill *et al.* (2010) requires a collection of sponge material in order to identify this species. Numerous additional specimens of *Dysidea* are available in the NIC

collections and Marine Invasives Taxonomy (MITS) collection, at NIWA, Wellington, but none have *in-situ* images, or images of freshly collected sponges. These specimens require careful histological, skeletal and morphological examination, but such work is beyond the scope of this project.

Acknowledgements

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Appendix 3

The biogeography of Taranaki sponges

Table A3.1 Geographic distribution of sponges recorded from stations in the Taranaki and Wellington Regions.

Species	Pariokariwa	Waitara	Waiwhakaiho	Hangatahua	Patea	Kapiti
Aaptos	√					√
Aaptos globosa		√			√	
Aaptos rosacea					√	
Aaptos sp.						√
Ancorina bellae						√
Ancorina sp.						√
Aplysilla rosea	√					√
Aplysilla sulfurea	√					√
Astrophorina					√	√
Axinella n. sp.						
Axinellida sp. (or spp.)	√					√
Biemna sp.	√					√
Cacospongia sp.	√					√
Callyspongia (Callyspongia) nuda	√					√
Callyspongia (Cladochalina) diffusa						√
Callyspongia cf. *ramosa*					√	
Callyspongia cf. *stellata*					√	
Callyspongia fistulosa				√		
Callyspongia sp.						√
Chelonaplysilla violacea	√					√
Chondropsis kirkii	√					√
Chondropsis sp.						√
Chondropsis sp. 1		√				
Chondropsis sp. 2		√				
Chondropsis wilsoni	√					√
Cinacyra sp.	√					√
Ciocalypta cf. *polymastia*	√					
Ciocalypta polymastia				√	√	
Ciocalypta sp. (cf *C. polymastia*)						√
Clathria (Microciona) sp.	√					√
Clathria (Microciona) sp.2 (pink)						√
Clathria (Microciona) sp.3 (orange)						√
Clathria (Microciona) sp.4 (red thinly encrusting)						√
Clathria coriacea	√					
Clathria sp.						√
Clathrina coriacea						√
Cliona celata	√					√
Crella incrustans	√	√			√	√
Cymbastela lamellata						√
Cymbastela tricalcyformis					√	
Dactylia varia					√	
Darwinella oxeata		√			√	
Demospongiae sp. 1		√				

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Species	Pariokariwa	Waitara	Waiwhakaiho	Hangatahua	Patea	Kapiti
Demospongiae sp. 2		√				
Desmacella dendyii	√		√			√
Desmacidon mamillatum					√	
Dictyoceratida sp. 1		√				
Dictyoceratida sp. 2		√				
Dictyoceratida sp. 3		√				
Dragmacidon australe						√
Dysidea sp. 1	√					√
Dysidea sp. 2						√
Dysidea sp.2 (light grey to light purple)						√
Ecionemia alata	√	√	√	√	√	√
Geodia regina	√					√
Geodia sp.			√			
Halichondria cf. moorei					√	
Halichondria sp. (or spp.)	√					√
Haliclona (Gellus) sp.		√				
Haliclona (Haliclona) sp. (or spp.)	√				√	√
Haliclona (Haliclona) sp.2 (yellow)						√
Haliclona (Reniera) sp.	√					√
Haliclona (Rhizoniera) brondstedi						√
<u>*Haliclona (Rhizoniera) rosea*</u>		√				
Haliclona sp.3 (purple)						√
Haliclona spp.	√					
Haliclona venustina						√
Haplosclerida sp. 1				√		
Haplosclerida sp. 2				√		
Haplosclerida sp. 3		√				
Heteroscleromorpha sp.			√			
Homaxinella sp.	√					
Hymedesmia (Stylopus) sp.1 (red)						√
Hymedesmia (Stylopus) sp.2 (orange)						√
Hymedesmia (Stylopus) sp.3 (yellow)						√
Hymedesmia sp.						√
Hymedesmia sp.2 (orange)						√
Hymedesmia sp.2 (pink)						√
Hymedesmia sp.3 (orange)						√
Hymedesmia sp.3 (pink)						√
Hymenacidon sp.1						√
Hymeniacidon perlevis				√		
Hymeniacidon sp. (or spp.)	√					√
Hymeniacidon sp. 1				√		
Hymeniacidon sp. 2		√				
Hymeniacidon sphaerodigitata			√			
Hymeniacidonidae		√				
Hyrtios sp.						√
Iophon minor	√		√		√	
Iophon proximum					√	
Ircinia sp.	√					√
Ircinia sp. 1			√			
Ircinia sp. 2			√			
Ircinia sp.2 (grey or white)						√
Latrunculia sp.	√					√
Leucosolenia sp.	√					

Species	Pariokariwa	Waitara	Waiwhakaiho	Hangatahua	Patea	Kapiti
Mycale (Carmia) hentscheli	√					
Mycale (Carmia) sp.						√
Mycale sp. (or spp.)	√					√
Myxilla (Styloptilon) fromontae		√				
Myxillidae		√				
Pararhaphoxya sinclairi		√	√	√		
Pararhaphoxya sp.	√					√
Penares tylaster	√					
Phorbas sp.	√	√				√
Poecilosclerid – unidentified	√					√
Poecilosclerid - unidentified (purple)						√
Poecilosclerida		√				
Polyfibrospongia sp.						√
Polymastia cf. *massalis*					√	
Polymastia crassa	√					
Polymastia crocea						√
Polymastia echinus						√
Polymastia fusca	√					√
Polymastia granulosa	√					√
Polymastia massillis			√			
Polymastia pepo		√				
Polymastia sp.	√		√			√
Psammocinia papillata				√		
Psammocinia sp.	√					√
Psammoclema sp. or *Chrondropisis* sp.					√	
Raspailia (Clathriodendron) arbuscula	√					√
Raspailia (Raspaxilla) topsenti	√				√	√
Sponge—encrusting						√
Sponge—encrusting orange (small)		√				
Sponge—encrusting orange sp. 1		√				
Sponge—orange		√				
Sponge—orange finger		√				
Sponge—orange globular		√				
Sponge—orange turret		√				
Sponge—purple		√				
Sponge—purple turret				√		
Sponge—purple turret (thickly encrusting)		√				
Sponge—red		√				
Sponge—red turret		√				
Sponge—rock		√				
Sponge—thickly encrusting orange		√				
Sponge—thin encrusting orange sp. 1		√				
Sponge—thinly encrusting orange		√		√		
Sponge—thinly encrusting orange sp. 1		√				
Sponge—thinly encrusting orange sp. 2		√				
Sponge—thinly encrusting orange with turrets		√				
Sponge—unidentified mix						√
Sponge—unidentified sp.1 (thin yellow)						√
Sponge—white		√				
Sponge—white with turrets		√				
Sponge—yellow		√		√		
Sponge—yellow finger		√				

Species	Pariokariwa	Waitara	Waiwhakaiho	Hangatahua	Patea	Kapiti
Sponge—yellow turret				√		
Spongia sp.	√				√	
Stelletta arenaria				√		
Stelletta columna					√	
Stelletta conulosa	√		√		√	√
Stelletta crater	√	√				√
Stelletta sandalinum	√					√
Strongylacidon conulosum						√
Strongylacidon sp. (blue or grey)						√
Stylissa haurakii		√				
Suberites axinelloides	√					√
Suberites sp.	√	√				
Sycon sp.	√					√
Tedania (Tedania) battershilli	√					√
Tedania (Tedania) connectens	√					√
Tedania (Tedania) sp.	√					√
Tedania sp. (orange encrusting)						√
Tethya aurantium	√					√
Tethya bergquistae		√	√		√	√
Tethya ingalli	√					√
Thorecta sp.	√					√

Table A3.2 Individual taxon names, number of individuals, total volume of all individuals representing the taxon and total area covered by taxa at each station along the Taranaki coastline.

Site name	Individual taxa	Number of individual Taxa	Total volume of combined individual taxa (cm³)	Total area covered by taxa (cm²)
Hangatahua coastal near, depth 17 m	Brown shell (unidentified)	2	NA	NA
	Cooks turban — (*Cookia sulcata*)	1	NA	NA
	Curly bryozoans — (*Cornuticella taurina*)	1	NA	NA
	Kelp — (*Ecklonia radiata*)	3	1500	375
	Sponge — (*Pararhaphoxya sinclairi*)	1	NA	NA
	Sponge — (*Ecionemia alata*)	3	5800	588
	Sponge — Purple turret	2	1212	216
	Sponge — Thinly encrusting orange	28	265	265
	Sponge — Yellow	1	27	9
	Sponge — Yellow turret	2	800	200
	Spotted tiger top-shell (*Meurea selectum*)	14	NA	NA
Waitara coastal distant, 19 m.	Ascidian — Purple (*Botrylloides leachii*)	1	NA	NA
	Hydroid	1	18	9
	Sponge — (*Stylissa haurakii*)	4	1680	270
	Sponge — (*Pararhaphoxya sinclairi*)	6	254	84
	Sponge — Orange finger	1	84	42
	Sponge — Red (*Crella incrustans*)	2	16	8
	Sponge — Thinly encrusting orange	5	78	74
	Spotted tiger top-shell — (*Meurea selectum*)	1	NA	NA

Site name	Individual taxa	Number of individual taxa	Total volume of combined individual taxa (cm³)	Total area covered by taxa (cm²)
Waitara coastal Near, 12 m.	Black nerita — (*Nerita malanotragus*)	1	NA	NA
	Coralline — knobby (*Sporolithon durum*)	1	NA	NA
	Clam, morning star — (*Tawera spissa*)	1	NA	NA
	Hydroid	1	NA	NA
	Nudibranchs — (*Goniobranchus aureomarginatus*)	2	NA	NA
	Oyster borer — (*Haustrum scobina*)	1	NA	NA
	Red turfing algae	1	150	25
	Sponge — (*Aaptos globosa*)	1	1000	100
	Sponge — Orange turret	4	160	40
	Sponge — (*Pararhaphoxya sinclairi*)	1	300	50
	Sponge — (*Polymastia pepo*)	1	480	80
	Sponge — Purple turret (thickly encrusting)	3	264	78
	Sponge — Red turret	2	58	14
	Sponge — Thickly encrusting orange	2	1200	600
	Sponge — encrusting orange sponge sp. 1	8	800	400
	Sponge — Thinly encrusting orange sp. 2	39	2050	1596
	Sponge — White with turrets	1	125	25
	Sponge — Yellow	1	25	25
	Sponge — Yellow finger	1	18	9
	Spotted tiger top-shell — (*Meurea selectum*)	1	NA	NA
	Top shells — (*Diloma aethiops*)	2	NA	NA
	Tube worm sp. 1	2	NA	NA
	Tube worms sp. 2	1	NA	NA
	Variable triple fin — (*Forsterygion varium*)	2	NA	NA

Site name	Individual taxa	Number of individual taxa	Total volume of combined individual taxa (cm³)	Total area covered by taxa (cm²)
Waiwhakaiho coastal distant	Ascidian (small)	1	12	6
	Brachiopods — (*Neothyris lenticularis*) in a clump	6	NA	NA
	Sponge — (*Ecionemia alata*)	1	NA	NA
	Hydroid	1	NA	NA
	Razor clam — (*Siliqua patula*)	1	NA	NA
	Red algae — (*Pterocladia* sp.*)*	1	4000	400
	Scarlet wrasse — (*Pseudolabrus miles*) [female]	1	NA	NA
	Sponge — Thinly encrusting orange sp. 1	3	59	59
	Sponge – Thinly encrusting orange sp. 2	2	8	8
	Sponge — Thinly encrusting orange with turrets	2	90	30
	Spotted tiger top-shell — (*Meurea selectum*)	8	NA	NA
Waiwhakaiho coastal near, 18 m.	Clam, morning star — *Tarawera spissa*	1	NA	NA
	Hydroid	2	NA	NA
	Scarlet wrasse (female) — (*Pseudolabrus miles*)	1	NA	NA
	Snake brittle star — (*Opiopsammus maculata*)	1	NA	NA
	Sponge — (*Ecionemia alata*)	1	4000	400
	Sponge — Encrusting orange (small)	40	1000	1000
	Sponge — Orange	6	900	300
	Sponge — Orange globular	10	270	90
	Sponge — (*Pararhaphoxya sinclairi*)	2	228	42
	Sponge — Purple	1	100	25
	Sponge — Red	1	48	16
	Sponge — Rock	1	120	30
	Sponge — Thin encrusting orange sp. 1	8	200	200

Site name	Individual taxa	Number of individual taxa	Total volume of combined individual taxa (cm³)	Total area covered by taxa (cm²)
Waiwhakaiho coastal near, 18 m.	Sponge — Thinly encrusting orange sp. 2	11	2225	1225
	Sponge — White	4	124	34
	Sponge — Yellow	1	27	9
	Spotted tiger top-shell — (*Meurea selectum*)	8	NA	NA
	Clam, morning star — *Tawera spissa*	1	NA	NA
	Turfing red algae — (*Pterocladia lucida*)	1	600	600
	Unidentified curvy turret shaped gastropod	1	NA	NA
	Variable triple fin — (*Forsterygion varium*)	7	NA	NA

Table A3.3 Taxa presence, and total number of taxa in each taxonomic family at each station: Pariokariwa reefs, Waitara reefs, Waiwhakaiho reefs, Hangatahua reefs, Patea reef, and Kapiti Island reefs.

Class	Sub-class	Order	Sub-order	Family	Pariokariwa	Waitara	Waiwhakaiho	Hangatahua	Patea	Kapiti	
Calcarea	Calcaronea	Leucosolenida	-	Leucosoleniidae	1						**1**
Calcarea	Calcaronea	Leucosolenida	-	Sycettidae	1					1	**2**
Calcarea	Calcinea	Clathrinida	-	Clathrinidae	1					1	**2**
Demospongiae	-	-	-	-		2					**2**
Demospongiae	Heteroscleromorpha	-	-	-			1				**1**
Demospongiae	Heteroscleromorpha	Axinellida	-	-	1					1	**2**
Demospongiae	Heteroscleromorpha	Axinellida	-	Axinellidae	1	1	1	1	1	3	**8**
Demospongiae	Heteroscleromorpha	Axinellida	-	Raspailiidae	2				1	2	**5**
Demospongiae	Heteroscleromorpha	Biemnida	-	Biemnidae	1					1	**2**
Demospongiae	Heteroscleromorpha	Desmacellida	-	Desmacellidae	1		1			1	**3**
Demospongiae	Heteroscleromorpha	Haplosclerida	-	-		1		2			**3**
Demospongiae	Heteroscleromorpha	Haplosclerida	-	Chalinidae	3	2			1	6	**12**
Demospongiae	Heteroscleromorpha	Haplosclerida	-	Callyspongiidae	1			1	3	3	**8**
Demospongiae	Heteroscleromorpha	Poecilosclerida	-	-	1	1				2	**4**
Demospongiae	Heteroscleromorpha	Poecilosclerida	-	Acarnidae	1		1		2		**4**
Demospongiae	Heteroscleromorpha	Poecilosclerida	-	Chondropsidae	2	2			1	5	**10**
Demospongiae	Heteroscleromorpha	Poecilosclerida	-	Crellidae	1	1			1	1	**4**
Demospongiae	Heteroscleromorpha	Poecilosclerida	-	Desmacididae					1		**1**
Demospongiae	Heteroscleromorpha	Poecilosclerida	-	Hymedesmiidae	1	1				9	**11**
Demospongiae	Heteroscleromorpha	Poecilosclerida	-	Latrunculiidae	1					1	**2**
Demospongiae	Heteroscleromorpha	Poecilosclerida	-	Microcionidae	2					6	**8**
Demospongiae	Heteroscleromorpha	Poecilosclerida	-	Mycalidae	2					2	**4**
Demospongiae	Heteroscleromorpha	Poecilosclerida	-	Tedaniidae	1					1	**2**
Demospongiae	Heteroscleromorpha	Poecilosclerida	-	Tedaniidae	2					3	**5**
Demospongiae	Heteroscleromorpha	Poecilosclerida		Myxillidae		2					**2**

Class	Sub-class	Order	Sub-order	Family	Pariokariwa	Waitara	Waiwhakaiho	Hangatahua	Patea	Kapiti	
Demospongiae	Heteroscleromorpha	Polymastiida	-	Polymastiidae	4	1	2		1	5	**13**
Demospongiae	Heteroscleromorpha	Scopalinida	-	Scopalinidae		1					**1**
Demospongiae	Heteroscleromorpha	Suberitida	-	Halichondriidae	3	2	1	3	2	4	**15**
Demospongiae	Heteroscleromorpha	Suberitida	-	Suberitidae	4	2			2	3	**11**
Demospongiae	Heteroscleromorpha	Tethyida	-	Tethyidae	2	1	1		1	3	**8**
Demospongiae	Heteroscleromorpha	Tetractinellida	Astrophorina	-					1	1	**2**
Demospongiae	Heteroscleromorpha	Tetractinellida	Astrophorina	Ancorinidae	4	2	2	2	3	4	**17**
Demospongiae	Heteroscleromorpha	Tetractinellida	Astrophorina	Geodiidae	2		1			1	**4**
Demospongiae	Heteroscleromorpha	Tetractinellida	Spirophorina	Tetillidae	1					1	**2**
Demospongiae	Heteroscleromorpha	Tetractinellida		Ancorinidae						2	**2**
Demospongiae	Keratosa	Dendroceratida	-	Darwinellidae	3	1			1	3	**8**
Demospongiae	Keratosa	Dictyoceratida	-	-		3					**3**
Demospongiae	Keratosa	Dictyoceratida	-	Dysideidae	1					3	**4**
Demospongiae	Keratosa	Dictyoceratida	-	Irciniidae	2		2	1	1	3	**9**
Demospongiae	Keratosa	Dictyoceratida	-	Spongiidae	1						**1**
Demospongiae	Keratosa	Dictyoceratida	-	Thorectidae	2					4	**6**
TOTALS					56	26	13	10	23	86	**214**

Table A3.4 Taxa presence, and percentage of total number of taxa in each taxonomic family at each station: Pariokariwa reefs, Waitara reefs, Waiwhakaiho reefs, Hangatahua reefs, Patea reef, and Kapiti Island reefs.

Orders	Pariokariwa Reefs	Waitara Reefs	Waiwhakaiho Reefs	Hangatahua Reefs	Patea Reef	Kapiti Island Reefs
Axinellida	7.14	0.00	7.69	0.00	18.40	6.98
Biemnida	1.79	0.00	0.00	0.00	9.80	1.16
Clathrinida	1.79	3.85	0.00	0.00	0.00	1.16
Dendroceratida	5.36	3.85	0.00	0.00	0.00	3.49
Desmacellida	1.79	0.00	7.69	0.00	0.00	1.16
Dictyoceratida	10.71	11.54	15.40	10.00	36.40	11.63
Haplosclerida	7.14	11.54	7.69	30.00	0.00	10.47
Leucosolenida	3.57	0.00	0.00	0.00	0.00	1.16
Poecilosclerida	25.00	26.92	7.69	0.00	0.00	34.88
Polymastiida	7.14	3.85	0.00	0.00	0.00	5.81
Suberitida	12.50	15.38	15.38	30.00	35.40	8.14
Scopalinida	0.00	3.85	0.00	0.00	0.00	0.00
Tetractinellida	12.50	7.69	23.08	20.00	0.00	10.47
Tethyida	3.57	3.85	7.69	0.00	0.00	3.49
Unknown	0.00	7.69	7.69	10.00	0.00	0.00

Appendix 4

From rivers to the sea: using stable isotopes C and N to reveal the critical role of marine sponges in processing terrestrially derived carbon

Table A4.1 Mean isotope signatures of sponge individual species and OTUs collected from each reef, Waiwhakaiho (WAIW), Waitara (WAI), and Hangatahua (HAN) (replicates, n = 1–5, ± SD not included).

Cryptic biota	n	WAIW Waiwhakaiho δ13C	WAIW Waiwhakaiho δ15N	WAI Waitara δ13C	WAI Waitara δ15N	HAN Hangatahua δ13C	HAN Hangatahua δ15N
Callyspongia fistulosa	1					-20.92	13.08
Chondropsis sp. 1	1			-20.18	9.09		
Chondropsis sp. 2	1			-19.98	9.12		
Ciocolypta polymastia	1					-21.11	9
Darwinella oxeata	1			-21.88	6.95		
Demospongiae sp. 1	1			-21.2	10.98		
Demospongiae sp. 2	1			-22.17	8.2		
Desmacella dendyi	1	-19.6	9.95				
Dictyoceratida sp. 1	1			-20.1	9.26		
Dictyoceratida sp. 2	1			-20.35	10.08		
Dictyoceratida sp. 3	1			-19.85	8.86		
Ecionemia alata	28	-18.32	9.64	-19.27	11.52	-18.8	8.01
		-18.78	12.29	-19.28	9.75	-18.76	8.52
		-18.64	9.71	-19.53	11.58	-18.82	8.92
		-18.56	8.98	-19.48	11.81	-18.9	8.57
		-18.99	9.35	-18.71	9.96	-18.89	9.28
		-19.27	9.17	-18.99	11.88	-19.03	9.02
		-18.84	9.88	-19.29	11.7		
		-19.07	9.22	-18.83	8.46		
		-19.12	10.65	-19.05	7.25		
				-19.1	7.65		
				-19.25	7.82		
				-19.12	9.92		
				-18.86	7.7		
Geodia sp. 1	1	-19.61	12.11				
Haliclona heterofibrosa	1			-18.54	8.59		
Haplosclerida sp. 1	1					-22.58	12.07
Haplosclerida sp. 2	1			-21.28	8.05		
Heteroscleromorpha sp.	1	-21.31	12.28				
Hymeniacidon perlevis	1					-20.83	7.84
Hymeniacidon sp. 1	1					-21.16	10.06
Hymeniacidon sp. 2	1			-20.99	11.38		
Hymeniacidon sphaerodigitata	1	-20.89	14.21				

Cryptic biota	n	WAIW Waiwhakaiho		WAI Waitara		HAN Hangatahua	
		δ13C	δ15N	δ13C	δ15N	δ13C	δ15N
Hymeniacidonidae	1			-20.9	10.47		
Iophon minor	1	-22.21	12.13				
Ircinia sp. 1	1	-19.3	10.09				
Myxilla (Styloptilon) fromontae	1			-21.04	9.4		
Myxillidae sp.	1			-21.4	13.07		
Myxillidae	1			-22.28	13.38		
Pararhaphoxya sinclairi	3	-20.62	12.54	-20.29	10.6		
				-21.21	12.81		
Phorbas sp. 1	1			-21.1	10.05		
Poecilosclerida	1			-21.03	14.06		
Polymastia massillis	1	-20.3	11.91				
Polymastia sp. 1	1	-20.9	11.87				
Psammocinia papillata	1					-18.27	8.28
Sigmadocia n. sp.	1			-21.45	13.16		
Stelleta crater	1			-19.02	8.14		
Stelletta arenaria	1					-16.03	8.62
Stelletta conulosa	1	-19.52	12.38				
Suberites sp.	1			-21.5	12.99		
Tethya berguistae	1			-20.69	9.38		
Tethya berguistae	1	-21.23	8.92				