

**A preliminary exploration of the rocky mesophotic communities of the
Wellington Region**

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Executive summary

Rocky mesophotic communities have been reported at several locations around New Zealand, where they are typically found within a depth range of ~30 – 150 m. However, although many deeper water rocky features occur in the Wellington region, the biological communities inhabiting these features have not been explored. In this study we surveyed rocky deep-water features on the Wellington South Coast (WSC) and Kapiti Coast to assess the benthic communities they support. We deployed our Remotely Operated Vehicle SAL at nine sites, three on the WSC and six on the Kapiti coast, covering a depth range from 26 to 57 m. The three sites on the WSC were all below 30 m, while the sites on the Kapiti coast ranged from 26-57 m. There was significant variation in the benthic community composition between sites and depth. Across all sites, sponges and bryozoans were by far the most abundant organisms, covering around 30% of the substrate, with all other groups having <5% cover. Very little bare space was found at any of the sites sampled. The sponges and bryozoans created complex three-dimensional structure to the seafloor, which is likely to serve an important role in providing habitat, refuge and food for other species. We recognise recreational fishing and changes in water quality (including nutrients and sedimentation/turbidity) as the most likely impacts on these mesophotic ecosystems. We discuss the value of these newly described ecosystems in the context of the 'Key Ecological Area' criteria and suggest further areas of research to better understand their wider distribution and ecological function.

1. Introduction

Mesophotic ecosystems in coastal regions have received very little attention when compared to shallower algal-dominated (infralittoral) zones. Furthermore, most of our understanding of mesophotic habitats is derived from tropical mesophotic coral ecosystems (MCEs) (e.g. Lesser et al. 2009; Kahng et al. 2014), while temperate mesophotic ecosystems (TMEs) have been largely overlooked, and only recently formally recognised (Cerrano et al. 2019; Turner, 2019; Bell et al. 2022). Given the extensive benthic habitat that TMEs encompass, and their connectivity with shallow habitats, the lack of research effort afforded to TMEs imposes significant limitations on our holistic understanding of coastal benthic ecosystems generally. This includes the ecological functions and services of TMEs, and their potential vulnerability to anthropogenic stressors.

Temperate Mesophotic Ecosystems (TMEs) occur throughout the world, at the limit of light availability for photosynthesis (Cerrano et al. 2019; Turner et al. 2019). A range of depths and environmental conditions (e.g. Micaroni et al. 2021) have been used to describe mesophotic ecosystems, but recently Cerrano et al. (2019) provided an unambiguous definition based on light attenuation. At its upper limit, the mesophotic zone receives $\sim 1\%$ of surface irradiance, and extends to the deepest extent of benthic primary producers. This zone has typically been reported to fall within a depth range of $\sim 30 - 150$ m, but animal-dominated systems can occur in shallower water depending on local environmental conditions (e.g. Micaroni et al. 2021).

Decreased light availability with depth is the primary environmental driver characterising the ecology of mesophotic zones in temperate systems (Bell et al. 2022). It generates a reduction in, and eventually, the exclusion of algae and other photosynthetic organisms (Lesser et al. 2009), changing competitive pressures on benthic fauna. The ecological dynamics of the mesophotic zone, therefore, are increasingly determined by the community composition and relative abundance of the benthic invertebrate fauna and the functions they perform, including sponges, bryozoans, ascidians, hard corals, and soft corals. The upper-extent of TMEs is likely to be highly location-specific, because temperate regions exhibit particularly dynamic and productive coastal environments (Harris et al. 2021).

In some circumstances, TME-like communities may occur in much shallower water than MCEs due to low light penetration (Micaroni et al. 2021), suggesting that some benthic habitats shallower than 40 m require consideration as TMEs when we begin to develop our understanding of these habitats. For example, the relatively shallow (15 - 25 m) environment of the Taranaki region of New Zealand's North Island has been suggested as more characteristic of deeper water (>30 m) reefs (Battershill & Page, 1996) exhibiting sponge-dominated benthic habitat. These shallower reefs have been posited as potential "surrogate TMEs" because they represent shallow-water examples of deeper-water communities. Due to the complex, three-dimensional habitat generated by so-called "sponge gardens" occurring here, they are likely to be particularly ecologically important, but not necessarily exclusive to the Taranaki region.

The Wellington region has a number of deeper water rocky reefs that might support animal-dominated mesophotic communities. These communities are likely to have important ecological functions, including the provisioning of complex three-dimensional habitat that may support recreational fisheries. However, despite their (possibly substantial) contribution to ecological services in a heavily utilized environment within close proximity to the capital city, these benthic communities have not been explored or quantified. Furthermore, the Wellington region is likely to be exposed to multiple local anthropogenic pressures such as acute pollution events and intense recreational fishing activity. These pressures are potentially threatening the ecological integrity of local TMEs before we have even been able to explore and understand their ecological significance.

With recent advancements in ROV technology, the exploration of TMEs is becoming much easier and more economically viable. Small, low-cost ROVs can be deployed from small vessels by a single user, and have been shown to be capable of generating species distribution and abundance data of comparable quality to those gathered using SCUBA (Boavida et al. 2016). This has also been demonstrated by other projects carried out in New Zealand by the Bell research group (see Harris et al. 2021). This advancement in technology provides an opportunity for non-commercial groups to explore and determine the community composition of TMEs at relatively low cost. This information will facilitate the continued development of effective management plans throughout New Zealand's coastal environment.

In this project we used a remotely operated vehicle (ROV) to explore deeper water rocky features in the Wellington region to:

- 1) Confirm the presence of TMEs in the Wellington region.
- 2) Quantify spatial and depth related variation in the benthic community structure between sites.
- 3) Generate initial habitat distribution polygons (where possible) for TMEs in the Wellington region.

2. Methods

2.1 Study sites

We investigated nine sites across two main locations within the Greater Wellington Region (Figure 1). All sites were chosen based on previous bathymetric assessments that indicate likely rocky-reef benthic habitats occurring within mesophotic depths (see Figure 2 for examples of mesophotic benthic habitat at both locations). Six sites were surveyed on the Kapiti Coast (KC) and three sites on the Wellington South Coast (WSC). Four of the six sites on the KC are distributed across the northern and southern ends of Mana Island with a total depth range of 30 – 57 m (Table 1 and Figure 1). Mana site 3, which is situated at the northern end of the island was considered as a shallow-mesophotic reef at a depth of 30 m, while the remaining sites at Mana Island were all situated deeper than 30 m. The remaining two sites on the KC are located on a shallow-mesophotic (26 – 33 m) and deeper mesophotic (45-57 m) region of Hunter Bank, situated between Mana Island and Kapiti Island (Figure 1). All KC sites receive high current flow outside of slack tide periods. These sites are currently fully open to recreational fishing activity. The remaining three sites on the WSC are considered shallow-mesophotic sites between 26 and 30 m and receive frequent strong swell and recreational fishing pressure outside of Taputeranga Marine Reserve.

Table 1. Metadata for nine surveyed mesophotic sites across the Wellington South Coast (WSC) and the Kapiti Coast including Mana Island.

Date	Site	Latitude	Longitude	Depth	Location
01/03/2022	Mana 1	41° 5.514' S	174° 45.629' E	38-45 m	South Mana
01/03/2022	Mana 2	41° 5.620' S	174° 45.495' E	46 m	South Mana
01/03/2022	Mana 3	41° 4.408' S	174° 47.281' E	30 m	North Mana
06/05/2022	Mana 4	41°06'23.4"S	174°45'50.8"E	45-50 m	South Mana
30/04/2022	Hunters Deep	40°58'17.4"S	174°48'54.1"E	45-57 m	Kapiti coast
30/04/2022	Hunters Shallow	40°58'18.1"S	174°48'48.0"E	26-33 m	Kapiti coast
23/03/2022	Arabella rocks	41° 24.703' S	174°51.344' E	26 m	WSC
23/03/2022	Taputeranga Island	41° 21.593' S	174°46.133' E	27 m	WSC

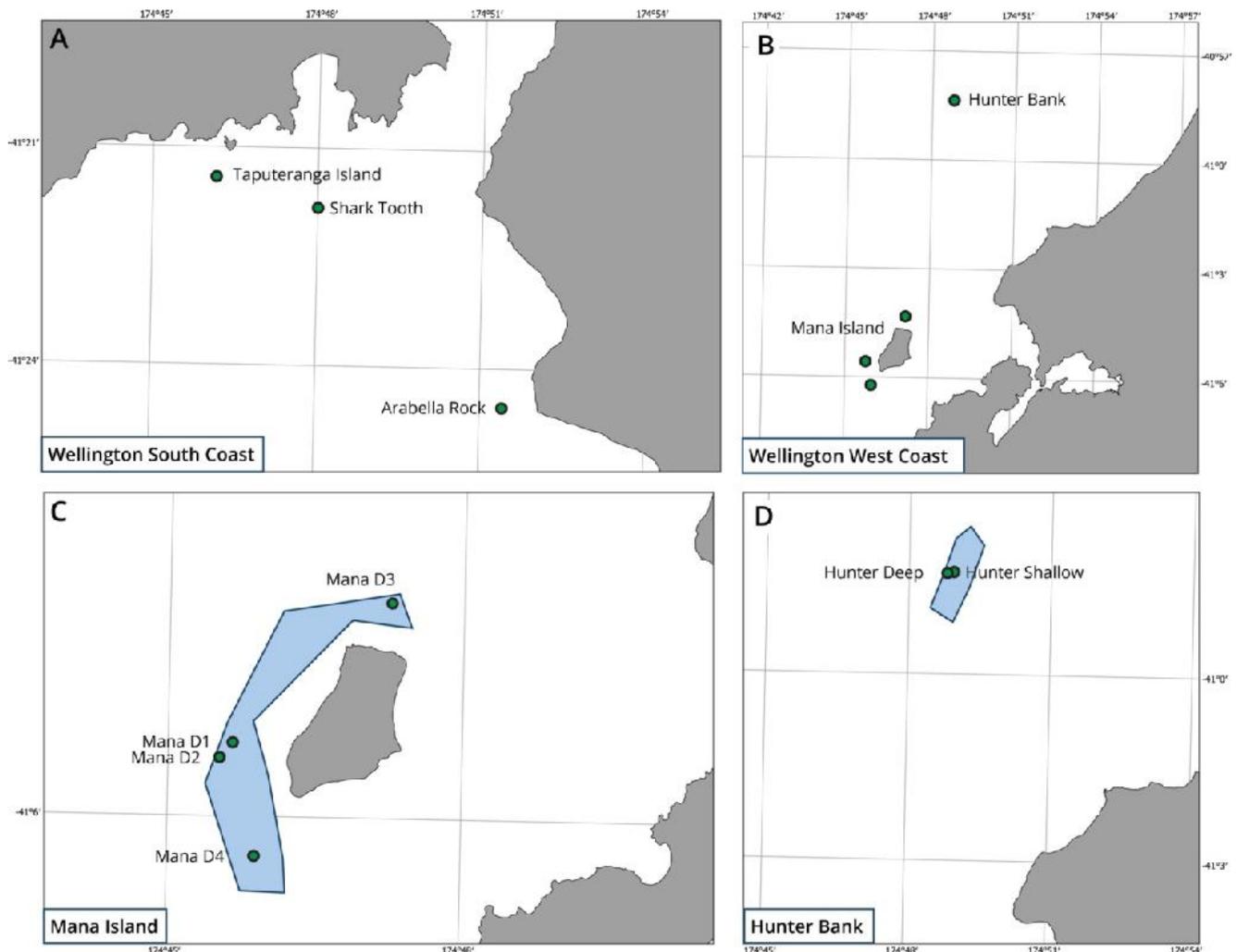


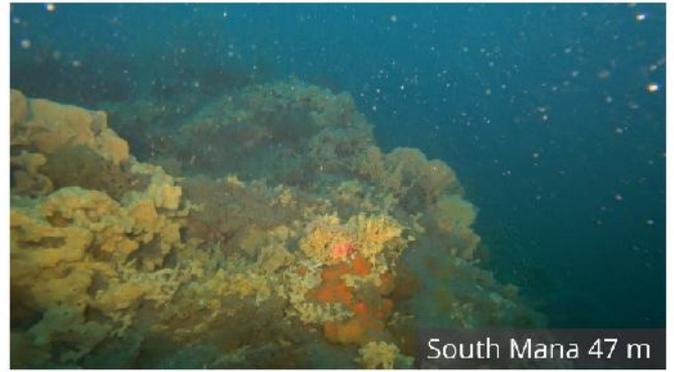
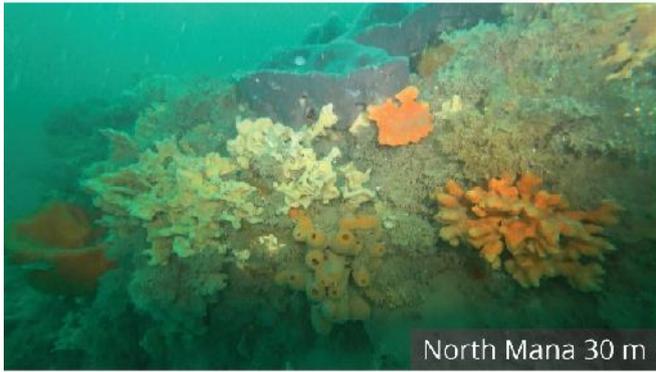
Figure 1. Locations of ROV deployments in the Wellington region. The approximate distributions of the mesophotic habitats in these areas are based on seafloor bathymetry. See Supplemental Table S2 for polygon coordinates.

2.2 Benthic video collection

The ROV DG2 (Deep Trekker Inc.) “SAL” with an internal (4k) camera mounted on an independent remotely controlled swivel was deployed at all sites. The camera was set to linear mode and angled perpendicular to the substrate to minimize parallax error as far as possible. The potential issue of parallax error (Rivero Calle, 2010 as discussed in Lesser & Slattery, 2019) was addressed further by employing a randomized point count approach for percentage cover analysis of images where the whole image area is not used (Scott et al. 2019). The ROV was deployed from the side of an 8.5 m tri-hull vessel The Raukawa Challenger. The ROV was driven vertically downwards from the vessel until reaching

approximately 1 m above the benthos and then driven along a transect approximately 1 m from the substrate for approximately 10 minutes. The internal swivel camera was angled downwards toward the horizontal substrate or adjusted accordingly to maintain the camera perpendicular when filming mounts and large three-dimensional reef features. ROV lasers were used to determine and then maintain distance from the benthos, producing frame grabs of similar scales. A more precise scale was not required for determining the abundance of benthic organisms using an area occupied approach. The maximum depth reached at all sites was 57 m at Hunters Bank (Table 1). Previous work using this same approach in similar habitats in New Zealand has yielded results indistinguishable from those obtained from photo-quadrats using SCUBA (Harris et al. 2021).

Kapiti Coast



Wellington South Coast



Figure 2. Examples of mesophotic benthic habitats found during this study.

2.3 Video analysis

Videos collected from ROV deployments were analysed using VLC media player; 10 frame grabs were extracted from each transect as replicates. The choice of frame grabs for analysis was dependent on the efficacy of each image. Frame grabs exhibiting the lowest occurrence of blurring and with the most perpendicular perspective of the substrate were prioritized. This ensured the greatest accuracy of the proceeding analyses and reduced potential selection bias toward images displaying specific community compositions or components. Coral Point Count with Excel extensions (CPCe) was used to estimate the percentage cover of categorized benthic groups. Thirty categories of benthic organisms (Table S1) were assigned to a CPCe codefile after preliminary analyses of video transects. These sub-categories were assigned under ten higher taxonomically ranked groups including Porifera, Bryozoa, Cnidaria and Ascidiacea, Annelida (only polychaetes observed) and the polyphyletic group Macroalgae. Crustose Coralline Algae (CCA) (no assigned sub-categories), and Biological Matrix (no assigned sub-categories) were also applied. Biological matrix was utilized to categorize a likely diverse group of small and tightly packed organisms unidentifiable from the resolution of the ROV camera. The categories Bare Substrate (no assigned sub-categories) and Sediment (no assigned sub-categories) were also included ensuring the total cover of each image equalled 100%. These 10 major categories covered every identifiable organism observed. A single analyst carried out all CPC image analyses to maintain quality control. CPCe randomly allocates points over an image; the user then manually identifies the substrate or benthic taxa beneath each point. The software uses this input to estimate substrate composition across the entire frame-grab (percentage cover of each substrate/ benthos), exporting the information as a comma-separated values (CSV) database. 120 points per quadrat was considered sufficient to reach a plateau of a species accumulation curve, based on other work by the authors in similar habitats.

2.4 Data analysis

Data was analysed using PRIMER V6 + PERMANOVA. Permutational multivariate analysis of variance (PERMANOVA) was used to determine the effect of fixed factors (depth and site) on multivariate data (community composition) using a Bray-Curtis similarity matrix. Where significant effects of fixed factors were found, PERMANOVA in PRIMER was also used to

determine any differences between factors or of multivariate data as post-hoc pairwise tests. PERMANOVA in PRIMER was also applied to univariate data (single organism categories) using a Euclidean-distance matrix to determine significant differences in single organism abundances across sites. All data was fourth root transformed to improve normality and reduce heteroscedasticity where appropriate, although this is not an underlying assumption for permutational tests. Multidimensional scaling (MDS) was used to visualise the dissimilarity between samples with overlaid factor indicators. Benthic group vectors were then overlaid according to a Pearson's rank correlation threshold of 0.45 to visualise the most important benthic community categories explaining these distribution patterns.

3. Results

3.1 Site and depth variation in benthic community composition

Benthic community composition was significantly different between sites (PERMANOVA, $F_{8,83} = 10.08$, $p < 0.001$) (Table S3), with clear differences evident from the multidimensional scaling plot (MDS) (Figure 3). *Post-hoc* pair-wise T tests revealed this effect was also significant between all individual site pairs (Table S4).

After separating the surveyed reefs into shallow (< 30 m) and deep (> 30 m) categories, a PERMANOVA test revealed depth also had a significant effect on overall community composition ($F_{1,83} = 11.52$, $p < 0.001$). PERMANOVA tests of interactive effect of depth and site on community composition could not be applied, due to the lack of depth profiles (multiple depth categories) within single sites. This also meant that conclusions drawn from PERMANOVA analyses alone are potentially insufficient for robust conclusions given that the fixed factor 'Depth' is nested within the fixed factor 'Site'. However, the MDS plot (Figure 3) showed a clear distinction between sites (groupings of symbol shapes) when embedded in the same depth categorization (symbol colour). Figure 3 shows a clear distinction between the composition of benthic communities at deep and shallow sites, but the cluster representing the shallow reef at Mana site 3 is nested within the deeper Mana sites. This suggests that Site is an important factor in driving community composition in this case. Furthermore, within both the shallow and deep groups, there are distinct separations of groups of symbols (sites) (e.g. see the variation between the deep reefs of Mana site 2 and

the deep reef of Hunters bank in Figure 3). These results suggest depth is important in driving community composition, independently of site-driven variation.

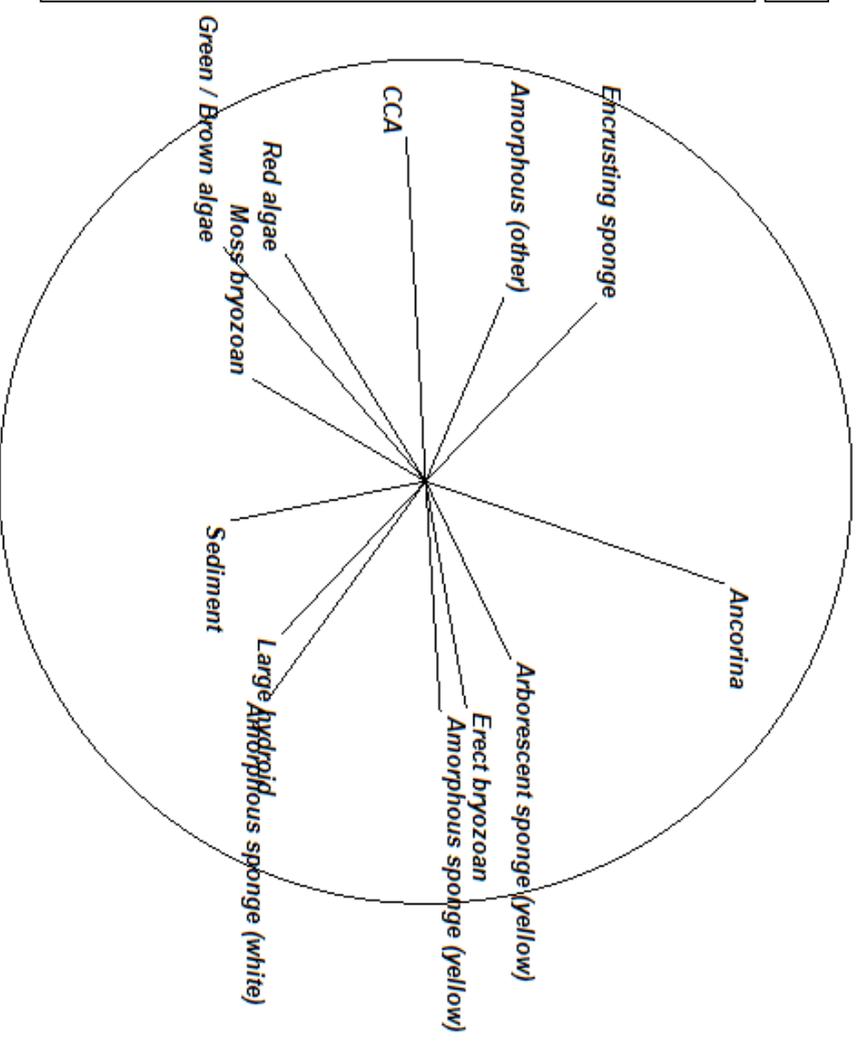
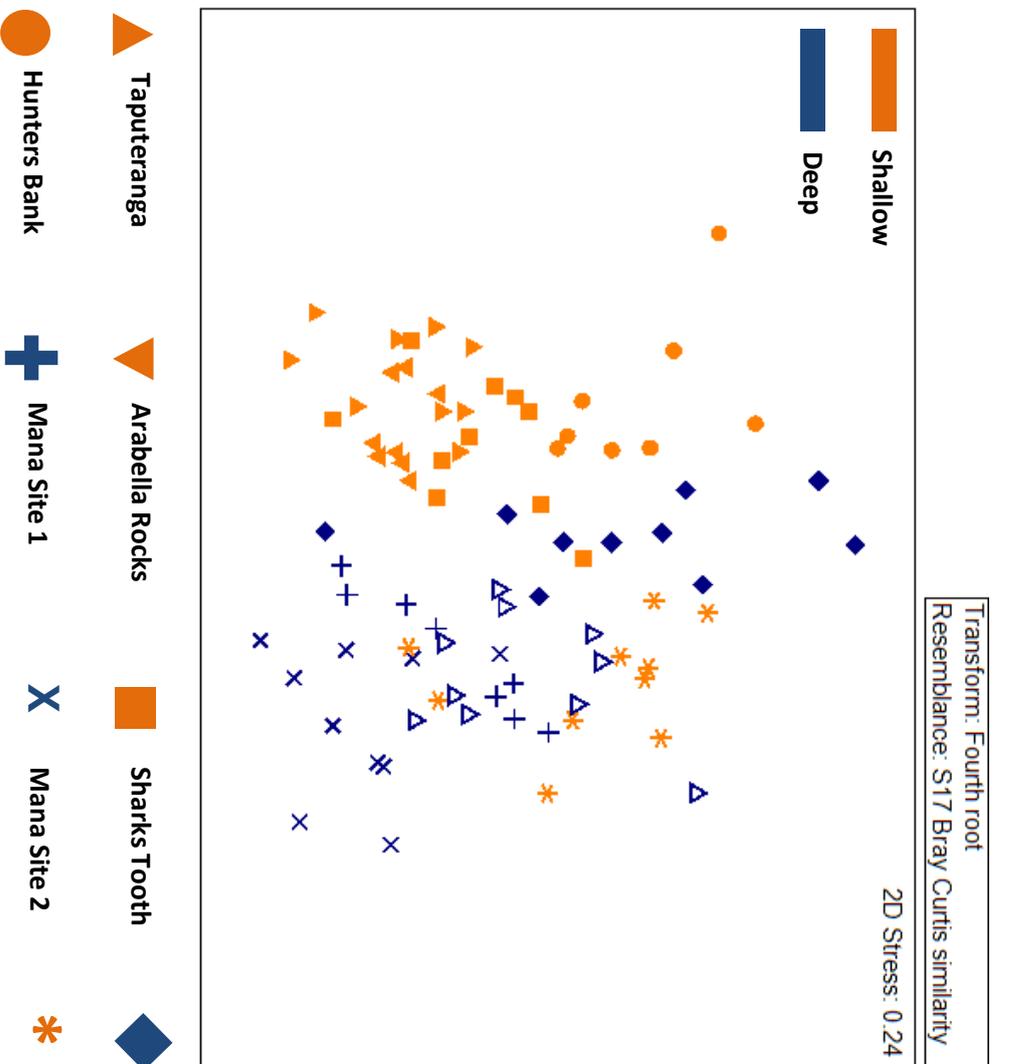


Figure 3. Multidimensional scaling (MDS) plot of centroids of benthic communities for a combination of site (represented by symbol shape) and depth (represented by symbol colour, shallow < 30 m, and deep > 30 m) for 9 mesophotic sites (left) with overlaid vector using Pearson correlation (> 0.45).

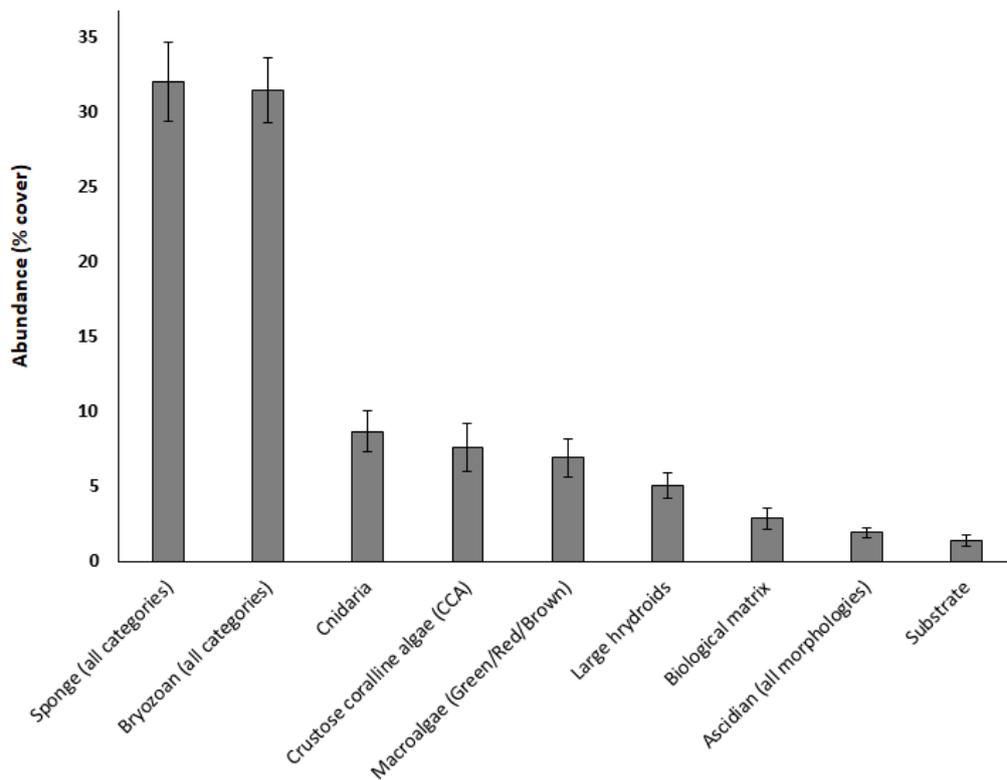


Figure 4. Average abundance (as % coverage) of the most abundant assigned major organism categories across all 9 study sites. Error bars are \pm SE.

3.2 Benthic community composition

Sponges and bryozoans were the most abundant of all the observed major benthic organism categories when averaged across all sites (Figure 4), covering $31.9 (\pm 2.6)$ % and $31.4 (\pm 2.1)$ % of the available substrate, respectively. This was more than 3.5 times the abundance of the next most abundant group Cnidaria ($8.7 \pm 1.4\%$), which predominantly consisted of large hydroids and dense *Parazoanthus* colonies. Overall, the presence of open rock-reef substrate was very low ($1.4 \pm 0.4\%$), where the remaining rocky reef habitat was colonized by living organisms. This is a conservative estimate as it is likely that areas identified as bare substrate harbour particularly small or finely encrusting organisms that were not visible at the image resolution or light availability provided by the ROV.

3.3 Sponge distribution

While sponges and bryozoans appeared to dominate the benthic communities overall, they exhibited significant variation in abundance between sites ($F_{8,83} = 7.601$, $p < 0.001$ and $F_{8,83} = 4.82$, $p < 0.001$ for sponges and bryozoans respectively; Figures 5 and 6). The apparent dominance of sponges overall is strongly driven by the high abundance of sponges at deeper sites with particularly high abundances exhibited at Hunters Bank Deep (57 m) and Mana 4 (50 m) (the two deepest sites) with $51.9 (\pm 7.4)\%$ and $53.4 (\pm 3.5)\%$ cover, respectively. The shallower sites on the Wellington South coast, however (Figure 6) had significantly lower sponge abundance than all deeper sites (see Table S5 for pairwise differences) explaining the significant overall effect of site on sponge abundance.

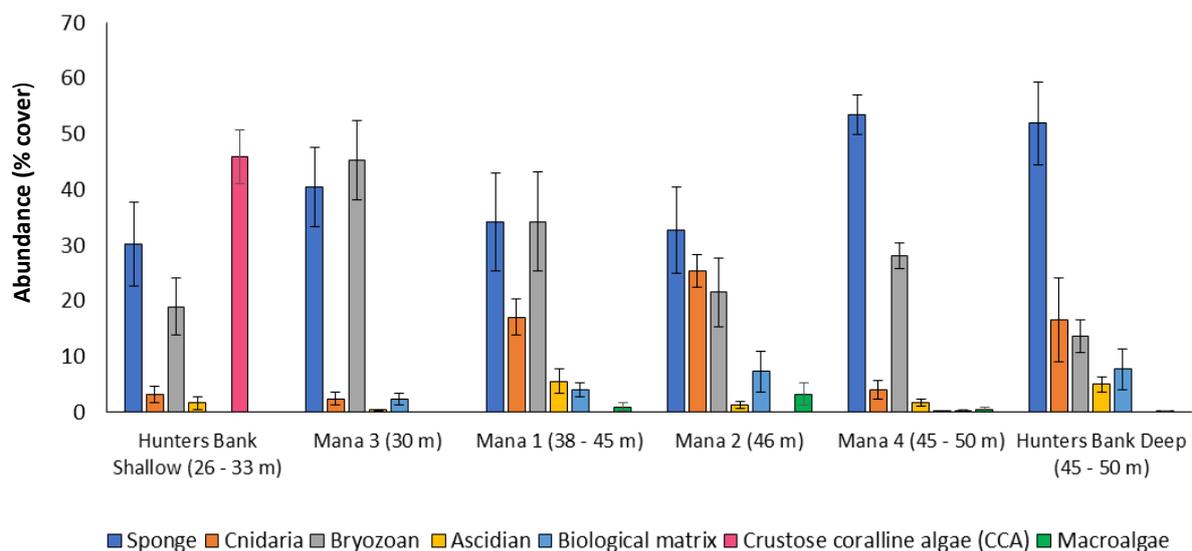


Figure 5. Percentage cover of the seven most abundant benthic groups at six mesophotic reef sites in order of depth on the Kapiti coast ranging from 26 – 57 m. Error bars are \pm SE.

3.4 Bryozoan distribution

The overall dominance of bryozoans (alongside sponges) (Figure 5 and 6) was particularly the result of high bryozoan abundance at the shallow WSC sites, where they were significantly more abundant than the deeper sites on the Kapiti coast. For example, the shallowest site at Arabella rocks (26 m) exhibited $50.6 (\pm 3.5)\%$ bryozoan cover, the highest of all sites, and was significantly higher ($t = 5.46$, $p < 0.001$) than the deepest site; Hunters Bank (45-57 m), which exhibited only $13.7 (\pm 2.9)\%$ bryozoan cover (see Table S6). Again, while this alone might

suggest depth as the primary driver in bryozoan abundance, Taputeranga (27 m) showed significantly lower bryozoan abundance than Mana 3 (30 m) despite both sites occurring at similar depths. This suggests that site is also likely to be contributing to bryozoan abundance independently of depth effects. The highest bryozoan abundance of all sites was at Arabella rocks, which coincided with the lowest sponge abundance of all sites at only $4.3(\pm 0.8)$ % cover. This was significantly lower than all other sites except for Taputeranga (see pairwise t-test results in Table S5).

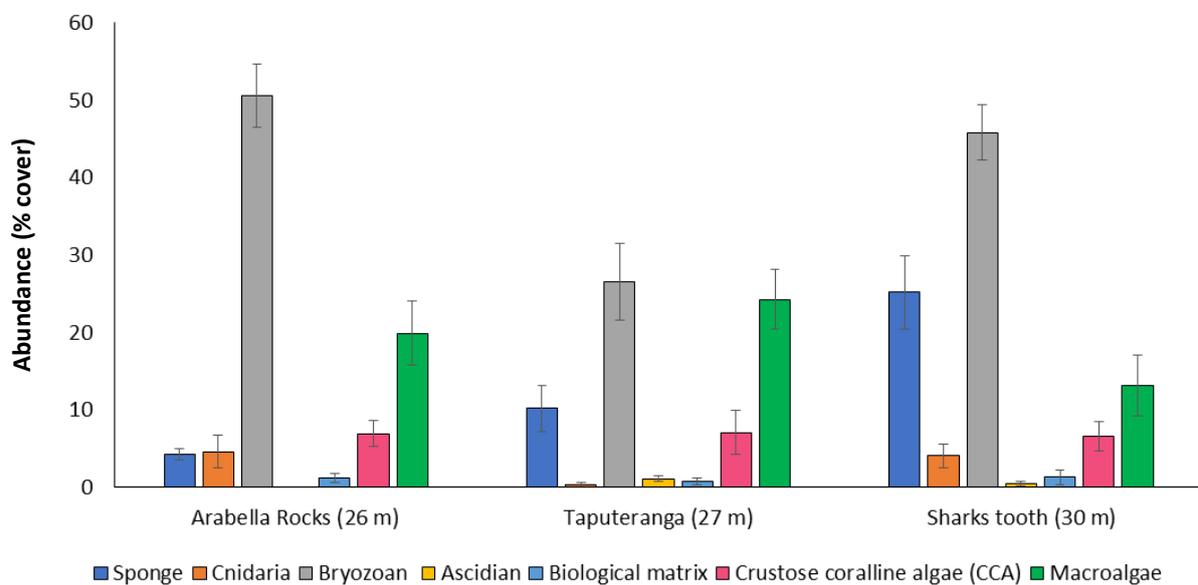


Figure 6. Percentage cover of the seven most abundant organism groups at three mesophotic reef sites on the Wellington south coast at approximately 30 m. Error bars are \pm SE.

3.5 Macroalgae distribution

Unsurprisingly, the shallowest sites exhibited the highest abundance of macroalgae with the highest cover of $24.3(\pm 3.9)$ % occurring at Taputeranga. However, while the other shallow sites, Arabella rocks and Sharks tooth, on the WSC also exhibited relatively high abundance of macroalgae, both shallow sites Mana 3 and Hunters Bank (shallow) on the KC were almost

entirely devoid of macroalgae cover, suggesting site rather than depth to be a particularly important factor in driving the variation in abundance of macroalgae.

3.6 Bryozoan and sponge assemblage composition

As the most abundant groups (Figures 5 and 6), the composition of the bryozoan and sponge assemblages observed are likely to be of particularly high ecological importance relative to the other benthic organisms reported. Bryozoans were categorized into three morphological groups; Encrusting, Erect, and Moss (see Table 2), which likely perform different ecological functions. Moss morphologies represented $65.3 (\pm 6.4)$ % of the total bryozoan cover averaged across all sites, which was significantly higher than branching forms (33.6 ± 4.5 %) which in turn were significantly more abundant than encrusting forms ($1.1 \pm 0.3\%$) (Figure 7). Sponges were assigned into a number of taxonomic and morphological categories (see Table 2). Despite likely representing an unconfirmed single species, the most abundant sponge category was an amorphous yellow form ($9.3 \pm 1.6\%$ average across all sites; closely followed by *Ancorina* at $7.9 \pm 1.7\%$ averaged across all sites) (Figure 8).

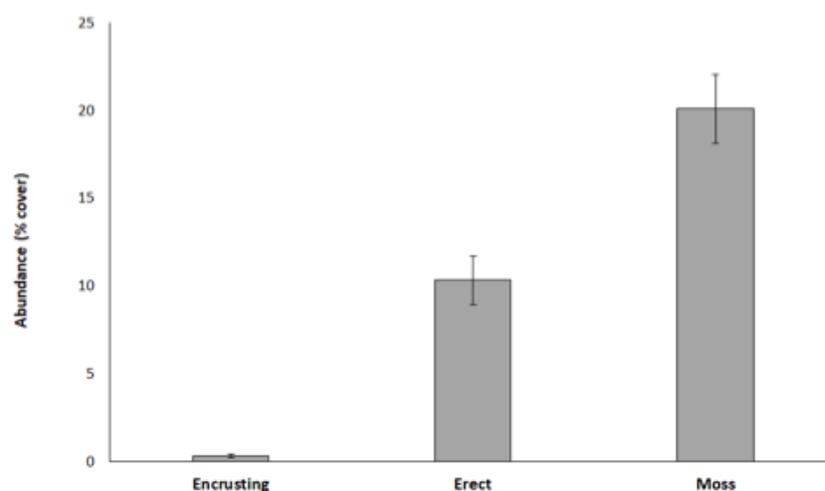


Figure 7. Percentage cover of the three assigned bryozoan morphological categories across all nine study sites. These categories encompass all bryozoans observed. Error bars are \pm SE.

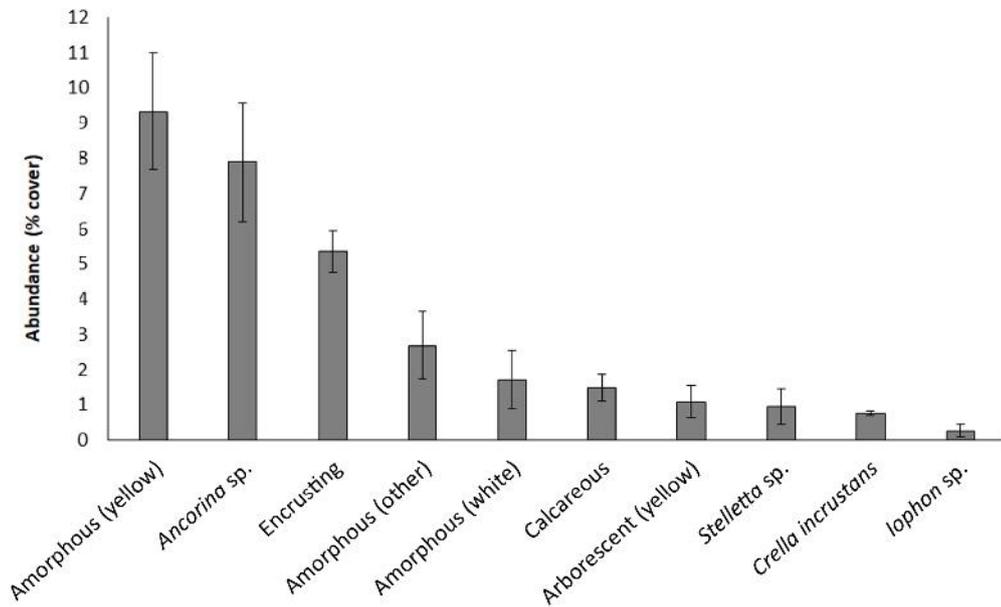
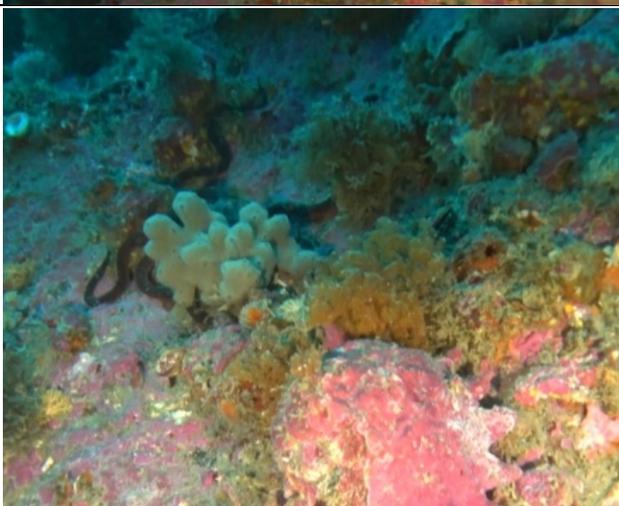


Figure 8. Percentage cover of the most abundant assigned sponge categories across all nine study sites. Assigned categories include identified species (e.g. *Crella incrustans*), unidentified species-specific morphologies (e.g. amorphous yellow), and inter-specific morphological categories (e.g. encrusting). Error bars are \pm SE.

Table 2. Screenshots from the ROV DG2 Deeptrekker of assigned sponge categories from 9 mesophotic sites in the Wellington South Coast and Wellington West Coast.

Assigned category	Location/Comments	Image
1. Amorphous sponge (yellow)	Mana Site 2. Highly abundant across Mana sites. Possible species include: <i>lophon</i> sp. Often associates with <i>Ancorina</i> sp. Or found on the top of mounts.	

2. <i>Ancorina</i> sp.	Mana Site 1. Easily identifiable. Large grey/black massive morphology. High abundance.	
3. Encrusting	Hunters bank shallow. Highly variable in colour and texture. Numerous species likely within this category. Seemingly less common relative to other TMEs assessed in New Zealand.	
4. Amorphous other	Hunters shallow. Very broad category of amorphous sponge species not otherwise categorized. Despite the breadth of this category, this group is less abundant than other more specific groups such as Amorphous yellow or <i>Ancorina</i> sp.	
5. Amorphous white	Mana site 2. Very similar morphology and apparent habitat preference to amorphous yellow, and possibly the same species. Differentiated due to distinct bleaching in colour.	

<p>6. Calcareous</p>	<p>Taputeranga. Multiple calcareous sponge species commonly occur in the shallow infralittoral zone around the southern reaches of the North Island including numerous <i>Clathrina</i>, and <i>Leucettusa</i> species. <i>Clathrina</i> sp. shown here.</p>	
<p>7. Arborescent yellow</p>	<p>More prevalent at deeper locations. Category likely encompasses multiple different species including <i>Callyspongia ramosa</i>, <i>Pararhaphoxya sinclairi</i>, and possibly <i>Iophon minor</i> and <i>Axinella</i> sp.</p>	
<p>8. <i>Stellatta crater</i></p>	<p>Mana site 2. Easily distinguished orange/yellow encrusting sponge <i>Desmacella denty</i> covering the massive/bowl morphology of <i>Stellatta crater</i>. Occur as single specimens but associated with a wide range of other organisms including hydroids, bryozoans and mobile vertebrate species.</p>	

9. *Crella
incrustans*

Very common at certain sites despite relatively less common compared to other categories when average abundance was considered across all sites. Occurs in a range of morphology from almost flat/encrusting to three-dimensional, plate-like forms.



Table 3. Screenshots from the ROV DG2 Deeptrekker of most abundant benthic community organism categories from 9 mesophotic sites in the Wellington South Coast and Wellington West Coast.

Assigned category	Comments/Location	Image
1. Bryozoan (Moss)	<p>Mana 2.</p> <p>Highly abundant at all sites beyond 30 m. Some range in colour from very pale pink to orange. Likely, <i>Cornuticella taurina</i>(orange) and <i>Amathia wilsoni</i> (pale / white).</p>	
2. Bryozoan (Erect/branching)	<p>Mana 1. Highly abundant at deeper sites. Wide range of morphologies and sizes. Likely to be a diverse mix including <i>Hornera robusta</i> and <i>Caberea zelandica</i>.</p>	

		
<p>3. Cnidaria (Parazoanthus)</p>	<p>Very abundant at Mana sites. Occurs in patches often underneath overhangs and appears to associate with massive sponge morphologies.</p>	
<p>4. Cnidaria (Large hydroids)</p>	<p>Seemingly diverse category with multiple different forms observed. Most often observed in groups on top or protruding from small mounts. Also often associated with massive sponge forms such as <i>Ancorina</i> sp.</p>	

5. Macroalgae (Red)	Uncommon at all sites. Predominantly filamentous forms.	
6. Macroalgae (Green/Brown)	Multiple staking species with diverse morphologies including: <i>Ecklonia radiata</i> (show in image), and <i>Lessonia</i> sp. Almost entirely absent from Kapiti sites beyond 30 m. Turfing / low profile species generally absent from all sites.	
7. Ascidian (encrusting)	Uncommon compared to encrusting sponge forms. Distinguished from sponge forms by white rim and often more evenly spaced apertures.	

4. Discussion

4.1 Overview of sponge gardens

Our preliminary study has shown that the Wellington region contains many previously unknown mesophotic communities, which are dominated by sponges and bryozoans. On the

Kapiti coast, there appears to be relatively rapid transition around 20-25 m from algal-dominated ecosystems to animal-dominated systems. On the Wellington south coast this transition appears to occur more gradually with the full transition to animal-dominated communities occurring in deeper water, although further sampling is needed to fully determine this since we only managed to reach 30-35 m. Importantly, the Bell-Rogers research groups have now explored mesophotic communities in Fiordland, Taranaki, Poor Knights and Bay of Islands, and those in Wellington, particularly on the Kapiti coast are very different. In particular the many massive thick 3D cushions and branching sponges, which create considerable biogenic structure to the benthos, are not something we have observed elsewhere. In the other locations we have sampled around New Zealand, the mesophotic communities are more dominated by thin encrusting sponge species, interspersed with branching and upright forms.

In all the mesophotic ecosystems we have explored around New Zealand sponges are the dominant fauna, and the mesophotic communities in the Wellington region are no different. Areas with lots of sponges have often been term 'sponge gardens', although this term has no formal definition. In general, this term has often been applied in the context of ecosystems that are dominated by mostly upright forms (e.g. branches and tubes) (Maldonado et al. 2017). However, there is no specific reason why this term should also not also be applied to communities that are dominated by mostly encrusting species (e.g. the Poor Knights) or cushion/massive species like those around Wellington. We consider the term 'sponge garden' to be best applied to describe ecosystems were sponges are most dominant benthic organism either in terms of biomass or area of the seabed occupied by sponges. We believe the term sponge garden should be extended to include ecosystems beyond those with extensive 3D structure.

4.2 Current and future impacts

We believe the most likely threats to the deep water communities we observed include recreational fishing and changes in water quality (including nutrients and sedimentation/turbidity; see recent for review by Bell et al. (2022) for a qualitative ranking of impacts on temperate mesophotic ecosystems). All of the areas we sampled are subject to recreational fishing pressure although there were no obvious impacts from these activities

based on our videos. However, although not detected in our videos it does seem likely (and has been reported by divers in the shallow areas) that there is discarded/caught fishing lines and nets in these areas, particularly on the Kapiti coast. For example, during sampling at Hunter Bank, we counted in excess of 30 boats fishing while we were sampling (noting this was a very sunny Saturday). In addition to fishing lining/net getting caught on the reef organisms, damage is also possible from anchoring, although the extent of anchoring on the actual reef is unknown. Given our sampling only represents a 'snap shot' of the condition of the deep water communities it is very hard to say if these ecosystems are degraded. However, given the low availability of bare unoccupied space, which is comparable to other NZ locations (see Harris et al. 2021), we believe these ecosystems to be relatively unimpacted.

The benthic communities we have observed are dominated by suspension feeding organisms, which are likely to be sensitive to changes in water column food availability and sediment loadings, and also smothering by sediment. Changes in land use (e.g. forest removal) or high levels of rain fall/changing rain fall patterns could cause increased sediment in coastal waters and impact these ecosystems.

Climate change, particularly increases in temperature, have the potential to strongly impact these ecosystems. At present we have very little understanding of how most NZ marine organisms will specifically respond to climate change.

4.3 Assessment of deeper water ecosystems against 'Key Ecological Area' criteria

Here we considered the features of the deeper water ecosystems we have described with respect to defining these areas as 'Key Ecological Areas' after Freeman et al. (2017). We do note here however, that much of our assessment is based on our knowledge of similar or related shallower water species and from mesophotic ecosystems more generally, since we know very little about the specific ecology of the Wellington mesophotic ecosystems and the organisms found.

Vulnerability, fragility, sensitivity, or slow recovery

The deeper (>30 m) biological communities that we have identified are dominated by sponges, many with complex three dimensional morphologies. While sponges can show a

range of life-history strategies they are generally considered to be slow growing, late colonisers of marine communities (Bell et al. 2022). There are also species of gorgonians that are also likely to be slow growing and sensitive to physical disturbance. Given recent work by the Bell group elsewhere on shallow water reefs (see Micaroni et al. 2021), if these ecosystems are lost they could take decades and perhaps even longer to recover. This also assumes that not all populations are lost and there are source populations remaining to provide replacement larvae.

Uniqueness/rarity/endemism

At present we have not seen mesophotic ecosystems like those reported in the Wellington region elsewhere in NZ, particularly those around Mana Island and at Hunter Bank, although our work elsewhere has only focused only Taranaki, Northland and Fiordland. At this stage is difficult to assess rarity and endemism without more extensive sampling, but there are likely species that are specific to these habitats types. As far as we are aware there are very few mesophotic communities that are protected by our existing reserve network.

Special importance for life history stages

The importance of mesophotic ecosystems for specific life-history strategies has not yet been determined. However, there are large amounts of mobile organisms associated with these reefs and given the complexity of the habitat it seems likely that its used by juvenile fish, and other fish for feeding. Given these areas are frequently visited by fishermen they are clearly recognised as areas where fish aggregate.

Importance for threatened/declining species and habitats

At present there is no evidence to suggest these ecosystems support any threatened or declining species.

Biological productivity

Several of the underwater features we have explored are surrounded by soft sediment environments and are therefore areas of much higher overall biological productivity. The

aggregations of fish species (including many recreational, customary and commercial species) around these mesophotic ecosystems make them localised centres of biological productivity.

Biological diversity

The ecosystems we have described have very high biological diversity, and are likely to contain many previously undescribed species. These areas support extensive sponge gardens, especially below around 25 m on the Kapiti coast. These areas also contribute to large scale biodiversity, as the communities found are very different to those in shallow water, where kelp and other seaweeds dominate.

Naturalness

We found little evidence to suggest that these ecosystems have been previously or currently impacted by human activity. However, since this is the first time these ecosystems have been explored it is possible they may have looked different in the past or have been impacted by humans. Without long-term data it is impossible to know this. Our ROV videos did not show any evidence of fishing line entangled on the reef. The domination of these ecosystems by three dimensional organisms does suggest they have not been impacted by bottom contact fisheries, such as trawling, recently.

Ecological function

While the ecological function of mesophotic ecosystems are still very poorly understood, we know these ecosystems provide habitat for a wide range of mobile species as a result of the complex structure. These deeper water habitats in tropical regions have also been considered an important source of larvae to shallow habitats, providing a 'rescue effect' to shallow water populations. This role of mesophotic ecosystems in temperate regions is less clear, since we still have a poor understanding of the overlap between species occurring in both shallower and deeper zones. Mesophotic ecosystems can also provide a thermal refuge for mobile organisms during warmer summer months. The nutrient cycling, particularly through the activities of the sponges and their ability to process DOC, also provides an important link between pelagic and benthic ecosystems (De Goeij et al. 2013). This carbon can then be cycled

through sponges to produce detritus that other organisms can feed on higher up the food chain. It is also likely that as well as using the sponge gardens for habitat, fish are feeding on all the small associated macrofauna living in these ecosystems.

Ecosystem services

The areas surveyed contained a very high abundance of filter feeding organisms and creates biogenic habitat, and are also important for nutrient recycling given they support lots of suspension feeders. The large number of fish associated with the survey areas means these areas are important for seafood provisioning.

4.4 Future research directions

Working on the mesophotic reefs in the Wellington region has been challenging. The very strong tidal currents in the region have seriously limited our ability to deploy the ROVs. Generally we have been limited to 30-45 minute sampling intervals either side of high/low tides, with weaker currents and therefore longer sampling times during neap tides. These tide times on parts of the Wellington coast have also been unpredictable at times (e.g Thoms Rock and Fishermans Rock), and sampling intervals even shorter and in some cases not possible at all. This aspect needs to be carefully considered in the future as this seriously limits deployment times. Here we describe possible future research directions for work on the mesophotic reefs in the Wellington region.

Other deep-water features

Through our discussions with fishers, desk-based research and field observations there are still a number of deeper rocky structures that we have identified throughout the Wellington region that are also likely to support the types of communities we have found in this study (e.g. Vern's Rock and 78 Meter Rise, plus many others). In addition, there are locations (e.g, Ohau point and Thoms rock) that we had hoped to sample as part of the current project but were unable to reach mostly because of the very specific sets of tide and weather conditions required to sample them. A future focus of mesophotic research should be to visit and explore these deeper structures and determine if they also harbour similar or different communities.

Several of these structures are considerably deeper than what we sampled here, so may harbour different communities. In addition, visiting further sites (and also areas in the vicinity of sites sampled in the current project) would provide further ground truthing for the polygons generated in the current project. Based on the data collected at part of the current project, we also expect these other locations to harbour rich biological communities. It would also be useful to connect with local fishermen and Iwi to draw on the local ecological knowledge and Mātauranga Māori to identify other potential deep reef locations.

1) Biotope identification

For operational reasons, we were limited to the use of our DeepTrekker DG3 for the current project and could not employ our new Boxfish Luna. This limited our ability to consistently identify some species between videos and limited the taxonomic resolution at which we could complete our quantitative analyses. However, we were still able to distinguish several common species or morphospecies. Our analysis showed some evidence for variation in the biological communities between the sampled sites on the south coast compared to the Kapiti coast, and very clearly with depth. In the future, we propose further exploration of some of these communities with our Boxfish Luna, which would mean we could distinguish more species and consistent morpho-species for these ecosystems. This would allow us to develop a biotope classification scheme for these mesophotic ecosystems in the Wellington region and allow us quantify spatial variation in these biological communities more accurately. This could be important if any future conservation measures were to be considered (e.g. further marine reserves) as we would be able to tell if all the mesophotic communities in the region are similar or different. Therefore this would aid in ensuring representativeness in protection.

Small-scale variation in mesophotic communities

We believe some finer scale mapping of the rock features we have identified would benefit our understanding of these ecosystems. This would allow us to understand the smaller-scale variation in these benthic communities and also allow us to explore specific variation from deeper reefs into the shallows. The topography/biogeography of the rock features in the region provides limited opportunity for examining the change in benthic communities with depth at a single location (compared to example with Fiordland). However, this could be

possible at Hunter Bank (also see below), since the rocky feature extends from 20 to 50 m. While this is not a huge depth range, this does appear to include a really important transition zone from algal- to animal-dominated communities. Furthermore, logistically for ROV deployment this site has lots of advantages, since we can anchor off the feature and drive the ROV towards the reef, rather than anchoring on the feature and driving the ROV over the edge of the reef, which is more likely to cause entanglement.

Establishment of deep water monitoring

Currently, it's difficult to determine the overall ecological status/quality of the deep water reefs, and we know virtually nothing about their temporal stability or patterns of variation. Monitoring mesophotic communities is logistically challenging since it is not possible to install permanent markers, and visiting exactly the same spot can be challenging. We suggest some effort is focused on the deep-water monitoring at Hunters Bank, and we propose that in combination with the finer scale biological mapping at this site, it is used as a focal area of understanding temporal variation. Clearly, understanding patterns of variation is important for distinguishing human impacts from natural variation. At present there is virtually no data to allow any such assessments to be made across the whole of NZ with the exception of our research in Fiordland and Poor Knights.

Physical environment

Although it is beyond the equipment capabilities of VUW it would be really useful to have high resolution multi-beam imagery for some of these deep water reefs areas, on which we could map the biological information. This would also help to explain some of the smaller-scale patterns in benthic community variation.

Biodiversity assessments

There are likely to be many new records and likely new species in the videos we have taken from the mesophotic communities around the Wellington region. Future work should focus on trying to collect specimens and identify/describe these species. However, while some might be relatively easy to collect with an ROV (e.g. erect or thick massive species), many are

encrusting species or are very thin/delicate, which will make it impossible to collect in this way. It would be worth considering the deployment of professional technical divers to collect a broader range of sponges. However, this will be expensive and based on recent estimates is likely to exceed \$8,000 per dive. These biodiversity questions could potentially be approached using eDNA techniques, although with the likelihood of many yet to be described species it is not clear exactly how valuable this would be.

Ecological function

We currently know very little about the ecological function of these mesophotic ecosystems. However, many of the ROV deployments showed high densities of fish, suggesting they are utilising these habitats for food or primary habitat (or both). Furthermore, these deep water reefs are areas where fishers are congregating, suggesting they are rich fishing grounds for a range of customary, recreationally and commercially important fish species. While we believe ecological function of these reefs is beyond an immediate phase 2 of this project, this is an area of active research for the Bell-Rogers research groups at VUW. Once we have a better understanding of the spatial and temporal variation in these reefs, we will then be better placed for studying function.

Susceptibility to stressors

We have no information at present on how any of the organisms living in these mesophotic ecosystems will respond to stress. We propose collecting specimens with the ROV (at least for those that are readily accessible to ROV collection) to conduct some specific stressor experiments, and we would suggest specifically focusing on the impact of sedimentation (both suspended and settled) and temperature, since we believe these are likely to be the main stressors that could impact on these in the future ecosystem.

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Supplemental material

Table S1. List of categories of benthic organisms identified from 9 mesophotic sites in the Wellington South Coast and Wellington West Coast.

Sponges	Algae
<i>Aaptos globosa</i>	Brown algae
Amorphous yellow sponge	Crustose coralline algae (CCA)
<i>Ancorina</i> sp.	<i>Ecklonia radiata</i>
Arborescent yellow sponge	Red flashy algae
Calcarea	Red filamentous algae
<i>Crella incrustans</i>	Cnidarians
<i>Darwinella oxeata</i>	Sea anemones (Actiniaria)
Encrusting orange sponge	<i>Corynactis australis</i>
Encrusting red sponges	Large Hydroids
Encrusting yellow sponge	<i>Parazoanthus elongatus</i>
<i>Iophon</i> sp.	Bryozoans
Other sponges	Encrusting Bryozoans
<i>Polymastia echinus</i>	Erect bryozoans
<i>Polymastia fusca</i>	Moss Bryozoans (Catenicellidae)
Repent sponges	Ascidians
<i>Stelletta</i> sp.	Encrusting ascidians
<i>Tedania connectens</i>	White colonial ascidians
<i>Tethya</i> sp.	Others
Massive yellow sponge	Brachipods
	Biological matrix

Table S2. Coordinates of the polygons' vertices of Mana and Hunter Bank mesophotic communities, based on substrate morphology and bathymetry.

	Mana Island		Hunter Bank		
	Latitude	Longitude	Latitude	Longitude	
Vertex 1	-40.978596	174.806748	Vertex 1	-40.969167	174.811815
Vertex 2	-41.109148	174.761547	Vertex 2	-40.959307	174.816198
Vertex 3	-41.095388	174.75569	Vertex 3	-40.955983	174.821588
Vertex 4	-41.087314	174.759714	Vertex 4	-40.961268	174.826493
Vertex 5	-41.072802	174.769416	Vertex 5	-40.973204	174.821121
Vertex 6	-41.070661	174.789286	Vertex 6	-40.982667	174.815120
Vertex 7	-41.075025	174.79137			
Vertex 8	-41.073992	174.781237			

Vertex 9	-41.087117	174.764026
Vertex 10	-41.094545	174.766613
Vertex 11	-41.105323	174.769003
Vertex 12	-41.10944	174.769182

Table S3. PERMANOVA table of results describing variance in community composition across 9 mesophotic sites on the WSC and WWC.

Source	df	SS	MS	Pseudo-F	P(perm)	perms
Site	8	81825	10228	10.077	0.0001	9849
Residual	75	76122	1015			
Total	83	1.5795E5				

Table S4. PERMANOVA table of results describing t-test pair-wise variance in community composition across 9 mesophotic sites on the WSC and WWC.

Groups	t	P(perm)	perms
Taputeranga, Arabella Rocks	2.6635	0.0001	8440
Taputeranga, Sharks tooth	2.553	0.0002	9140
Taputeranga, Hunters Bank Deep	3.3647	0.0001	9211
Taputeranga, Hunters Bank Shallow	3.2584	0.0001	8376
Taputeranga, Mana 1	3.763	0.0001	8409
Taputeranga, Mana 2	4.4184	0.0001	9203
Taputeranga, Mana 3	4.0333	0.0001	9176
Taputeranga, Mana 4	4.1039	0.0001	9139
Arabella Rocks, Sharks tooth	2.1653	0.0003	8871
Arabella Rocks, Hunters Bank Deep	3.7869	0.0001	8918
Arabella Rocks, Hunters Bank Shallow	3.6355	0.0004	5071
Arabella Rocks, Mana 1	3.8427	0.0003	5094
Arabella Rocks, Mana 2	4.3966	0.0001	8898
Arabella Rocks, Mana 3	3.9822	0.0001	8952
Arabella Rocks, Mana 4	4.5408	0.0001	8857
Sharks tooth, Hunters Bank Deep	2.866	0.0001	9428
Sharks tooth, Hunters Bank Shallow	2.8333	0.0001	8894
Sharks tooth, Mana 1	2.9107	0.0001	8913
Sharks tooth, Mana 2	3.8973	0.0001	9424
Sharks tooth, Mana 3	3.3664	0.0001	9488
Sharks tooth, Mana 4	3.3811	0.0001	9429
Hunters Bank Deep, Hunters Bank Shallow	2.7627	0.0001	8879
Hunters Bank Deep, Mana 1	2.1497	0.0002	8894
Hunters Bank Deep, Mana 2	3.3112	0.0001	9461
Hunters Bank Deep, Mana 3	2.2936	0.0001	9413
Hunters Bank Deep, Mana 4	3.0336	0.0002	9448
Hunters Bank Shallow, Mana 1	2.8316	0.0004	5071

Hunters Bank Shallow, Mana 2	3.7296	0.0002	8905
Hunters Bank Shallow, Mana 3	3.0732	0.0001	8902
Hunters Bank Shallow, Mana 4	3.2039	0.0001	8912
Mana 1, Mana 2	2.0738	0.0001	8888
Mana 1, Mana 3	1.8266	0.0046	8898
Mana 1, Mana 4	2.0636	0.0007	8862
Mana 2, Mana 3	2.8062	0.0001	9457
Mana 2, Mana 4	2.794	0.0001	9438
Mana 3, Mana 4	1.7608	0.0059	9438

Table S5. PERMANOVA table of results describing t-test pair-wise variance in sponge abundance across 9 mesophotic sites on the WSC and WWC.

Groups	t	P(perm)	Unique perms
Taputeranga, Arabella Rocks	0.11092	0.9088	6964
Taputeranga, Sharks tooth	2.591	0.0105	7397
Taputeranga, Hunters Bank Deep	4.1883	0.0003	8252
Taputeranga, Hunters Bank Shallow	2.2708	0.0359	7701
Taputeranga, Mana 1	2.2465	0.0398	7777
Taputeranga, Mana 2	2.4106	0.023	8694
Taputeranga, Mana 3	3.0851	0.0053	8735
Taputeranga, Mana 4	4.7275	0.0001	8759
Arabella Rocks, Sharks tooth	5.7145	0.0002	8252
Arabella Rocks, Hunters Bank Deep	8.9367	0.0001	8311
Arabella Rocks, Hunters Bank Shallow	4.0491	0.003	3940
Arabella Rocks, Mana 1	3.5913	0.0065	2705
Arabella Rocks, Mana 2	3.7024	0.0032	8364
Arabella Rocks, Mana 3	5.0239	0.0005	7489
Arabella Rocks, Mana 4	16.684	0.0001	8430
Sharks tooth, Hunters Bank Deep	2.9752	0.0083	9037
Sharks tooth, Hunters Bank Shallow	0.16591	0.875	8848
Sharks tooth, Mana 1	0.26878	0.7841	8745
Sharks tooth, Mana 2	0.19825	0.8454	9360
Sharks tooth, Mana 3	1.1371	0.2706	9350
Sharks tooth, Mana 4	4.5087	0.0005	9332
Hunters Bank Deep, Hunters Bank Shallow	2.0475	0.058	8825
Hunters Bank Deep, Mana 1	1.7025	0.1123	8785
Hunters Bank Deep, Mana 2	1.9064	0.0739	9361
Hunters Bank Deep, Mana 3	1.148	0.2656	9320
Hunters Bank Deep, Mana 4	0.56157	0.6015	9142
Hunters Bank Shallow, Mana 1	9.6628E-2	0.9208	5017
Hunters Bank Shallow, Mana 2	3.2931E-2	0.9743	8868
Hunters Bank Shallow, Mana 3	0.76686	0.455	7803
Hunters Bank Shallow, Mana 4	2.8318	0.0036	8778
Mana 1, Mana 2	6.6417E-2	0.9458	8813
Mana 1, Mana 3	0.60425	0.5474	8259
Mana 1, Mana 4	2.2785	0.0282	8897
Mana 2, Mana 3	0.73033	0.4687	9353
Mana 2, Mana 4	2.4962	0.0241	9338

Mana 3, Mana 4	1.7098	0.101	9285
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Table S6. PERMANOVA table of results describing t-test pair-wise variance in bryozoan abundance across 9 mesophotic sites on the WSC and WWC.

Groups	t	P(perm)	perms
Taputeranga, Arabella Rocks	2.7526	0.006	7702
Taputeranga, Sharks tooth	2.6572	0.0056	7630
Taputeranga, Hunters Bank Deep	1.58	0.1317	9049
Taputeranga, Hunters Bank Shallow	1.0425	0.3431	8402
Taputeranga, Mana 1	0.58921	0.558	8318
Taputeranga, Mana 2	0.68941	0.5029	9085
Taputeranga, Mana 3	2.0338	0.0583	9095
Taputeranga, Mana 4	0.88419	0.4044	8683
Arabella Rocks, Sharks tooth	0.86908	0.3937	8338
Arabella Rocks, Hunters Bank Deep	5.4553	0.0002	8409
Arabella Rocks, Hunters Bank Shallow	2.8574	0.0012	3992
Arabella Rocks, Mana 1	1.9674	0.0676	3971
Arabella Rocks, Mana 2	3.3932	0.0035	8440
Arabella Rocks, Mana 3	0.91427	0.3826	7018
Arabella Rocks, Mana 4	5.0294	0.0002	7746
Sharks tooth, Hunters Bank Deep	5.5424	0.0001	9290
Sharks tooth, Hunters Bank Shallow	2.9424	0.0006	8814
Sharks tooth, Mana 1	1.7877	0.0917	8755
Sharks tooth, Mana 2	3.3989	0.0028	9327
Sharks tooth, Mana 3	0.44418	0.6632	9332
Sharks tooth, Mana 4	4.2826	0.0005	9072
Hunters Bank Deep, Hunters Bank Shallow	5.604E-3	0.9953	8408
Hunters Bank Deep, Mana 1	2.1581	0.0486	8811
Hunters Bank Deep, Mana 2	0.76077	0.4648	8748
Hunters Bank Deep, Mana 3	4.2536	0.0006	9291
Hunters Bank Deep, Mana 4	3.4399	0.0013	9140
Hunters Bank Shallow, Mana 1	1.3753	0.1917	5083
Hunters Bank Shallow, Mana 2	0.5141	0.6354	8777
Hunters Bank Shallow, Mana 3	2.5349	0.0068	8841
Hunters Bank Shallow, Mana 4	1.8112	0.0358	7757
Mana 1, Mana 2	1.2111	0.2435	8894
Mana 1, Mana 3	1.2471	0.2243	8830
Mana 1, Mana 4	3.1566E-2	0.976	8407
Mana 2, Mana 3	2.7349	0.0141	9268
Mana 2, Mana 4	1.74	0.0962	9061
Mana 3, Mana 4	2.0794	0.0504	9051

