A preliminary exploration of the rocky mesophotic communities of the Wellington Region (Combined report for Phases 1 and 2)

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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 Vehicles at seventeen sites, three on the WSC and 14 on the Kapiti coast, covering a depth range from 26 to 72 m. The three sites on the WSC were all shallower than 30 m, while the sites on the Kapiti coast ranged from 26-72 m. We also deployed a baited underwater video camera system (BUV) at one site at Hunters Bank to explore fish assemblages at mesophotic depths. 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 (although this was masked by sediment in many locations). 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. Our BUV deployment identified seven fish species, with Blue cod being the most abundant 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 ~ 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 ~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 proposed 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", they are likely to be particularly ecologically important.

The Wellington region has several 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/customary 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 (particularly during periods of calm weather). 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 remotely operated vehicle (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. This project was split into two phases.

Phase 1 aims:

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.

Phase 2 aims:

1) Explore more sites (minimum 5) to confirm the further presence of TMEs and describe the dominant fauna with a view to determine the spatial extent of TMEs in each location and be able to delineate boundaries;

2) Quantify the abundance of benthic organisms to the lowest taxonomic level for a minimum of 4 locations around Hunter Bank to assess the level of local scale variability in TME communities.

3) Conduct preliminary assessments of the fish populations at Hunter Bank and a minimum of one other TME location in the Wellington region. This may include some Baited Underwater Camera deployments and/or ROV deployments.

4) Where possible collect examples of the dominant TME organisms for identification purposes.

2. Methods

2.1 Study sites

We used ROV deployments to investigate nine sites (Figure 1; Table 1) in Phase 1 (predominantly 2022) and an additional nine sites in Phase 2 (predominately 2023) across two main locations within the Greater Wellington Region. 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). Fourteen sites were surveyed on the Kapiti Coast (KC) and three sites on the Wellington South Coast (WSC). Six of the fourteen sites on the KC are distributed across the northern and southern ends of Mana Island (Mana D1-D6) with a total depth range of 30 – 52 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. Five sites (Hunters D1-D5) sampled on the KC were located on a shallow-mesophotic (26 – 33 m) and deeper mesophotic (45-57 m) region of Hunters Bank, situated between Mana Island and Kapiti Island (Figure 1). Three further sites (Verns Rock D1-D3) were sampled in the deeper water (>70 m) at Verns Rock (noting this is a series of rocky areas rather than a single rock). All KC sites receive high current flow outside of slack tide periods. These sites are currently fully open to recreational fishing activity. The 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. We also deployed a baited underwater camera at one site (Hunters D6) at Hunters Bank.

Table 1. Metadata for surveyed mesophotic sites across the Wellington South Coast (WSC) and the Kapiti Coast (KC). The shaded cell indicates the location of the Baited Underwater Camera Deployment.

	Date	Project	Location	Area	Depth	Latitude (EPSG:4326)	Longitude (EPSG:4326)
1	1/03/22	Phase 1	Wellington West Coast	Mana D1	38-45 m	-41.0919	174.7604833
2	1/03/22	Phase 1	Wellington West Coast	Mana D2	46 m	-41.09366667	174.75825
3	1/03/22	Phase 1	Wellington West Coast	Mana D3	30 m	-41.07346667	174.7880167
4	23/03/22	Phase 1	Wellington South Coast	Arabella rocks	26 m	-41.41171667	174.8557333
5	23/03/22	Phase 1	Wellington South Coast	Taputeranga Island	27 m	-41.35988333	174.7688833
6	24/03/22	Phase 1	Wellington South Coast	Shark Tooth	30 m	-41.366964	174.799598
7	30/04/22	Phase 1	Kapiti Coast	Hunters D1	45-57 m	-40.971488	174.81503
8	30/04/22	Phase 1	Kapiti Coast	Hunters D2	26-33 m	-40.971686	174.813342

9	6/05/22	Phase 1	Wellington West Coast	Mana D4	45-50 m	-41.106491	174.764098
10	23/08/22	Phase 2	Wellington West Coast	Mana D5	42-52 m	-41.104942	174.763703
11	23/08/22	Phase 2	Wellington West Coast	Mana D6	43-51 m	-41.103162	174.764493
12	5/12/22	Phase 2	Wellington West Coast	Verns Rock D1	70-72 m	-41.138859	174.720262
13	30/04/23	Phase 2	Kapiti Coast	Hunters D3	30 m	-40.9701	174.81655
14	30/04/23	Phase 2	Kapiti Coast	Hunters D4	54-59 m	-40.969854	174.814402
15	30/04/23	Phase 2	Kapiti Coast	Hunters D5	70 m	-40.969779	174.813953
16	1/05/23	Phase 2	Wellington West Coast	Verns Rock D2	70 m	-41.13896667	174.7202667
17	1/05/23	Phase 2	Wellington West Coast	Verns Rock D3	70 m	-41.138288	174.720531
18	30/4/23	Phase 2	Kapiti Coast	Hunters D6 – BUV	50 m	-40.958873,	174.858232

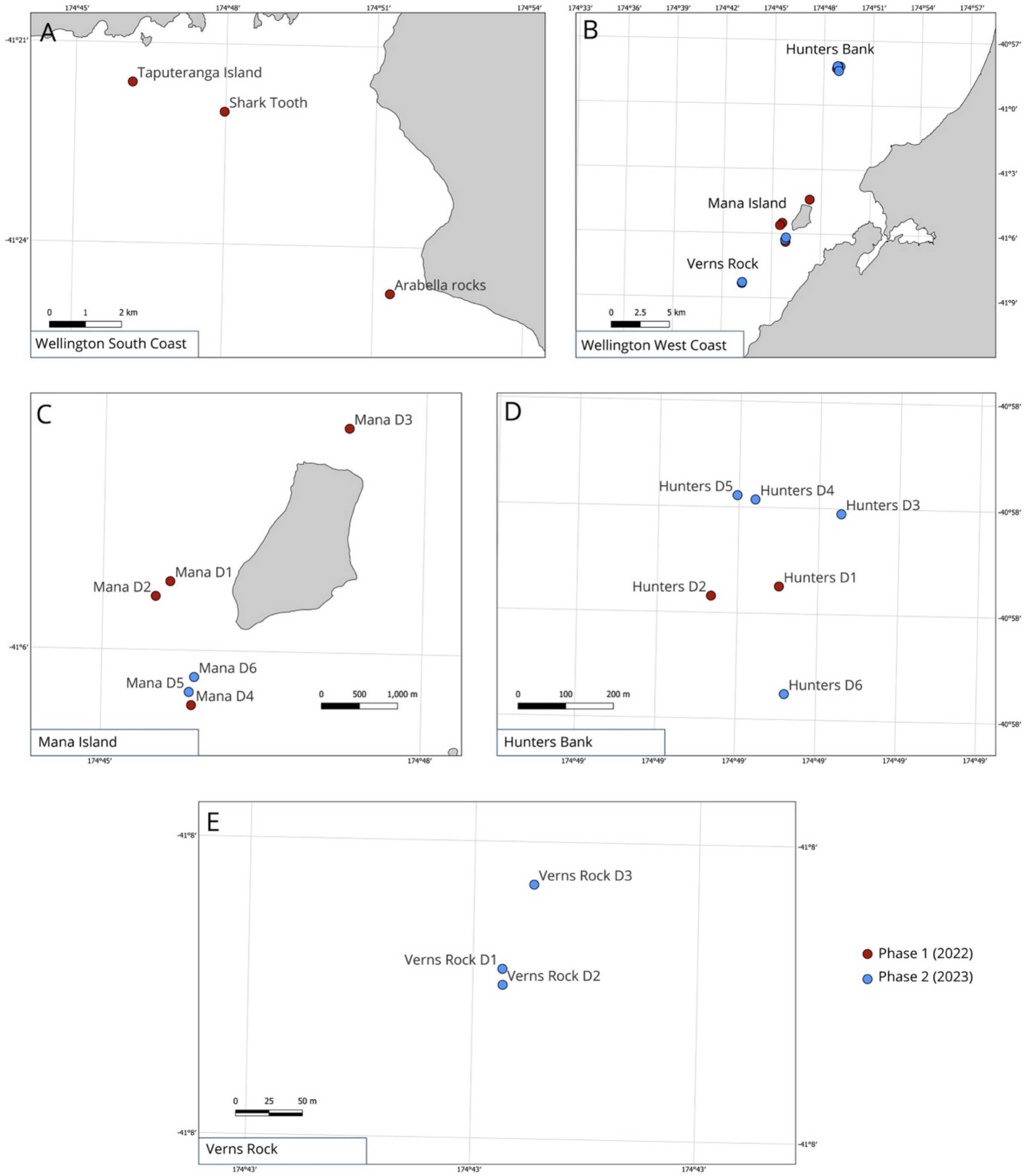


Figure 1. Locations of ROV deployments in the Wellington region between 2022 and 2023. A) Site locations on the Wellington south coast. B) Site locations on the Kapiti coast. Sampled locations around Mana Island (C), Hunters Bank (D) and Verns Rock (E). See Table 1 for specific details of each location. Note: that site D6 was the location for the deployment of the Baited Underwater Video Camera.

2.2 Benthic video collection

For sites sampled in phase 1, 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. In Phase 2 we used our Boxfish Alpha and Chasing ROVs to capture video footage at each of the sample sites. Different ROVs were used based on weather conditions on deployment days, and availability of the Boxfish (which captures the highest resolution videos). The potential issue of parallax error (Rivero Calle, 2010 as discussed in Lesser & Slattery, 2019) was addressed 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 VUW vessel The Raukawa Challenger and the commercial vessel the Black Pearl. 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. For the DG2 deployments, 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. The Boxifsh and Chasing ROVs are fully vectored, meaning the camera is fixed and the ROV can move on any axis to become perpendicular to the substrate. 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 72m at Verns rock (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).

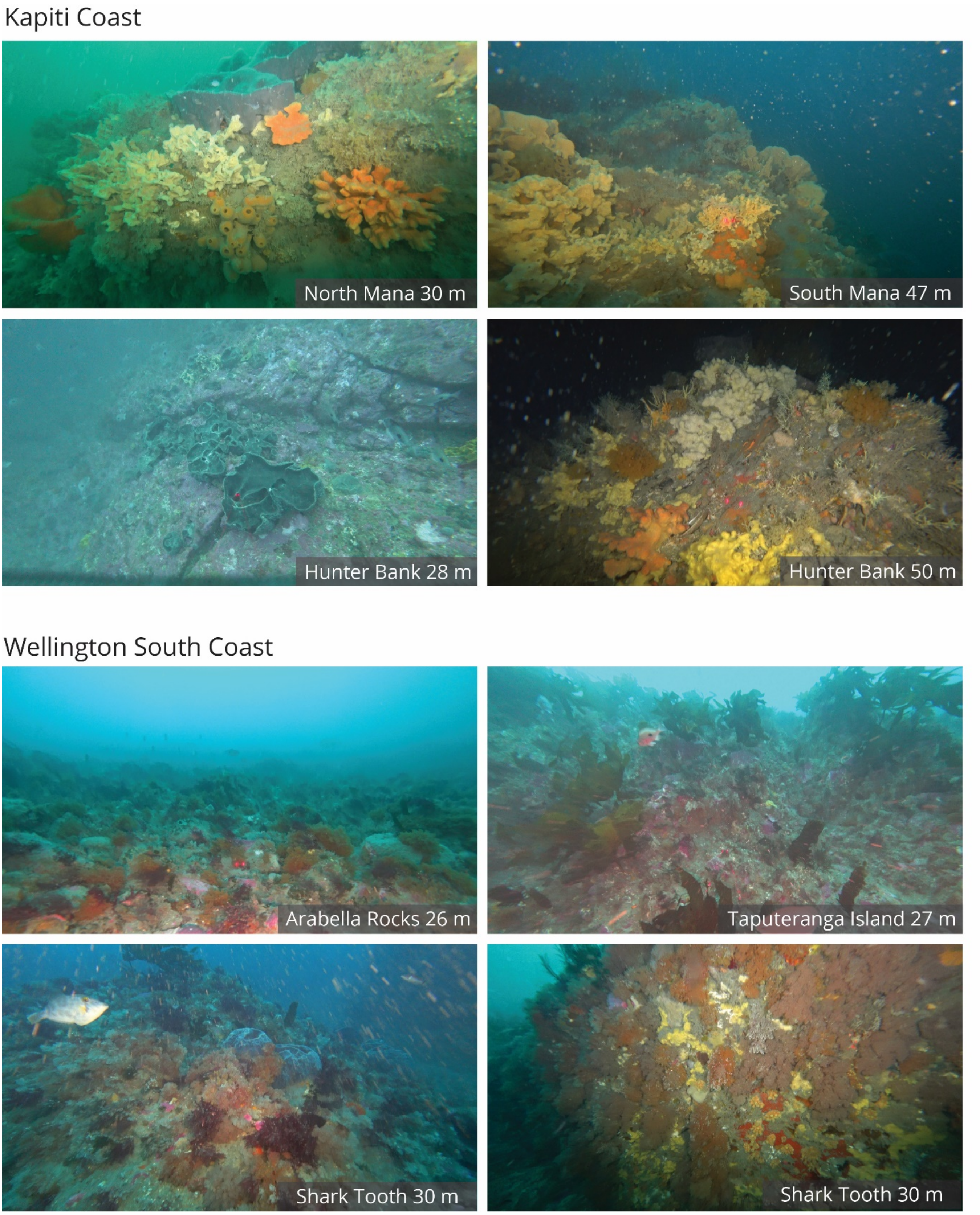


Figure 2. Examples of mesophotic benthic habitats found during this study.

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 category bare substrate/sediment (defined as sediment in figures) was also included ensuring the total cover of each image equalled 100%. Sediment included areas of the reef where the substrate could not be seen and it was covered in sediment. These major categories covered every identifiable organism observed. 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 Video data analysis

Data was analysed using PRIMER V6 + PERMONOVA. 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 across all sampling sites. In addition, we conducted a separate analysis at Hunter Bank to look at small scale variation. 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. MDS plots were created for the entire dataset and also separately for the data collected from Hunters Bank to assess smaller-scale variation in benthic communities.

2.5 Baited Underwater Video deployment

The assessment of carnivorous/scavenging fish assemblages was conducted using a Baited Underwater Video (BUV) system tethered to a surface buoy. The system was designed based on that described by Willis & Babcock (2000) and equipped with a GoPro camera and single 1500 lumen light housed within a GroupBinc housing (Jensen Beach, Florida, USA). The bait was housed in a perforated bucket that was positioned 1 m horizontally from the camera. Mackerel was used as bait (approx. 100g). The BUV deployed at site D6 in 50 m (Figure 1 and Table 1) to the southeast of Hunters Bank for approximately 2-hour period. The first 20-25 minutes of the deployment the light was off (using a timer system) to allow fish to become accustomed to the presence of the BUV. Unfortunately, the BUV system was extensively damaged during this first deployment when retrieved and therefore we were only able to make one deployment.

2.6 Baited Underwater Video analysis

After retrieval of the BUV, 2 hours of video was analysed to record fish abundance (from when the light turned on). The 2 hour video was analysed in 30 second segments (120) for the entire BUV deployment. The the maximum number of individuals of each species was recorded for each segment. Species abundance was measured in terms of: 1) MaxN; the highest abundance of each species in any of the 30 second segments across the entire deployment; and 2) The mean highest abundance of each species averaged across all 30 second segments.

3. Results

3.1 Site and depth variation in benthic community composition

Benthic community composition was significantly different between sites (PERMANOVA, $F_{16,157} = 14.08$, $p < 0.001$) (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 ($F_{16,157} = 15.52$, $p < 0.001$). 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.

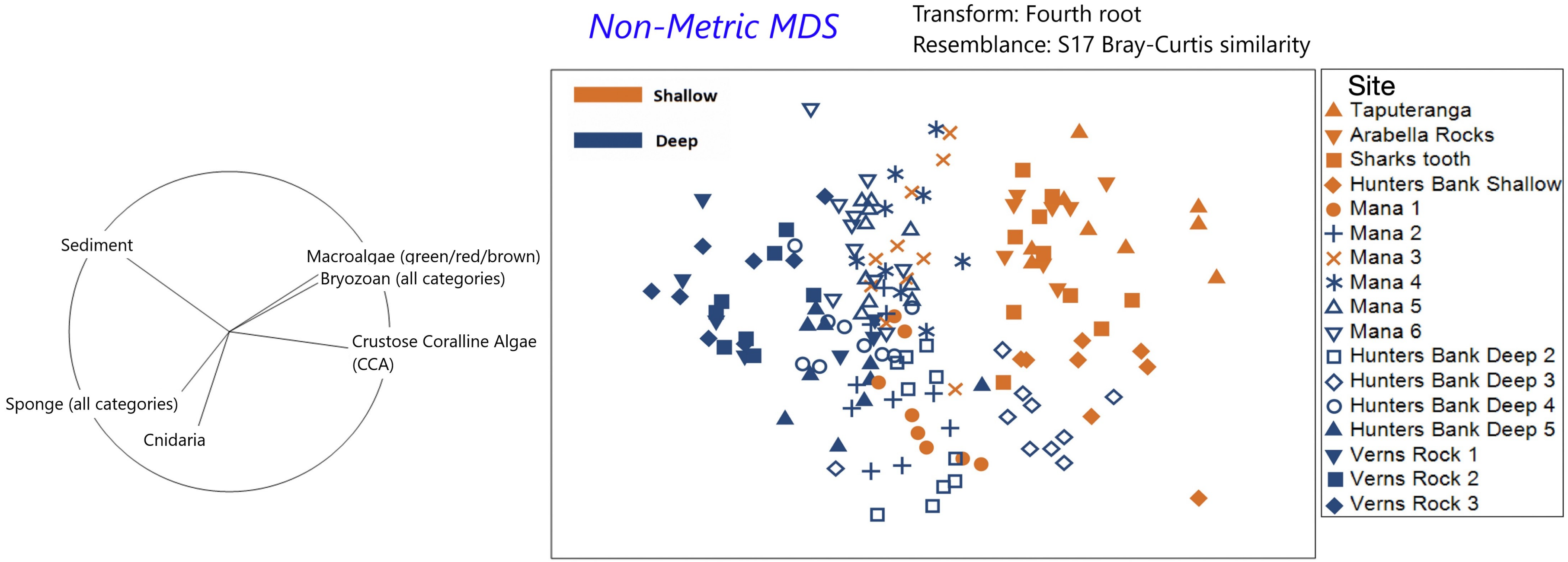


Figure 3. Multidimensional scaling (MDS) plot of centroids of benthic communities for a combination of site (represented by symbol shape) and depth (represented by symbol colour, shallow < 30 m, and deep > 30 m) for 17 mesophotic sites (left) with overlaid vector using Pearson correlation (> 0.45).

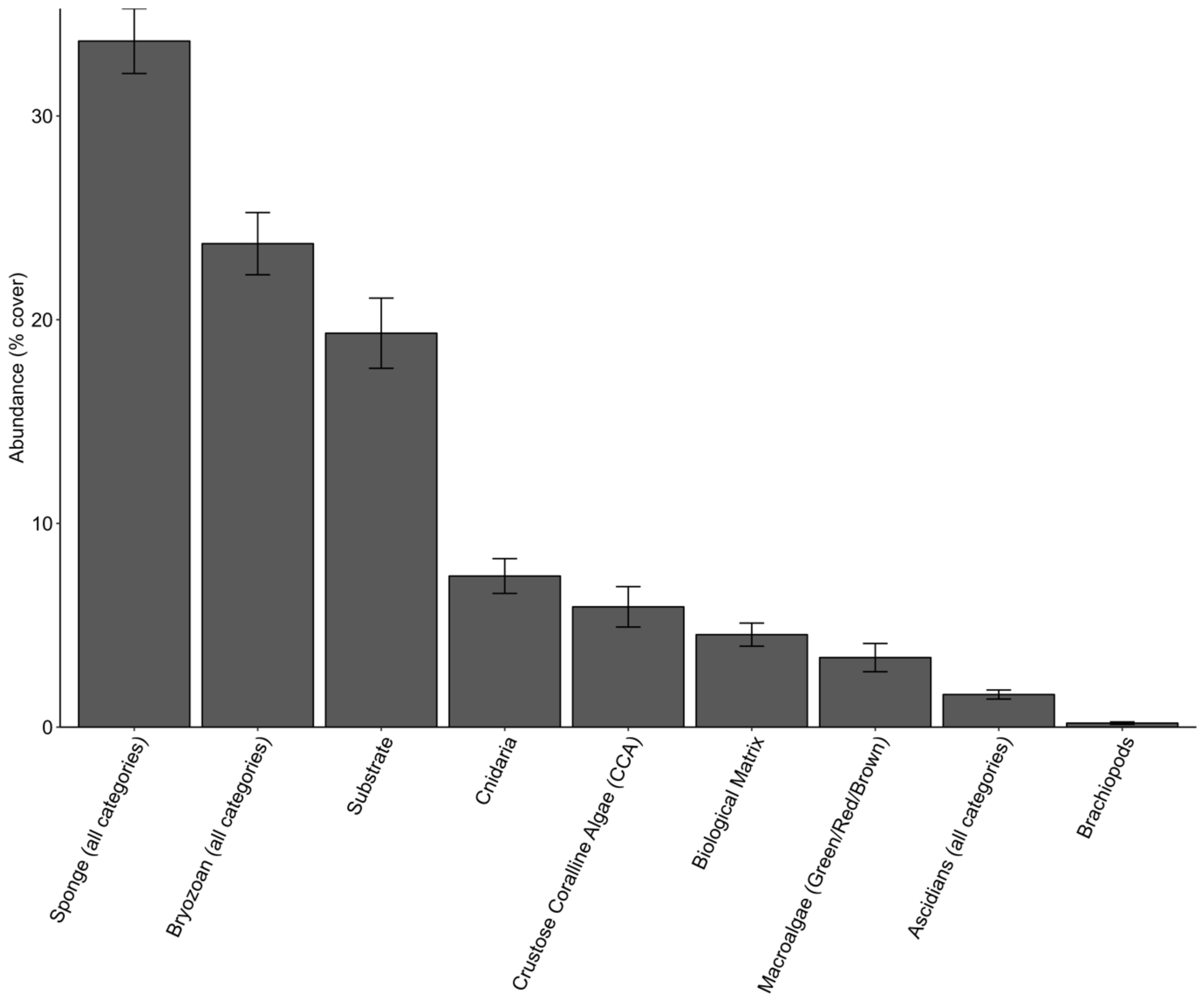


Figure 4. Average abundance (as % coverage) of the most abundant major organisms across all 17 benthic study sites. Error bars are ± SE.

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 33.1 (± 2.6) % and 24.5 (± 2.3) % of the available substrate, respectively. This was more than 3.5 times the abundance of the next most abundant biological group Cnidaria (8.8 ± 1.4%), which predominantly consisted of large hydroids and dense *Parazoanthus* colonies (although this was highly variable). Overall, the presence of sediment covered substrate was high (19.4 ± 3.1%).

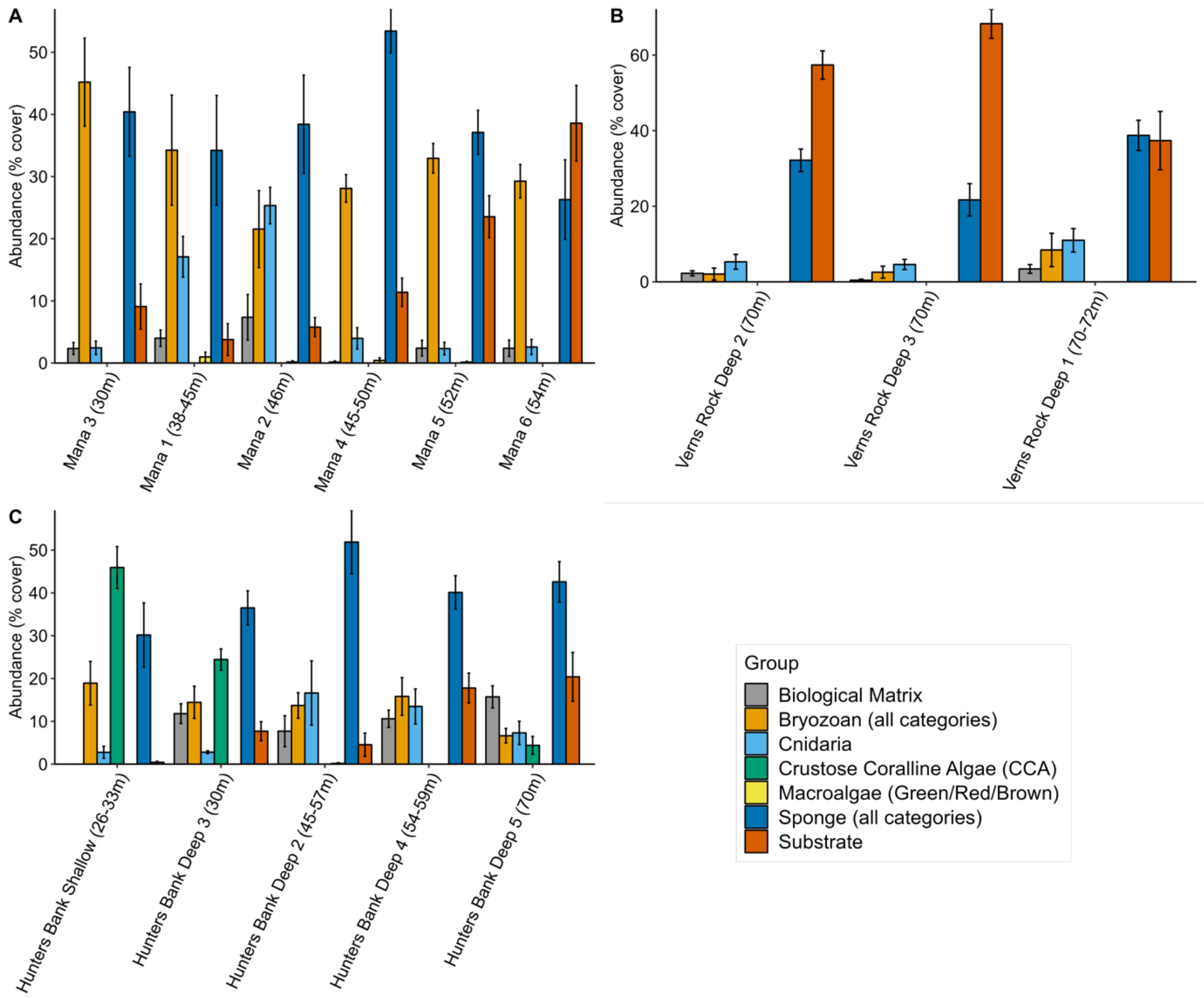


Figure 5. Percentage cover of the seven most abundant benthic groups at 17 mesophotic reef sites in order of depth on the Kapiti coast ranging from 26 – 57 m. Error bars are ± SE. A) Mana Island; B) Verns rock; and C) Hunters Bank.

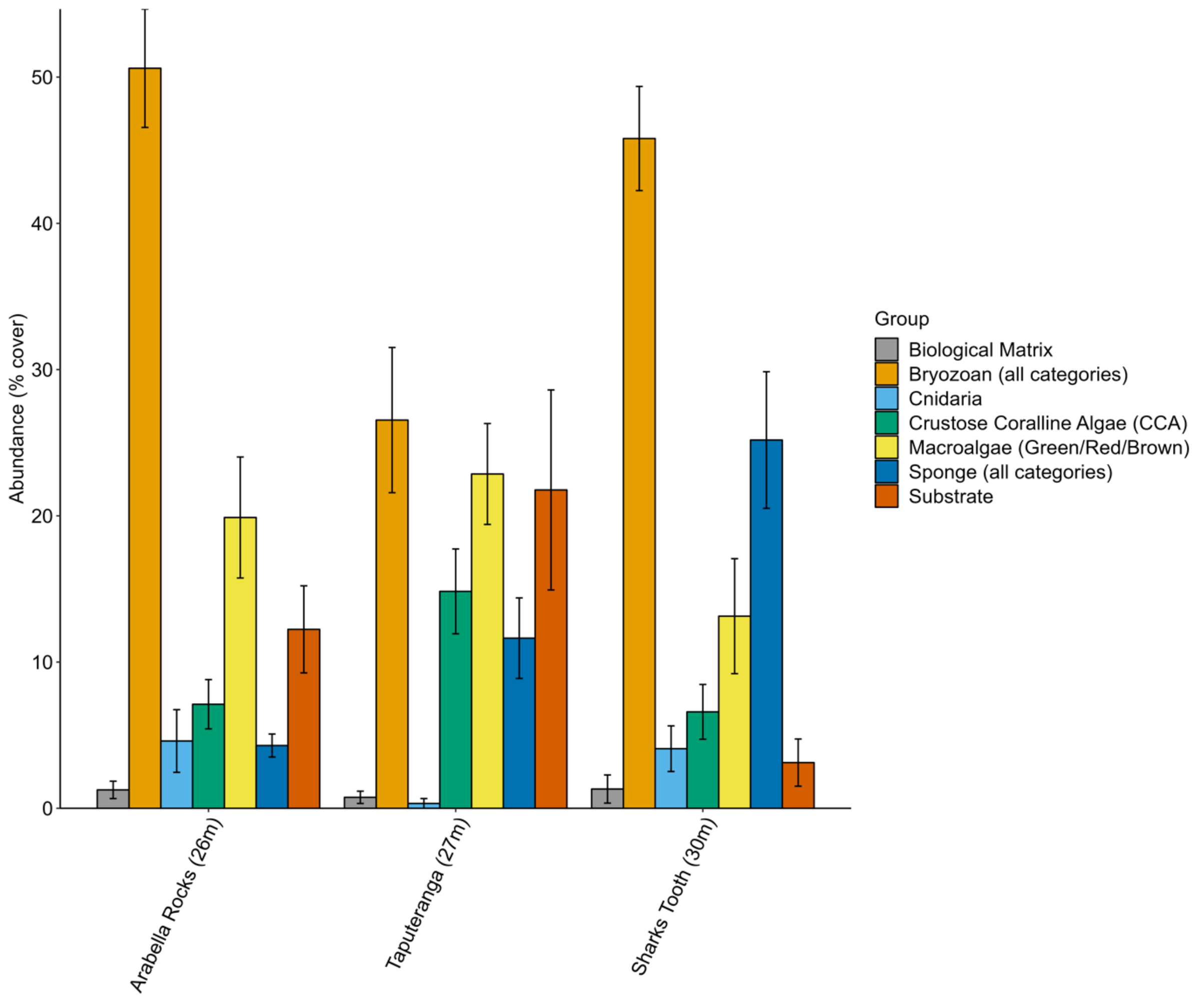


Figure 6. Percentage cover of the seven most abundant benthic groups at three mesophotic reef sites on the Wellington south coast at approximately 30 m. Error bars are ± SE.

3.3 Sponge distribution

While sponges and bryozoans appeared to dominate the benthic communities overall, they exhibited significant variation in abundance between sites ($F_{16,157} = 15.78$, $p < 0.001$ and $F_{16,157} = 12.24$, $p < 0.001$ 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 and Mana sites with the highest sponge abundance being found at Mana Site 4 with 53.4 (± 3.5) % cover. 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.

3.4 Bryozoan distribution

The overall dominance of bryozoans (alongside sponges) (Figure 5 and 6) was driven by 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 all the sites on the KC. 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).

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 $\pm$ 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). The most abundant sponge was Iophon sp. (identified in Phase 2; 10.3 ± 1.6% average across all sites; closely followed by *Ancorina* at 8.6 ± 1.7% averaged across all sites) (Figure 8).

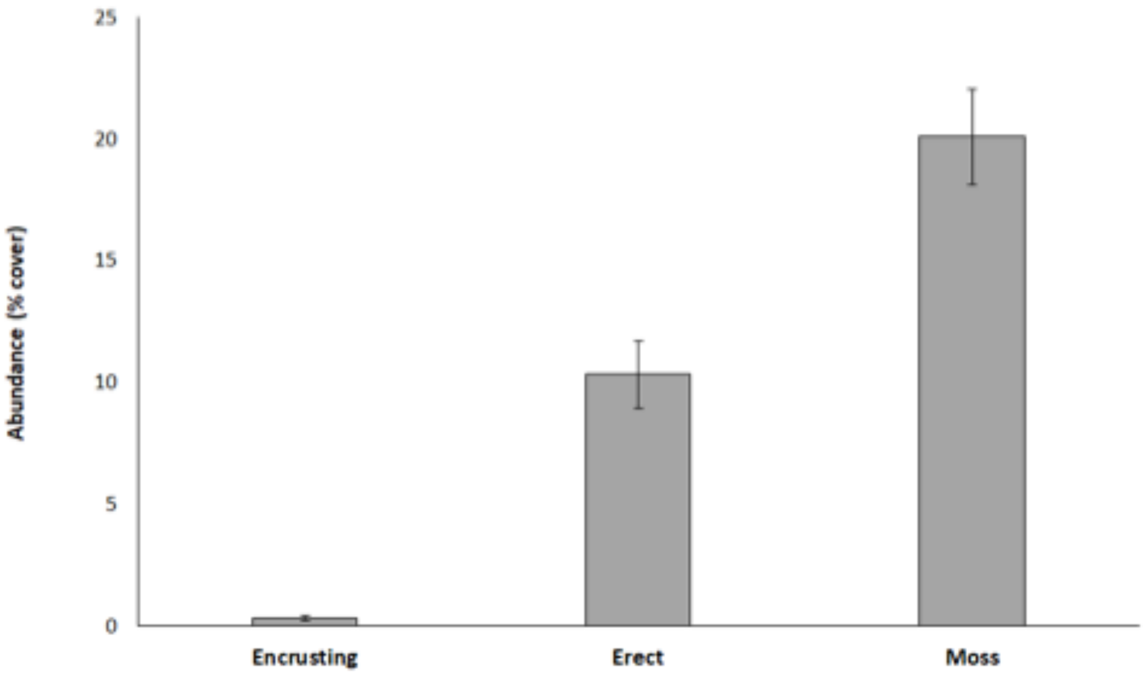


Figure 7. Percentage cover of the three assigned bryozoan morphological categories across all nine study sites. These categories encompass all bryozoans observed. Error bars are ± SE.

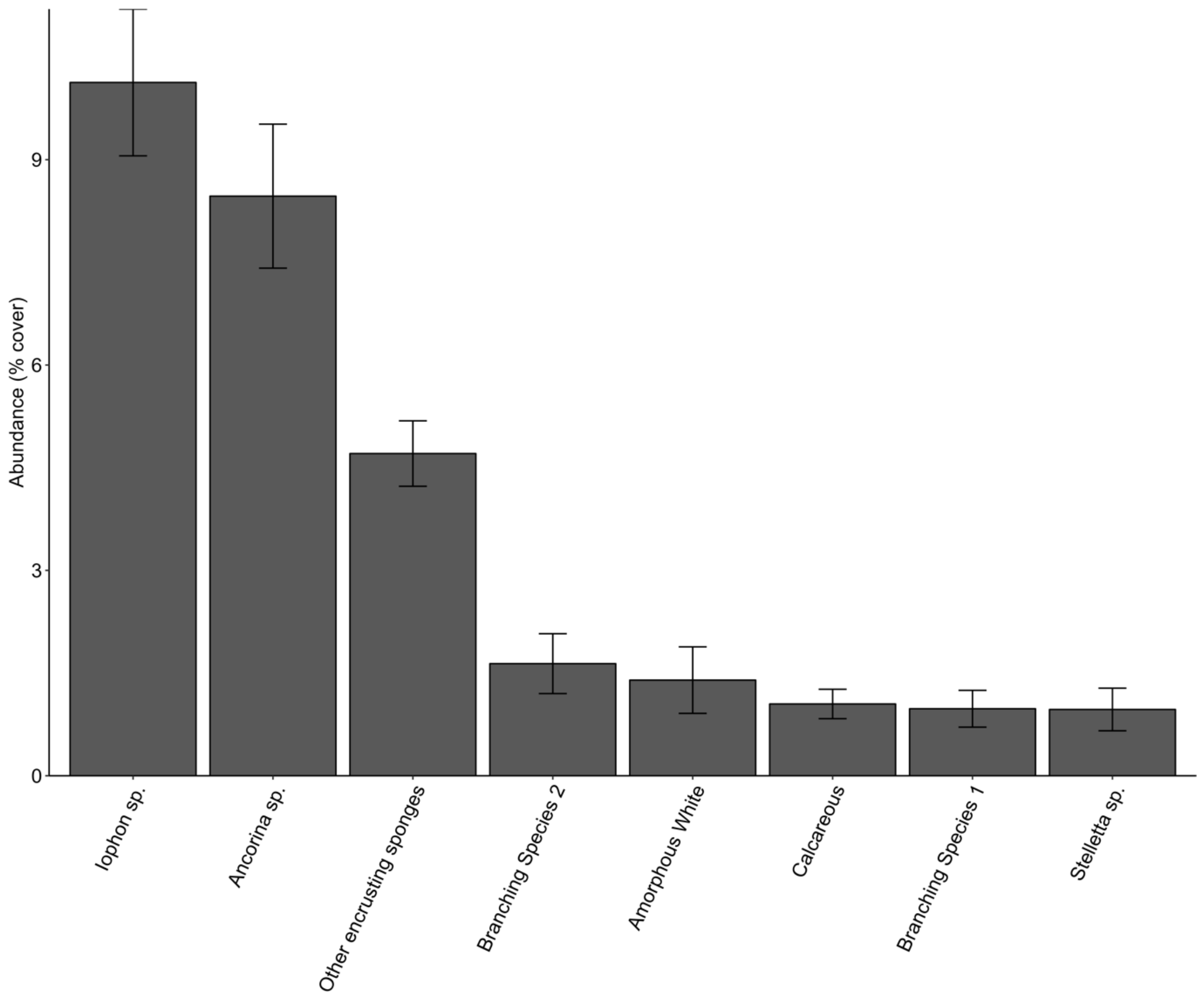
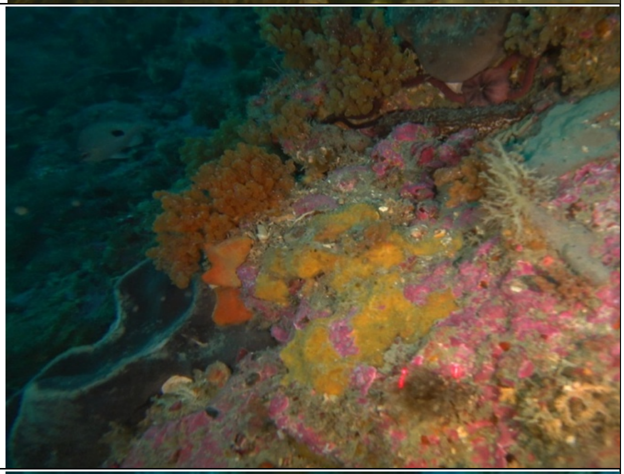


Figure 8. Percentage cover of the most abundant assigned sponge categories across all fourteen study sites (See Table 2). Error bars are ± SE.

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. Iophon sp.	Mana Site 2. Highly abundant across Mana sites, Vern's rock and Hunter Bank.	

<table>
<tr><td>2. Ancorina sp.</td><td>Mana Site 1. Easily identifiable. Large grey/black massive morphology. High abundance.</td><td></td></tr>
<tr><td>3. Other Encrusting sponges</td><td>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.</td><td></td></tr>
<tr><td>4. Branched species Type 1 -</td><td>Hunters shallow. Very broad category of amorphous sponge species. Includes a number of white and orange species.</td><td></td></tr>
<tr><td>5. Amorphous white</td><td>Mana site 2. Very similar morphology and apparent habitat preference to Iophon, and possibly the same species. Differentiated due to distinct colour difference.</td><td></td></tr>
</table>

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

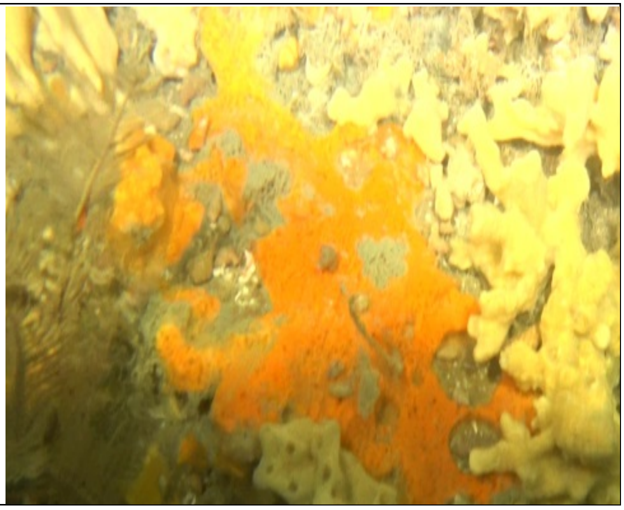
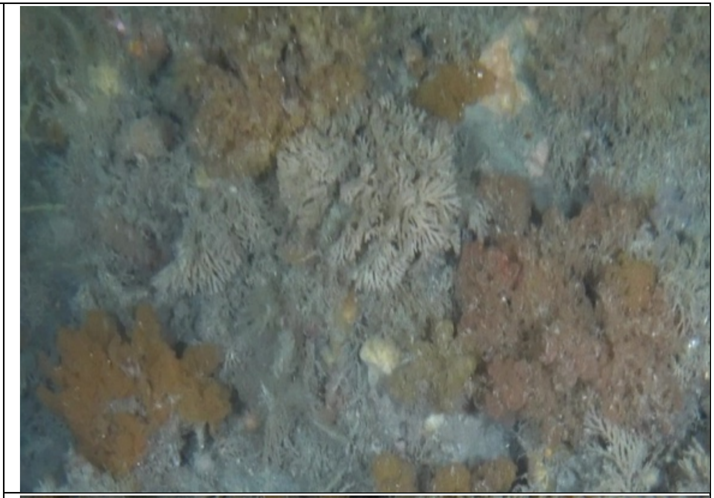
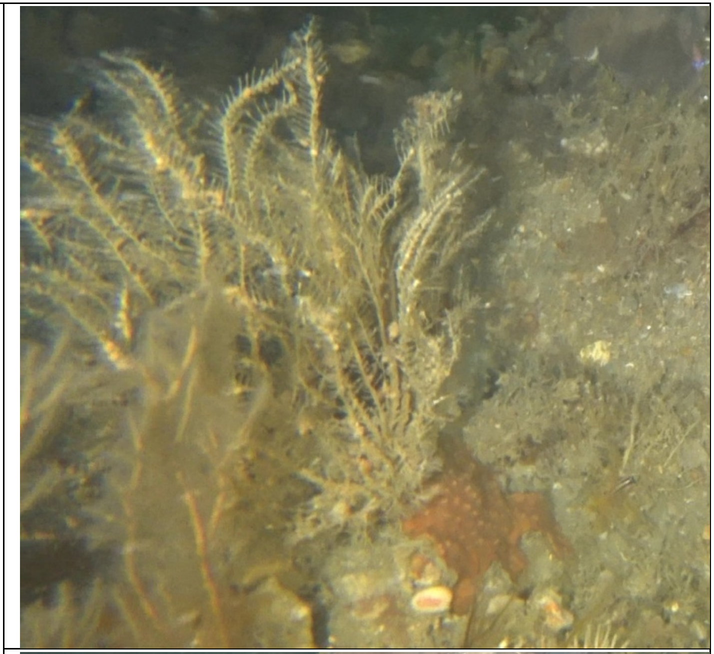
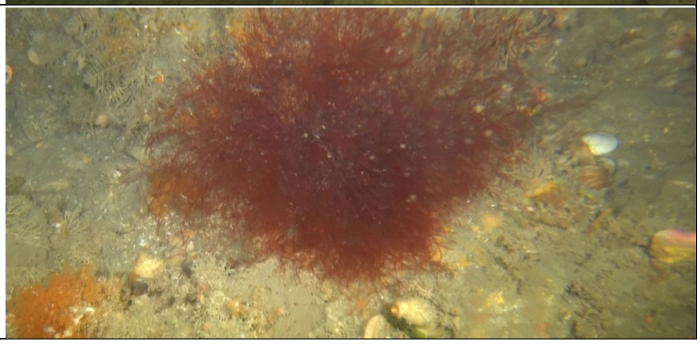
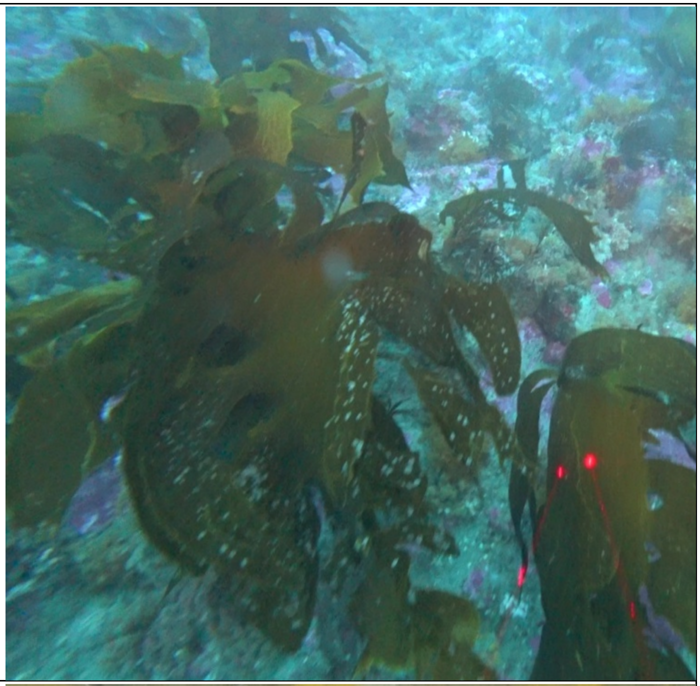
9. *Crella incrustans*	Very common at certain sites despite relatively less common compared to other categories when average abundance was considered across all sites. Occurs in a range of morphology from almost flat/encrusting to three-dimensional, plate-like forms.	

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)	Mana 2. Highly abundant at all sites beyond 30 m. Some range in colour from very pale pink to orange. Likely, *Cornuticella taurina*(orange) *and Amathia wilsoni* (pale / white).	 

2. Bryozoan (Erect/branching)	Mana 1. Highly abundant at deeper sites. Wide range of morphologies and sizes. Likely to be a diverse mix including *Hornera robusta* and *Caberea zelandica.*	 
3. Cnidaria (Parazoanthus)	Very abundant at Mana sites. Occurs in patches often underneath overhangs and appears to associate with massive sponge morphologies.	

4. Cnidaria (Large hydroids)	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 *Ancorina* sp.	 
5. Macroalgae (Red)	Uncommon at all sites. Predominantly filamentous forms.	

6. Macroalgae (Green/Brown)	Multiple stalking species with diverse morphologies including: *Ecklonia radiata* (show in image), and *Lessonia* 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.	

3.7 Small scale variation at Hunter Bank

We found evidence for small scale variation in the benthic communities at Hunters Bank (Figure 9). Consistent with the patterns for the entire dataset, the single shallow site at Hunters Bank was different to the deep-water sites. However, there was evidence from the MDS plot that sites D2, D4, D5 to the west of Hunters Bank have different community composition to sites on the eastern side and D1 and D3. This pattern was largely driven by differences in CCA, biological matrix and amount of 'free' substrate and brachiopod abundance.

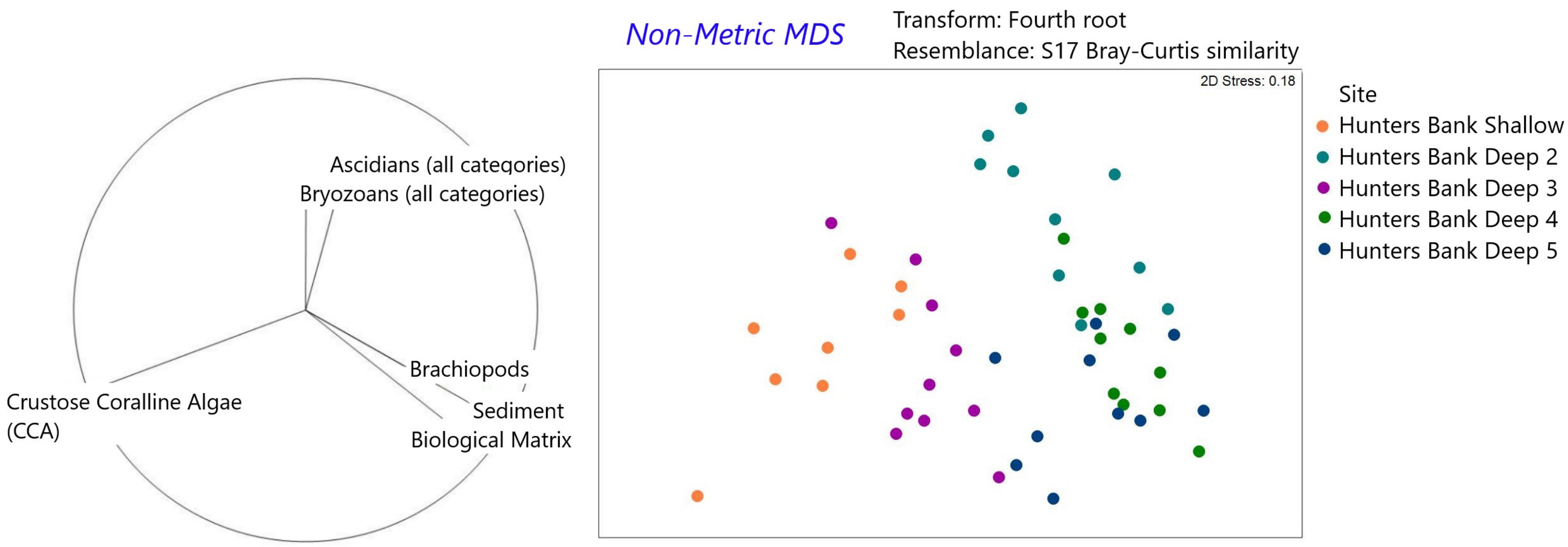


Figure 9. Multidimensional scaling (MDS) plot of centroids of benthic communities for a combination of site for the five mesophotic sites (right) at Hunters Bank with overlaid vectors using Pearson correlation (> 0.45) (left).

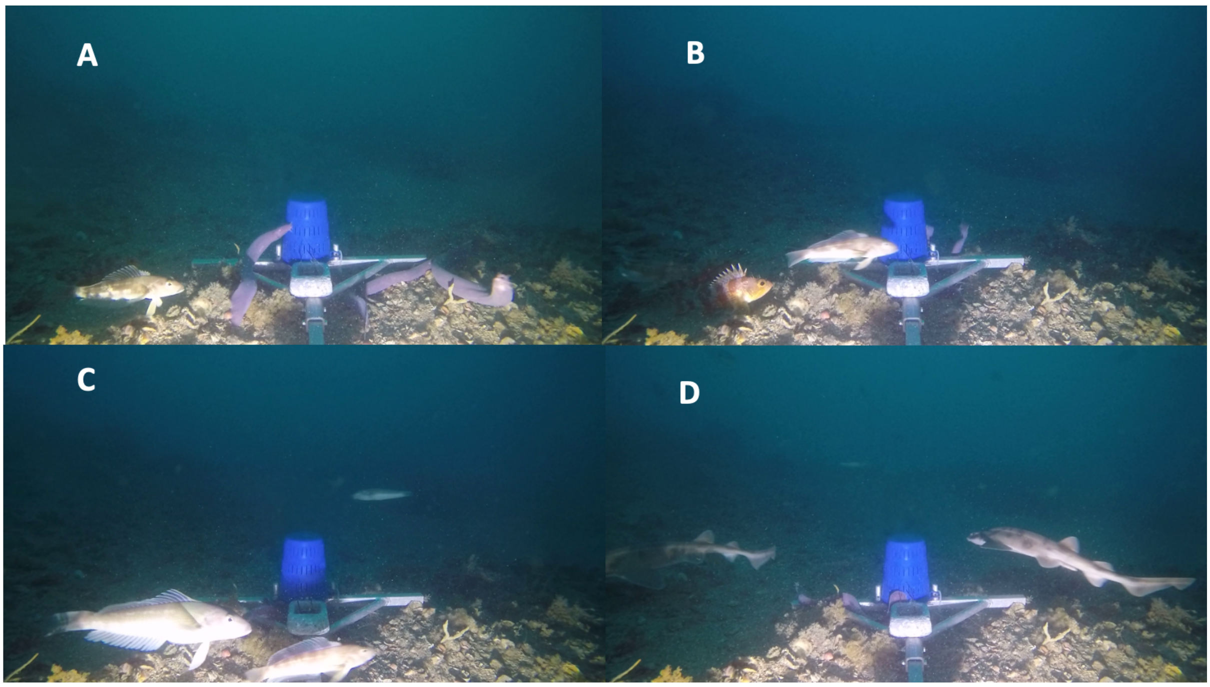
3.8 Baited underwater video

We identified seven species from the baited underwater camera footage (Table 4). The most abundant fish were Blue cod, which were observed in virtually every video. This was followed by Hagfish, Butterfly Perch and Jock Stewart (Figure 10).

Table 4. Fish species identified from the Baited Underwater Video analysis at Hunter Bank, and the percentage of video clips where each species was found (presence/absence), Nmax and Mean Nmax.

	Species	Presence/Absence(%)	Nmax	Mean Nmax
Blue Cod	*Parapercis colias*	96	6	2.5
Hagfish	*Eptatretus cirrhatus*	50	2	0.72
Butterfly perch	*Caesiopera lepidoptera*	45	4	0.54
Jock Stewart	*Helicolenus percoides*	37	5	0.58
School Shark	*Galeorhinus galeus*	18	2	0.15
Tarakihi	*Nemadactylus macropterus*	12	2	0.12
Leather Jacket	*Meuschenia scaber*	2	1	0.02

Figure 10. Examples of the fish species identified from the Baited Underwater Video camera at Hunters Bank. A) Blue cod and Hagfish; B) Blue cod and Jock Stewart; C) Blue cod; and D) School Sharks.



4. Discussion

4.1 Overview of sponge gardens

Our 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 termed ‘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.

We did find evidence for smaller-scale variation in the benthic community composition around Hunters Bank, with support for east-west community differentiation. This difference seems likely to be driven by the orientation of the reefs into the prevailing swells, although the differences were generally driven by the less abundant organisms. From a management perspective it does mean than if in the future any protection was afforded to Hunters Bank it would need to account for this variation.

4.2 Mesophotic fish assemblages

Despite only conducting one deployment of the Baited Underwater Video camera (due to system being damaged), we found extensive fish assemblages in mesophotic depths, which include recreationally, culturally, and commercially important species. We saw large numbers of Blue cod, although due to the nature of baited underwater camera deployments these are likely to be many of the same individuals observed in multiple frames. This is expected for this survey technique. However, our observations do highlight that mesophotic reefs are home to many fish. While we did not explicitly measure size of the fish observed, approximate sizing based on the size of the bar holding the bait suggested that all the Blue Cod observed were below the legal catch size (33 cm). It was not possible to size the other species.

We do note that while we did see some Butterfly perch (*Caesiopera lepidoptera*) in the baited camera, when using the ROV we saw large schools of this species (many 100s). This is not surprising since Butterfly perch feed on planktonic organisms and bottom-dwelling invertebrates and therefore would not have been attracted to the bait and were just likely passing by the camera. It will be important in the future to attempt to quantify fish abundance using other methods such as newly available long-term monitoring cameras or possibly ROV transects (noting this will be very hard given the low visibility at most sites).

4.3 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). In phase 1, despite the areas we sampled being subject to recreational fishing pressure there were no obvious impacts from these activities based on our videos. However, we did detect human impacts in our videos from the second phase, including several cases of what looked like lost anchor ropes, particularly at

Verns Rock. It also 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 three sampling visits to 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 line/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.

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, sediment loadings, and sediment smothering. Changes in land use (e.g. forest removal, urban development) or high levels of rain fall/changing rain fall patterns could cause increased sediment loads being delivered to coastal waters and so 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.

4.4 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 it's 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 predominance of three dimensional organisms in these ecosystems does suggest they have not been impacted by bottom contact fisheries, such as trawling, recently.

Ecological function

While the ecological functions 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 dissolved organic carbon , 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 and suspension feeding organisms, creating valuable biogenic habitats and recycling nutrients. The large number of fish associated with the survey areas means these areas are important for seafood provisioning.

4.5 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 often been unpredictable (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. 78 Meter Rise and Fishermens rock). 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 support 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 as part of the current project, we also expect these other nearby 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

Using ROV technology 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 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, 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 further 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, further work could be possible at Hunters Bank (also see below) to assess depth variation, 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. 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 $10,000 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

- *Aaptos globosa*
- *Iophon* sp.
- *Ancorina* sp.
- Arborescent yellow sponge
- Calcarea
- *Crella incrustans*
- *Darwinella oxeata*
- Encrusting orange sponge
- Encrusting red sponges
- Encrustingy yellow sponge
- Other sponges
- *Polymastia echinus*
- *Polymastia fusca*
- Repent sponges
- *Stelletta* sp.
- *Tedania connectens*
- *Tethya* sp.
- Massive yellow sponge

Algae

- Brown algae
- Crustose coralline algae (CCA)
- *Ecklonia radiata*
- Red flashy algae
- Red filamentous algae

Cnidarians

- Sea anemones (Actiniaria)
- *Corynactis australis*
- Large Hydroids
- *Parazoanthus elongatus*

Bryozoans

- Encrusting Bryozoans
- Erect bryozoans
- Moss Bryozoans (Catenicellidae)

Ascidians

- Encrusting ascidians
- White colonial ascidians

Others

- Brachipods
- Biological matrix

Table S2. Coordinates of possible for Mana and Hunters 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	16	82720	5170	15.787	0.0001	9879
Residuals	140	45847	327.48			
Total	156	1.2857E+05				

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	2.8132	0.0004	8451
Taputeranga, Sharks tooth	2.6576	0.0004	9221
Taputeranga, Hunters Bank Shallow	4.5536	0.0001	8381
Taputeranga, Mana 1	5.3587	0.0001	8462
Taputeranga, Mana 2	5.655	0.0001	9234
Taputeranga, Mana 3	5.1809	0.0001	9206
Taputeranga, Mana 4	5.2263	0.0001	9207
Taputeranga, Mana 5	5.7023	0.0001	9191
Taputeranga, Mana 6	5.2907	0.0001	9207
Taputeranga, Hunters Bank Deep 2	5.0541	0.0001	9144
Taputeranga, Hunters Bank Deep 3	4.709	0.0001	9179
Taputeranga, Hunters Bank Deep 4	6.5366	0.0001	9187
Taputeranga, Hunters Bank Deep 5	5.5196	0.0001	9211
Taputeranga, Verns Rock 1	5.8121	0.0001	6987
Taputeranga, Verns Rock 2	6.904	0.0001	8451
Taputeranga, Verns Rock 3	6.4915	0.0002	8365
Arabella Rocks, Sharks tooth	1.8827	0.0033	8869
Arabella Rocks, Hunters Bank Shallow	5.1131	0.0006	5064
Arabella Rocks, Mana 1	4.8878	0.0002	5065
Arabella Rocks, Mana 2	5.2055	0.0001	8907
Arabella Rocks, Mana 3	4.4715	0.0001	8951
Arabella Rocks, Mana 4	5.2774	0.0001	8906
Arabella Rocks, Mana 5	5.4501	0.0001	8896
Arabella Rocks, Mana 6	4.6518	0.0002	8938
Arabella Rocks, Hunters Bank Deep 2	5.5896	0.0001	8859
Arabella Rocks, Hunters Bank Deep 3	6.0368	0.0001	8892
Arabella Rocks, Hunters Bank Deep 4	6.1612	0.0001	8919
Arabella Rocks, Hunters Bank Deep 5	5.1486	0.0001	8888
Arabella Rocks, Verns Rock 1	5.3931	0.0002	5133
Arabella Rocks, Verns Rock 2	6.7384	0.0002	5070
Arabella Rocks, Verns Rock 3	6.1813	0.0004	5100
Sharks tooth, Hunters Bank Shallow	3.3321	0.0002	8840
Sharks tooth, Mana 1	3.226	0.0001	8918
Sharks tooth, Mana 2	3.7241	0.0001	9424
Sharks tooth, Mana 3	3.2171	0.0001	9432
Sharks tooth, Mana 4	3.5489	0.0001	9486
Sharks tooth, Mana 5	4.01	0.0001	9421
Sharks tooth, Mana 6	3.9291	0.0001	9426
Sharks tooth, Hunters Bank Deep 2	3.7331	0.0001	9440
Sharks tooth, Hunters Bank Deep 3	4.0093	0.0001	9465
Sharks tooth, Hunters Bank Deep 4	4.6343	0.0002	9429
Sharks tooth, Hunters Bank Deep 5	4.2234	0.0001	9418
Sharks tooth, Verns Rock 1	4.5229	0.0001	7795
Sharks tooth, Verns Rock 2	5.4716	0.0001	8903
Sharks tooth, Verns Rock 3	5.3039	0.0001	8901
Hunters Bank Shallow, Mana 1	4.3604	0.0001	5075
Hunters Bank Shallow, Mana 2	4.6892	0.0001	8892
Hunters Bank Shallow, Mana 3	4.1892	0.0002	8831
Hunters Bank Shallow, Mana 4	4.4007	0.0001	8874
Hunters Bank Shallow, Mana 5	5.3303	0.0001	8898
Hunters Bank Shallow, Mana 6	4.9913	0.0002	8930
Hunters Bank Shallow, Hunters Bank Deep 2	4.0535	0.0001	8959
Hunters Bank Shallow, Hunters Bank Deep 3	3.0154	0.0001	8905

Hunters Bank Shallow, Hunters Bank Deep 4	5.7761	0.0001	8881
Hunters Bank Shallow, Hunters Bank Deep 5	4.5979	0.0001	8879
Hunters Bank Shallow, Verns Rock 1	5.0657	0.0001	5014
Hunters Bank Shallow, Verns Rock 2	6.1017	0.0002	5035
Hunters Bank Shallow, Verns Rock 3	5.6605	0.0005	5057
Mana 1, Mana 2	1.2342	0.2248	8874
Mana 1, Mana 3	2.252	0.0012	8861
Mana 1, Mana 4	2.9303	0.0002	8902
Mana 1, Mana 5	3.3361	0.0001	8871
Mana 1, Mana 6	3.1787	0.0004	8846
Mana 1, Hunters Bank Deep 2	1.2675	0.1714	8909
Mana 1, Hunters Bank Deep 3	3.9005	0.0001	8938
Mana 1, Hunters Bank Deep 4	2.4033	0.0028	8879
Mana 1, Hunters Bank Deep 5	2.6378	0.0001	8906
Mana 1, Verns Rock 1	3.284	0.0002	5091
Mana 1, Verns Rock 2	4.0855	0.0001	5082
Mana 1, Verns Rock 3	4.2697	0.0002	5019
Mana 2, Mana 3	2.382	0.0002	9443
Mana 2, Mana 4	2.7434	0.0002	9436
Mana 2, Mana 5	3.2427	0.0001	9431
Mana 2, Mana 6	3.0737	0.0002	9507
Mana 2, Hunters Bank Deep 2	1.7632	0.0246	9444
Mana 2, Hunters Bank Deep 3	4.0635	0.0001	9441
Mana 2, Hunters Bank Deep 4	1.9283	0.0057	9442
Mana 2, Hunters Bank Deep 5	2.5671	0.0002	9399
Mana 2, Verns Rock 1	2.7892	0.0001	7838
Mana 2, Verns Rock 2	3.6039	0.0001	8942
Mana 2, Verns Rock 3	3.9289	0.0001	8908
Mana 3, Mana 4	1.4645	0.0942	9426
Mana 3, Mana 5	1.3596	0.1474	9455
Mana 3, Mana 6	1.6957	0.0349	9414
Mana 3, Hunters Bank Deep 2	2.4351	0.0002	9448
Mana 3, Hunters Bank Deep 3	4.6656	0.0001	9420
Mana 3, Hunters Bank Deep 4	2.5342	0.0002	9447
Mana 3, Hunters Bank Deep 5	3.069	0.0001	9472
Mana 3, Verns Rock 1	2.9894	0.0001	7763
Mana 3, Verns Rock 2	3.8212	0.0001	8885
Mana 3, Verns Rock 3	3.987	0.0001	8867
Mana 4, Mana 5	1.458	0.0894	9400
Mana 4, Mana 6	1.8705	0.0111	9421
Mana 4, Hunters Bank Deep 2	2.4054	0.0002	9425
Mana 4, Hunters Bank Deep 3	5.2002	0.0001	9436
Mana 4, Hunters Bank Deep 4	3.0674	0.0001	9454
Mana 4, Hunters Bank Deep 5	3.5731	0.0001	9463
Mana 4, Verns Rock 1	3.1385	0.0001	7793
Mana 4, Verns Rock 2	4.1284	0.0001	8972
Mana 4, Verns Rock 3	3.9565	0.0001	8905
Mana 5, Mana 6	1.0096	0.4288	9444
Mana 5, Hunters Bank Deep 2	3.2018	0.0001	9441
Mana 5, Hunters Bank Deep 3	6.0068	0.0001	9453
Mana 5, Hunters Bank Deep 4	2.6255	0.0013	9422
Mana 5, Hunters Bank Deep 5	3.1838	0.0002	9441
Mana 5, Verns Rock 1	2.5972	0.0004	7768
Mana 5, Verns Rock 2	3.519	0.0001	8942
Mana 5, Verns Rock 3	3.5918	0.0003	8957
Mana 6, Hunters Bank Deep 2	3.277	0.0003	9430
Mana 6, Hunters Bank Deep 3	5.5543	0.0001	9469
Mana 6, Hunters Bank Deep 4	2.5502	0.001	9444

Mana 6, Hunters Bank Deep 5	3.1119	0.0001	9414
Mana 6, Verns Rock 1	2.3223	0.0003	7836
Mana 6, Verns Rock 2	2.8937	0.0002	8863
Mana 6, Verns Rock 3	2.8588	0.0001	8883
Hunters Bank Deep 2, Hunters Bank Deep 3	3.4027	0.0001	9431
Hunters Bank Deep 2, Hunters Bank Deep 4	2.5481	0.0018	9429
Hunters Bank Deep 2, Hunters Bank Deep 5	2.649	0.0005	9457
Hunters Bank Deep 2, Verns Rock 1	3.2987	0.0001	7819
Hunters Bank Deep 2, Verns Rock 2	4.0368	0.0001	8930
Hunters Bank Deep 2, Verns Rock 3	4.2166	0.0001	8914
Hunters Bank Deep 3, Hunters Bank Deep 4	4.7712	0.0001	9464
Hunters Bank Deep 3, Hunters Bank Deep 5	3.4283	0.0001	9449
Hunters Bank Deep 3, Verns Rock 1	5.0298	0.0001	7791
Hunters Bank Deep 3, Verns Rock 2	5.9851	0.0001	8905
Hunters Bank Deep 3, Verns Rock 3	6.2824	0.0001	8898
Hunters Bank Deep 4, Hunters Bank Deep 5	1.2088	0.2457	9448
Hunters Bank Deep 4, Verns Rock 1	2.003	0.0204	7834
Hunters Bank Deep 4, Verns Rock 2	2.7963	0.0001	8901
Hunters Bank Deep 4, Verns Rock 3	3.2725	0.0001	8895
Hunters Bank Deep 5, Verns Rock 1	2.0472	0.0093	7807
Hunters Bank Deep 5, Verns Rock 2	2.6617	0.0003	8891
Hunters Bank Deep 5, Verns Rock 3	3.3376	0.0001	8911
Verns Rock 1, Verns Rock 2	Negative		
Verns Rock 1, Verns Rock 3	1.3683	0.1665	5076
Verns Rock 2, Verns Rock 3	1.1084	0.3339	5103

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)	perms
Taputeranga, Arabella Rocks	1.7283	0.0051	7829
Taputeranga, Sharks tooth	0.99294	0.4351	9193
Taputeranga, Hunters Bank Shallow	1.3982.	0.0996	8483
Taputeranga, Mana 1	1.8542.	0.0224	8435
Taputeranga, Mana 2	3.6365	0.0001	9158
Taputeranga, Mana 3	2.9226	0.0003	9167
Taputeranga, Mana 4	3.2249	0.0007	9181
Taputeranga, Mana 5	2.7708	0.0003	9175
Taputeranga, Mana 6	2.2737	0.0018	8798
Taputeranga, Hunters Bank Deep 2	2.0455	0.0008	9149
Taputeranga, Hunters Bank Deep 3	3.5341	0.0002	9202
Taputeranga, Hunters Bank Deep 4	2.4044	0.0015	9173
Taputeranga, Hunters Bank Deep 5	2.9538	0.0004	9191
Taputeranga, Verns Rock 1	1.8325	0.0194	6968
Taputeranga, Verns Rock 2	2.3146	0.0023	7786
Taputeranga, Verns Rock 3	1.6828	0.0192	6745
Arabella Rocks, Sharks tooth	3.3226	0.0001	8901
Arabella Rocks, Hunters Bank Shallow	1.9033	0.0168	5096
Arabella Rocks, Mana 1	3.087	0.0005	5050
Arabella Rocks, Mana 2	4.9684	0.0001	8880
Arabella Rocks, Mana 3	3.8162	0.0001	8903
Arabella Rocks, Mana 4	5.167	0.0002	8922
Arabella Rocks, Mana 5	3.7518	0.0001	8890
Arabella Rocks, Mana 6	3.0799	0.0002	8914
Arabella Rocks, Hunters Bank Deep 2	3.0491	0.0002	8911
Arabella Rocks, Hunters Bank Deep 3	4.9681	0.0001	8947
Arabella Rocks, Hunters Bank Deep 4	4.0093	0.0001	8969
Arabella Rocks, Hunters Bank Deep 5	5.0686	0.0001	8897
Arabella Rocks, Verns Rock 1	2.83	0.0001	5045
Arabella Rocks, Verns Rock 2	3.4818	0.0004	5094
Arabella Rocks, Verns Rock 3	2.4087	0.0004	4023
Sharks tooth, Hunters Bank Shallow	2.1041	0.0037	8905
Sharks tooth, Mana 1	1.8543	0.0239	8866
Sharks tooth, Mana 2	4.4338	0.0001	9396
Sharks tooth, Mana 3	3.1736	0.0001	9445
Sharks tooth, Mana 4	3.5612	0.0001	9420
Sharks tooth, Mana 5	2.9776	0.0002	9418
Sharks tooth, Mana 6	2.4395	0.0001	9445
Sharks tooth, Hunters Bank Deep 2	2.6175	0.0007	9394
Sharks tooth, Hunters Bank Deep 3	4.1585	0.0002	9428
Sharks tooth, Hunters Bank Deep 4	2.3414	0.0043	9437
Sharks tooth, Hunters Bank Deep 5	3.2607	0.0003	9467
Sharks tooth, Verns Rock 1	1.9514	0.0119	7808
Sharks tooth, Verns Rock 2	2.4879	0.0002	8906
Sharks tooth, Verns Rock 3	1.8936	0.0031	8408
Hunters Bank Shallow, Mana 1	1.4978	0.1082	5072

Hunters Bank Shallow, Mana 2	3.3627	0.0001	8923
Hunters Bank Shallow, Mana 3	1.9709	0.0147	8910
Hunters Bank Shallow, Mana 4	2.6841	0.0011	8885
Hunters Bank Shallow, Mana 5	1.9749	0.0143	8951
Hunters Bank Shallow, Mana 6	1.5891	0.031	8879
Hunters Bank Shallow, Hunters Bank Deep 2	1.7373	0.0381	8888
Hunters Bank Shallow, Hunters Bank Deep 3	2.9923	0.0005	8906
Hunters Bank Shallow, Hunters Bank Deep 4	2.0549	0.0081	8927
Hunters Bank Shallow, Hunters Bank Deep 5	2.3159	0.0023	8928
Hunters Bank Shallow, Verns Rock 1	1.3411	0.167	4991
Hunters Bank Shallow, Verns Rock 2	1.5822	0.0497	5078
Hunters Bank Shallow, Verns Rock 3	1.4415	0.0721	4014
Mana 1, Mana 2	2.7956	0.0001	8926
Mana 1, Mana 3	1.461	0.0899	8893
Mana 1, Mana 4	1.4444	0.0851	8947
Mana 1, Mana 5	1.1668	0.272	8892
Mana 1, Mana 6	0.75635	0.7582	8937
Mana 1, Hunters Bank Deep 2	2.4207	0.001	8959
Mana 1, Hunters Bank Deep 3	2.8724	0.0009	8922
Mana 1, Hunters Bank Deep 4	1.4229	0.1161	8907
Mana 1, Hunters Bank Deep 5	1.6073	0.0501	8898
Mana 1, Verns Rock 1	0.81009	0.5961	5043
Mana 1, Verns Rock 2	0.94982	0.5027	5060
Mana 1, Verns Rock 3	0.79239	0.7271	3989
Mana 2, Mana 3	3.148	0.0001	9440
Mana 2, Mana 4	3.4453	0.0001	9431
Mana 2, Mana 5	2.5871	0.0007	9447
Mana 2, Mana 6	2.2255	0.0004	9449
Mana 2, Hunters Bank Deep 2	5.0145	0.0002	9432
Mana 2, Hunters Bank Deep 3	4.9424	0.0001	9415
Mana 2, Hunters Bank Deep 4	4.0947	0.0002	9442
Mana 2, Hunters Bank Deep 5	4.2247	0.0001	9426
Mana 2, Verns Rock 1	2.6134	0.0001	7849
Mana 2, Verns Rock 2	2.439	0.0003	8891
Mana 2, Verns Rock 3	1.8885	0.0011	8388
Mana 3, Mana 4	2.0341	0.0096	9439
Mana 3, Mana 5	1.1226	0.295	9446
Mana 3, Mana 6	1.1259	0.2861	9458
Mana 3, Hunters Bank Deep 2	2.523	0.0001	9449
Mana 3, Hunters Bank Deep 3	1.9114	0.0131	9425
Mana 3, Hunters Bank Deep 4	1.7359	0.0207	9437
Mana 3, Hunters Bank Deep 5	1.9029	0.0087	9440
Mana 3, Verns Rock 1	0.7537	0.6828	7803
Mana 3, Verns Rock 2	0.85053	0.6401	8866
Mana 3, Verns Rock 3	1.3365	0.0937	8457
Mana 4, Mana 5	0.83431	0.62	9424
Mana 4, Mana 6	0.87288	0.6316	9460
Mana 4, Hunters Bank Deep 2	4.4317	0.0001	9445
Mana 4, Hunters Bank Deep 3	4.5871	0.0001	9448
Mana 4, Hunters Bank Deep 4	2.6817	0.0001	9434

Mana 4, Hunters Bank Deep 5	2.7272	0.0003	9443
Mana 4, Verns Rock 1	1.4289	0.1141	7782
Mana 4, Verns Rock 2	1.4204	0.0477	8911
Mana 4, Verns Rock 3	1.5222	0.0272	8406
Mana 5, Mana 6	Negative		
Mana 5, Hunters Bank Deep 2	3.2304	0.0001	9446
Mana 5, Hunters Bank Deep 3	3.0054	0.0002	9437
Mana 5, Hunters Bank Deep 4	1.7928	0.0178	9418
Mana 5, Hunters Bank Deep 5	1.5728	0.047	9485
Mana 5, Verns Rock 1	0.92858	0.4901	7769
Mana 5, Verns Rock 2	0.79674	0.729	8910
Mana 5, Verns Rock 3	1.0151	0.4051	8428
Mana 6, Hunters Bank Deep 2	2.7188	0.0001	9450
Mana 6, Hunters Bank Deep 3	2.7933	0.0001	9454
Mana 6, Hunters Bank Deep 4	1.5633	0.0215	9440
Mana 6, Hunters Bank Deep 5	1.5283	0.0269	9453
Mana 6, Verns Rock 1	0.7644	0.6961	7783
Mana 6, Verns Rock 2	0.7503	0.8202	8431
Mana 6, Verns Rock 3	0.53734	0.9744	7527
Hunters Bank Deep 2, Hunters Bank Deep 3	2.7706	0.0002	9443
Hunters Bank Deep 2, Hunters Bank Deep 4	2.0535	0.0021	9434
Hunters Bank Deep 2, Hunters Bank Deep 5	3.0544	0.0001	9402
Hunters Bank Deep 2, Verns Rock 1	1.621	0.0474	7815
Hunters Bank Deep 2, Verns Rock 2	2.4942	0.0001	8874
Hunters Bank Deep 2, Verns Rock 3	2.2247	0.0002	8399
Hunters Bank Deep 3, Hunters Bank Deep 4	2.841	0.0003	9438
Hunters Bank Deep 3, Hunters Bank Deep 5	3.9178	0.0001	9431
Hunters Bank Deep 3, Verns Rock 1	2.1697	0.0119	7787
Hunters Bank Deep 3, Verns Rock 2	2.2776	0.001	8891
Hunters Bank Deep 3, Verns Rock 3	2.3074	0.0002	8421
Hunters Bank Deep 4, Hunters Bank Deep 5	0.5779	0.808	9442
Hunters Bank Deep 4, Verns Rock 1	0.098396	0.9229	7873
Hunters Bank Deep 4, Verns Rock 2	1.6513	0.0091	8948
Hunters Bank Deep 4, Verns Rock 3	1.4645	0.0406	8447
Hunters Bank Deep 5, Verns Rock 1	0.51542	0.8119	7800
Hunters Bank Deep 5, Verns Rock 2	1.7351	0.0016	8874
Hunters Bank Deep 5, Verns Rock 3	1.578	0.0095	8405
Verns Rock 1, Verns Rock 2	0.9236	0.5061	5048
Verns Rock 1, Verns Rock 3	0.69676	0.8125	4020
Verns Rock 2, Ve			