Benthic community composition of temperate mesophotic ecosystems (TMEs) in New Zealand: sponge domination and contribution to habitat complexity

Benjamin Harris*, **Simon K. Davy, James J. Bell**

School of Biological Sciences, Victoria University of Wellington, PO Box 600, Wellington, New Zealand

ABSTRACT: Temperate mesophotic ecosystems (TMEs) typically occur between 30 and 150 m depth and support rich benthic communities. However, despite their widespread distribution and ecological importance, TMEs are one of the most poorly studied marine ecosystems globally. We measured changes in the benthic community composition of rocky reefs through the infralittoral and mesophotic zone from 5 to 120 m at 6 locations across New Zealand (the Poor Knights Islands, the inner, mid-, and outer regions of the Fiordland Marine Area [FMA], and the North and South Taranaki Bights) which we considered as potential shallow-water TME surrogates due to these sites having environmental conditions and biological communities similar to deeper-water communities. Benthic community data were analysed from videos and photographs collected using SCUBA (<30 m) and a remotely operated vehicle (ROV) (>30 m). We found significant changes in community composition with depth at all locations, suggesting that TMEs provide habitats different from those in shallower water. We consistently found that TME benthic communities were dominated by sponges, but their abundance varied significantly with depth at 3 out of 4 locations, while the morphological composition of these assemblages changed with depth at all locations. Given their particularly high abundance and morphological complexity, we suggest that sponge assemblages make an important contribution to habitat complexity in benthic TME communities.

KEY WORDS: Benthic community · Habitat complexity · Temperate mesophotic ecosystem · Sponge · Community composition · Sponge morphology

1. INTRODUCTION

Determining the drivers of biodiversity patterns and understanding how different organisms contribute to ecosystem functioning is critical for the implementation of effective biodiversity monitoring and conservation management strategies (Balmford & Gaston 1999, Costello et al. 2010). However, this first requires the distribution and abundance of organisms to be determined, which poses many practical challenges for marine species compared to terrestrial species. As a result, significant gaps persist in our understanding of many marine ecosystems (Bouchet 2006, Costello et al. 2010), which limits our ability to make effective management decisions (van Jaarsveld et al. 1998).

Coastal benthic marine ecosystems are among the most bio-diverse and productive on Earth (Poore & Wilson 1993). These ecosystems occur in a broad range of geophysical spaces and environmental conditions (Covich et al. 2004), where particularly active hydrological regimes play an important role in ecosystem dynamics (Austen et al. 2002). Intertidal and shallow coastal benthic communities have received a high level of research effort compared to deeper water, so-called mesophotic habitats, which generally occur deeper than 30 m, approaching the limits of recreational SCUBA (Kahng et al. 2010). First-person

access to these environments requires substantially greater expertise, training, and is more costly. Furthermore, observation time is limited due to decompression considerations, which may reduce the spatial coverage of sampling and replication (Lam et al. 2006). While the use of remotely operated vehicles (ROVs) in these zones is possible, in the past this has often been prohibitively expensive.

Past mesophotic ecosystem research has predominantly focused on tropical mesophotic coral ecosystems (MCEs) (e.g. Lesser et al. 2009, Kahng et al. 2014), with comparable ecosystems from temperate environments having been only recently formally recognised (Cerrano et al. 2019, Turner et al. 2019). The definition of MCEs remains ambiguous, with researchers often providing their own criteria, but generally, this zone extends from approximately the edge of recreational SCUBA limits at 40 m, where zooxanthellate corals decline (Hinderstein et al. 2010), down to 150 m, where light availability becomes significantly reduced (<1% of the surface light). Studies of equivalent depth zones in temperate mesophotic ecosystems (TMEs) are far fewer (see James et al. 2017, Cerrano et al. 2019). Furthermore, no studies have considered the transition of entire benthic communities through the complete infralittoral (here classified as 5–30 m) and mesophotic (30–150 m) range (5–150 m) (Cerrano et al. 2019). This research gap is likely due to the practical obstacles of working below recreational SCUBA limits, with projects employing large ROVs and autonomous underwater vehicles (AUVs) instead prioritising exploration far into the bathyal or even abyssal zones, capitalising on extreme pressure ratings in areas truly inaccessible to first-person exploration (Danovaro et al. 2014). However, in recent years, robotics technology has advanced considerably, with ROVs becoming smaller and cheaper, providing more opportunities for researchers to investigate previously overlooked TMEs. Low-cost ROVs are capable of generating species distribution and abundance data of comparable quality to those gathered using SCUBA (Boavida et al. 2016), but from deeper depths.

The reduction in light availability is the primary environmental driver characterising the ecology of mesophotic zones in both temperate and tropical climates. It generates declines 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, appear to be 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. Marine sponges (Porifera) are among the most abundant sessile benthic invertebrates in shallow rocky-reef environments (Bell & Barnes 2000, Schlacher et al. 2007), frequently occurring on hard substrate across all global marine bioregions (van Soest et al. 2012). These suspension feeders perform a wide range of important ecological functions including moving substantial amounts of carbon (and other nutrients) from the water column to the benthos, substrate stabilisation and bio-erosion, acting as strong spatial competitors, and providing 3-dimensional habitat (Bell 2008). The distribution abundance and ecological functions of sponges have been well documented in shallow, accessible areas (<30 m) in temperate (e.g. Roberts et al. 2006, Bell 2007), tropical (e.g. Diaz & Rützler 2001, Lesser & Slattery 2013) and polar (McClintock et al. 2005) environments, but again, assemblages in the mesophotic zone are less understood, especially in temperate regions. Although sponges are effective spatial competitors (Bell & Barnes 2003), they are expected to increase in abundance with depth, as has been demonstrated in tropical regions (Lesser & Slattery 2018) as light penetration declines through the infralittoral zone and their competition with algae reduces (Cárdenas et al. 2012), although generalisations of these patterns require caution (see Scott & Pawlik 2019). As a result, the functions that sponges perform may play an increasingly important role with increasing depth into the mesophotic zone.

A particularly important function that sponges perform in temperate regions is the creation of habitat complexity to the wider benthic community, as temperate environments generally lack the complex habitat structures provided by reef-building corals that characterize tropical reefs (Graham & Nash 2013). Furthermore, the transition from the infralittoral to the mesophotic zone in temperate regions sees a significant decline and the eventual exclusion of light-dependent habitat-forming organisms, such as canopy-forming macroalgae species and branching forms of crustose coralline algae. Therefore, the relative importance of habitat complexity provided by sponges is likely to be increasingly important with depth, regardless of whether sponges show significant increases in abundance. The habitat complexity provided by sponge assemblages can increase the abundance and biodiversity of associated organisms (Maldonado et al. 2017, Folkers & Rombouts 2020) in numerous ways, including providing refugia for prey organisms (Ryer et al. 2004), hunting habitat for predators (Miller et al. 2012), and direct sponge habi-

tat for obligate sponge dwellers (Henkel & Pawlik 2005). Three-dimensional morphologically complex sponge assemblages are also likely to alter local hydrodynamics by reducing surface boundary layers and providing greater environmental heterogeneity (Beazley et al. 2013). Quantifying changes in sponge cover and complexity with changes in benthic community composition through the infralittoral and mesophotic zones is therefore an essential component in understanding the overall ecological dynamics and functions of coastal benthic communities.

Despite a particularly high abundance and diversity of sponges in New Zealand (Downey et al. 2012), less research effort has been afforded to this South Pacific region compared to other temperate areas (Bell et al. 2020). Furthermore, the mesophotic zones where sponges are potentially most abundant and functionally significant as provisioners of habitat complexity have been largely overlooked (but see taxonomy assessments of specimens found at 190 m by Kelly & Rowden 2019).

Here we focus on the full transitional depth range from the infralittoral to the mesophotic zone across multiple sites in New Zealand, within the same depths considered to be mesophotic on tropical coral reefs (30–150 m). We propose that mesophotic habitats in temperate regions are location-specific due to highly dynamic coastal environments, where in some circumstances, TME-like communities may occur in much shallower water than MCEs due to particularly low light penetration. Therefore, we also considered some shallow benthic habitats without depth profiles (<30 m) in the Taranaki region of New Zealand's North Island, which have been previously considered to be more characteristic of deeper water reefs (Battershill & Page 1996). Here, particularly high turbidity reduces light availability, potentially reducing the persistence of algal species. Algae are generally highly abundant in the shallow (<20 m) coastal areas of New Zealand reefs and often compete effectively with the wider benthic community for habitat space (Choat & Schiel 1982). A reduction in algal abundance due to low light availability could facilitate the proliferation of invertebrates, such as those sponges that would normally be found in deeper habitats. Comparing these low light shallow habitats with deeper water mesophotic zones may help elucidate the mechanisms driving the benthic community composition and distribution of TMEs in temperate ecosystems. If these shallow-water sites resemble deeper water TME communities, then they might act as models for future TME studies, as they are much easier to access.

The aims of this study were to (1) describe how benthic community structure changes from shallow water to the mesophotic zone (5–120 m) on New Zealand rocky reefs; and (2) characterize sponge abundance and morphological complexity across these zones allowing an assessment of their contribution to TME habitat complexity.
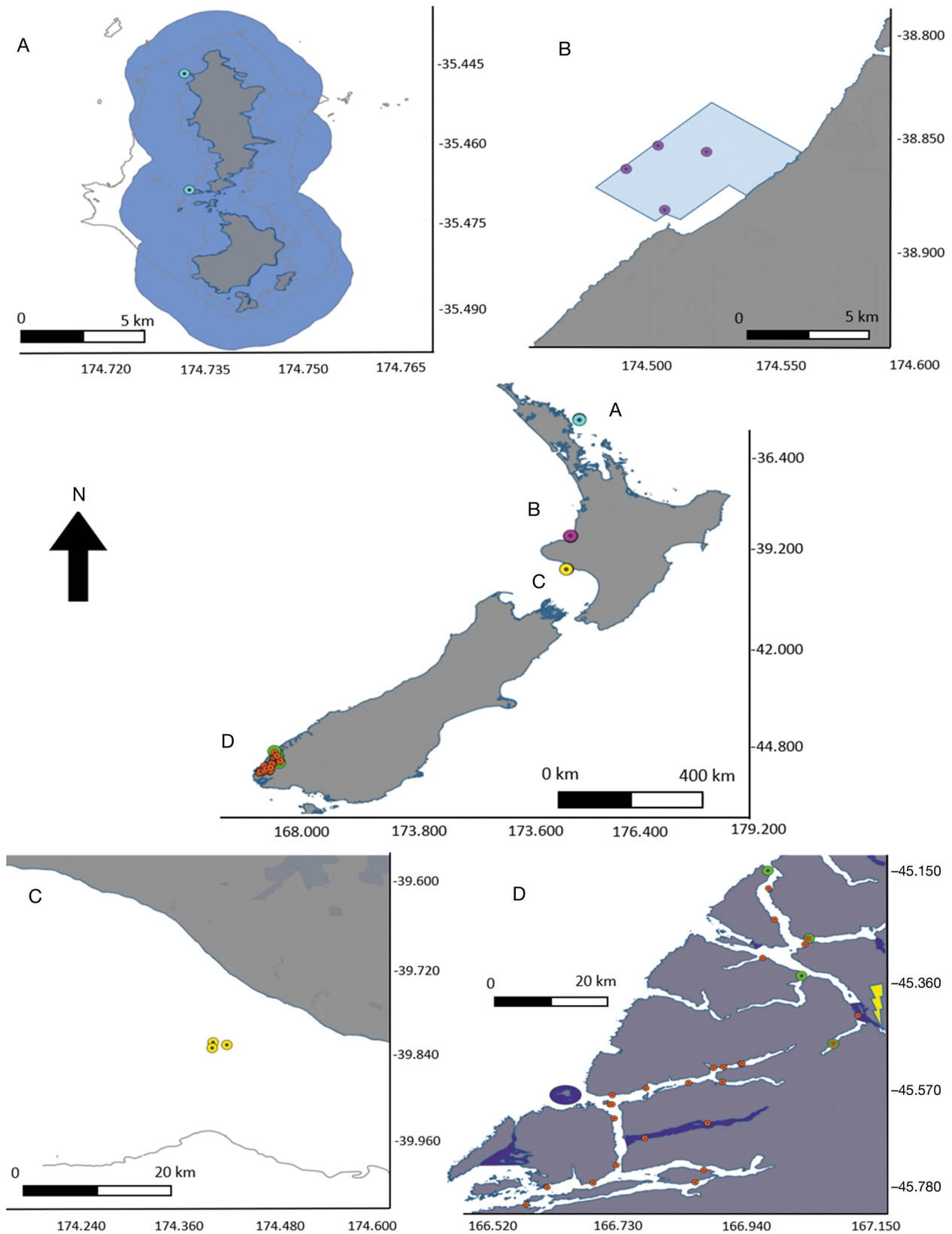
2. MATERIALS AND METHODS

2.1. Study sites

Four geographic regions were chosen to represent a wide range of potential shallow water (<30 m) and deeper water mesophotic habitats (30–150 m), in New Zealand: Fiordland National Park, South Taranaki Bight, North Taranaki at Parininihi Marine Reserve, and Poor Knights Marine Reserve (Fig. 1). Surveys took place between 2018 and 2019 (Table S1 in the Supplement at www.int-res.com/articles/suppl/m671p021_supp.pdf).

2.1.1. Fiordland National Park

The Fiordland Marine Area (FMA) is in the southwest of New Zealand's South Island (Fig. 1D) and covers 928 000 ha that includes the waters of 14 fiords with 10 marine reserves (Ministry for the Environment 2014). Surveys took place over 2 yr in February 2018 and 2019 at 28 and 4 sites, respectively (Table S1). Sites surveyed in both years were categorised into inner, mid, and outer regions, according to their relative distance to the open ocean. The mid-region (8.1–12.5 km from the open ocean) contained more sites than the inner (16.9–20.2 km) and outer (0.8–6.8 km) regions, as weather conditions restricted accessibility at outer sites and fewer deep-water vertical walls were available at inner sites. Fiord systems are characterised by submerged vertical walls that provide a habitat for diverse biological communities that are usually very different from those communities found on the adjacent open coast (Howe et al. 2010). The high annual rainfall (>6400 mm) and rapid runoff from the steep topography in the FMA, results in a tannin-rich freshwater surface layer 1–4 m deep that is maintained throughout the year creating strong depth gradients in salinity and temperature (Goodwin & Cornelisen 2012). This phenomenon is particularly apparent in the inner-most reaches of each fiord, where the exchange of water from the open ocean is most limited. This is artificially accen-

tuated at Deep Cove at the inner reaches of Doubtful Sound, where freshwater arrives via a hydroelectric power station from Lake Manapouri, 10 km to the northeast. It is likely that the high-level input of freshwater strongly influences patterns of community composition and abundance (Howe et al. 2010), but still very little is known about the benthic community in this region.

2.1.2. South Taranaki Bight: Patea

Sampling in South Taranaki took place at 3 sites separated by no more than 500 m in June 2018 (Fig. 1C). The area consists of a large shallow bay (<50 m deep) that extends south and east from the south coast of Taranaki on New Zealand's North Island. The surveyed reef is situated approximately 11 km offshore from the mouth of the Patea River, consisting of broken boulders and rocky ledges ranging from 15 to 30 m deep. The extensive shallow areas are mainly soft sediment habitats and experience regular high energy swells that generate high turbidity and relatively low visibility. Periodic large inputs of turbid freshwater from the Patea River (last peak open-source data available at >110 m^3 s^{-1}, March 2018) may also contribute to this effect.

2.1.3. North Taranaki Bight (Parininihi Marine Reserve)

Fieldwork in North Taranaki took place at 4 locations separated by a maximum of 3 km in March 2019 (Fig. 1B). The Pariokariwa reef at Parininihi Marine Reserve extends 5 km northeast from the 'White Cliffs' in the southwest corner of the North Taranaki bight. The reef consists of rocky boulders and ledges ranging from approximately 10 to 25 m deep. This area receives frequent, high energy swells generating high turbidity. The reserve has been an area of scientific interest since Battershill & Page (1996) described a particularly dense and diverse sponge assemblage thought to be more normally associated with deeper waters.

Fig. 1. Survey locations at (A) the Poor Knights, (B) Parininihi Marine Reserve, (C) South Taranaki Bight, and (D) Fiordland Marine Area (FMA). Orange and green circles in the FMA represent survey locations in 2018 and 2019, respectively. Blue shaded regions show the locations of Marine Reserves. The yellow 'lightning bolt' symbol in (D) indicates the location of freshwater in-put from Manapouri hydroelectric power station

2.1.4. Poor Knights Marine Reserve

Fieldwork at the Poor Knights Marine Reserve took place in March 2018 and December 2019 at 2 sites (Fig. 1A). Sites were chosen according to the largest depth profiles available (maximum of 85 m). The reserve covers an area of 15 km^2 and is situated 22 km offshore east of Matapouri on the northeast coast of New Zealand's North Island. Consisting of 2 main islands, vertical walls descend to an observed maximum of approximately 85 m before reaching a sandy bottom with intermittent boulder complexes. The area is exposed to strong currents and oceanic water, with deep light penetration and low turbidity, which supports abundant and diverse pelagic, coastal, and benthic communities. This includes very diverse and abundant sponge assemblages with over 140 species being recorded (see Kelly & Sim-Smith 2009), with many species in shallow water, thought to be facilitated by the shade provided by a macroalgal canopy (Battershill & Page 1996).

2.2. Benthic video collection

The ROV 'SAL', Model DG2 (Deep Trekker Inc.) with an internal and external mounted GoPro 4 silver camera (set at 60 fps at 1080p resolution) and an internal (4k) camera mounted on an independent remotely controlled swivel was deployed at all locations. Studies using AUVs and ROVs for quantitative assessments of benthic communities have been criticised for overlooking potential parallax error (e.g. Rivero Calle 2010 as discussed in Lesser & Slattery 2019). This issue is less problematic when employing a randomized point-count approach for percentage cover analysis of images whereby the whole area is not used (Scott et al. 2019). However, we set the internal camera to linear mode and kept the camera angled perpendicular to the substrate to minimize parallax error as far as possible.

ROV deployment protocol varied slightly according to each location. At Fiordland and the Poor Knights, the ROV was driven vertically downwards from the vessel and then towards the wall once the estimated maximum depth of the wall had been reached. Approaching the wall from the deepest possible depth reduced the likelihood of entanglement with features on the wall itself. The ROV was driven along the wall on a horizontal transect for approximately 10 min. Lasers were used on the ROV to determine distance from the wall (1 m) producing frame grabs of similar scales. A precise scale was not re-

quired for determining the abundance of benthic organisms using an area occupied approach. The ROV was then driven upwards 10 m and another transect completed. This process was repeated at 10 m depth increments until the shallowest transect at 30 m was completed at each site. The maximum depth reached was 120 m at Fiordland and 80 m at the Poor Knights.

The ROV protocol for the south and north Taranaki locations was tailored for horizontal rather than vertical reef structures. The ROV was driven vertically down from the vessel, set at an angle of approximately 85°, and then driven along a horizontal transect for approximately 10 min.

Other benthic communities less than 30 m deep were sampled using SCUBA, whereby the same diver would swim horizontally along a wall at 3 transect depths of 25, 15, and 5 m, taking photographs (Nikon D800 with Ikelite Housing and YS50 TTL strobe) approximately every meter and 1 m from the substrate.

Preliminary tests were undertaken to test the consistency between data derived from ROV deployments and SCUBA. We employed the same protocols as described above for both ROV deployments and SCUBA to assess the same designated area of substrate. We found no significant differences between data derived from ROV and SCUBA images of the same quadrats (Fig. S1).

2.3. CTD deployment

CTD model RBRconcerto/201801 was set to log temperature (°C), turbidity (NTU), salinity (PSU), chlorophyll *a* (mg l^{-1}), depth (m), and conductivity (SI) every second. Two replicate deployments were made at each site down to the deepest ROV transect. Descent rate was approximately 2 m s^{-1}, and the ascent rate was approximately 1 m s^{-1}. The CTD was deployed at all sites at all locations. CTD data were extracted using the RBR software. The use of CTD data allowed us to determine if any correlations existed between environmental variables and benthic community distributions. CTD data were averaged according to the same 10 m increments as categorized in the community distribution data to allow for statistical correlations. Extreme outliers in the CTD data only occurred for turbidity at the lowest 50 cm of each deployment due to disturbance of soft sediment when touching the seafloor; these obvious outliers were removed. As this study was undertaken across a relatively large geographic scale and with some temporal variability, the precise values of the

environmental variables measured were not used for between-location comparisons.

2.4. Video analysis

Videos collected from ROV deployments were analysed using VLC media player; 10 frame grabs were extracted from each transect as replicates. The selection of frame grabs was randomized but was largely reliant upon the availability of quality still images. Coral point count (CPC) was used to estimate the percentage cover of (1) 9 benthic groups at the phylum level, namely Porifera, Bryozoa, Cnidaria, Ascidiacea, Annelida (only polychaetes observed), Echinodermata, Mollusca, Chordata, Brachiopoda; (2) 3 mixed levels of algae, namely crustose coralline algae (CCA), macroalgae, and branching coralline algae; and (3) 'unidentified' organisms that could not be confidently assigned to any of the predefined phyletic groups due to indistinguishable gross morphological traits or the obstruction of view due to overlapping organisms in the image. Bare substrate was included ensuring the total cover of each image quadrat equalled 100%. The 9 phyla described, covered every identifiable organism observed. A single analyst carried out all CPC image analyses to maintain quality control. All 9 phyla were included in statistical analyses. However, we only provide figures for the 6 overall most abundant groups (Fig. 2), as the abundance of the remaining groups was extremely low in most transects.

A second database was created from CPC where the sponges were broken down into 10 morphological types based on, but not exclusive to, those categorized by Bell & Barnes (2001): encrusting, repent, digitate, massive, branching, flabellate, globular, tube, calcareous, and other. Calcareous was applied as a description specifically for the species *Leucettusa lancifera*, which was particularly common at Fiordland and morphologically distinct from the other categories. Repent refers to both cushion and repent forms as described by Bell & Barnes (2001), as these could not be easily distinguished due to perpendicular ROV camera angles restricting perspectives required to differentiate them. 'Other' refers to any morphology that could not be assigned to any of the 9 specific categories. To determine the contribution of sponge assemblages to habitat complexity, all morphologies described above were binned into levels of high, medium, and low complexity (Table S2). The relative complexity levels were assigned based on the true surface area of different morphologies relative to their individual cover as observed in a
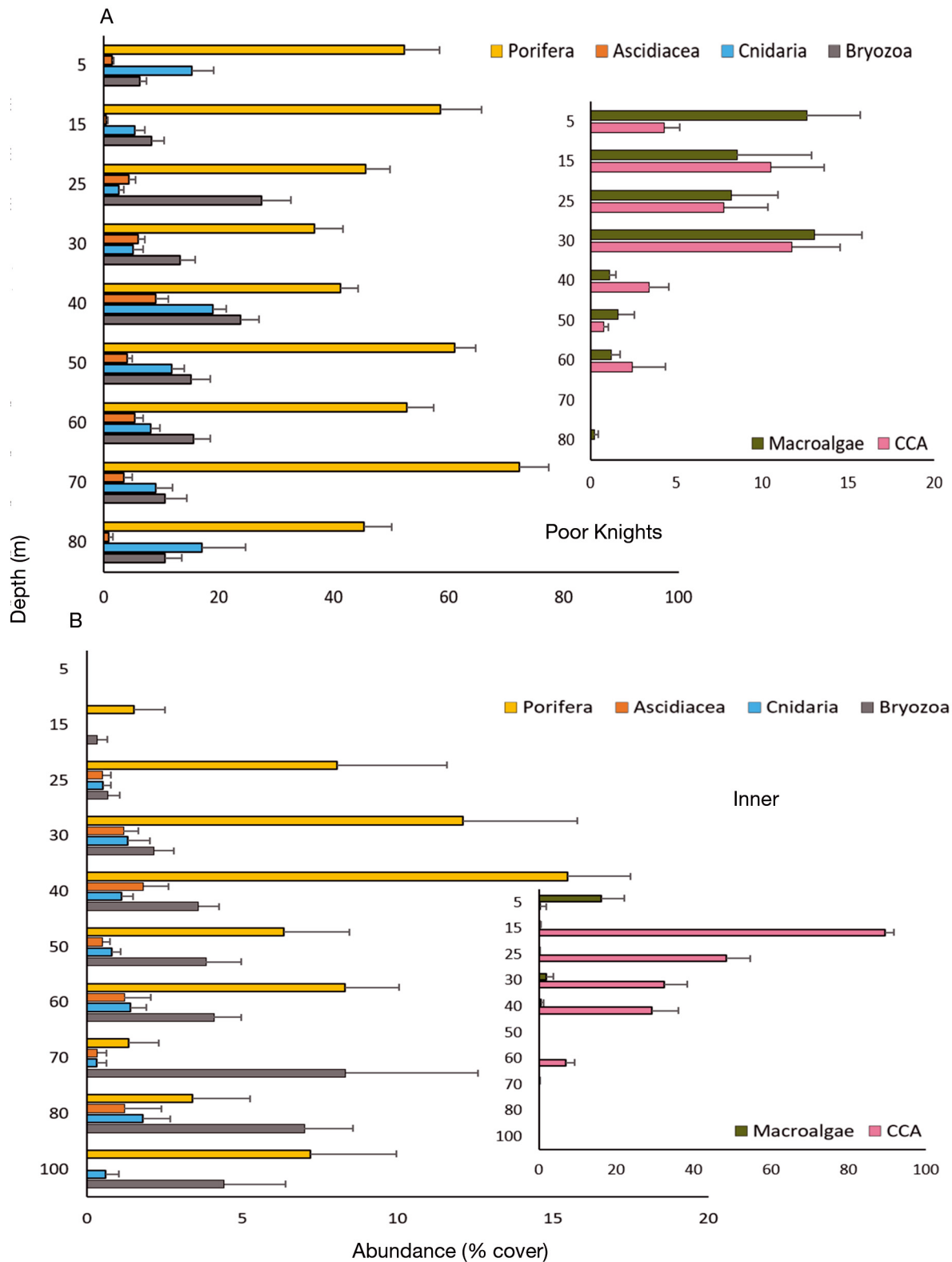
Fig. 2. (Above and next page.) Abundance (as % coverage) of the 6 most abundant benthic groups at (A) Poor Knights, (B) inner, (C) mid, and outer (D) Fiordland, and (E) Patea and Parininihi at 25 m only. Algal groups have been separated to maintain meaningful visualisation of invertebrate groups due to large differences in abundance values. Values are means ± SE. CCA: crustose coralline algae

Fig. 2. (continued)
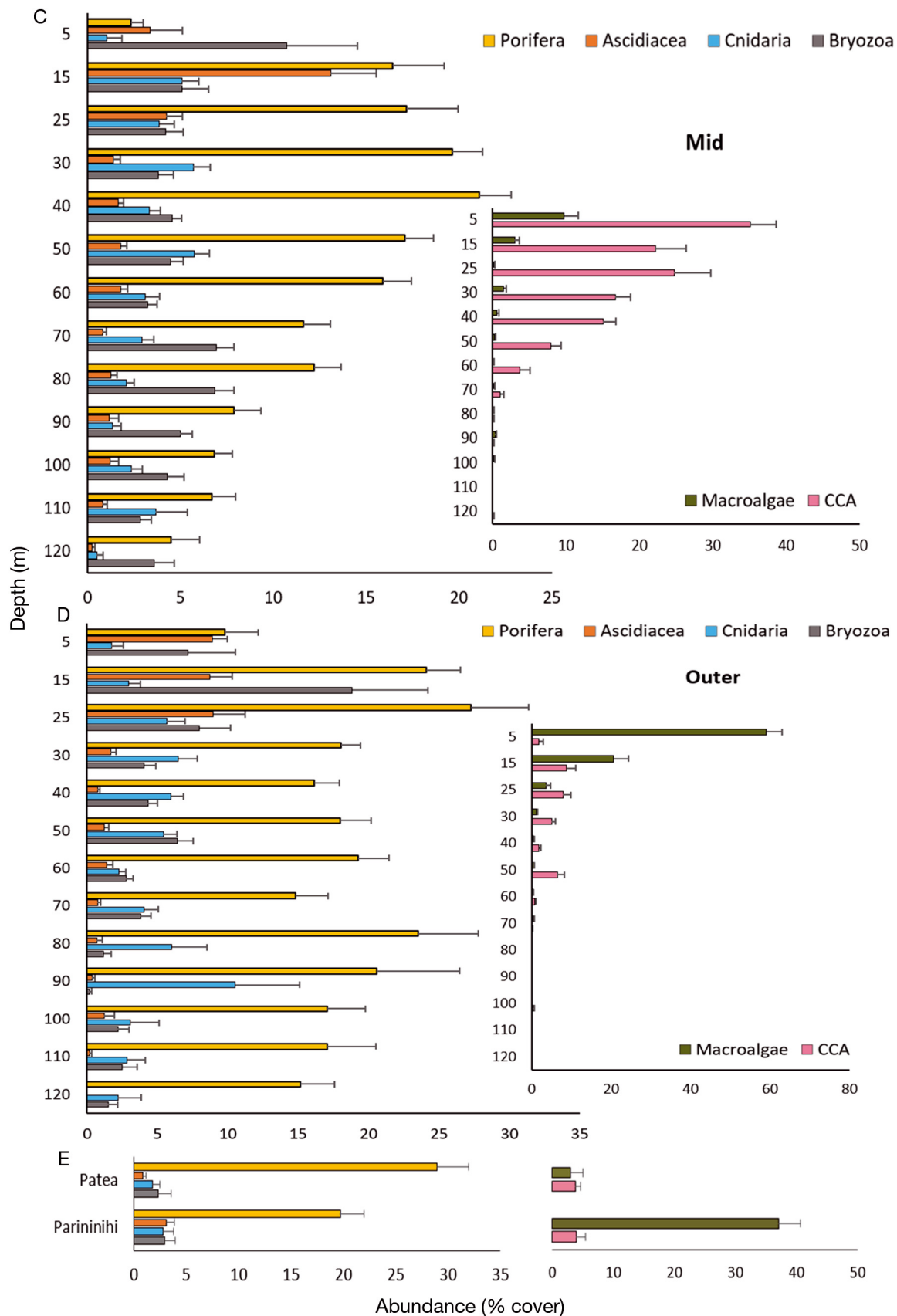
2-dimensional image (Fig. S2). Images were taken of upright specimens of each morphology, and surface area was determined using foil closely wrapped around the entire specimen. The 3 morphologies with the lowest ratios were categorized as low complexity, the next 4 morphologies that exhibited larger but similar ratios were categorized as medium complexity, and the 3 morphologies with the largest ratios were categorized as high complexity. These categories are qualitative and were designed to demonstrate the relative changes in the overall (% cover) and relative (% of sponge assemblage) contributions of different morphological complexities across different depths. Changes in the cover of each morphological group can be seen in Fig. S3. We also applied a full quadrat complexity score to sponge assemblages in each depth bin to assess the changes in the overall complexity of the sponge assemblage across depth. These scores were derived from the same image cover/surface area ratios as described above but were assigned a value of 1–5 in complexity (1 = lowest complexity, 5 = highest complexity; see Table S2). With a particularly low image cover/surface area ratio, encrusting forms were given a lower score (1) than the other low complexity forms (2), while branching forms were given a higher score (5) than the other high complexity forms (4) due to a particularly high ratio. The assigned scores were then multiplied by the abundance value (% cover) of each morphology in a quadrat to provide an overall complexity score in a quadrat that also considers the total cover of each morphology. Complexity values (1–5) were also qualitative and used to estimate relative (as opposed to actual) changes in sponge provisioning to habitat complexity.

CPC 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. A maximum of 100 points was sufficient to reach the plateau of species accumulation curves (Fig. S4) for each location. These were generated from tests of randomised frame-grabs assigned with: 10, then 20, 60, 80, 100, 120, 140 points.

2.5. Data analysis

CSV files were analysed using Rstudio 3.5.1 and PRIMER V6 + PERMONOVA. Permutational multivariate analysis of variance (PERMANOVA) was used to determine the effect of fixed factors (i.e. depth) on multivariate data (i.e. community composition and sponge assemblage morphological composition) using a Bray-Curtis resemblance matrix. PERMANOVA in PRIMER was also used to determine any differences between depth categories of univariate (i.e. sponge cover) and multivariate data as post-hoc pairwise tests. Data were checked in Rstudio 3.5.1 for homoscedasticity and that assumptions of normality were met by observing standardized residuals plotted against theoretical quantiles (QQ plot), as well as residuals vs. fitted and leverage values. Data was log-transformed to improve normality and reduce heteroscedasticity where appropriate, although this is not an underlying assumption for permutational tests. Raw CTD environmental data were visualized as line graphs. SIMPER analysis was used to determine those groups most responsible for the differences between depths. Canonical analysis of principal coordinates (CAP) was used to visualise the variation in community data and sponge assemblage morphological composition based on depth, whereby the distances amongst centroids were calculated from a Bray-Curtis resemblance matrix. CAP analysis was chosen, as this method finds axes through the multivariate cloud of data points, which discriminate among *a priori* groups. Benthic group vectors from multidimensional scaling (MDS) were then overlaid according to a Pearson's rank correlation threshold of 0.4 to visualise the most important community or sponge categories explaining these distribution patterns. Sponge complexity bins from the relative image cover/surface area ratios were analysed both as the percentage cover of the substrate and as a proportion of the total sponge assemblage cover. This took into consideration of how relative assemblage complexity changed with depth, while controlling for any changes in overall sponge cover.

3. RESULTS

3.1. Benthic community composition

At the Poor Knights, overall community composition varied considerably with depth (Pseudo-$F_{8,133} = 7.675$, p < 0.001) (Figs. 2A & 3), with significant differences between almost every 10 m increment (Table S3 for *post-hoc t*-test results and pattern exceptions). This was attributed to an overall significant decline in macroalgae and significant changes in ascidian and cnidarian cover with depth (Fig. 2A, Table S4). While sponges showed significant varia-
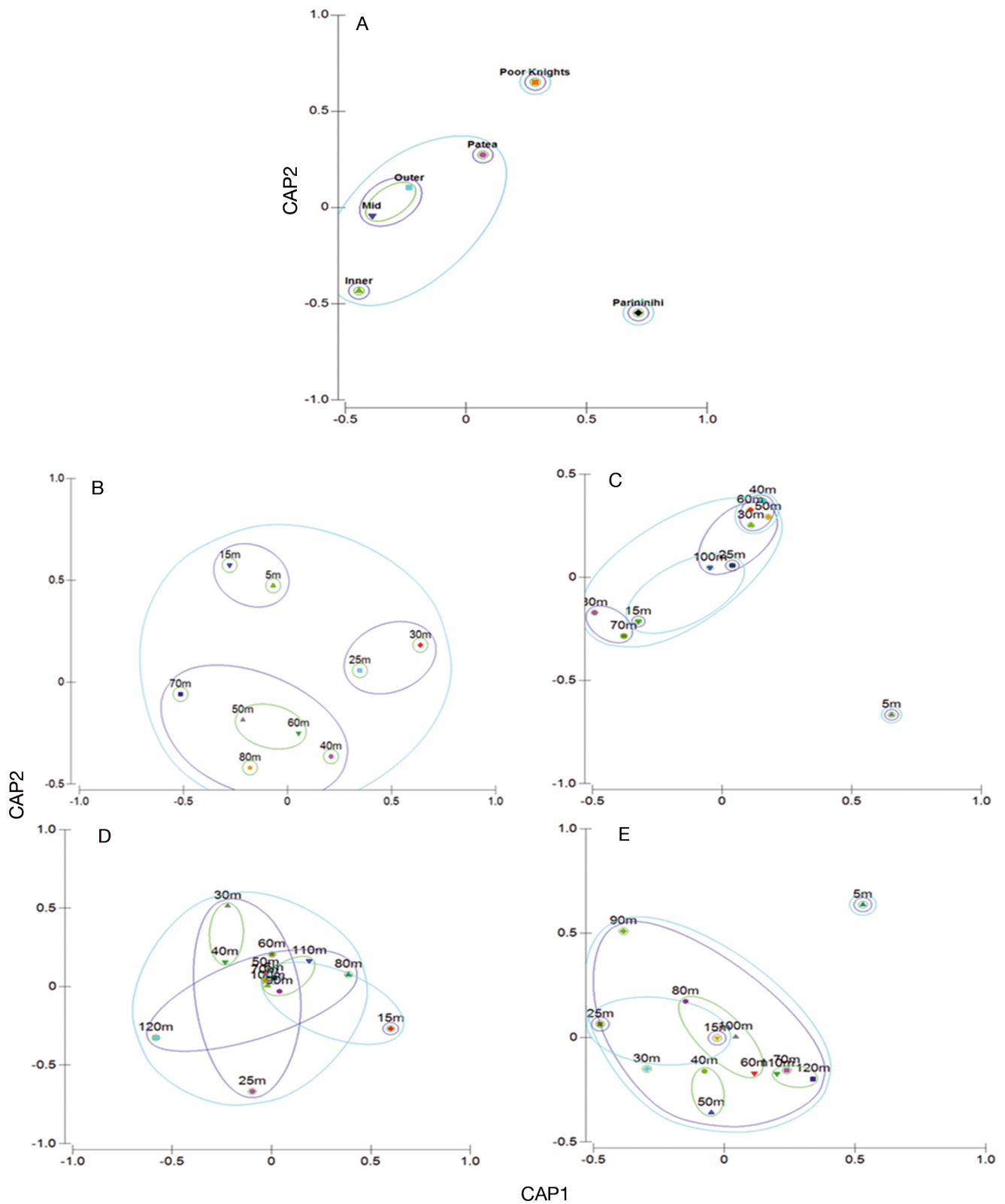
Fig. 3. Canonical analysis of principal coordinates (CAP) ordination of sampled benthic community composition at all survey locations across all depths with groups factored as location (A). Groups were then factored as depth at (B) the Poor Knights, (C) inner Fiordland, (D) mid Fiordland, and (E) outerFiordland. Analysis is based on a Bray-Curtis similarity matrix of percentage cover data. Clusters are based on resemblance levels at 10% (green), 20% (blue), and 30% (turquoise)

tion in their cover with depth, they were the most abundant benthic group at every depth, ranging from a low of 36.6% (±5 SE) cover at 30 m to 72.3% (±5.2 SE) at 70 m, compared with the next most overall abundant group (bryozoans), which ranged from a low of 6.2% (±1.2 SE) at 5 m to a high of 27.5% (±5.1 SE) cover at 25 m (Fig. 2A).

At the inner Fiordland sites community composition also changed significantly with depth (Pseudo-$F_{9,116}$ = 12.341, p < 0.001). Here, a particularly distinct community was found at 5 m (Fig. 3C) as a result of particularly high macroalgal cover and an absence of sponges and CCA (Fig. 2B). There were significant changes in community composition across the shallow depth range (15−30 m), resulting from further declines in macroalgae, a significant decline in CCA from a very high cover (89.3% ± 2.3 SE) at 15 m, and a corresponding increase in sponge cover (Fig. 2B, Table S5). Community composition was similar within the 30−60 m depth range, but it was distinct from the shallower and deeper depths (Fig. 2B). The 30−60 m region was characterised by a relatively high abundance of polychaetes (ranging from 3.7% ± 1.1 to 5.9% ± 0.9 SE). Community composition changed again into a distinct deeper depth zone (70−100 m), characterised by a higher bryozoan cover and reduced sponge and polychaete cover. Limited change in community composition occurred within this depth zone (Table S5 & S6).

At the mid Fiordland sites, community composition changed significantly with depth (Pseudo-$F_{12,577}$ = 17.071, p < 0.001). The change down to 70 m (Figs. 2C & 3, Table S7) was primarily due to a reduction in CCA cover, where the shallowest depths (5−25 m) were characterised by high CCA cover (35.1% ± 3.6−24.7% ± 5 SE). The initial increase and then decline of sponges at this same depth was also responsible for the overall changes seen in community composition (Fig. 2C, Tables S7 & S8). However, the community then changed beyond 70 m and remained similar down to 120 m (Table S7). This deeper region was characterized by higher polychaete cover but lower ascidian, cnidarian and sponge cover (Fig. 2C) compared to other shallower depths, and an absence of macroalgae. However, sponge cover remained high relative to other groups (ranging from 4.5% ± 1.5 to 12.1% ± 1.4 SE).

Outer Fiordland sites showed a significant (Pseudo-$F_{12,293}$ = 6.821, p < 0.001) but less rapid change in community composition with depth than the mid Fiordland sites (Fig. 2D, Table S9). CCA showed a large decline from 5 to 30 m, while macroalgae also showed a major decline from 15 to 30 m (Fig. 2D) ex-

plaining community composition differences both within this region and between shallower and deeper depths. However, no significant changes in community structure were seen throughout the entire depth range of 60−120 m, with this zone being characterised by consistently high sponge cover and an absence of all algal groups (Fig. 2D, Tables S9 & S10). The significant difference in community composition between shallow and deeper depths was attributed to the disappearance of algae. Sponges showed consistently higher cover relative to other groups, with the average similarity in community composition across the full depth range being most attributed to sponges, except for at 5 m (Fig. 2D, Table S10).

3.2. Changes in sponge cover with depth

Sponges were the most abundant invertebrate community group at all locations and were particularly abundant at the Poor Knights with a range of 36% (±5 SE) to 72% cover (±5.2 SE) (Fig. 2). Sponge cover was also significantly different between depths at Poor Knights ($F_{8,133}$ = 4.338, p < 0.001, inner Fiordland ($F_{9,116}$ = 4.482, p < 0.0001), mid Fiordland ($F_{12,577}$ = 11.01, p < 0.0001), but not at outer Fiordland ($F_{12,293}$ = 1.476, p < 0.132).

At the Poor Knights sites, sponge cover was highly variable with the highest peak of cover occurring in the mesophotic zone. Sponge cover showed a significant decline from 15 m (58.5% ± 7.1 SE) to 30 m (36.6% ± 5) (p < 0.05) before significantly increasing again at 50 m (60.1% ± 4.7 SE) (p < 0.001), which was maintained down to 70 m (72.3% ± 5.2 SE) before a non-significant decrease at 80 m (45.3% ± 4.8 SE) (Fig. 2A). At the inner Fiordland sites, sponge cover increased from no cover at 5 m to a peak of 15.46% (±2 SE) cover at 40 m (Fig. 2B), which was significantly higher than all other depth bins (range of p < 0.05 to p < 0.001), except at 30 m. A significant decline occurred beyond 40 m, where cover remained below 10% at all remaining depths sampled (Fig. 2B). At the mid Fiordland sites, sponge cover was lowest at 5 m (2.4% ± 4.8 SE cover) and then increased rapidly between 5 and 15 m to 16.4% (±2.8 SE) (p < 0.001), reaching a peak at 40 m (21.1% ± 1.7 SE). Abundance then significantly declined from 40 down to 120 m (p < 0.001). After an initial significant increase between 5 and 15 m (from 9.8% ± 2.3 to 24.1% ± 2.4 SE) (p < 0.001) (Fig. 2D), the outer Fiordland sites showed no further significant change in sponge cover across depth categories. Sponge cover at Patea (25 m) was particularly high (30% ± 3

SE) and higher than macroalgae and CCA cover (3.1 ± 1.9 to 3.9% ± 0.8 SE, respectively). Parininihi had lower sponge cover (19.6% ± 2.3 SE) but with high corresponding macroalgae cover (37.4% ± 3.6 SE) (Fig. 2E).

3.3. Sponge assemblage morphological composition

Sponge assemblage morphological composition was significantly different between depths at all locations with depth profiles: Poor Knights ($F_{8,133}$ = 5.65, p < 0.001); inner Fiordland ($F_{9,116}$ = 4.53, p < 0.0001); mid Fiordland ($F_{12,577}$ = 6.99, p < 0.0001); and outer Fiordland ($F_{12,293}$ = 3.37, p < 0.001), (Tables S11–S14).

At the Poor Knights, encrusting sponges (low complexity, Table S2) were the most abundant morphologies at all depths except 80 m (Figs. 4B & S3A), where their cover declined significantly from a peak of 50.6% (±7.6 SE) at 15 m to 4.1% (±1.9 SE) at 80 m (p < 0.001). Here, branching and massive sponges became the most dominant forms (both > 9% total cover at 80 m) having both increased in cover significantly from where they first appeared at 15 m (p < 0.01) and 5 m (p < 0.001), respectively. Repent and flabellate forms also increased significantly at deeper depths from 3.9% (±0.9 SE) at 5 m to a peak of 17.3% (±2.9 SE) at 50 m (p < 0.001), and 0% at 5–15 m to a peak of 6.4% (±4.4 SE) at 80 m (p < 0.001), respectively (Fig. S3A).

Depth-related changes in the morphological composition of sponge assemblages at inner Fiordland sites were more difficult to elucidate given the low overall sponge cover (Figs. 2B & S3B). However, encrusting, globular, and repent sponges were the most abundant forms overall (Fig. S3B). These forms all increased in cover at mid-range depths, all peaking at 30 or 40 m (encrusting: 11.4% ± 2.1 SE; repent: 1.3% ± 0.5 SE; globular: 2.3% ± 0.5 SE) and then declining into the deeper depth zones where at 100 m repent forms disappeared entirely, and globular and encrusting forms dropped to 0.6% (±0.3 SE) and 3.6% (±1.4 SE), respectively (Fig. S3B). SIMPER analysis showed that similarities in assemblage morphological composition between depth bins were explained by the presence of encrusting morphologies due to their consistently high relative abundance.

At the mid Fiordland sites, each morphological type was represented across a wider depth range than at inner Fiordland sites (Fig. S3C). Overall, encrusting sponges were again the most dominant form at every depth (Fig. S3C). However, after peak-

ing at 40 m (14.9% ± 1.4 SE), encrusting forms then declined significantly with increasing depth down to 120 m (2.1% ± 1.2 SE) (p < 0.001), (Fig. S3C). Globular forms followed a similar pattern to encrusting forms, peaking at 30 m (1.8% ± 0.3 SE) and then declining down to 120 m (0.3% ± 0.1 SE) (p < 0.001). Repent forms peaked at a shallower depth of 15 m (2.6% ± 0.9 SE), and then steadily declined, but non-significantly, with depth until 60 m (0.9% ± 0.2 SE) beyond which their cover changed very little with increasing depth. Massive forms showed no obvious pattern with depth. At both depth extremes, sponge assemblages were generally defined by lower cover of all morphologies (Fig. 2 & S3).

While most sponge morphologies were more abundant at every depth at the outer Fiordland sites than mid Fiordland sites, the relative abundance patterns were similar. However, encrusting sponges were an exception, where their cover did not change as much with depth as found at the mid Fiordland sites, only showing a non-significant drop in cover after 90 m, ranging from a low of 4.2% (±1.6 SE) to a high of 5.2% (±2 SE) cover (Fig. S3D). Repent sponges were the next most abundant form and followed a similar depth pattern to that at mid Fiordland sites, with a peak in cover at 15 and 25 m (7.5% ± 2.7 SE and 5.1% ± 0.5 SE, respectively). This was significantly higher than all other depths (p < 0.001) and steadily declined with depth (Fig. S3D) with the exception of a second smaller peak occurring at 120 m (4.3% ± 1.5 SE). As with the mid Fiordland sites, globular sponges peaked from 30–50 m (3.0% ± 0.4 to 2.2% ± 0.3 SE), but again, as with repent forms, a second peak in cover occurred at 120 m (4.3% ± 1.4 SE) (Fig. S3D). Massive forms showed no obvious pattern with depth except for a peak in cover between 80 and 110 m that was significantly higher than at all depths above 80 m and below 25 m (p < 0.01). A maximum cover of 4.5% (±1.9 SE) was reached at 110 m before significantly reducing in abundance, declining to 0.2% (±0.2 SE) cover at 120 m (p < 0.05) (Fig. S3D).

3.4. Sponge assemblage contribution to habitat complexity

Sponge assemblage morphological complexity (as assemblage complexity score, see Table S2) changed significantly with depth at all locations (Fig. 5). Poor Knights ($F_{8,133}$ = 10.8, p < 0.0001) showed a significant increase beyond 40 m ($F_{8,133}$ = 5.05, p < 0.0001), while overall morphological complexity at inner
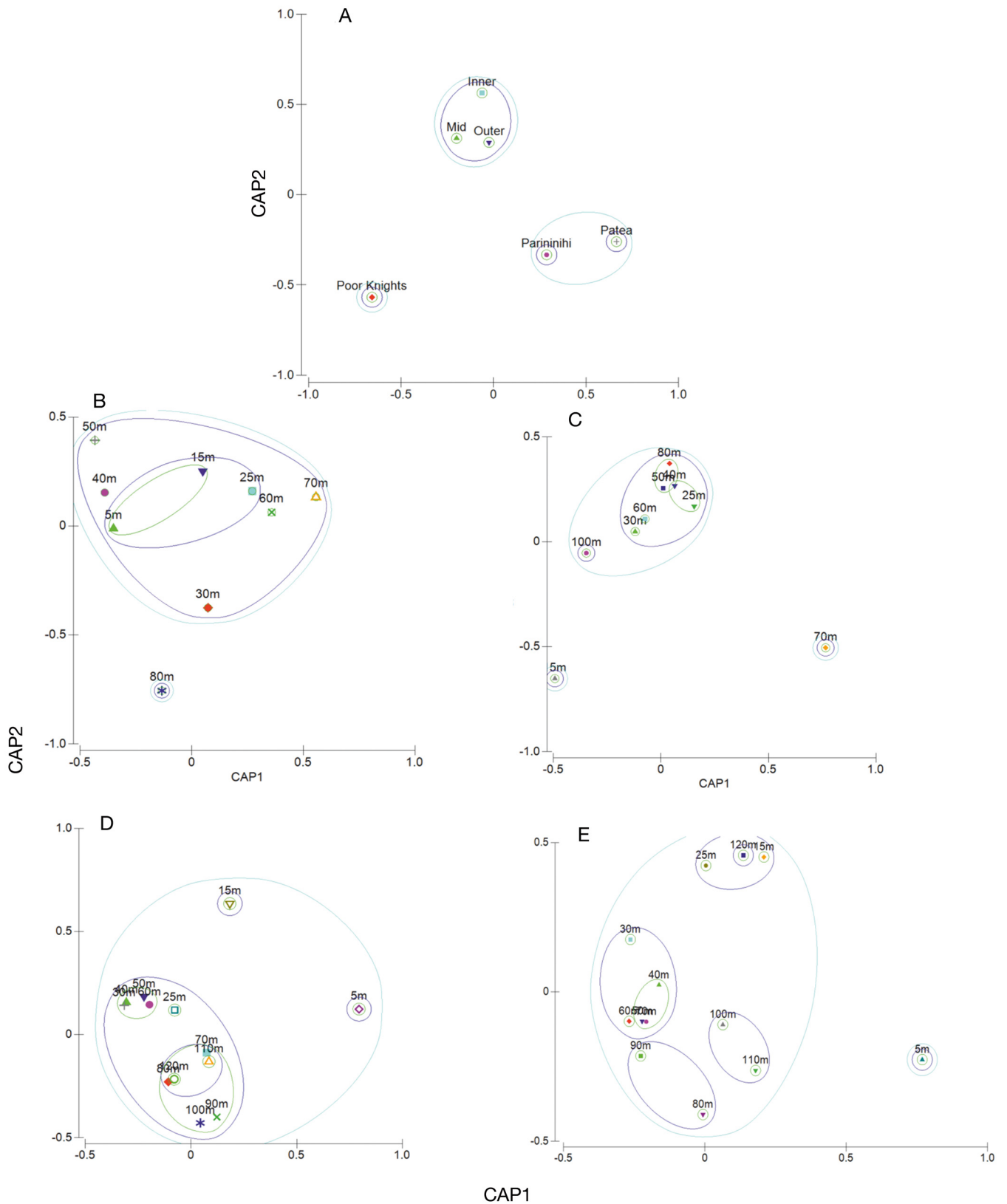
Fig. 4. Canonical analysis of principal coordinates (CAP) ordination of sponge assemblage morphological composition at all survey locations across all depths with groups factored as location (A). Groups were then factored as depth at (B) the Poor Knights, (C) inner Fiordland, (D) mid Fiordland, and (E) outer Fiordland. Analysis is based on a Bray-Curtis similarity matrix of percentage cover data. Clusters are based on resemblance levels at 10% (green), 20% (blue), and 30% (turquoise)
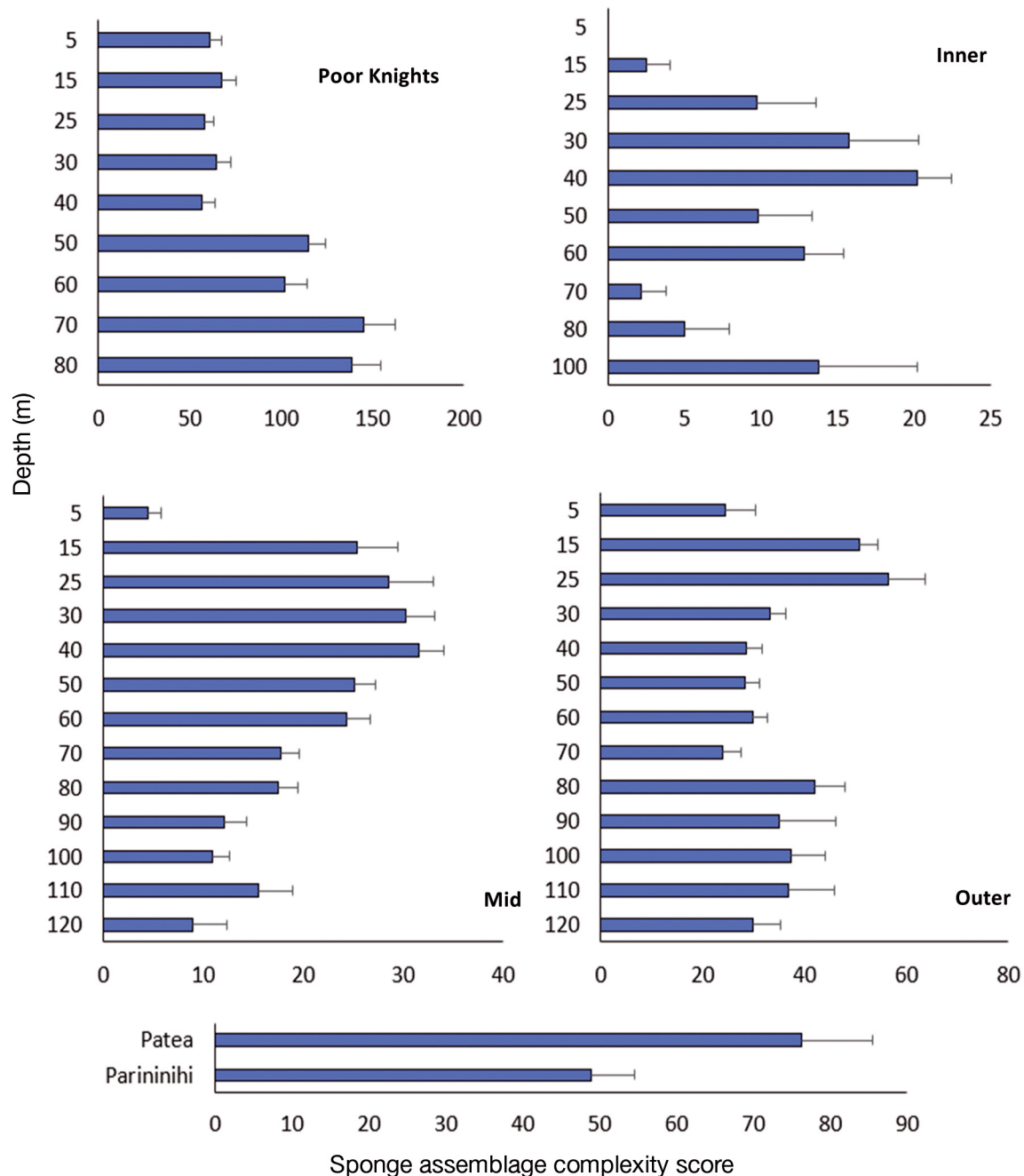
Fig. 5. Sponge assemblage morphological complexity scores at 10 m depth increments at Poor Knights, inner, mid, and outer Fiordland, Patea, and Parininihi. Assemblage complexity scores equal the sum of the complexity score assigned to each morphological type of sponge (ranging from 1–5, Table S2) multiplied by the abundance of each morphology in a quadrat. Figure shows mean of quadrat scores + SE

Fiordland ($F_{9,116}$ = 4.02, p < 0.0001) peaked at 30 and 40 m. At mid Fiordland ($F_{12,577}$ = 9.72, p < 0.0001) overall morphological complexity also peaked at 40 m, but with a reduction in complexity beyond this depth. At outer Fiordland ($F_{12,293}$ = 2.79, p < 0.001) overall sponge morphological complexity peaked at 15 m (Fig. 5).

Low complexity morphologies were consistently the most abundant group followed by medium and high complexity forms throughout the infralittoral and upper mesophotic regions of all locations (Fig. 6). However, the deeper depths (>70 m) at all locations showed an increase in medium and high complexity forms compared to shallow regions in respect to
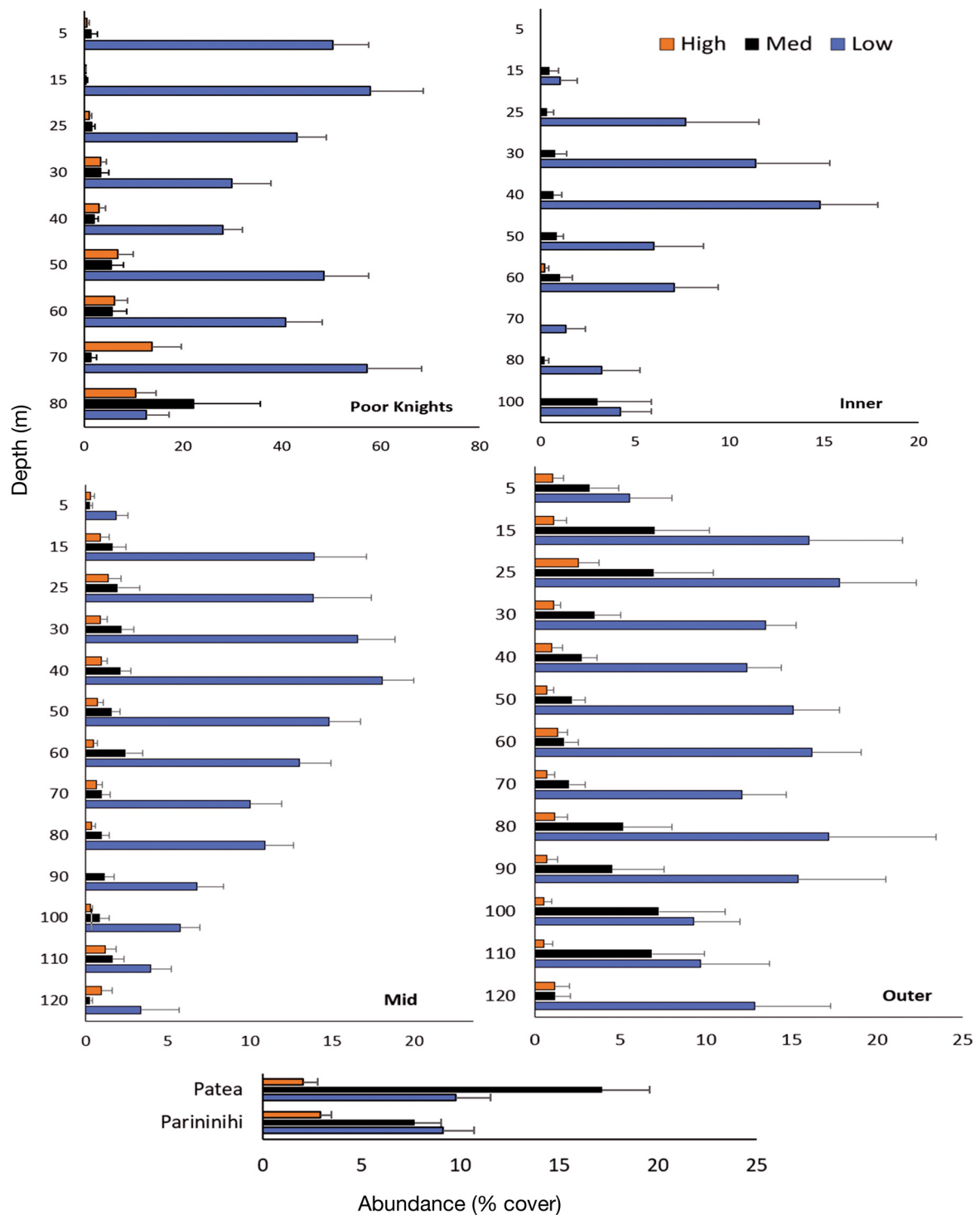
Fig. 6. Total sponge cover as binned into high, medium, and low complexity at 10 m depth increments at Poor Knights, inner, mid, and outer Fiordland, Patea, and Parininihi

actual cover (Fig. 6) and proportionally to the full sponge assemblage (Fig. 7).

At the Poor Knights, low complexity forms initially declined significantly with depth (p < 0.01) from a

peak at 15 m (57.9% ± 7 SE) (Fig. 6) representing 99.1% of the total sponge assemblage (Fig. 7), down to 28.1% (±3.2 SE) at 40 m. Cover of low complexity forms was variable below 40 m, but at 80 m there was
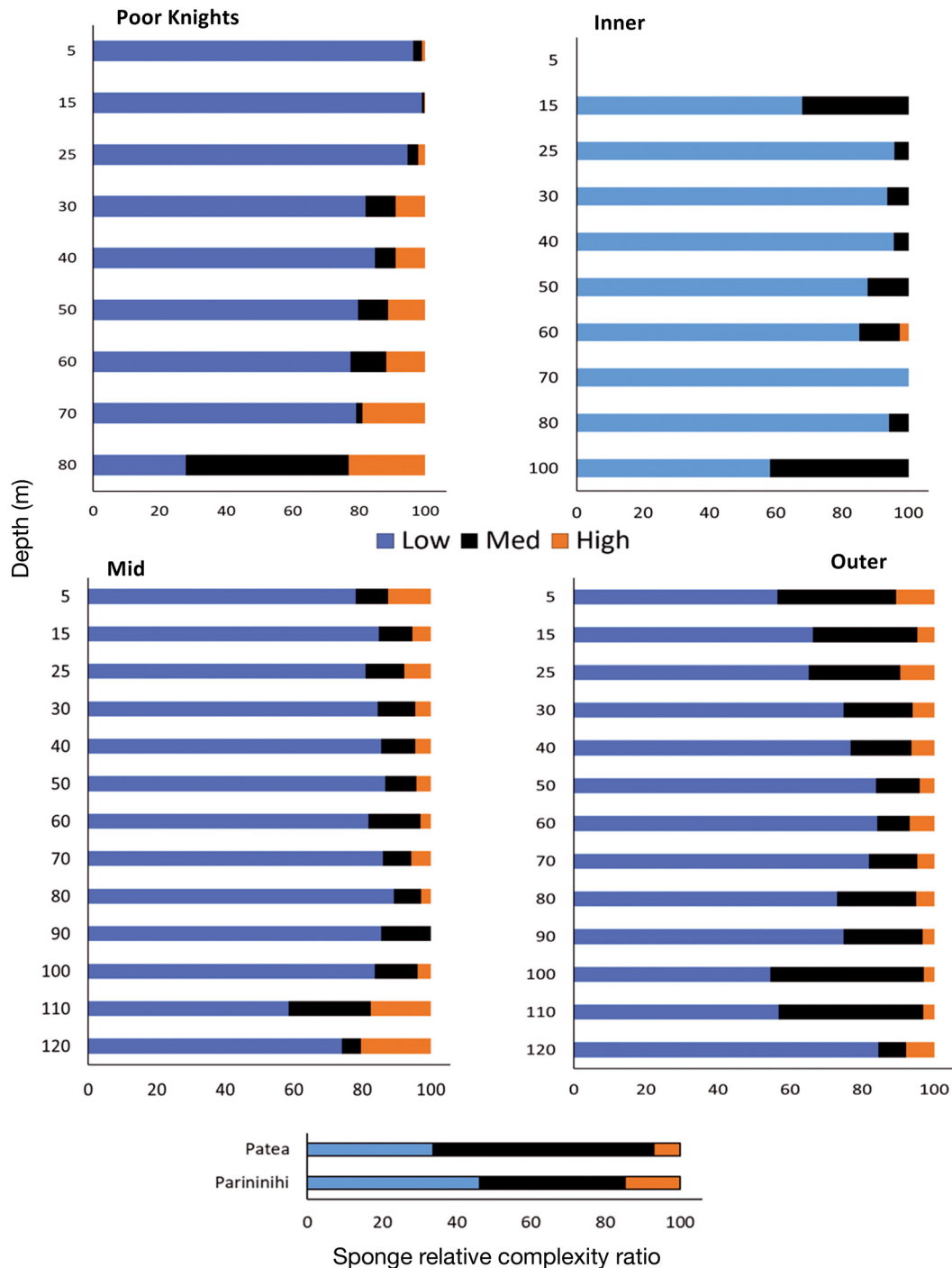
Fig. 7. Relative abundance (of sponge assemblage) of low, medium, and high complexity sponge morphologies over 10 m depth increments at Poor knights, inner, mid, and outer Fiordland, Patea, and Parininihi

significantly lower coverage (12.6% ± 3.1 SE) compared to all other depth bins (except for 30 m) (p < 0.01), representing only 27.9% of the total sponge assemblage. Medium and high complexity forms were generally more abundant below 40 m. Medium complexity forms had significantly more coverage at

80 m (22.2% ± 6.8 SE) than all other depth bins (p < 0.01). High complexity forms peaked in coverage (13.7% ± 4.3 SE) at 70 m, which was significantly higher than all depth bins in the infralittoral zone (below 30 m) (p < 0.05) (Fig. 6). Medium and high complexity forms represented 49 and 23.1%, respec-

tively, of the sponge assemblage at 80 m (Fig. 7). The relative increase of high complexity forms below 60 m was positively correlated with the overall increase in sponge cover ($F_{1,75}$ = 2.96, p < 0.01). At inner Fiordland, medium complexity forms were most abundant at 100 m with 3% (±1.9 SE) total cover (Fig. 6), representing 41.7% of the total sponge assemblage (Fig. 7). High complexity forms only occurred at 60 m and at very low overall cover (0.2% ± 0.2 SE), representing only 2.6% of the total sponge assemblage. Low complexity forms were significantly more abundant than medium and high complexity forms at all depths (p < 0.0001) but dropped to a low of 58.3% of the total sponge assemblage cover at 100 m, indicating a relative increase in importance of medium complexity forms (Figs. 6 & 7). At mid Fiordland, high complexity forms were generally low in overall cover with a maximum of 1.3% (±0.5 SE) cover at 25 m (Fig. 6). However, high complexity forms became increasingly abundant relative to the overall sponge assemblage, reaching highest proportional cover (20.4%) at the deepest surveyed depth bin (120 m) (Fig. 7). Medium complexity forms showed a similar pattern, becoming more proportionally abundant below 80 m, reaching a high of 23.9% at 110 m (Fig. 7) but peaking in overall cover at 60 m (2.4% ± 0.7 SE) (Fig. 6). At outer Fiordland, the highest sponge cover recorded (27.3% ± 4.1 SE) at 25 m (Fig. 2) coincided with the greatest coverage of high complexity forms (2.6% ± 0.8 SE) (Fig. 6). This represented 9.4% of the sponge assemblage (the highest proportion of high complexity forms recorded at this location) (Fig. 7). The cover of medium complexity forms showed two peaks of high cover at 15 and 25 m (7% ± 2.1 and 7% ± 1.4 SE, respectively) and 100–110 m (7.2% ± 2 to 6.8% ± 2.1 SE, respectively) (Fig. 7). However, the assemblage-relative abundance of medium complexity forms significantly increased through the lower mesophotic region from 60 to 110 m (8.9 and 40.2%, respectively) (p < 0.0001) and correlated with overall sponge cover ($F_{1,165}$ = 2.35, p < 0.05) with a significant assemblage-relative reduction in low complexity forms over the same depth range (84.2 to 56.7%) (p < 0.01) (Fig. 7). Patea showed the highest sponge assemblage complexity score of all locations at 25 m (Fig. 5) with an overall cover of 17.2% (±3.5 SE) of medium complexity forms (Fig. 6) representing 59.3% of the sponge assemblage (Fig. 7) and the only location to exceed the proportion of low complexity forms (9.8%) at this depth. Parininihi showed a lower overall sponge complexity than Patea (Fig. 5) coinciding with lower overall sponge cover (Fig. 2E). The

lower overall complexity score is unsurprising, as the overall sponge complexity metric considers cover as well as morphological complexity scores. However, Parininihi showed the highest overall cover of high complexity forms (2.9% ± 0.6 SE) of all locations at 25 m (Fig. 6), which also represented the largest proportion of high complexity forms of any assemblage (14.7%) at 25 m across all locations (Fig. 7).

3.5. Environmental variables

Temperature declined with increasing depth at all locations but plateaued before reaching the depth limits of all sites (Fig. S5C). Chlorophyll *a* concentrations also decreased with depth at all locations, dropping most significantly and rapidly with depth at inner Fiordland sites, while Poor Knights and outer Fiordland chlorophyll *a* showed little decline with depth (Fig. S5D). Salinity was significantly lower in the first 20 m at inner Fiordland sites than all other locations but rapidly increased with depth, reaching similar concentrations to mid and outer Fiordland sites by 20 m (Fig. S5A). Poor Knights showed very little change in salinity with depth (Fig. S5A). Inner Fiordland sites and Poor Knights showed similar average turbidity values with no significant change with depth (Fig. S5B). While turbidity decreased gradually with depth at mid Fiordland sites, it increased with depth at outer Fiordland sites (Fig. S5B). These environmental variables showed strong multi-collinearity with depth in linear models; beyond acceptable thresholds of variance inflation factors (>5 VIF). This restricts the evaluation of independent effects of specific environmental variables on community distributions without carrying out experimental tests.

4. DISCUSSION

Very little is known about the community composition, abundance, and ecological significance of TMEs. Our study is the first to demonstrate how benthic community composition (at the phylum level) changes from the upper reaches of the infralittoral zone (> 5 m) through mesophotic depth ranges (down to 120 m) for TMEs in New Zealand. Our results show that TMEs have abundant benthic communities with significantly different compositions to those occurring at shallow depths (Figs. 2 & 3, Tables S4– S10) and are therefore likely to provide different ecological services and functions, compared to shallow water communities. However, our study also sug-

gests that TME community compositions can vary significantly across relatively small geographical scales as sampling location had a significant effect on the depth-related patterns of all TMEs sampled. This suggests that the environmental drivers that determine the benthic community distribution patterns of TMEs are not exclusively associated with depth. Our results also show how shallow-water reefs with reduced light availability are not necessarily appropriate surrogates for deeper water TMEs but instead harbour their own local communities. We also show the substantial contribution of sponges to TMEs relative to other benthic groups and their importance in providing habitat complexity especially in areas below 50 m.

4.1. TME benthic community patterns

The most abundant invertebrate phyla occurring across all TMEs were (in descending order) Porifera, Bryozoa, Ascidia, Cnidaria, and Annelida. While sponges were consistently among the most important organisms in characterising the benthic community throughout the infralittoral and mesophotic zone, the high variability in benthic community composition across the locations surveyed likely prevents generalised descriptions of the depth-related patterns of New Zealand TMEs being possible. Indeed, all locations had different depth-related community composition patterns. However, as expected, both macroalgae and CCA declined rapidly with depth and were generally absent below 60 m. As algae are important provisioners of habitat in shallow regions, the exclusion of algae from mesophotic zones is likely to increase the relative importance of sponges to habitat complexity.

At the Poor Knights, the decline in algal cover with increased depth is likely responsible for the increase in benthic animals into the upper mesophotic zone (40 m) as spatial competition between algae and the benthic invertebrate community is reduced. This has been shown in other temperate regions (e.g. Bell & Barnes 2000, Cárdenas et al. 2012) and is perhaps similar to the relief of spatial competition from algae (Scott et al. 2019) and corals (see Lesser et al. 2018, Bell et al. 2019) in MCEs. However, this relationship is not necessarily causal, as other abiotic factors, such as substratum inclination (Preciado & Maldonado 2005), have been shown to have a more significant effect than algal presence on the abundance of benthic organisms in temperate environments. Furthermore, benthic invertebrate groups have also been

shown to exhibit high abundance and diversity in conjunction with high algal abundances at shallow depths (e.g. Konar & Iken 2005). Indeed, the possibility of the co-occurrence of high abundances of algae and sponges was supported by our observations from Parininihi Marine Reserve. It has also been suggested that canopy-forming algae (e.g. *Ecklonia radiata*) can facilitate the abundance and diversity of other benthic invertebrate groups (Cárdenas et al. 2016). These observations from other temperate regions indicate that the mechanisms driving benthic community diversity patterns in TMEs are likely to be context-specific whereby algal abundance may only be an important driver in some locations. This was also confirmed by our own observations of TMEs at inner Fiordland sites, where diversity increased with depth (down to 60 m), which cannot have been a consequence of relief from spatial competition with macroalgae, as algae were almost completely absent below 5 m. While spatial competition from algae might be important in MCEs and certain TMEs with high light availability, such as the Poor Knights, the ecological mechanisms driving the depth-related patterns in community composition and diversity in low light habitats with low algal abundances are likely to be very different.

The reduction in macroalgae with depth is one of the few taxon-specific patterns that occurred at all locations albeit at very different rates and with variable consequences for the wider benthic community. Importantly, the relationship between algae and the wider benthic community becomes more complex when considering that the relationship is interactive, as some benthic invertebrate groups can also directly determine the distribution and abundance of algae, for example via predation (Tuya et al. 2004). Furthermore, algae comprise an extremely broad group and individual species are likely to respond differently to the abiotic and biotic factors occurring throughout TMEs depending on species-specific traits. For example, CCA persisted much deeper than other macroalgal species at all locations surveyed, and in some cases, continued far into the mesophotic zone (>60 m), with potentially limiting (Breitburg 1984) and facilitative (Nelson 2009) effects on the deeper community components of these TMEs.

The only other taxon-specific depth pattern found at all locations was the higher cover of polychaetes (Annelida) at deeper depths (>60 m), where they occupied up to 6% of the substrate (at 60 m at inner Fiordland). Every organism counted in this category was either *Spirobranchus cariniferus* (Gray, 1843) or *Galeolaria hystrix* (Mörch, 1863), 2 species of filter-

feeding fan worms. These tube-building polychaetes are endemic to New Zealand and southern Australia. While both these species have been observed in the intertidal zone (Riedi & Smith 2015), our results suggest an overwhelming preference for deeper environments, the reasons for which are not immediately obvious. However, at the Poor Knights, polychaetes were almost completely absent throughout the full depth range where other groups across the benthic invertebrate community (especially sponges) were particularly abundant. Inter-phyletic spatial competition might, therefore, be playing a significant role in the overall exclusion of this group in shallow waters (Bell & Barnes 2003). Another explanation for the apparent absence of this phylum at the Poor Knights is that the species occurring here, and in the shallower depth zones of other locations are less conspicuous than the large and gregarious reef-building polychaetes found further south, and therefore, were missed during image analysis. This group might not be subject to the spatial competition imposed by other benthic groups and are instead directly utilizing the habitat that more spatially competitive organisms (such as sponges) provide.

4.2. Sponge assemblage patterns

We found that sponges were the most dominant benthic community group at every location, through the infralittoral and mesophotic zone reaching very high cover in some cases in the lower mesophotic zone (Fig. S6). For example, sponge cover exceeded 70% cover in the lower mesophotic regions of the Poor Knights (Fig. 2A), approaching some of the highest reported abundances in MCEs (Lesser & Slattery 2018) and exceeding those reported for the shallow reefs of other temperate regions (e.g. Bell et al. 2020). The mesophotic-like reefs in Taranaki also exhibited high sponge cover relative to those reported on other temperate reefs within the same depth range (15–25 m), particularly Patea, which had 30% total sponge cover; higher than reported for any other shallow temperate reefs outside of the Mediterranean (see Bell et al. 2020). The TMEs at all the other locations surveyed had mean sponge cover similar to those observed in temperate infralittoral zones (<30 m) elsewhere in the world which range from 8 to 18% cover, with the exception of the particularly high abundances found in shallow waters of the Mediterranean (see Bell et al. 2020). However, quantitative information of sponge abundance in the mesophotic zones of other temperate regions is sparse

and often derived from narrower depth ranges (e.g. Heyns et al. 2016 [45–75 m], Ferrari et al. 2018 [25–50 m], Idan et al. 2018 [95–120 m]) or is derived from a specimen count approach (number of specimens m^{-2}) without specific depth considerations (e.g. Bo et al. 2012).

We observed high sponge cover occurring beyond the infralittoral zones where sponges remained the dominant benthic invertebrate group throughout depth profiles at all sites. However, full depth profile patterns were highly variable. This high degree of variability does not support the sponge increase hypothesis as suggested by Lesser (2006) and Lesser & Slattery (2013), who observed increases in sponge abundance with depth in MCEs. Our results are more reflective of those reported by Scott et al. (2019), who also demonstrated high variablilty in sponge abundance with depth and supported by a review of the sponge increase hypothesis in Scott & Pawlik (2019), but again, this study was carried out in tropical environments with likely different ecological dynamics driving sponge distributions.

It has been suggested that macroalgae are likely to have important contributions to sponge distributions either as facilitative (Cárdenas et al. 2016) or competitive (Easson et al. 2014) interactions. Indeed, we observed a negative correlation between macroalgae and sponge cover within the infralittoral zone, but this was only correlative, and relief from competition from macroalgae might not necessarily be the dominant driver of any observed increases in sponge abundance as demonstrated by Preciado & Maldonado (2005). Furthermore, spatial competition with macroalgae cannot explain the continued variation in sponge cover throughout the deeper regions of the TMEs observed where macroalgae are absent. The variation in sponge cover throughout TMEs is, therefore, likely to be in response to different drivers to those occurring at shallow depths. In particularly diverse and abundant TME benthic communities, this might include spatial competition with other benthic invertebrates rather than just algae, such as bryozoans (Russ 1982) and ascidians (de Voogd et al. 2004, Chadwick & Morrow 2011). In more depauperate TME benthic communities, where the substrate is more freely available, limiting factors to sponge distributions might include other ecological mechanisms, such as food availability. The effect of food limitation on the distribution of sponge assemblages remains a contentious topic in certain MCEs (e.g. Slattery & Lesser 2015, Pawlik et al. 2018), but evidence from other regions supports the hypothesis that food availability could be an important factor in

the ecological dynamics of sponges generally (Wooster et al. 2019). To our knowledge, no studies have investigated the role of food limitation on sponge assemblage distributions in TMEs, but given our understanding of sponge responses to temporal variability in food availability from shallow (Perea-Blázquez et al. 2013) and abyssal (Kahn et al. 2012) temperate zones, investigations of food limitation will be important for increasing our understanding of the mechanisms driving sponge assemblage distributions through TMEs.

4.3. Sponge morphology and contribution to habitat complexity

Different sponge morphologies can provide different ecosystem functions (Bell 2008, Folkers & Rombouts 2020), particularly the provision of habitat (Bell 2008, Maldonado et al. 2017), which is likely to be particularly important in temperate ecosystems that lack 3D reef-building corals (Graham & Nash 2013). For example, sponges have been shown to (1) provide important biogenic habitat structure for commercially important species (e.g. Miller et al. 2012); (2) form local biodiversity centres in deep-sea environments (e.g. Hogg et al. 2010); and (3) provide refuge from predation pressure for benthic invertebrates (Henkel & Pawlik 2005) and fishes (Ryer et al. 2004). Furthermore, sponge morphology has been shown to be closely related to the abundance and diversity of their associated macrofauna (Gherardi et al. 2001). Changes in sponge morphological complexity with depth (as assemblage complexity scores, Table S2) were site specific (Fig. 5) and closely resembled sponge cover–depth patterns (Fig. 2). This was not unexpected due to the inclusion of sponge cover in the assemblage morphological complexity metric. However, categorizing sponge morphologies into high, medium and low complexity bins revealed how levels of complexity changed with depth independent of overall sponge cover, both in terms of substrate cover (Fig. 6) and relative to the overall sponge assemblages (Fig. 7). While the specific details of depth patterns of sponge assemblage contributions to habitat complexity varied across TME locations, the overall pattern is one of increasing importance of medium and high complexity sponge assemblages with progression into the mesophotic zone. This has important ecological implications for TMEs harbouring high sponge abundances. The ecological functions of TMEs will involve different ecological community dynamics to shallow regions where the relative importance and

contribution of sponges to habitat complexity is less pronounced due to the higher relative abundance of other habitat-forming organisms, including macroalgae. Indeed, with the significant reduction in abundance of bryozoans, particularly low ascidian abundance, and the absence of macroalgae and CCA, the sponge assemblage in the lower mesophotic region of the Poor Knights appears to be the primary source of biotic habitat complexity in this ecosystem. A similar pattern was reflected at mid Fiordland sites albeit to a lesser extent, whereby the cover of medium and high complexity forms at mid Fiordland remained relatively stable with depth while low complexity forms declined significantly. This resulted in a much higher cover of high and medium complexity forms proportionally to the overall sponge assemblage in the lower mesophotic zones. Outer Fiordland sites showed a significant increase of total (Fig. 6) and proportional (Fig. 7) cover of medium complexity sponges between 100 and 110 m. Even in circumstances of low overall cover, again, sponges appear to be the primary source of habitat complexity in these TMEs.

While the importance of the sponge assemblages to numerous ecological functions, including the provision of habitat complexity, have been discussed, the mechanisms generating these observed patterns observed remain unknown, whereby the environmental variables considered in this study do not show any obvious correlations with sponge distributions. Further study is required to consider a wider range of both abiotic and biotic variables to determine these drivers. Sponge assemblages have been observed to be most affected by substrate inclination relative to a number of quantified biotic and abiotic factors in a multivariate analysis by Preciado & Maldonado (2005). Although changing substrate complexity and inclination with depth were not quantified in this study, these factors provide a possible explanation for the total and proportional morphological complexity depth patterns of sponge communities that were observed in the deeper zones (>70 m) of the TMEs surveyed. The environmental variables that were measured in these zones were relatively stable at these deeper zones (Fig. S5) and, therefore, are unlikely to be fully responsible for the observed changes in the morphological composition of the sponge community.

4.4. Mesophotic TME surrogates

Parininihi and Patea were only surveyed across a limited depth profile between 15 and 25 m, beyond which, rocky reef becomes homogeneous sandy ha-

bitat. However, these locations are known to have poor light penetration and visibility (Battershill & Page 1996) and as such were chosen to determine if low-light shallow reefs can harbour benthic communities analogous to those found at deeper locations and potentially act as shallow surrogates for deeper TMEs more generally. Our results suggest that this was not the case and that these reefs harbour different community compositions to those occurring in TMEs, but also from those occurring at the same depths in other locations in New Zealand. However, these reefs do appear to be more similar to deeper habitats in regard to their sponge assemblages and the particularly high morphological complexity of these assemblages. High and medium sponge morphologies were significantly more abundant at both Patea and Parininihi than in the infralittoral zones of the other locations surveyed. As such, while these shallow reefs may not be suitable direct surrogates for the wider benthic communities of TMEs, they provide valuable opportunities to develop our understanding of the ecological functions of sponge assemblages more typical of TMEs and are also likely to provide valuable insights into the driving mechanisms behind TME community compositions generally, since they experience limited light availability. Furthermore, it is likely that these shallow mesophotic-like ecosystems are common along the west coast of New Zealand and, therefore, require further investigation.

Our results suggest that TMEs can support abundant benthic communities distinct from those occurring at shallow depths in the infralittoral zone. However, depth-related patterns were very location-specific, making it difficult to generalise between TMEs. More direct assessments of TME benthic communities at the species-level would help elucidate any common benthic community patterns that might exist. However, one consistent characterisation of all the sites surveyed was the domination of sponges throughout TME depth profiles. Furthermore, as a consequence of their high cover relative to other phyla within the wider benthic community, and particularly high gross morphological variation, our results suggest that these sponge assemblages are providing important ecological functions through the provisioning of habitat complexity. This is especially important in the deeper regions of the TMEs we studied, as other important habitat complexity provisioners such as macroalgae and branching forms of crustose coralline algae decline in the infralittoral and upper mesophotic zones. We suggest that TME research should prioritise multivariate analyses of the ecological drivers of TME community distributions, including abiotic drivers such as substrate inclination, habitat complexity and the direct quantification of light availability, and biotic considerations such as spatial competition, habitat provisioning, predation, anthropogenic disturbance, and food availability.

LITERATURE CITED

Austen MC, Lambshead PJD, Hutchings PA, Boucher G, Snelgrove PVR, Heip C, Smith C (2002) Biodiversity links above and below the marine sediment–water interface that may influence community stability. Biodivers Conserv 11:113–136

Balmford A, Gaston KJ (1999) Why biodiversity surveys are good value. Nature 398:204–205

Battershill CN, Page MJ (1996) Preliminary survey of Pariokariwa Reef North Taranaki. National Institute of Water and Atmosphere (NIWA), Kilbirnie, Wellington

Beazley LI, Kenchington EL, Murillo FJ, Sacau MDM (2013) Deep-sea sponge grounds enhance diversity and abundance of epibenthic megafauna in the Northwest Atlantic. ICES J Mar Sci 70:1471–1490

Bell JJ (2007) The ecology of sponges in Lough Hyne Marine Nature Reserve (south-west Ireland): past, present and future perspectives. J Mar Biol Assoc UK 87:1655–1668

Bell JJ (2008) The functional roles of marine sponges. Estuar Coast Shelf Sci 79:341–353

Bell JJ, Barnes DKA (2000) The influences of bathymetry and flow regime upon the morphology of sublittoral sponge communities. J Mar Biol Assoc UK 80:707–718

Bell JJ, Barnes DKA (2001) Sponge morphological diversity: A qualitative predictor of species diversity? Aquat Conserv 11:109–121

Bell JJ, Barnes DKA (2003) The importance of competitor identity, morphology and ranking methodology to outcomes in interference competition between sponges. Mar Biol 143:415–426

Bell JJ, Jompa J, Haris A, Werorilangi S, Shaffer M, Mortimer C (2019) Domination of mesophotic ecosystems in the Wakatobi Marine National Park (Indonesia) by sponges, soft corals and other non-hard coral species. J Mar Biol Assoc UK 99:771–775

Bell JJ, McGrath E, Kandler N, Marlow J and others (2020) Interocean patterns in shallow water sponge assemblage structure and function. Biol Rev Camb Philos Soc. 95: 1720–1758

Bo M, Bertolino M, Bavestrello G, Canese S, Giusti M, Angiolillo M, Taviani M (2012) Role of deep sponge grounds in the Mediterranean Sea: a case study in southern Italy. Hydrobiologia 687:163–177

Boavida J, Assis J, Reed J, Serrão EA, Gonçalves JMS (2016) Comparison of small remotely operated vehicles and diver-operated video of circalittoral benthos. Hydrobiologia 766:247–260

Bouchet P (2006) The magnitude of marine biodiversity. In: Duarte CM (ed) The exploration of marine biodiversity: scientific and technological challenges. Fundación BBVA, Mexico City, p 31–62

Breitburg DL (1984) Residual effects of grazing: inhibition of competitor recruitment by encrusting coralline algae. Ecology 65:1136–1143

Cárdenas CA, Davy SK, Bell JJ (2012) Correlations between algal abundance, environmental variables and sponge distribution patterns on southern hemisphere temperate rocky reefs. Aquat Biol 16:229–239

Cárdenas CA, Davy SK, Bell JJ (2016) Influence of canopy-forming algae on temperate sponge assemblages. J Mar Biol Assoc UK 96:351–362

Cerrano C, Bastari A, Calcinai B, Di Camillo C and others (2019) Temperate mesophotic ecosystems: gaps and perspectives of an emerging conservation challenge for the Mediterranean Sea. Eur Zool J 86:370–388

Chadwick NE, Morrow KM (2011) Competition among sessile organisms on coral reefs. In: Dubinsky Z, Stambler N (eds) Coral reefs: an ecosystem in transition. Springer, Dordrecht, p 347–371

Choat JH, Schiel DR (1982) Patterns of distribution and abundance of large brown algae and invertebrate herbivores in subtidal regions of northern New Zealand. J Exp Mar Biol Ecol 60:129–162

Costello MJ, Coll M, Danovaro R, Halpin P, Ojaveer H, Miloslavich P (2010) A census of marine biodiversity knowledge, resources, and future challenges. PLOS ONE 5(8): e12110

Covich AP, Austen MC, Bärlocher F, Chauvet E, Cardinale BJ, Biles CL, Moss B (2004) The role of biodiversity in the functioning of freshwater and marine benthic ecosystems. Bioscience 54:767–775

Danovaro R, Snelgrove PVR, Tyler P (2014) Challenging the paradigms of deep-sea ecology. Trends Ecol Evol 29: 465–475

de Voogd NJ, Becking LE, Hoeksema BW, van Soest RWM (2004) Sponge interactions with spatial competitors in the Spermonde Archipelago. Boll Museo Istitu Biol Univ Genova 68:253–261

Diaz MC, Rützler K (2001) Sponges: an essential component of Caribbean coral reefs. Bull Mar Sci 69:535–546

Downey RV, Griffiths HJ, Linse K, Janussen D (2012) Diversity and distribution patterns in high Southern latitude sponges. PLOS ONE 7(7):e41672

Ferrari R, Marzinelli EM, Ayroza CR, Jordan A, Figueira WF, Byrne M, Steinberg PD (2018) Large-scale assessment of benthic communities across multiple marine protected areas using an autonomous underwater vehicle. PLOS ONE 13(3):e0193711

Folkers M, Rombouts T (2020) Sponges revealed: a synthesis of their overlooked ecological functions within aquatic ecosystems. In: Jungblut S, Liebich V, Bode-Dalby (eds) YOUMARES 9 — The oceans: our research, our future. Springer, Cham, p 181–193

Gherardi M, Giangrande A, Corriero G (2001) Epibiontic and endobiontic polychaetes of *Geodia cydonium* (Porifera, Demospongiae) from the Mediterranean Sea. Hydrobiologia 443:87–101

Goodwin E, Cornelisen CD (2012) Near-surface water temperatures in Doubtful Sound and response to natural and anthropogenic drivers. NZ J Mar Freshw Res 46:1-19

Graham NAJ, Nash KL (2013) The importance of structural complexity in coral reef ecosystems. Coral Reefs 32: 315–326

Henkel TP, Pawlik JR (2005) Habitat use by sponge-dwelling brittlestars. Mar Biol 146:301–313

Heyns ER, Bernard ATF, Richoux NB, Götz A (2016) Depth-related distribution patterns of subtidal macrobenthos in a well-established marine protected area. Mar Biol 163:1–15

Hinderstein LM, Marr JCA, Martinez FA, Dowgiallo MJ and others (2010) Theme section on 'Mesophotic coral ecosystems: characterization, ecology, and management'. Coral Reefs 29:247–251

Hogg MM, Tendal OS, Conway KW, Pomponi SA and others (2010) Deep-sea sponge grounds: reservoirs of biodiversity. World Conservation Monitoring Centre (UNEP regional seas report and studies, no. 189) (UNEP–WCMC Biodiversity Series, 32), Cambridge

Howe JA, Austin WEN, Forwick M, Paetzel M, Harland R, Cage AG (2010) Fjord systems and archives: a review. Geol Soc Spec Publ 344:5–15

Idan T, Shefer S, Feldstein T, Yahel R, Huchon D, Ilan M (2018) Shedding light on an east-Mediterranean mesophotic sponge ground community and the regional sponge fauna Mediterranean. J Mar Sci 19:84–106

James LC, Marzloff MP, Barrett N, Friedman A, Johnson CR (2017) Changes in deep reef benthic community composition across a latitudinal and environmental gradient in temperate Eastern Australia. Mar Ecol Prog Ser 565: 35–52

Kahn AS, Ruhl HA, Smith KL (2012) Temporal changes in deep-sea sponge populations are correlated to changes in surface climate and food supply. Deep Sea Res I 70: 36–41

Kahng SE, Garcia–Sais JR, Spalding HL, Brokovich E, Wagner D, Weil E, Toonen RJ (2010) Community ecology of mesophotic coral reef ecosystems. Coral Reefs 29:255–275

Kahng SE, Copus JM, Wagner D (2014) Recent advances in the ecology of mesophotic coral ecosystems (MCEs). Curr Opin Environ Sustain 7:72–81

Kelly M, Rowden AA (2019) New sponge species from hydrothermal vent and cold seep sites off New Zealand. Zootaxa 4576:401–438

Kelly M, Sim-Smith C (2009) A literature review on the Poor Knights Islands Marine Reserve. Department of Conservation, Northland Conservancy, Whangarei, Northland

Konar B, Iken K (2005) Competitive dominance among sessile marine organisms in a high Arctic boulder community. Polar Biol 29:61–64

Lam K, Shin PKS, Bradbeer R, Randall D, Ku KKK, Hodgson P, Cheung SG (2006) A comparison of video and point intercept transect methods for monitoring subtropical coral communities. J Exp Mar Biol Ecol 333:115–128

Lesser MP (2006) Benthic–pelagic coupling on coral reefs: feeding and growth of Caribbean sponges. J Exp Mar Biol Ecol 328(2): 277-288

Lesser MP, Slattery M (2013) Ecology of Caribbean sponges: Are top-down or bottom-up processes more important? PLOS ONE 8:e79799

Lesser MP, Slattery M (2018) Sponge density increases with depth throughout the Caribbean. Ecosphere 9:e02525

Lesser MP, Slattery M (2019) Sponge density increases with depth throughout the Caribbean: reply. Ecosphere 10(4): e02690

Lesser MP, Slattery M, Leichter JJ (2009) Ecology of mesophotic coral reefs. J Exp Mar Biol Ecol 375:1–8

Lesser MP, Slattery M, Mobley CD (2018) Biodiversity and functional ecology of mesophotic coral reefs. Annu Rev Ecol Evol Syst 49:49–71

Maldonado M, Aguilar R, Bannister RJ, Bell JJ and others (2017) Sponge grounds as key marine habitats: a synthetic review of types, structure, functional roles and conservation concerns. In: Rossi S, Bramanti L, Gori A, Orejas Saco del Valle C (eds) Marine animal forests. Springer, Cham, p 1–39

McClintock JB, Amsler CD, Baker BJ, Van Soest RW (2005) Ecology of Antarctic marine sponges: an overview. Integr Comp Biol 45:359–368

Miller RJ, Hocevar J, Stone RP, Fedorov DV (2012) Structure-forming corals and sponges and their use as fish habitat in Bering Sea submarine canyons. PLOS ONE 7:e33885

Ministry for the Environment (2014) Fiordland (Te Moana o Atawhenua) Marine Management Act (2005). New Zealand Government, Wellington

Nelson WA (2009) Calcified macroalgae — critical to coastal ecosystems and vulnerable to change: a review. Mar Freshw Res 60:787–801

Pawlik JR, Loh TL, Mcmurray SE (2018) A review of bottom-up vs top-down control of sponges on Caribbean fore-reefs: what's old, what's new, and future directions. PeerJ 6:e4343

Perea-Blázquez A, Davy SK, Magana-Rodríguez B, Bell JJ (2013) Temporal variation in food utilisation by three species of temperate demosponge. Mar Ecol Prog Ser 485:91–103

Poore GCB, Wilson G (1993) Marine species richness (with reply from R.M. May). Nature 361:597–598

Preciado I, Maldonado M (2005) Reassessing the spatial relationship between sponges and macroalgae in sublittoral rocky bottoms: a descriptive approach. Helgol Mar Res 59:141–150

Riedi MA, Smith AM (2015) Tube growth and calcification of two reef-building ecosystem engineers in southern New Zealand: *Galeolaria hystrix* and *Spirobranchus cariniferus* (Polychaeta: Serpulidae). Mar Geol 367:212–219

Rivero Calle S (2010) Ecological aspects of sponges in mesophotic coral ecosystems. PhD thesis, University of Puerto Rico, Mayaguez

Roberts DE, Cummins SP, Davis AR, Chapman MG (2006) Structure and dynamics of sponge-dominated assemblages on exposed and sheltered temperate reefs. Mar Ecol Prog Ser 321:19–30

Russ GR (1982) Overgrowth in a marine epifaumal community: competitive hierarchies and competitive networks. Oecologia 53:12–19

Ryer CH, Stoner AW, Titgen RH (2004) Behavioural mechanisms underlying the refuge value of benthic habitat structure for two flatfishes with differing anti-predator strategies. Mar Ecol Prog Ser 268:231–243

Schlacher TA, Schlacher-Hoenlinger MA, Williams A, Althaus F, Hooper JNA, Kloser R (2007) Richness and distribution of sponge megabenthos in continental margin canyons off southeastern Australia. Mar Ecol Prog Ser 340:73–88

Scott AR, Pawlik JR (2019) A review of the sponge increase hypothesis for Caribbean mesophotic reefs. Mar Biodivers 49:1073–1083

Scott AR, Battista TA, Blum JE, Noren LN, Pawlik JR (2019) Patterns of benthic cover with depth on Caribbean mesophotic reefs. Coral Reefs 38:961–972

Slattery M, Lesser MP (2015) Trophic ecology of sponges from shallow to mesophotic depths (3 to 150 m): Comment on Pawlik et al. (2015). Mar Ecol Prog Ser 527:275–279

Turner JA, Andradi-Brown DA, Dominic A, Gori A and others (2019) Key questions for research and conservation of mesophotic coral ecosystems and temperate mesophotic ecosystems. In: Loya Y, Puglise K, Bridge T (eds) Mesophotic coral ecosystems. Coral Reefs of the World, Vol 12. Springer, Cham, p 989–1003

Tuya F, Boyra A, Sanchez–Jerez P, Barbera C, Haroun RJ (2004) Relationships between rocky-reef fish assemblages, the sea urchin *Diadema antillarum* and macroalgae throughout the Canarian Archipelago. Mar Ecol Prog Ser 278:157–169

van Jaarsveld AS, Freitag S, Chown SL, Muller C, Koch S, Hull H, Scholtz CH (1998) Biodiversity assessment and conservation strategies. Science 279:2106–2108

van Soest RWM, Boury-Esnault N, Vacelet J, Dohrmann M, Erpenbeck D, de Voogd NJ, Hooper JNA (2012) Global diversity of sponges (Porifera). PLOS ONE 7(4):e35105

Wooster MK, McMurray SE, Pawlik JR, Morán XAG, Berumen ML (2019) Feeding and respiration by giant barrel sponges across a gradient of food abundance in the Red Sea. Limnol Oceanogr 64:1790–1801