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Invertebrate Biodiversity Associated With a Unique Bryozoan Biogenic Reef Complex (Western Port, Victoria, Australia)

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ABSTRACT

A unique biogenic bryozoan reef has been recently discovered in Western Port (a temperate embayment), Victoria, Australia. This reef is significant owing to its contiguous, regular, linear rows of densely stacked bryozoan colonies with large vertical relief. We aimed to (1) document the biodiversity of the macroinvertebrate epifauna associated with this unique linear bryozoan reef, and (2) to determine if there were differences in invertebrate matrix epifauna associated with each of the three bryozoan species which differ in structural complexity. This was achieved by collecting samples from colonies of the three dominant bryozoan species that make up the reef: *Triphyllozoon munitum*, *Triphyllozoon moniliferum* and *Celleporaria foliata*. The *Triphyllozoon* species (*T. moniliferum*, *T. munitum*) are fenestrate forming rounded colonies with intricate laminal folding, with *T. moniliferum* exhibiting a higher degree of folding, while *C. foliata*, a non-fenestrate species, forms plate-like colonies. Based on their differing morphology, we sought to determine if *Celleporaria foliata* and the two *Triphyllozoon* species harboured different matrix fauna and/or differing abundances. In total, bryozoan reef samples contained 7266 individuals, representing 120 different morphospecies from 57 different families across nine phyla. The assemblage was dominated by crustaceans (78% of the total abundance of taxa from 66 morphospecies). There was no significant difference in overall species richness or abundance of matrix fauna between the bryozoan species, although *C. foliata* harboured a significantly higher number of annelid species. Matrix epifauna richness was significantly higher in spring for all three bryozoan species. The relatively high invertebrate abundance and diversity associated with the Western Port bryozoan reefs potentially represents a spatially constrained area of enhanced foraging by demersal fishes and other taxa with links to other ecosystem functions. Further research is required to establish the conservation value of these reefs and determine what protective measures, if any, are required.

1 | Introduction

Biogenic reefs are typified by rigid calcareous skeletal frameworks that are topographically higher than surrounding sediments and composed of biological deposits produced over geological time (Hallock 1997). Bryozoans are a phylum of aquatic, non-photosynthesizing, filter-feeding invertebrates (Cook et al. 2018) and are described as 'ecosystem engineers' that can enhance local biodiversity when clustered together, or in reef form (Jones 2006). Bryozoan-dominated habitats are considered complex habitats for macroinvertebrates and support diverse assemblages at the centimetre to kilometre scale (Wood et al. 2012). These complex structures can harbour an array of epifaunal macroinvertebrates, both sessile and mobile, which we term 'matrix fauna' (Bradstock and Gordon 1983; Wood 2005; Wood et al. 2012; Wood and Probert 2013). As such,

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bryozoan habitat can be a biodiversity hotspot with the number of associated species per unit of habitat often exceeding that of adjacent non-biogenic habitat 10-fold or more (Jackson and Sala 2001; Lenihan and Peterson 1998).

Complex habitats can also decrease predation rates by providing refugia and protection to prey species, not only by way of hiding opportunities, but also by altering local environmental conditions such as wave action and current speed (Bell and Westoby 1986; Pederson and Peterson 2002; Wood et al. 2012). Additionally, they provide living space and attachment opportunities (Wood et al. 2012) for epifauna at various stages of development as well as spawning and nursery habitat for juvenile fish, as demonstrated at Separation Point and Foveaux Strait, New Zealand (Carbines et al. 2004; Jiang and Carbines 2002; Saxton 1980; Vooren 1975).

These sessile, mostly colonial organisms are found in all oceans, from the infralittoral zone to the deep-sea (up to 8000 m) and in all major benthic habitat types, including soft sediments, seagrass meadows, temperate reefs and hard bottoms (Cook et al. 2018; McKinney and Jackson 1991; Wood et al. 2012). Bryozoa generally establish and live attached to a substratum like rock, algae, or shell (Cocito et al. 2000; Cook et al. 2018; Wood et al. 2012). Colonies vary widely in growth habits ranging from 1 mm to more than 1 m, and can be soft with gelatinous exoskeletons, or hard but fragile with mineralised exoskeletons (Class Stenolaemata and Gymnolaemata) (Cook et al. 2018). Modern bryozoans tend to occur as isolates or patches of colonies and individual colonies are known to grow on infralittoral and circalittoral reefs, jetty pylons and among seagrass and *Caulerpa* spp. beds in Western Port and Port Phillip Bay, Victoria, Australia (Dutka et al. 2022). Colonies may become aggregated to form biogenic habitat (see Dutka et al. 2022). While bryozoan habitat can extend over thousands of square kilometres, patch size is typically less than one square metre (Wood et al. 2012). It is thought there are approximately 5700–6500 extant bryozoan species and perhaps > 15 000 species in the fossil record (Bock and Gordon 2013; Bock et al. 2018; Clarkson 1998; Cook et al. 2018; Gordon and Costello 2016; Horowitz and Pachut 1994).

Most reports of bryozoan biogenic habitat relate to 'encrusting' bryozoan-rich rock formations, patch reefs, thickets and bioherms rather than extant and extensive large biogenic habitat (e.g., Abrolhos Shelf, Brazil Bastos et al. 2018) and bryozoan-rich fossil bioherms (Cuffey et al. 1977; Ernst and Königshof 2008) and sediments (e.g., Tasmanian continental shelf, James et al. 2008). Globally, it appears that bryozoans mostly occur in deep clear water (see table 1 in Dutka et al. 2022). Light intensity decreases with depth, so deep water is conducive to bryozoan life as they are not outcompeted by algae; however, at depth the water is cooler and most likely limits growth. As stated in Bock et al. (2018) 'Murky water and high suspended sediment loads, characteristic of Broad Sound/Shoalwater Bay and the Gulf of Carpentaria, do not prevent substantial bryozoan growth.' In fact, the diversity and dominant taxa in the Gulf of Carpentaria are quite different from those of the Great Barrier Reef. There have been 56 genera recorded from 57 sites within the Gulf of Carpentaria (Bock et al. 2018). Species of *Celleporaria* are common in the Gulf of Carpentaria and are also part of the Western Port bryozoan reefs. Western Port is similar to the Gulf of Carpentaria in that they are both relatively shallow, murky, and have a high suspended sediment load.

A variety of mobile and sessile infauna and epifauna taxa have been associated with biogenic bryozoan reefs in New Zealand (Bradstock and Gordon 1983; Wood et al. 2012) and elsewhere (Ferdeghini and Cocito 1999; Morgado and Tanaka 2001), including echinoderms, crustaceans, molluscs, hydroids, tunicates, annelids, brachiopods and other bryozoans. Bryozoan communities in New Zealand are hotpots for biodiversity, especially in Foveaux Strait where at least 190 species representing 82 families across 12 phyla were identified from a dredge survey (Rowden et al. 2004). Bryozoan-dominated communities elsewhere have demonstrated similarly high species richness. For example, 115 species in Brazil (Morgado and Tanaka 2001) and 84 species in the Ligurian Sea (Italy) (Ferdeghini and Cocito 1999) are associated with a single bryozoan species. Many of these habitats also demonstrate high levels of intra-phyla richness, the highest of which occur in molluscs (Ferdeghini and Cocito 1999; Willan 1981), annelids (Morgado and Tanaka 2001) and crustaceans (Lindberg and Stanton 1988).

1.1 | Western Port

Extensive areas of significant biogenic bryozoan reefs have recently been documented in Western Port, Victoria, Australia (Dutka et al. 2022). These reefs occupy a total area of 1.74 km^2 and contain linear reefs that are in an approximately north–south orientation perpendicular to the local tidal currents and in an area of eddying currents due to the influence of the Eastern Entrance.

There are three dominant bryozoan species in the reef: *Triphyllozoon munitum* (Hincks 1880), *Triphyllozoon moniliferum* (MacGillivray 1860) and *Celleporaria foliata* (MacGillivray 1888). The *Triphyllozoon* species are mounded fenestrate (net-like) colonies that collectively make up the majority of the linear biogenic reefs, while *C. foliata* is a non-fenestrate, plate-like species that can be mounded, spreading, or encrusting (see Dutka et al. 2022; Figure 1).

Virtually nothing is known about the Western Port biogenic bryozoan reefs. However, previous biodiversity studies on other biogenic reef habitats worldwide (Buhl-Mortensen and Mortensen 2005; Morrison et al. 2014; Sciberras et al. 2009), bryozoan-dense habitats (Wood et al. 2012) and other Western Port habitats (Butler and Bird 2010; Coleman et al. 1978; Harvey and Bird 2008; Watson et al. 1984) show that biogenic reefs harbour rich assemblages across a wide range of taxa.

The aim of this study is twofold. First, this study sought to provide an understanding of the co-occurring invertebrate biodiversity and conservation values of the Western Port linear bryozoan reef. Second, we aimed to determine if there were differences in macrofaunal biodiversity associated with each of the three bryozoan species comprising the linear bryozoan reef

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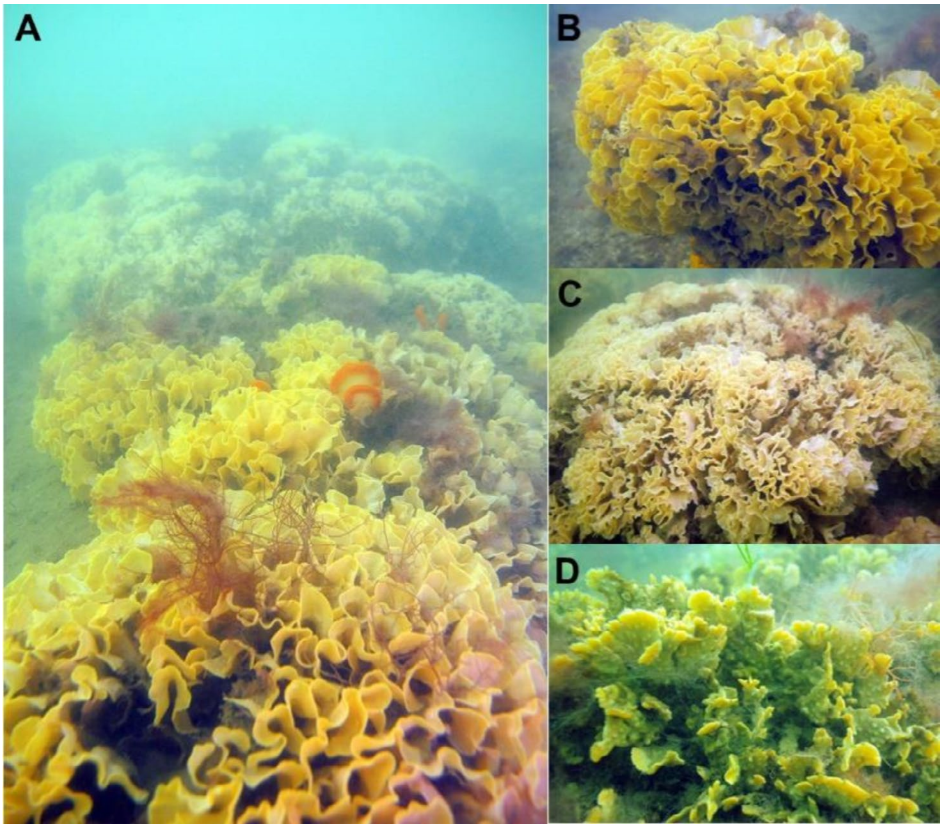

FIGURE 1 | A linear row of biogenic bryozoan habitat (A). Linear rows are comprised exclusively of three bryozoan species: *Triphyllozoon munitum* (B), *Triphyllozoon moniliferum* (C) and *Celleporaria foliata* (D). Modified from Dutka et al. (2022).

to establish whether the morphology of each bryozoan species plays a role in the composition of the associated faunal assemblages. It was hypothesised that each bryozoan species would harbour different community compositions given the differences in their structural complexity. The thick, plate-like structure of *C. foliata* colonies and the larger, intricately folded, and fragile *Triphyllozoon* species may offer different types of habitat values for matrix fauna. Additionally, the difference in the degree of laminar folding between the two *Triphyllozoon* species may drive changes in composition due to available space within the colony structures.

2 | Materials and Methods

2.1 | Study Area

Western Port is a temperate embayment fringed by mangroves and silty mudflats (Jenkins and Conron 2015). Typically, with the exception of the Eastern and Western Entrances to the bay, the substrate in Western Port is characterised by silty muds, and the water column is highly turbid, with wind-waves contributing to sediment resuspension and mobilisation (Wallbrink and Hancock 2003). These conditions are conducive to the settlement of larvae and may also serve to entrain and locally enhance the production of phytoplankton, which are the main food source for bryozoans (Cranfield et al. 2003; James et al. 2008). There are two distinct structural categories of the bryozoan reef: the 'linear' bryozoan reef, which is characterised by continuous bryozoan colonies orientated in the north–south pattern with a vertical relief, and 'patch-like' bryozoan reef that is characterised by conglomerate colonies with no regular orientation.

The linear bryozoan reef sampled in this study is located in the eastern arm of Western Port in an area termed the 'Rhyll Segment' (Jenkins et al. 2013; see Figure 2). The linear reefs were sampled as they represent densely packed biogenic bryozoan habitat. In contrast, the patch reefs are interspersed with other habitat types such as *Caulerpa cactoides*. GPS waypoints were recorded so the same patch of reef could be returned to at different seasons, albeit in a different linear section.

2.2 | Sampling of Bryozoan Reef

Fifteen to 20 linear rows of bryozoan mounds occur centred within the largest contiguous bryozoan reef site. Bryozoan samples and associated fauna were collected under Victorian Fisheries Authority research permit RP1363 in strict adherence to La Trobe University's Animal Ethics Committees approval (AEC19007). Samples were collected from colonies of the three bryozoan species in random positions along a single linear row. To spread the sampling burden across the site and to prevent pseudo-replication, samples were collected from different (adjacent) rows of reef during each season. Owing to poor visibility, it was sometimes necessary to use touch to identify the bryozoans. This meant that although the samples were collected randomly, the distance between each sample was difficult to precisely quantify once out of view. Sample

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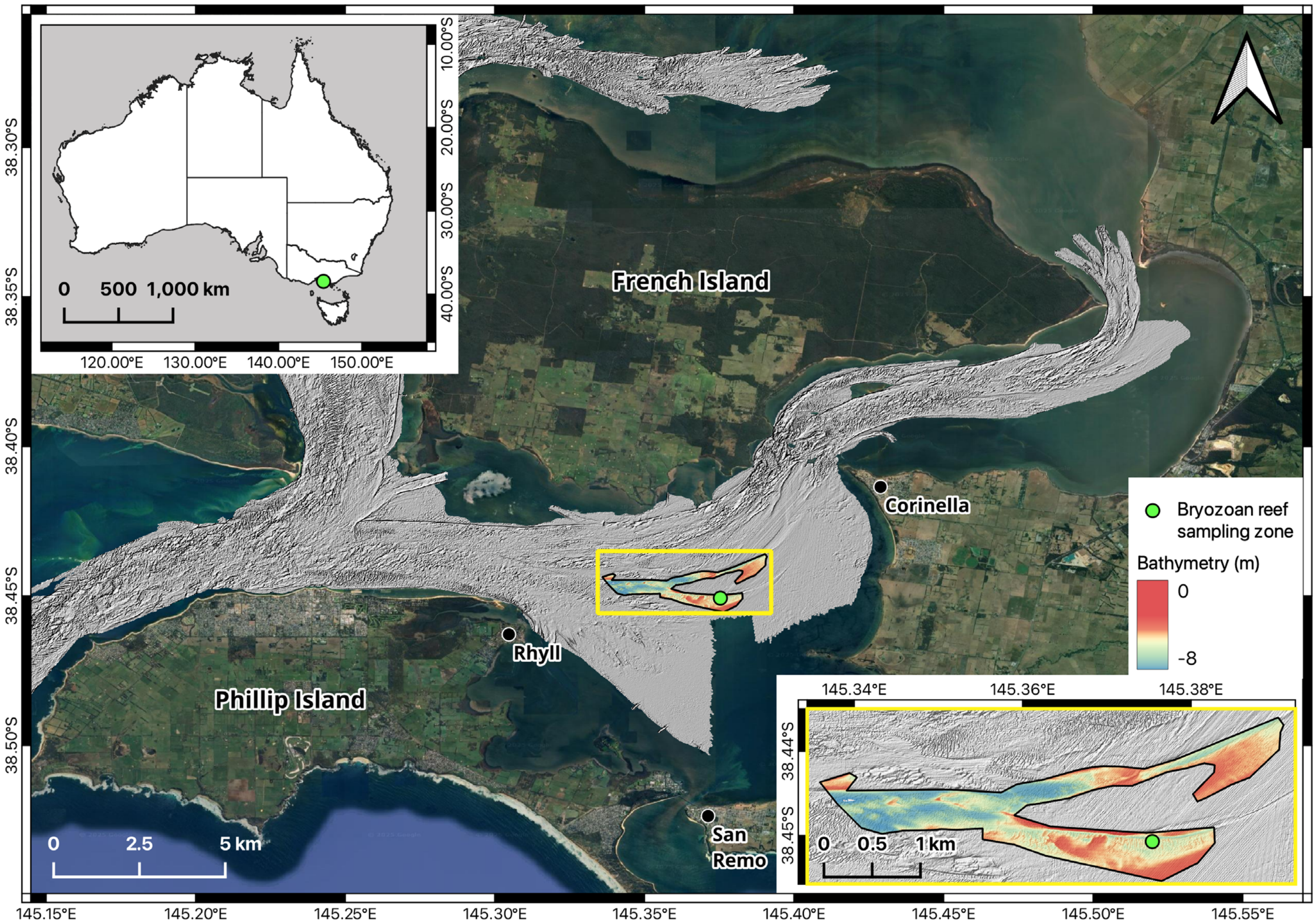

FIGURE 2 | Western Port and the bryozoan study site. The study site is located in the 'Rhyll segment' and contains linear rows of bryozoans (inset is a 3D reconstruction of multibeam bathymetry adapted from Dutka et al. 2022). Sampling area is denoted by a green circle.

collections occurred once per season for four consecutive seasons (late autumn, winter, spring and summer). The rationale for sampling once per season was to control for fluctuations which might have underestimated or overestimated species richness and abundance. Further, selecting one season in preference to another would require justification of the significance of that particular season. Sampling days were planned based on neap tides, targeting slack tide periods on days with low wind to maximise visibility in the high turbidity conditions, and thus, accuracy in underwater identification of bryozoan species for sampling.

Diver-operated hand corers with a volume of 5301 cm^3 (height = 30 cm, radius = 7.5 cm) were lined with a 0.5 mm^2 wire mesh (biodiversity screening minimum limit) to allow for displacement of water but retention of fauna. These dimensions were chosen to ensure it was sufficiently large to capture enough fauna to make it a good measure of richness and abundance so as to have statistical power. Samples were taken from the middle of each row when visibility allowed for the determination of the end of a linear reef.

Divers aimed to collect three samples from each of the bryozoan species (*T. munitum, T. moniliferum* and *C. foliata*) per season. Due to both environmental and technical challenges, 35 samples were collected in total.

2.3 | Bryozoan Sample Processing

Immediately following collection, sample contents were placed onto a 0.5-mm^2 mesh sieve and rinsed carefully with seawater to remove as much fine sediment as possible to facilitate the extraction of fauna from the sample in the laboratory and to screen and liberate any protected (e.g., fish and seahorses) or potentially dangerous species (e.g., blue-ringed octopus *Hapalochlaena maculosa*). The samples were then placed back into the sampler, capped, bagged and taken to a laboratory (La Trobe University Bundoora, Victoria), where they were refrigerated overnight at 4°C–8°C prior to processing the next day. Samples were placed in shallow containers and sorted through by two pickers with a magnifying glass and forceps to collect conspicuous fauna. Owing to the amount of fine silt, mud and crushed substrate, samples were rinsed thoroughly during the sorting process with the filtrate being collected at all stages using a 0.5 mm^2 sieve to ensure no small fauna were lost during the entire procedure. The removal of silt and sediment from all samples meant that the contents of the corer could not be normalised against the amount of sample in the corer and instead the volume of the standard collected core sample was used.

The two pickers cross-checked each other's samples to minimise observer biases. Specimens were placed into jars

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containing 95% ethanol for later counting, identifying and preservation. Specimens were counted and photographed using a stereomicroscope (Zeiss Stemi SV 11) fitted with a digital camera (Olympus DP27). In the case of partial specimens, only the head ends of dismembered annelids and crustaceans were recorded to avoid duplicate counts of individuals. The small number of colonial tunicates recorded were classified as individual colonies. Gastropods were counted if they were > 3 mm in size (as crushing them was required to see the presence/absence of an animal inside and this was problematic with those < 3 mm) and were found to contain an animal inside.

2.4 | Fauna Identification

Relevant literature (including Glasby 2000; Gowlett-Holmes 2008) was used to assist with identifying taxa to the lowest possible taxonomic level. Representative specimens were then sent to infauna specialist Lynda Avery of Infauna Data Pty Ltd for confirmation and further identification. Due to the morphologically cryptic nature of many of the crustaceans and annelids, only 12.5% of taxa were identified to species level, with the majority (68%) of taxa identified to family level. However, although those taxa were only identified to family level, each morphologically different taxa were counted as a different morphospecies.

2.5 | Statistical Analysis

All analyses were completed in the statistical and graphical software R (R Core Team 2025).

Variation in invertebrate morphospecies richness and abundance was investigated using generalised linear mixed effects models (GLMMs) with a Poisson distribution and log link function. Separate sets of models were tested for richness and abundance, using models with bryozoan habitat type (three levels: *C. foliata*, *T. munitum* and *T. moniliferum*) and season (four levels) fitted as fixed effects, in addition to models with habitat as a fixed effect and season as a random factor to account for the lack of sample independence. Model selection was informed using second-order Akaike Information Criterion (AICc) and the most parsimonious model for each response variable was selected (see Tables S1 and S2). Model fits and assumptions were assessed using simulated residual plots, which were satisfactory in all cases. All models were fit using the GLMM-TMB package (Brooks et al. 2017). Post hoc comparisons of model estimates among bryozoan habitat type and season were completed using the Sidak *p*-value adjustment method.

Patterns in invertebrate community composition were visualised using a non-metric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarities calculated from fourth-root scaled and Wisconsin double-standardised abundance data. To reduce noise and the disproportionate influence of rare taxa on dissimilarity measures, morphospecies occurring in fewer than 5% of core samples were excluded prior to transformation. This ensured the ordination reflected ecologically meaningful patterns. Differences in invertebrate community composition among bryozoan habitats and seasons were tested using permutational multivariate analysis of variance (PERMANOVA) with 999 permutations. Permutational analysis of multivariate dispersion (PERMDISP) was used to test the assumption of homogeneity of dispersion for the PERMANOVA. All multivariate analyses were completed using the vegan package (Oksanen et al. 2025).

3 | Results

3.1 | Bryozoan Reef Matrix Fauna Assemblage

Within the bryozoan linear reef, a total of 7266 individuals were sampled, representing 120 different morphospecies from at least 57 different families across 9 phyla. A full list of morphospecies and counts recorded across all bryozoan samples is shown in Data S1. Further, a breakdown of morphospecies and abundance in each sample is provided in Data S2.

Taxa smaller than ~5 mm dominated the matrix fauna contributing to 69% of the total abundance of fauna within the bryozoan reef. The most common conspicuous taxa (> 5 mm) in the bryozoan matrix were banded arks (*Barbatia pistachio*), beaded hairy crabs (*Pilumnus serratifrons*), fat-handed snapping shrimp (*Synalpheus tumidomanus*), southern mud oyster (*Ostrea angasi*), sea squirts (*Pyura stolonifera*), Eunicid worms (*Eunice* spp.) and cage worms (Flabelligeridae). Crustaceans were the most dominant taxa, making up 78% of the total abundance and 52% of the total number of morphospecies. Annelids (15% abundance and 31% morphospecies) and molluscs (4% abundance and 9% morphospecies) were relatively common across samples, while rare taxa like Brachiopoda, Sipuncula, Echinodermata, Cnidaria and Porifera together accounted for less than 8% of morphospecies and 4% of abundance. Fifty percent of the total abundance of invertebrates within the bryozoan reef was attributed to four dominating crustacean morphospecies—sea fleas (*Paranebalia tiparra*), Tanaidacea sp.indet., Apseudidae sp.indet. and amphipods (Corophiidae sp.), whereas 114 morphospecies (88% of the total identified) accounted for ≤ 1% each of the total abundance.

3.2 | Bryozoan Reef Matrix Fauna Morphospecies Richness

Morphospecies richness ranged from nine to 43 morphospecies per core. Morphospecies richness was highest in spring (Figure 3). Bryozoan habitat had no effect on morphospecies richness. However, significant differences were detected between seasons, with spring exhibiting the highest morphospecies richness when compared to autumn across the three bryozoan habitats (Sidak pairwise test, $p < 0.05$) (see Tables S1 and S2).

3.3 | Bryozoan Reef Matrix Fauna Morphospecies Abundance

Total abundance ranged from 25 to 905 individuals per core (Figure 4). Abundance was highest in spring, attributed

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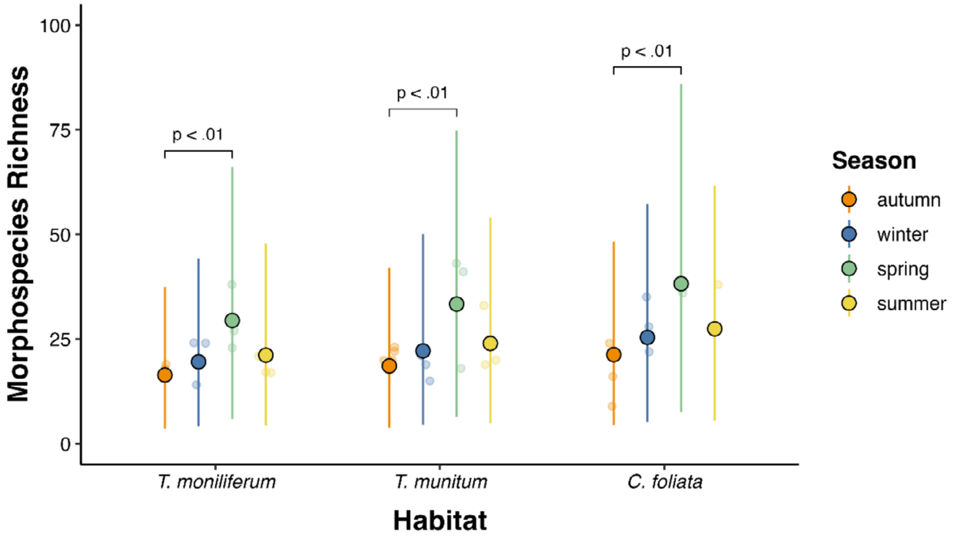

FIGURE 3 | Morphospecies richness of bryozoan matrix fauna for three bryozoan species sampled at four timepoints between May 2019 and January 2020. Coloured points are the mean predicted fits of a generalised linear mixed effects model (Poisson distribution with log link). Coloured vertical lines represent 95% confidence intervals. Raw data are shown as faint-coloured points. Brackets indicate statistically significant differences in morphospecies richness between seasons.

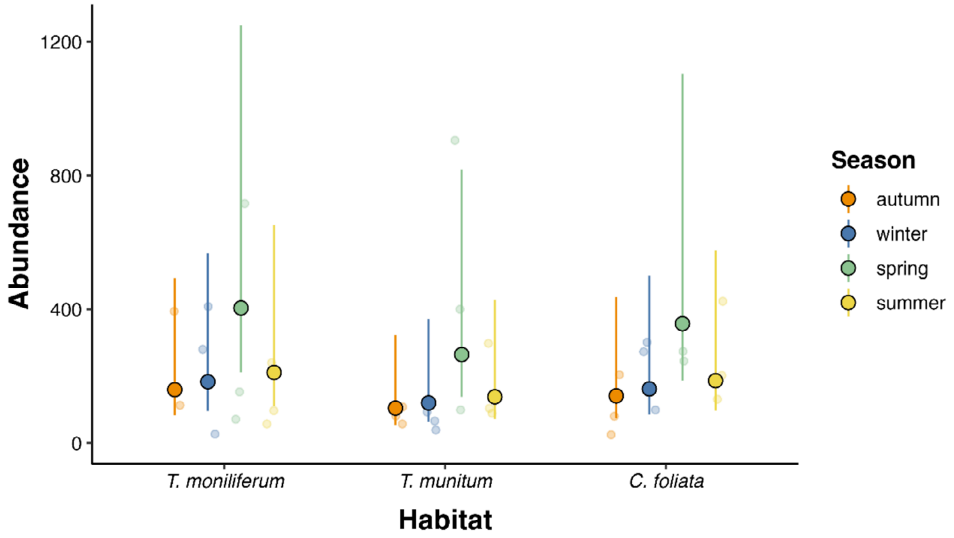

FIGURE 4 | Total abundance of all bryozoan matrix fauna for three bryozoan species sampled at four timepoints between May 2019 and January 2020. Coloured points are the mean predicted fits of a generalised linear mixed effects model (Poisson distribution with log link). Coloured vertical lines represent 95% confidence intervals. Raw data are shown as faint-coloured points.

largely to increased abundance of crustaceans and annelids. Between-sample variability was high, particularly in spring. Neither bryozoan habitat nor season had a significant effect on abundance (GLMM, groups = 12, $p > 0.05$) (see Tables S1 and S2).

3.4 | Bryozoan Reef Matrix Fauna Community Composition

Out of 120 morphospecies, 58 were removed prior to transformation to reduce the influence of rare taxa on dissimilarity measures. Ordination plots showed that there was no significant distinction in community composition among bryozoan habitats (PERMANOVA: $F(2, 34) = 3.62$, $r^2 = 0.16$, $p = 1$) (Figure 5). Clustering indicated that the matrix fauna associated with the *C. foliata* habitat was somewhat differentiated from that in the two *Triphyllozoon* species, although there was a relatively high stress value associated with the 2D ordination.

Ordination plots identified no significant distinction in community composition among seasons (PERMANOVA: $F(3, 34) = 3.10$, $r^2 = 0.20$, $p = 1$) (see Figure 6).

4 | Discussion

Soft sediments are the prevailing habitat of Western Port, covering approximately two thirds of the bay (Harvey and

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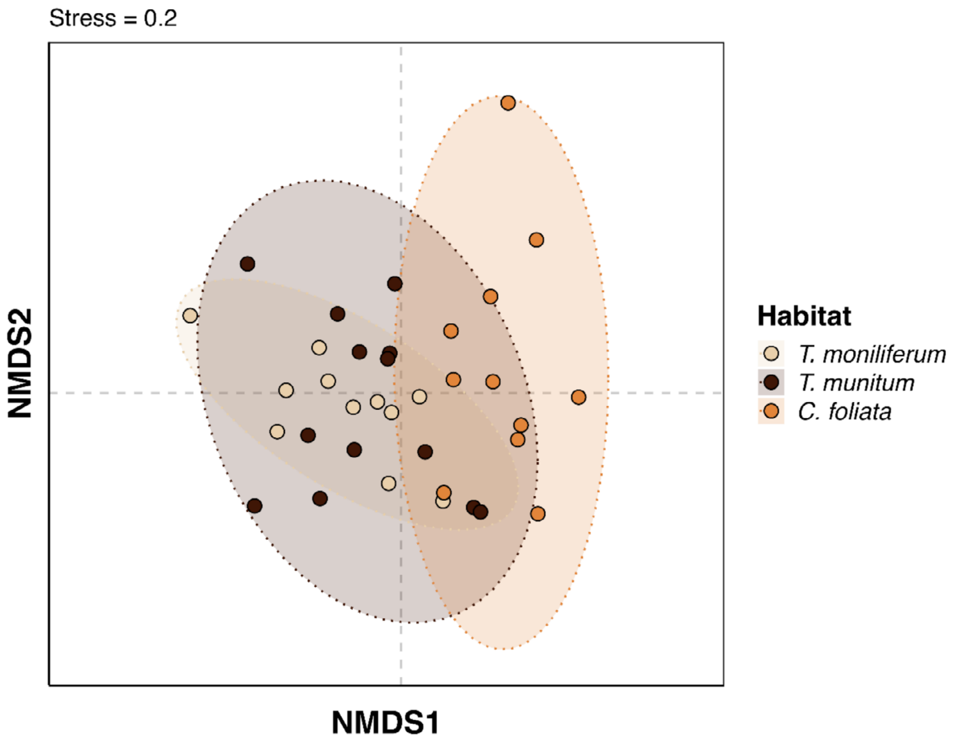

FIGURE 5 | Non-metric multidimensional scaling (NMDS) ordination of $N = 35$ sampling units based on Bray–Curtis dissimilarity indices of fourth-root scaled and Wisconsin double standardised abundance data. Coloured points represent the location of each core sample in multivariate space. 95% confidence ellipses are shown for each habitat (bryozoan species).

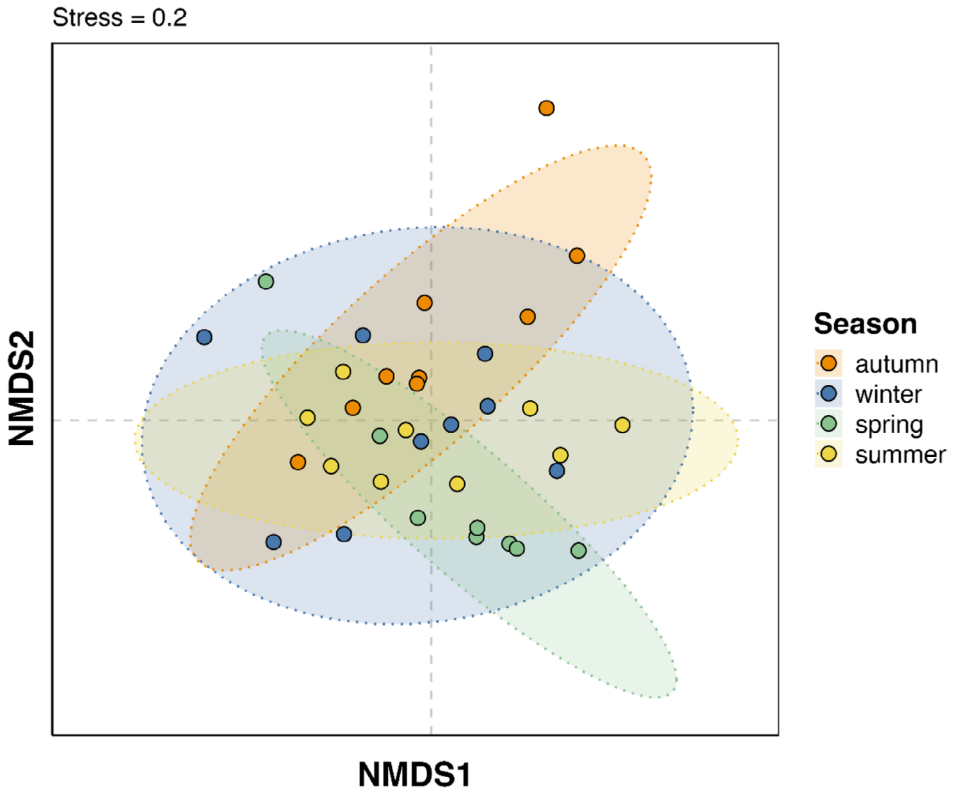

FIGURE 6 | Non-metric multidimensional scaling (NMDS) ordination of $N = 35$ sampling units based on Bray–Curtis dissimilarity indices of fourth-root scaled and Wisconsin double standardised abundance data. Coloured points represent the location of each core sample in multivariate space. 95% confidence ellipses are shown for each season.

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Bird 2008). It is known that there is a positive correlation between habitat complexity and ecosystem production (Barnard and Drummond 1978), thus making it likely that these rigid, elevated, biogenic bryozoan structures play an important role in ecosystem productivity within the bay. In this regard, these complex biogenic structures may provide a function similar to that of hard corals (Giampaoletti et al. 2020). It is essential that the faunal assemblages of the more complex habitats of the bay, such as bryozoans, are more extensively researched. Some lines of enquiry that may be considered include ecosystem functions and food webs, comparisons against other habitat types such as rocky reef and seagrass beds, and similar biodiversity studies over a greater spatial and temporal scale.

4.1 | Bryozoan Reef Assemblage

In this study, 120 morphospecies were found within a single section of bryozoan linear reef comprising three dominant bryozoan species. This is remarkably consistent with the bryozoan associated invertebrate community on the Otago Shelf, New Zealand, where 138 invertebrate species were associated with three habitat-forming bryozoan species (Wood 2005; Wood and Probert 2013). The most abundant group was deposit and suspension feeding crustaceans, followed by annelids. This is also in accordance with bryozoan biodiversity studies from New Zealand (Wood and Probert 2013) and elsewhere (Ferdeghini and Cocito 1999; Morgado and Tanaka 2001). These studies have demonstrated that crustacean- and annelid-dominated assemblages are typical of habitat-forming bryozoans. The dominance of crustaceans, annelids and molluscs appears to not only be characteristic of bryozoan dominated habitat but also a bay-wide pattern in Western Port. For instance, an extensive quantitative survey of the macroinvertebrates of Western Port by Coleman et al. (1978) found that the fauna was dominated by annelids (54%), crustaceans (32%) and molluscs (7%) and accounted for 36%, 48% and 10% of morphospecies, respectively. The bryozoan reefs were not part of that survey because they had not yet been identified or characterised until recently. Edgar et al. (1994) also reported a more diverse assemblage of macroinvertebrates in seagrass habitat than in unvegetated habitat, with the seagrass habitats being dominated by crustaceans (39%), annelids (33%) and molluscs (18%) in terms of abundance.

The nearby (San Remo) rhodolith beds (biogenic bed formed by free-living calcified coralline red algae) have been found to be dominated by polychaete worms, both in abundance (89% of the total assemblage) and number of morphospecies, with the family Terebellidae comprising 53% of the annelid community (Harvey and Bird 2008). Like bryozoans, biogenic rhodolith beds provide a hard substratum for invertebrates such as crustaceans, polychaetes and molluscs to attach to, burrow into, mimic or hide within (Harvey and Bird 2008). In general, biodiversity in rhodolith beds has proven to be remarkably higher than in surrounding habitats (Foster 2001). Consistent with the findings of this current study, the shallow biogenic rhodolith beds in Western Port display high levels of biodiversity compared to soft sediment communities elsewhere in the bay (Harvey and Bird 2008). Given Western Port's relatively young geological age (~10 000 years) (Shapiro 1975), endemicity is likely to be low suggesting that radiation of taxa occurred elsewhere and they simply invaded the bay.

Small crustaceans, such as Amphipoda, which are present across at least 15 different families, made up approximately 70% of the total abundance of invertebrates collected from the reefs and are important dietary items for many demersal (bottom-dwelling) fish (Edgar and Shaw 1995b) and other taxa. Analysis of gut contents of 91 fish species from Western Port by Edgar and Shaw (1995a, 1995b) revealed that $>25\%$ of species fed on polychaetes, while the majority (69%) fed on crustaceans, with many small fish at every site particularly ingesting amphipods. Therefore, the bryozoan reefs may represent areas of enhanced prey abundance for fish species preferentially targeting Crustacea. Further, the large increase in both abundance and morphospecies richness, particularly in crustaceans and annelids occurring in spring, may be an important food resource for larval fish in the warmer months.

It was noted by Probert et al. (1979) on the Otago shelf and more recently by Dutka et al. (2022) in the Western Port reefs that, while habitat-forming bryozoans provide habitat for a variety of small species, large ‘macro’ invertebrates also shelter on and around bryozoan colonies. Coleman et al. (1978) reported that where sediments had a greater abundance of attachment substrate (e.g., rock, shell and bryozoan fragments), the epifauna were more diverse. Many motile taxa observed here are not strictly infaunal or epifaunal within a phylum (e.g., annelids, crustaceans and molluscs). The brain ascidian, *Sycozoa cerebriformis*, was found attached to all bryozoan species and had three colour variants (red, yellow and white). There is no information available on the significance of this variation. It was difficult to quantify how abundant they were as the hand corer was typically smaller than the ascidian colony and frequently cut into them. Exploratory remote operated vehicle (ROV) footage and underwater photographs collected from 2017 to 2020 examined by the Western Port Bryozoan Reefs Research Project suggested that *S. cerebriformis* was in the top five most abundant species detected on the bryozoan reef. Our counts, therefore, may underestimate the occurrence of this species (Dutka et al. 2022).

4.2 | Differences Among Bryozoan Species

It was expected that many of the taxa observed within the bryozoan matrix would be found in all three bryozoan species given that mobile species likely move through the close interlinked colonies that create the reefs' unique linear row structures. Despite the morphological differences between the fragile, fenestrate bryozoans (*T. munitum* and *T. moniliferum*) and the more robust, plate-like *C. foliata*, there was no difference in the mean abundance or mean taxon richness observed between these species. Interestingly, Wood (2005) reported that the taxon composition of macroinvertebrates differs depending on the form that habitat-forming bryozoans take (e.g., fenestrate, dendroid, encrusting, plated and foliaceous) (McKinney and Jackson 1991). For instance, they found that *Cinctipora elegans*, a bushy bryozoan that forms tubular, bifurcating branches, provided attachment points for ascidians, while the honeycomb growth form of *Hippomenella vellicata* was more suited to mobile species like munidid squat lobsters which use the large, sheltered spaces for

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protection (Wood 2005). The lack of a significant difference in morphospecies richness and abundance between the three bryozoan species reported here is presumably driven by the large variation within samples (see Data S2) and habitat usage by matrix fauna not being exclusive. However, a significant increase in morphospecies richness occurred during spring across all three bryozoan species (Figure 3).

Although there was no difference in the mean abundance or morphospecies richness, differing patterns in assemblages were observed between the bryozoan species driven by colony structure. *C. foliata* only contributes to approximately 5% of the bryozoan cover in the reefs in comparison to the dense coverage (~95%) of the *Triphyllozoon species* (Dutka et al. 2022). Despite this, the plate-like, solid colonies appear to provide opportunities to a larger range of unique taxa than the other genera. The abundance of eunicids in *C. foliata* (231) in comparison to the *Triphyllozoon species* (10) may suggest either aggregating behaviour or that perhaps the folding skeletal structure of *Triphyllozoon species* is not preferred over *C. foliata*. No information on associations between bryozoans and eunicid worms is available. Further research into the ecological processes of the reefs is required to ascertain the role that these carnivorous polychaetes play.

4.3 | Ecological Variables and Drivers of Biodiversity

The focus of this study was to record the co-occurring macroinvertebrate fauna and to investigate how abundance and richness were influenced by the different structural complexity of three bryozoan species. In all three bryozoans, there was a significant increase in richness in spring compared to other seasons but no difference between the three species. The lack of differences in richness and abundance between the three bryozoan species might be due to the spatial proximity and consequent spillover of taxa between bryozoan species. Alternatively, the differences in microhabitats created by the three bryozoan species may be inconsequential to the matrix fauna analysed. Scale may also play a role as the bryozoan colonies sampled are a small part of a larger biogenic reef structure which is expected to support macroinvertebrate communities that differ from the surrounding bare sediments and respond differently to environmental variables. Environmental variables such as temperature, turbidity, and organic matter production were not measured directly due to the limitations of the study. However, future work could investigate their relative importance in driving changes in abundance and richness. Temperature, light, and organic matter production have been identified in temperate marine ecosystems as being important drivers of seasonality in benthic soft sediment and reef macrofauna abundance (Gammal et al. 2025; Leppäranta and Myrberg 2009). Since marine invertebrates are ectothermic, it is not surprising that temperature is a key driver of substantial variations in production owing to related variations in metabolic rate (Kautsky and Evans 1987). Primary production peaks in spring and autumn, shaping food resources for benthic communities (Gili and Coma 1998; Molinero et al. 2008). These changes in trophic dynamics have been shown to alter the diet and community structure of benthic invertebrates across seasons (Coma and Ribes 2003).

Studies of benthic communities in Western Port Bay and Port Phillip Bay have shown that factors such as temperature, resource availability and hydrodynamic conditions strongly influence assemblage structure, with spring often associated with peaks in productivity and recruitment (Butler and Bird 2010; Edmunds et al. 2011; Poore 1998; Wilson et al. 1993). Here, spring showed higher invertebrate richness. This suggests that increased springtime temperature and productivity may enhance recruitment and growth, reinforcing that substrate complexity alone does not fully explain biodiversity patterns without considering environmental seasonality. The Western Port biogenic bryozoan reefs are not within a Marine National Park and are currently not afforded protection under any legislation. The area is popular with recreational fishers, and physical damage from anchoring and fishing equipment is a potential threat. Given bryozoans are not photosynthetic, increased turbidity and sedimentation (due to changes in the sediment regime over the last century) could potentially smother colonies or clog their feeding structures and is therefore another key threat to the Western Port bryozoan reefs.

5 | Concluding Remarks

This study identified the macroinvertebrate biodiversity associated with the newly characterised unique bryozoan reefs of Western Port. We have established that they support a highly diverse community of matrix macrofauna comprised of 120 morphospecies across 57 families and 9 phyla. This study revealed that 97% of total abundance could be attributed to crustaceans (78%), molluscs (15%) and annelids (4%), which is consistent with other bryozoan communities elsewhere (e.g., Otago Shelf, New Zealand) and an indication of the role they play in supporting these epifauna. Further, matrix epifauna richness was significantly higher in spring for all three bryozoan species when compared to other seasons. This is likely important as a food resource for larval fish (Edgar and Shaw 1995a, 1995b) and other taxa in warmer months frequenting Western Port. Future studies on growth rates, establishment, larval dispersion and threatening processes will provide the critical information necessary to guide recommendations on management and protection.

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Ethics Statement

Bryozoan samples and associated fauna were collected under Victorian Fisheries Authority research permit RP1363 in strict adherence to La Trobe University's Animal Ethics Committees approval (AEC19007).

Conflicts of Interest

The authors declare no conflicts of interest.

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Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

References

Barnard, J. L., and M. M. Drummond. 1978. "Gammaridean Amphipoda of Australia, Part III. The Phoxocephalidae." *Smithsonian Contributions to Zoology* 245: 1–551. https://doi.org/10.5479/si.00810282.245.

Bastos, A. C., R. L. Moura, F. C. Moraes, et al. 2018. "Bryozoans Are Major Modern Builders of South Atlantic Oddly Shaped Reefs." *Scientific Reports* 8: 1–11.

Bell, J. D., and M. Westoby. 1986. "Abundance of Macrofauna in Dense Seagrass Is due to Habitat Preference, Not Predation." *Oceologia* 68, no. 2: 205–209.

Bock, P. E., P. L. Cook, and D. P. Gordon. 2018. "Bryozoans in the Marine Benthos." In *Australian Bryozoa Volume 1: Biology, Ecology and Natural History*, edited by P. L. Cook, P. E. Bock, D. P. Gordon, and H. J. Weaver, 157. CSIRO Publishing.

Bock, P. E., and D. P. Gordon. 2013. "Phylum Bryozoa Ehrenberg, 1831." *Zootaxa* 3703, no. 1: 67–74.

Bradstock, M., and D. P. Gordon. 1983. "Coral-Like Bryozoan Growths in Tasman Bay, and Their Protection to Conserve Commercial Fish Stocks." *New Zealand Journal of Marine and Freshwater Research* 17, no. 2: 159–163.

Brooks, M. B., K. Kristensen, K. J. van Benthem, et al. 2017. "glmmTMB Balances Speed and Flexibility Among Packages for Zero-Inflated Generalized Linear Mixed Modeling." *R Journal* 9, no. 2: 378–400. https://doi.org/10.32614/RJ-2017-066.

Buhl-Mortensen, L., and P. B. Mortensen. 2005. "Distribution and Diversity of Species Associated With Deep-Sea Gorgonian Corals Off Atlantic Canada." In *Cold-Water Corals and Ecosystems*, 849–879. Springer.

Butler, S., and F. L. Bird. 2010. "Monitoring the Macroinvertebrates and Soft Sediments in the Marine National Parks in Western Port." Parks Victoria Technical Series No. 60. Parks, Victoria, Melbourne.

Carbines, G., W. Jiang, and M. P. Beentjes. 2004. "The Impact of Oyster Dredging on the Growth of Blue Cod, *Parapercis colias*, in Foveaux Strait, New Zealand." *Aquatic Conservation: Marine and Freshwater Ecosystems* 14, no. 5: 491–504.

Clarkson, E. N. K. 1998. *Invertebrate Palaeontology and Evolution*. John Wiley & Sons.

Cocito, S., F. Ferdeghini, C. Morri, and C. N. Bianchi. 2000. "Patterns of Bioconstruction in the Cheilostome Bryozoan *Schizoporella errata*: The Influence of Hydrodynamics and Associated Biota." *Marine Ecology Progress Series* 192: 153–161.

Coleman, N., W. Cuff, M. Drummond, and J. D. Kudenov. 1978. "A Quantitative Survey of the Macrobenthos of Western Port, Victoria." *Marine and Freshwater Research* 29, no. 4: 445–466.

Coma, R., and M. Ribes. 2003. "Seasonal Energetic Constraints in Mediterranean Benthic Suspension Feeders: Effects at Different Levels of Ecological Organization." *Oikos* 101, no. 1: 205–215. https://doi.org/10.1034/j.1600-0706.2003.12028.x.

Cook, P. L., H. Weaver, P. Bock, and D. Gordon, eds. 2018. *Australian Bryozoa Volume 2: Taxonomy of Australian Families*. CSIRO Publishing.

Cranfield, H. J., B. Manighetti, K. P. Michael, and A. Hill. 2003. "Effects of Oyster Dredging on the Distribution of Bryozoan Biogenic Reefs and Associated Sediments in Foveaux Strait, Southern New Zealand." *Continental Shelf Research* 23, no. 14–15: 1337–1357.

Cuffey, R. J., S. S. Fonda, D. F. Kosich, C. D. Gebelein, D. M. Bliefnick, and L. G. Soroka. 1977. "Modern Tidal-Channel Bryozoan Reefs at Joulters Cays (Bahamas)." In *Proceedings: Third International Coral Reef Symposium*, 339–345. University of Miami.

Dutka, T. L., A. J. Fejer, T. Williams, D. M. Donnelly, and A. J. Flynn. 2022. "Extent and Characteristics of a Newly Discovered Unique Bryozoan Biogenic Reef Complex." *Frontiers in Marine Science* 9: 841131.

Edgar, G. J., and C. Shaw. 1995a. "The Production and Trophic Ecology of Shallow Water Fish Assemblages in Southern Australia I. Species Richness, Size-Structure and Production of Fishes in Western Port, Victoria." *Journal of Experimental Marine Biology and Ecology* 194: 53–81.

Edgar, G. J., and C. Shaw. 1995b. "The Production and Trophic Ecology of Shallow Water Fish Assemblages in Southern Australia. II. Diets of Fishes and Trophic Relationships Between Fishes and Benthos at Western Port, Victoria." *Journal of Experimental Marine Biology and Ecology* 194: 83–106.

Edgar, G. J., C. Shaw, G. F. Watsona, and L. S. Hammond. 1994. "Comparisons of Species Richness, Size-Structure and Production of Benthos in Vegetated and Unvegetated Habitats in Western Port, Victoria." *Journal of Experimental Marine Biology and Ecology* 176, no. 2: 201–226.

Edmunds, M., K. Stewart, and K. Pritchard. 2011. "Victorian Subtidal Reef Monitoring Program: The Reef Biota in the Port Phillip Bay Marine Sanctuaries." Parks Victoria Technical Series No. 67. Parks Victoria.

Ernst, A., and P. Königshof. 2008. "The Role of Bryozoans in Fossil Reefs—An Example From the Middle Devonian of the Western Sahara." *Facies* 54, no. 4: 613.

Ferdeghini, F., and S. Cocito. 1999. "Biologically Generated Diversity in Two Bryozoan Buildups." *Biologia Marina Mediterranea* 6, no. 1: 191–197.

Foster, M. S. 2001. "Rhodoliths: Between Rocks and Soft Places." *Journal of Phycology* 37, no. 5: 659–667.

Gammal, J., M. Järnström, J. Norkko, E. Bonsdorff, and A. Norkko. 2025. "Seasonal Variation in the Role of Benthic Macrofauna Communities for Ecosystem Functioning in Shallow Coastal Soft-Sediment Habitats." *Estuaries and Coasts* 48, no. 3: 62.

Giampaoletti, J., F. Cardone, G. Corriero, M. F. Gravina, and L. Nicoletti. 2020. "Sharing and Distinction in Biodiversity and Ecological Role of Bryozoans in Mediterranean Mesophotic Bioconstructions." *Frontiers in Marine Science* 7: 581292.

Gili, J.-M., and R. Coma. 1998. "Benthic Suspension Feeders: Their Paramount Role in Littoral Marine Food Webs." *Trends in Ecology & Evolution* 13, no. 8: 316–321. https://doi.org/10.1016/S0169-5347(98)01365-2.

Glasby, C. J. 2000. *Polychaetes & Allies: The Southern Synthesis*. CSIRO Publishing.

Gordon, D. P., and M. J. Costello. 2016. "Bryozoa—Not a Minor Phylum." *New Zealand Science Review* 73: 63–66.

Gowlett-Holmes, K. L. 2008. *A Field Guide to the Marine Invertebrates of South Australia*. Notomares Publishing.

Hallock, P. 1997. "Reefs and Reef Limestones in Earth History." In *Life and Death of Coral Reefs*, 13–42. Chapman-Hall Science.

Harvey, A. S., and F. L. Bird. 2008. "Community Structure of a Rhodolith Bed From Cold-Temperate Waters (Southern Australia)." *Australian Journal of Botany* 56, no. 5: 437–450.

Hincks, T. 1880. "Contributions Towards a General History of the Marine Polyzoa." *Journal of Natural History* 6, no. 31: 69–92.

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Horowitz, A. S., and J. F. Pachut. 1994. "Lyellian Bryozoan Percentages and the Fossil Record of the Recent Bryozoan Fauna." *PALAIOS* 9, no. 5: 500–505.

Jackson, J. B., and E. Sala. 2001. "Unnatural Oceans." *Scientia Marina* 65, no. S2: 273–281.

James, N. P., R. C. Martindale, I. Malcolm, Y. Bone, and J. Marshall. 2008. "Surficial Sediments on the Continental Shelf of Tasmania, Australia." *Sedimentary Geology* 211, no. 1–2: 33–52.

Jenkins, G., and S. Conron. 2015. "Characterising the Status of the Western Port Recreational Fishery in Relation to Biodiversity Values: Phase." Technical Report. School of Biosciences, Melbourne University.

Jenkins, G., T. Kenner, and A. Brown. 2013. *Determining the Specificity of Fish–Habitat Relationships in Western Port*. Melbourne Water.

Jiang, W., and G. Carbines. 2002. "Diet of Blue Cod, *Parapercis colias*, Living on Undisturbed Biogenic Reefs and on Seabed Modified by Oyster Dredging in Foveaux Strait, New Zealand." *Aquatic Conservation: Marine and Freshwater Ecosystems* 12, no. 3: 257–272.

Jones, E. J. 2006. *Bryozoan Thickets on Otago Shelf, New Zealand: A Quantitative Assessment of the Epibenthos Using Underwater Photography*. University of Otago.

Kautsky, N., and S. Evans. 1987. "Role of Biodeposition by *Mytilus edulis* in the Circulation of Matter and Nutrients in a Baltic Coastal Ecosystem." *Marine Ecology Progress Series* 38: 201–212.

Lenihan, H. S., and C. H. Peterson. 1998. "How Habitat Degradation Through Fishery Disturbance Enhances Impacts of Hypoxia on Oyster Reefs." *Ecological Applications* 8, no. 1: 128–140.

Leppäranta, M., and K. Myrberg. 2009. *Physical Oceanography of the Baltic Sea*. Springer Berlin Heidelberg.

Lindberg, W. J., and G. Stanton. 1988. "Bryozoan-Associated Decapod Crustaceans: Community Patterns and a Case of Cleaning Symbiosis Between a Shrimp and Crab." *Bulletin of Marine Science* 42, no. 3: 411–423.

McKinney, F. K., and J. B. Jackson. 1991. *Bryozoan Evolution*. University of Chicago Press.

Molinero, J. C., F. G. Figueiras, and C. Marrasé. 2008. "Primary Productivity and Seasonal Zooplankton Dynamics: Implications for Benthic Invertebrate Diversity." *Journal of Marine Systems* 72, no. 3–4: 391–403. https://doi.org/10.1016/j.jmarsys.2007.03.010.

Morgado, E. H., and M. O. Tanaka. 2001. "The Macrofauna Associated With the Bryozoan *Schizoporella unicornis* in Southeastern Brazil." *Scientia Marina* 65, no. 3: 173–181.

Morrison, M., E. G. Jones, M. Consalvey, and K. Berkenbusch. 2014. *Linking Marine Fisheries Species to Biogenic Habitats in New Zealand: A Review and Synthesis of Knowledge*. Ministry for Primary Industries.

Oksanen, J., G. Simpson, F. Blanchet, et al. 2025. "vegan: Community Ecology Package." R package version 2.6-10. https://CRAN.R-project.org/package=vegan.

Pederson, E., and M. Peterson. 2002. "Bryozoans as Ephemeral Estuarine Habitat and a Larval Transport Mechanism for Mobile Benthos and Young Fishes in the North-Central Gulf of Mexico." *Marine Biology* 140, no. 5: 935–947.

Poore, G. C. B. 1998. "Changes in Benthic Communities of Port Phillip Bay, Australia, Between 1969 and 1995." *Marine and Freshwater Research* 49, no. 8: 847–861. https://doi.org/10.1071/MF97164.

Probert, P. K., E. J. Batham, and J. B. Wilson. 1979. "Epibenthic Macrofauna Off Southeastern New Zealand and Mid-Shelf Bryozoan Dominance." *New Zealand Journal of Marine and Freshwater Research* 13: 379–392.

R Core Team. 2025. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. https://www.R-project.org/.

Rowden, A. A., R. M. Warwick, and D. P. Gordon. 2004. "Bryozoan Biodiversity in the New Zealand Region and Implications for Marine Conservation." *Biodiversity and Conservation* 13: 2695–2721.

Saxton, F. L. 1980. "The Coral Beds of Tasman and Golden Bay." Ministry of Agriculture and Fisheries. Unpublished Report.

Sciberras, M., M. Rizzo, J. R. Mifsud, et al. 2009. "Habitat Structure and Biological Characteristics of a Maerl Bed Off the Northeastern Coast of the Maltese Islands (Central Mediterranean)." *Marine Biodiversity* 39, no. 4: 251–264.

Shapiro, M. A., ed. 1975. *Westernport Bay Environmental Study, 1973–1974*. Environmental Study Series No. 502. Ministry for Conservation.

Vooren, C. M. 1975. "Nursery Grounds of Tarakihi (Teleostei: Cheilodactylidae) Around New Zealand." *New Zealand Journal of Marine and Freshwater Research* 9, no. 2: 121–158.

Wallbrink, P. J., and G. Hancock. 2003. *Western Port Sediment Study: Background and Literature Review*. CSIRO Land and Water.

Watson, G. F., A. I. Robertson, and M. J. Littlejohn. 1984. "Invertebrate Macrobenthos of the Seagrass Communities in Western Port, Victoria." *Aquatic Botany* 18, no. 1–2: 175–197.

Willan, R. C. 1981. "Soft-Bottom Assemblages of Paterson Inlet, Stewart Island." *New Zealand Journal of Zoology* 8, no. 2: 229–248.

Wilson, R. S., B. F. Cohen, and G. C. Poore. 1993. *The Role of Suspension-Feeding and Deposit-Feeding Benthic Macroinvertebrates in Nutrient Cycling in Port Phillip Bay*. CSIRO.

Wood, A. C. L. 2005. "The Macrofaunal Communities Associated With Bryozoan Thickets on Otago Shelf, South-Eastern New Zealand." PhD thesis, Otago University.

Wood, A. C. L., and P. K. Probert. 2013. "Bryozoan-Dominated Benthos of Otago Shelf, New Zealand: Its Associated Fauna, Environmental Setting and Anthropogenic Threats." *Journal of the Royal Society of New Zealand* 43, no. 4: 231–249.

Wood, A. C. L., P. K. Probert, A. A. Rowden, and A. M. Smith. 2012. "Complex Habitat Generated by Marine Bryozoans: A Review of Its Distribution, Structure, Diversity, Threats and Conservation." *Aquatic Conservation: Marine and Freshwater Ecosystems* 22, no. 4: 547–563.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** aec70183-sup-0001-DataS1.xlsx. **Data S2:** aec70183-sup-0002-DataS2.xlsx. **Table S1:** aec70183-sup-0003-TablesS1-S2.docx.

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