

Biodiversity and Seasonal Fluctuations of Invertebrates Associated with Western Port
(Victoria, Australia) Bryozoan Biogenic Reefs

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Statement of Authorship

Declaration

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Nicole Wilson

13th April 2021

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Abstract

Biogenic reefs are significant marine habitats, providing food and attachment opportunities for numerous and varied sessile organisms, shelter from wave action and strong currents, and concealment from predators for both adult and larval stages. Consequently, these complex habitats are often biodiversity hotspots compared to surrounding habitats. Although most biogenic reef types are well represented worldwide, biogenic bryozoan reefs are extremely rare. Recently, large areas of biogenic bryozoan reef were documented in Western Port (WP), Victoria, Australia at depths typically of 5 - 12 m. These unique reefs are potentially globally significant due to their structure and extent. In this study, we aimed to examine the biodiversity of the matrix fauna associated with these reefs by collecting cores from the three dominant bryozoan species within the reefs: *Triphyllozoon munitum*, *Triphyllozoon moniliferum* and *Celleporaria foliata*, and two neighbouring habitats (bare sediment bed and *Caulerpa cactoides* bed). Within the bryozoan reef, 127 different species across 9 phyla were identified and the assemblage was dominated by crustaceans (75% of the total abundance of taxa). The reef had significantly higher species richness, abundance, and diversity, than the neighbouring habitats. 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. Secondly, we examined differences in species richness and abundance in the bryozoan matrix fauna across four consecutive seasons. Both species richness and abundance were considerably increased in spring compared to the other seasons, especially the colder autumn and winter seasons. The spring matrix fauna assemblage represented enhanced prey abundance and diversity for many taxa, in particular, commercially and recreationally important fish in WP. This ecosystem is potentially under threat from anthropogenic activities and further research is

60 required to establish the conservation value of these reefs and determine what protective
61 measures, if any, are required.

1 WESTERN PORT BIOGENIC BRYOZOAN REEFS

Biogenic reefs

Biogenic reefs are ecologically important marine habitats. They 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). These structures form biodiversity hotspots with the number of associated species per unit of habitat often exceeding that of adjacent non-biogenic habitat 10-fold or more (Lenihan & Peterson 1998; Jackson & Sala 2001). Most biogenic habitats, such as seagrass meadows (Heck & Wetstone 1977; Kirkman 2013), corals (Austin et al. 1980; Buhl-Mortensen and Mortensen 2005), rhodolith beds (Steller et al. 2003; Harvey et al. 2017), macroalgal turfs (Holbrook et al. 1990), sponges (Klitgaard 1995), tube-building polychaetes (Moore et al. 1998), and mollusc beds (Lenihan et al. 2001; Grabowski & Powers 2004; Ford & Hamer 2016) are relatively well documented. However, despite being well represented in the fossil record (James et al. 2000; Taylor et al. 2015) and early literature (Hincks 1880), reef-forming bryozoan habitats are rarely encountered. Consequently, there is a paucity of studies that describe these habitats and document their importance and usage by other organisms.

Bryozoa are a phylum of aquatic, non-photosynthesizing, filter-feeding, invertebrates. These sedentary, mostly colonial organisms are found in freshwater and all oceans from the sublittoral zone to the deep sea (up to 8000 m) in all major benthic habitat types including soft sediments, seagrass meadows, temperate reefs, and hard bottoms (McKinney & Jackson 1991; Wood et al. 2012; Cook et al. 2018). Colonies can be soft to touch with gelatinous exoskeletons, or hard but fragile with mineralized exoskeletons (Cook et al. 2018). Commonly referred to as lace corals, colonies vary widely in growth habits and range from

1 mm to more than 1 m (Cook et al. 2018). Bryozoa generally live attached to a substratum like rock, algae, or shell, though they often colonise other animals such as gorgonians (order Alcyonacea) and hydroids (class Hydrozoa) or grow root-like structures that hold fast in soft substrata (Cocito et al. 2000; Wood et al. 2012; Cook et al. 2018). There are approximately 5,700 known extant species of bryozoans (Horowitz & Pachut 1994) and 15,000 species known from fossil records (Amini et al. 2004). Continuous carbonate sediments dominated by bryozoan skeletons on the southern continental shelf of Australia occur between 80 – 200 m as single and multiple mounds standing at 65 m tall, 10 km long, and 720 m wide (James et al. 2008). Elsewhere, modern bryozoans tend to occur as isolates or patches of colonies, otherwise known as ‘thickets’ (Wood & Probert 2013). Habitat generated by bryozoans can extend over thousands of square kilometres, however, patch sizes are typically less than one square metre in size (Wood et al. 2012). Individual colonies and circalittoral reefs occur throughout Western Port (WP) and Port Phillip Bay (PPB), Victoria, are found growing on jetty pylons and among seagrass and *Caulerpa* spp. (Flynn et al. 2019). Bryozoan colonies are generally considered large or ‘frame-building’ if the species typically grow to 50 mm in three dimensions, as defined by Batson and Probert (2000). The term ‘habitat-forming’ is generally reserved for cases where frame-building bryozoans dominate large areas of the seafloor and are a significant contributor to habitat complexity (Wood et al. 2012).

Globally, there are 54 known sites that have a high bryozoan density, including three Australian sites (prior to the discovery of the WP reefs); Coorong Lagoon (South Australia), Bathurst Channel (Tasmania), and the Tasman Sea (near the Victoria-New South Wales border) (Wood et al. 2012). Most of these reports, however, relate to bryozoan-rich rock formations, patch reefs, thickets, sediments, and bioherms rather than extant and extensive

large biogenic habitat (Probert et al. 1979; Ernst & Königshof 2008, James et al. 2008; Bastos et al. 2018). Biogenic bryozoan habitats typically occur either in the lower limits of the photic zone, or in turbid, shallow waters with abundant phytoplankton where they do not need to compete with photosynthetic algae (Cook et al. 2018). Two noteworthy sites in New Zealand host true extant biogenic bryozoan reefs – Foveaux Strait and Three Kings Plateau (Rowden et al. 2004).

Western Port

Western Port (WP) is a temperate bay located in Victoria, Australia, fringed by mangroves and silty mudflats and subdivided into segments based on physical features; the Lower North Arm, Upper North Arm, Corinella Segment, Rhyll Segment and Western Entrance Segment (Jenkins & Conron 2015). Between French Island, Corinella, and Rhyll, extensive patches of globally significant bryozoan biogenic reefs have recently been identified in depths of 5 to 12 m (Flynn pers. Comm., 2016; Flynn et al. 2019). The WP bryozoan reefs are in the Rhyll Segment which is a broad subtidal sedimentary plain characterised by communities of seagrass, macroalgae and sessile invertebrate isolates with relatively weak tidal movements and eddies (Blake et al. 2013). It represents a key region for biodiversity and recreationally/commercially important fish species including snapper (*Pagrus auratus*), King George whiting (*Sillaginodes punctatus*), gummy shark (*Mustelus antarcticus*) and other teleosts (Keough & Bathgate 2011). The area is historically known to fishers as “The Corals”; a misnomer given that bryozoans belong to a different phylum. The area was the site of a commercial oyster dredge fishery in the early 19th to 20th centuries with commercial fishing ceasing in 2007 (Hannan & Bennett 2010). This bryozoan habitat was not represented in the literature, however, until as late as 2013 when Blake et al. (2013) identified it as isolated occurrences of “patches of reef colonised by dense bryozoans and

sparse sponges”. The ecological significance of the habitat was not appreciated until a biotope mapping study of WP by the Department of Environment, Land, Water and Planning (DELWP) revealed extensive, contiguous mounds of bryozoan reef; a new biotope for Victoria (Fathom Pacific 2020). They occupy a total area of 1.74 km² and the mounds are arranged in a linear, approximately north-south orientation, ranging between 3 – 30 m in length, with a vertical relief of up to 120 cm above the surrounding sediment (Flynn et al. 2019). Observations of the site indicate that tidal currents are slower in the area compared to neighbouring channels and generally display a counter-clockwise circulation pattern (Flynn et al. 2019). These conditions would be conducive to the settlement of larvae and may also serve to enhance the production of the main source of bryozoan food, phytoplankton (Cranfield et al. 2003; James et al. 2008). These reefs have escaped attention for several reasons. Firstly, this part of WP has typically poor visibility and generally dangerous currents not conducive to diving and snorkelling activities. Secondly, this area falls outside of Marine National Parks (MNP’s) and has not been extensively surveyed until now. Finally, this area is currently not of any commercial interest. Therefore, it has been ‘out-of-sight and out-of-mind’.

There are three dominant bryozoan species in the reef: *Triphyllozoon munitum* (Hincks, 1878), *Triphyllozoon moniliferum* (MacGillivray, 1860), and *Celleporaria foliata* (MacGillivray, 1888). The *Triphyllozoon* species are mounded fenestrate (netted) colonies and collectively make up >90% of the composition, while *C. foliata* is a non-fenestrate, less brittle, plate-like species that can be mounded, spreading, or encrusting (Fathom Pacific 2020) (Figure 1). No other known *Triphyllozoon*-dominant biogenic reefs have been documented anywhere else in the world. Recent mapping by Flynn et al. (2019), discovered locally dense patches of reef elsewhere in the Rhyll section of WP, although ground-truthing

of these areas has not yet been as extensively targeted owing to prohibitively expensive techniques of high resolution multibeam scanning. Compared to the linear reefs, field observations of these patch-like reefs indicate that they too represent enhanced localised macrofauna biodiversity compared to surrounding sediments. The bryozoan reef formations recorded by Cocito et al. (1998) in the Ligurian Sea are most similar to the WP reefs and are composed of *Pentapora fascialis*; a non-fenestrate species but with thinly folded sheets akin to *Triphyllozoon*.

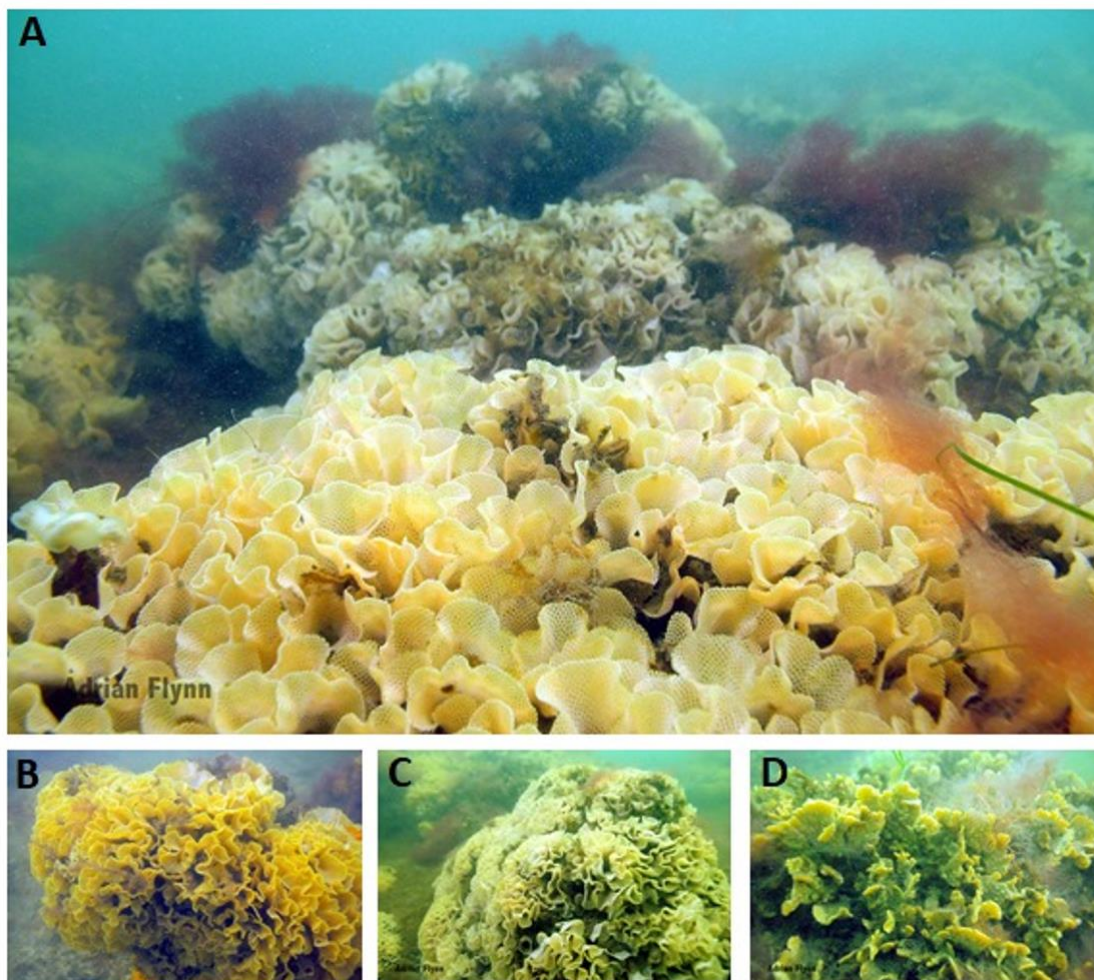


Figure 1. Western Port bryozoan reef matrix (A), *Triphyllozoon munitum* (B), *Triphyllozoon moniliferum* and (C) *Celleporaria foliata* (D) (photos taken and reproduced here with the permission of Adrian Flynn-Fathom Pacific Pty. Ltd.).

The Western Port reefs are unique because they:

- 1) Occur in shallow water - although individual bryozoan colonies have been reported in WP and PPB, no other biogenic reef habitat is known to persist in shallow water in Australia
- 2) Are dominated by delicate fenestrate colonies of *Triphyllozoons*, unlike the reefs in the Ligurian Sea (Cocito et al. 1998) and New Zealand which are composed of different species forming non-fenestrate colonies (Cranfield et al. 2003; Wood & Probert 2013).
- 3) Form regular North-South oriented rows of complex structure interspersed with ultrafine silt sediment deposits, potentially driving important sediment trapping and regimes (Flynn et al. 2019).
- 4) Form extensive linear mounds with a vertical relief of up to approximately 1.2 m, among the largest recorded in the world of non-encrusting bryozoa (Flynn et al. 2019).

Potential threats to the bryozoans of Western Port

Increasing coastal urbanisation and recreational use of marine spaces are considered serious threats to global marine biodiversity (Halpern et al. 2007; Stuart-Smith et al. 2015). Our ability to make predictions about the vulnerability of bryozoan biogenic reefs is severely limited by our lack of historical information, and most of what we do know comes from oyster dredging impact studies from other parts of the world such as New Zealand (Cranfield et al. 1999; Wood et al. 2012).

Sedimentation in WP is viewed as the primary threatening process to most habitats within the port (Hancock et al. 2001) and it is likely that regimes in the bay have changed dramatically over the past century due primarily to anthropogenic impacts (Wilkinson et al. 2016). Sediments from coastal erosion and agricultural run-off enter the bay north of French

Island (Wallbrink & Hancock 2003) and are resuspended by tidal flow, wind, and wave action, resulting in highly turbid waters (Jenkins et al. 2013). Resuspended sediments are then redistributed by tidal currents from North of French Island in a clockwise direction to the Corinella and Rhyll sectors of the port, which experiences high levels of deposition (Hancock et al. 2001; Jenkins & Conron 2015). High turbidity and sedimentation levels have been known to impact negatively on bryozoans elsewhere (Best & Thorpe 1996) and other biogenic habitats such as rhodolith beds (Harvey & Bird 2008). For bryozoans, this means delicate feeding structures may become clogged, the soft integuments scraped or scoured, and colonies smothered, which may impact on their growth potential (Gordon 2003). Additionally, it is possible that the silty mud substrate that now characterises the area is unsuitable for bryozoan recolonization (Flynn et al. 2019) necessary to sustain the reefs into perpetuity.

Physical damage, from fishing gear and anchors, is a key threat to bryozoan habitats due to the fragility of these brittle colonies (Cranfield et al. 2003). In Torrent Bay, NZ, a bryozoan biogenic reef of more than 300 km² was destroyed in the 1960's through commercial fishing (Saxton 1980). Although the WP reefs are not commercially fished currently, photographs from Fathom Pacific (2020) show visible damage that appears to represent recreational fishing gear and anchor damage. It is common for large volumes of recreational fishing boats to anchor in the area around the reefs throughout the spring - summer fishing season when *P. auratus* enter the port to spawn, and the area is relatively easy to locate due to access to GPS coordinates in the grey literature, coupled with the features being recognisable on recreational echosounders (Fathom Pacific 2020).

Toxicants and pollution are potential threats not only to the bryozoans themselves, but also the faunal assemblages. Bioaccumulation of heavy metals can affect the entire benthic food web (Waring et al. 2006). Agriculture, industry, and urban development can impact on the water quality in WP (Wilkinson et al. 2016). Surprisingly, levels of toxicants such as pesticides in sediments in WP were found to be low and relatively harmless to many biota (ANZECC 2000). Future tests should consider the impacts that these toxicants have on other local communities, such as the bryozoan reefs.

Marine pests can modify ecosystem processes and reduce biodiversity (Vitousek et al. 1997). Successful eradication of these non-native pests is almost impossible once a population is established (Parry et al. 2000). To date, WP has avoided major outbreaks of marine pests that plague PPB, such as the invasions of the Northern Pacific sea-star (*Asterias amurensis*), Japanese kelp (*Undaria pinnatifida*) and the European fanworm (*Sabella spallanzanii*) (Parks Victoria 2018. Reports from the National Introduced Marine Pest Information System (NIMPIS) on the spread of *A. amurensis* through recreational and commercial fishing gear stated that gear and vessels have a high probability of spreading the invasive sea-star to new locations in Australia (Dommissie & Hough 2002).

The WP bryozoan reefs are not within a Marine National Park (MNP) and are currently not afforded protection under any legislation. The WP Bryozoan Reefs Project intend to use the results of this study, in conjunction with others currently being undertaken, to propose that the reefs should be listed as a community under the ‘*Victoria Flora and Fauna Guarantee Act 1998 (FFG)*’. If accepted, this will mean that their ecological value will be considered as part of any future management planning and/or development plans for the area.

2 GENERAL MATERIALS AND METHODS

Survey area

The WP bryozoan reefs are in an area between French Island, Corinella, and Rhyll in a water depth range of 5 - 12 m but more commonly between 5 - 8 m (Figure 2). The substrate is characterised by silty muds and the water column is highly turbid with wind-waves contributing to sediment resuspension and mobilisation (Wallbrink & Hancock 2003). The bryozoan reefs form North-South oriented linear features that are acoustically discernible. Textures in multibeam bathymetry suggest that they potentially occupy an area of approximately 3 km² with >70 sites having been verified with a drop-camera/scuba diver. To date, they are associated with subtidal banks and not channels (Flynn et al. 2019). The bryozoan reef study site (approximately 16 kms South-East of Stony Point boat ramp launch point) was previously verified and the GPS waypoints (-38.451043°, 145.376471°) recorded so that the same reef patch can be returned to each season. Two other habitat types were used as a comparison to the bryozoan habitat; sediment predominantly comprised of dead shell bed and silty mud, and a lightly vegetated green algae (*C.cactoides*) bed. The sediment site (-38.455453°, 145.376220°) was located by travelling approximately 500 m south of the bryozoan site and the *C. cactoides* bed site (-38.458500°, 145.358462°) is approximately 2 km's South-West of the reef and was discovered when ground-truthing for bryozoan reef (Figure 2).

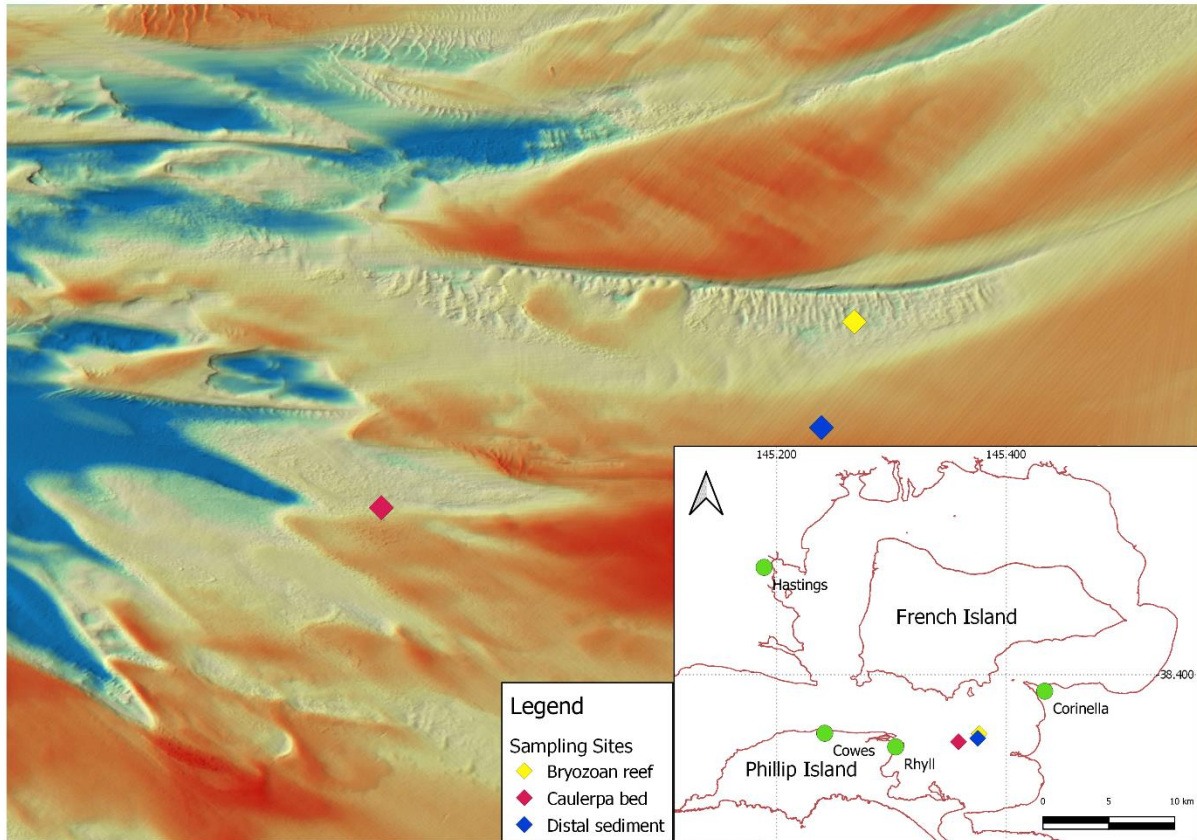


Figure 2. Map of Western Port highlighting the location of the sampling sites within the bay. Textures in the multibeam imagery show the North-South linear orientations of the rows of bryozoan reefs in contrast to the flat sediment and *C. cactoides* sites. The colour gradient represents a depth profile with bright red being the shallowest water depth (3.3 m), and the bright blue indicating the deepest water (≥ 12 m), while the light yellow where the bryozoan reef site occurs represents water depths of 5 – 8 m.

Study design

Fifteen to twenty linear columns of bryozoan mounds occur centred within the largest contiguous bryozoan reef site. Bryozoan samples were collected (May 2019 - January 2020) from a central site in the reef to remove edge effects. To spread the sampling burden across the site and to prevent pseudo-replication, samples were collected from different rows of reef during each season. Sample collections occurred temporally, once per season for four consecutive seasons (late autumn, late winter, late spring and late summer). Sampling days were planned based on the smallest tidal movements for the month (neap tide), optimal tide changes in the middle of the day and then on days with the least wind.

An echosounder (Simrad Evo 3 NSS9) and a transducer (Lowrance TotalScan Transducer) were utilised to visualise the columns of bryozoans and choose an optimal position to place the shot line to avoid damaging the bryozoans. Polyvinyl chloride (PVC) cylinders were used to craft the 15 sampling corers (height = 30 cm, radius = 7.5 cm, and total volume, $v = 5301 \text{ cm}^3$). A pole was inserted near to the top of the cylinder to act as handles to allow the diver to control the corer. The tops of the cylinders were lined with a 0.5 mm^2 wire mesh (our biodiversity screening minimum limit). The bottom of each corer was open with an attached cap to seal it off once the sample was collected (Figure 3). These demensions 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 and investigate many relationships. However, consideration was given to its size to minimize the damage such coring would cause.

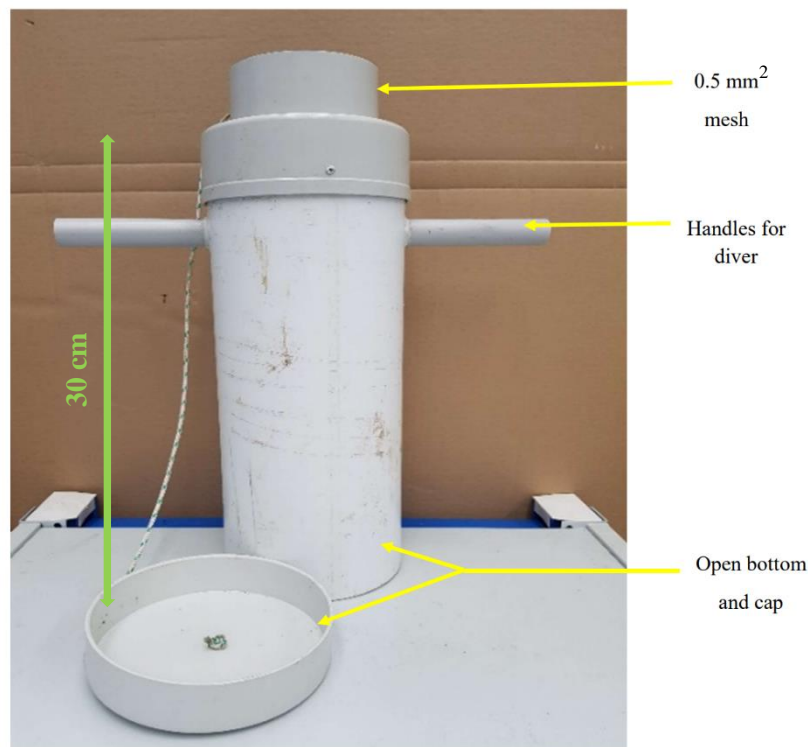


Figure 3. PVC hand-corer design used to collect samples.

The empty hand corers were placed in catch-bags and hooked onto evenly spaced knots in the shot line. The line was weighted for the catch-bags to remain on the seabed for the diver as the visibility was very poor (an average less than 1 m) due to the highly turbid water column and agitation of the fine silt on the seafloor by the diver's activities.

'Proximal sediment' (sediment between the rows of bryozoans, within 1 m) and 'Distal sediment' (~500 m South of the reef) were sampled in the first round of sampling; however, proximal sediment was omitted subsequently as it was found to contain very fine silt and showed extremely low faunal richness and abundance, presumably as the ultrafine silt clogs respiratory surfaces and feeding apparatus. Hence, resources (time, effort, and diver's air) were redirected and subsequent sampling efforts targeted the *C. cactoides* bed (~2 km South-West of the reef) instead as this was considered an under-studied neighbouring habitat (Figure 2). The data obtained from the proximal sediment was not used in any analysis but is included in Appendix 1, and distal sediment was renamed 'Sediment'. Where possible and to the diver's best ability for given environmental conditions on the day, three samples from each of the bryozoan species (*T. munitum*, *T. moniliferum* and *C. foliata*), sediment, and the *C. cactoides* bed were collected. At varying depths beneath the sediment and *C. cactoides* sites there were mud and dead shell-beds which was often difficult to penetrate and required the diver to search for appropriate sampling locations to obtain a core. The dead shells were not counted. Owing to poor visibility, it was sometimes necessary to use touch to identify the bryozoans by touch. This meant that although the samples were collected randomly, the distance between each sample was difficult to precisely quantify once out of view.

Sample processing

Immediately following collection, the sample contents were placed onto a 0.5 mm² mesh filtering system attached to the side of the boat and rinsed carefully with seawater to remove as much fine sediment to facilitate the extraction of fauna from the sample. Additionally, this process was used to screen and liberate any protected (e.g., fish or seahorses) or potentially dangerous species (e.g., blue-ringed octopus (*Hapalochlaena maculosa*). The samples were then placed back into the coring sampler, capped and bagged in case of leakage, then taken to a laboratory (La Trobe University Bundoora, Victoria), where they were refrigerated overnight at 4 – 8 °C to reduce specimen decay prior to being processed.

On the following day, samples were placed into a shallow container and sorted through by two pickers with a large free-standing magnifying glass and forceps to collect conspicuous fauna. Owing to the amount of fine silt, mud, crushed substrate etc, samples were rinsed thoroughly during the sorting process with the filtrate being collected at all stages using a 0.5 mm² sieve to ensure no small fauna were lost during the entire procedure. The sorting process took on average one hour per sample and the two pickers cross-checked each other's samples to minimise observer biases. Specimens were placed into jars containing 95% ethanol for later counting, identifying, and to preserve for eventual DNA analysis (not possible owing to covid restrictions). Three samples over the course of the study were noticeably different in volume compared to the other two samples from the same season and same bryozoan species. The invertebrate counts associated with those samples were adjusted accordingly. For example, given the volume of one spring *T.munitum* sample was approximately half the volume of the other two spring *T.munitum* samples, all abundance and morphospecies values for that sample were doubled.

Specimens were counted and photographed using a stereomicroscope (Zeiss Stemi SV 11) fitted with a digital camera (Olympus DP 27). This secondary sorting process took approximately one week per sample as each was meticulously picked through and each animal counted. All fauna were recorded as opposed to randomly sub-sampling the contents to give an estimate. Only the head ends of annelids and crustaceans were recorded to avoid duplicate counts of individuals. Many tunicates were encrusting species and regardless of the size, each separate piece of animal observed was counted as one individual. The sediment and *C. cactoides* samples were predominantly made up of dead shell necessitating a list of criteria when counting them. Bivalves were counted as an individual if they were 1) still intact, and 2) contained an animal inside. Gastropods were counted if they were 1) >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 2) contained an animal inside.

Fauna identification

Due to COVID19, access to the laboratory in 2020 was limited and, consequently, the original plan to use DNA analysis to identify the fauna was not possible. 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 an infauna specialist for confirmation and further identification. Due to the morphologically cryptic nature of many of the crustaceans and annelids, only 15 % of taxa were identified to species level, with the majority (60 %) of species identified down to family level (Appendix 2).

Statistical analysis

Given the primary aim was to compare the bryozoan reef matrix biodiversity to neighbouring habitats, the samples from all bryozoan species were pooled to create a data

set named “Pooled bryozoans”. To account for high replicates (n) in the pooled bryozoans relative to the other habitats, each sample was randomly allocated into one of three groups (Subset1 (n = 12) Subset2 (n = 12) and Subset3 (n = 11) so that each group represented a random subset of the total bryozoan pool. The same analyses were used across all 3 groups to gauge whether the results were similar across models and could therefore be reasonably applied. The statistical package SPSS 27.0.1.0 was used for all univariate analyses. PRIMER (Plymouth Routines in Multivariate Ecological Research) v7 with the PERMANOVA + add-on was used for multivariate analyses. When variances were not homogenous, data was transformed by square root to reduce the effect of dominant species.

The total number of different morphospecies, total abundance of taxa, and Shannon-Weiner’s Diversity Index (H') were calculated for each habitat. One-way ANOVA’s were used to assess whether there were significant differences in species richness and abundance between the bryozoan reefs and neighbouring habitats, between the three species of bryozoan, and between seasons. A two-way ANOVA was used to verify that differences across seasons could not be explained by different habitat types. Tukey’s post hoc tests were used for pairwise comparisons. Significant differences in the diversity of annelids, crustaceans, and molluscs (being the most common phyla) were assessed in the same way. The Bray-Curtis index was used to create a similarity matrix and the similarities in assemblage composition between the habitats was displayed using non-metric multidimensional scaling (nMDS).

To visualise some of the dis/similarities between the bryozoan reef assemblages and other Victorian marine habitats, a presence/absence table displaying the 20 most abundant families found in each study was created using data sourced from a number of previous

395 studies, including; WP seagrass (Watson et al. 1984; Edgar et al. 1994), WP Rhodoliths
396 (Harvey & Bird 2008), WP unvegetated sediment (Edgar et al. 1994), and PPB mud and
397 sand (Wilson et al. 1998).

3 INVERTEBRATE BIODIVERSITY OF WESTERN PORT BRYOZOAN REEFS

Introduction

Biogenic structures typically lead to a higher diversity of species at all trophic levels (Menge & Sutherland 1976). Virtually nothing is known about the WP bryozoan reef habitat. However, based on previous biodiversity studies on biogenic reef habitats worldwide (Buhl-Mortensen & Mortensen 2005; Sciberras et al. 2009; Morrison et al. 2014), bryozoan-dense habitats (Wood et al. 2012), and other WP habitats (Coleman et al. 1978; Watson et al. 1984; Harvey & Bird 2008; Butler & Bird 2010), it is highly likely that these reefs will harbour rich assemblages across a wide range of taxa. Bryozoans have been described as “bioconstructors” that can enhance local biodiversity when clustered together, or in reef form, like those in WP (Jones 2006). Bryozoan-dominated habitats are considered complex habitat for macroinvertebrates and support diverse assemblages at the centimetre to kilometre scale (Attrill et al. 2000; Wood et al. 2012). They provide opportunities that may not be otherwise available in neighbouring habitats. Organisms can live in greater densities in these complex habitats because the increased surface area and variety of niches (in comparison to surrounding sediment) reduces competition for resources, like space and food (Bruno et al. 2003). Complex habitats can decrease predation rates by providing refuge and protection often making these habitats favourable to prey species (Bell & Westoby 1986; Pederson & Peterson 2002). 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 Straight, New Zealand (Vooren 1975; Saxton 1980; Jiang & Carbines 2002; Carbines et al. 2004). The structure and height of the colonies can alter local environmental conditions such as wave

423 action and current speed which not only offers shelter for a range of macroinvertebrates but
424 may also affect the distribution of sediment in the immediate area (Wood et al. 2012).
425 Sediment heterogeneity (a mixture of different particle sizes) has been associated with
426 higher local biodiversity (Gray, 1974; Jones 2006).

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

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442 Given the WP bryozoans reefs offer extensive rows of complex habitat surrounded by
443 predominantly bare soft sediment, it is expected that the invertebrate assemblage associated
444 with them will be similarly diverse. Additionally, since the *Triphyllozoon* species and *C.*
445 *foliata* are characterized by different growth forms, it is possible that parameters like species
446 density, and physical structure (solid and plate-like versus fragile, folded, and fenestrate)
447 could affect the invertebrate assemblages directly associated with each (Wood 2005).

Aims of this study

Given the very recent discovery of, and paucity of data associated with the WP bryozoan reefs, the current project aims to provide an understanding of the co-occurring biodiversity and conservation values of these reefs. In this study, the macrofauna within the matrix of the WP bryozoan reefs will be examined by collecting samples from the reefs and comparisons made to neighbouring habitats. Specifically, the aims are to:

- 1) Determine the macrofaunal biodiversity associated with the bryozoan reefs compared to neighbouring habitats including sediment and nearby *C. cactoides* bed, and
- 2) Compare the macrofaunal biodiversity of the three bryozoan species as separate entities to explore whether the morphology of each species plays a role in the composition of the associated faunal assemblages.

It was hypothesized that species richness and abundance would be greater in the bryozoan reefs compared to neighbouring habitats, and that each bryozoan species would harbour a similar richness and abundance but with a somewhat different composition.

Results

The total number of samples were 35, 11 and 9 for bryozoan, sediment and *C. cactoides* respectively (Table 1). The overall highest number of morphospecies (47) and abundance (923) in a single sample was recorded in a Spring *T. munitum* sample, while one sample of *C. cactoides* contained no invertebrates (greater than 0.5 mm²) at all. The highest number of different species within a habitat was observed in *C. foliata* (102), while only 38 morphospecies were observed in the sediment (Table 1).

Table 1. Number of samples, total abundance, number of morphospecies, and species diversity (Shannon Weiner's Index, H') observed in the three bryozoan species (*C. foliata*, *T. munitum*, and *T. moniliferum*), and neighbouring habitats (sediment and *C. cactoides* bed).

Habitat	N	Abundance	No. morphospecies	Shannon Weiner (H')
<i>C. foliata</i>	11	2409	102	2.6301
<i>T. munitum</i>	13	2562	88	2.6908
<i>T. moniliferum</i>	11	2603	70	2.3309
Sediment	11	281	38	1.8728
<i>C. cactoides</i>	9	157	40	1.5745

Within the bryozoan matrix a total of 7,574 individuals were captured representing 127 different morphospecies from 59 different families across 9 phyla. The full listing of morphospecies recorded in each season is shown in Table 2.

Table 2. Occurrence and abundance of macroinvertebrate taxa ≥ 0.5 mm² in three dominant bryozoan species (*C. foliata*, *T. munitum*, and *T. moniliferum*), and two neighbouring habitats (sediment and *C. cactoides* bed) in Western Port. The numbers in brackets represent the number of morphospecies. Morphospecies unique to a habitat are denoted by ^.

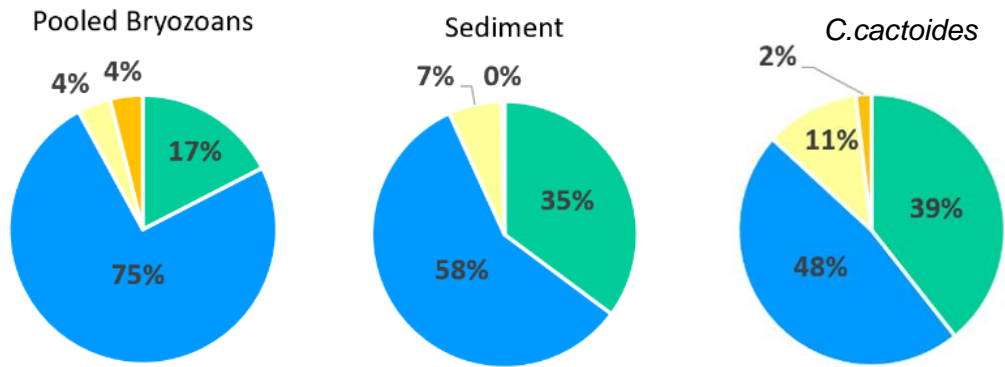
	Taxon	<i>C. foliata</i>	<i>T. munitum</i>	<i>T. moniliferum</i>	Sediment	<i>C. cactoides</i>
Annelida						
Ampharetidae	<i>Melinninas</i> sp.		1^			
Capitellidae	Capitellidae spp. (2)	12	1	32	32	9
Cirratulidae	Cirratulidae sp.	2	2			
Eunicidae	Eunicidae spp. (2)	33	2			7
	<i>Eunice</i> spp. (3)	254	6	1		
	<i>Lysidice</i> spp. (2)	2	1		6	9
Flabelligeridae	<i>Pherusa</i> sp.	54	78	54		
Glyceridae	Glyceridae sp.		1		1	
Goniadidae	Goniadidae sp.		1	4	5	2
Lumbrineridae	Lumbrineridae spp. (3)	19	39	22	16	23
Nephtyidae	Nephtyidae sp.			1^		
Nereididae	Nereididae spp. (6)	54	20	28		2
	<i>Australonereis</i> sp.	2	5	3		
	<i>Simplisetia</i> sp.	6	6	15		
Opheliidae	<i>Armandia</i> sp.	44	57	56	36	4
Orbiniidae	Orbiniidae spp. (2)	3	1		1	
Phyllodocida	Phyllodocida			1		1
Polynoidae	Polynoidae spp. (4)	8	12	9		1
Sigalionidae	Sigalionidae sp.	1^				
Syllidae	Syllidae spp. (4)	71	222	42	5	2
Terebellidae	Terebellidae sp.			1^		
Trichobanchidae	Trichobanchidae spp. (2)	8	14	4	1	2
Brachiopoda						
Terebratulidae	<i>Magellania flavescentis</i>	3	15	8	1	2
Crustacea						
Alpheidae	Alpheidae spp. (2)	2	1	1		
	<i>Alpheus</i> spp. (2)	4^				
	<i>Alpheus villosus</i>	1^				
	<i>Alpheus astrinx</i>			2^		
	<i>Synalpheus tumidomanus</i>	61	83	58	1	
Amaryllididae	Amaryllididae spp. (8)	14	18	7	1	1
	<i>Amaryllis</i> sp.	1^				
Ampeliscidae	Ampeliscidae sp.	1^				
Amphilocidae	Amphilocidae spp. (3)	7	4		2	
Amphipoda	Amphipoda (2)	2			2	3
Anthuriidae	Anthuriidae sp.	6	24	5	6	1
	<i>Mesanthura</i> sp.	1^				
Bodotriidae	Bodotriidae sp.	7	32	30	24	
Callianassidae	Callianassidae spp. (3)		3		7	3
Caprellidae	Caprellidae sp.		2	15	9	
Cirolanidae	Cirolanidae sp.				2^	
Colomastigidae	Colomastigidae sp.	1	5	3		
	<i>Colomastix</i> sp.	1	26	7		
Corophiidae	Corophiidae spp. (2)	293	377	524	43	33
	<i>Monocorophium insidiosum</i>	11	9			3
	<i>Xenocheira fasciata</i>	23	36	75	10	1
Cyclopidae	Cyclopidae sp.		2^			
Cylindroleberididae	Cylindroleberididae sp.	4	6			
Galatheididae	Galatheididae spp. (3)	6^				

Table 2 continued.

	Taxon	<i>C. foliata</i>	<i>T. Munitum</i>	<i>T. moniliferum</i>	Sediment	<i>C. cactoides</i>
	<i>Galathea australiensis</i>	1	1	1		
Hyperiididae	Hyperiididae sp.	1	4		1	
Impheimediidae	Impheimediidae sp.	3	10	25		1
Joeropsidae	Joeropsidae sp.	24	64	76		
Leucothoidae	Leucothoidae sp.	23	13	9		
Liljebergiidae	Liljebergiidae sp.	47	11	31	3	
Lysianassidae	Lysianassidae sp.	1	7	3	1	
Maeridae	Maeridae sp.	19	5	3		
Munididae	Munididae sp.	3	1			
Mysidae	Mysidae sp.	50	190	79	3	
Paguridae	Paguridae sp.				2^	
Paranebaliidae	Paranebaliidae sp.		10^			
	<i>Levinebalia</i> sp.	6	8	53		1
	<i>Paranebalia tiparra</i>	98	217	486	1	2
Paranthuridae	Paranthuridae sp.	2	12	9	7	3
Phoxocephalidae	Phoxocephalidae spp. (5)	12	24	4	2	3
	<i>Birubius</i> sp.	5	39	19	11	10
	<i>Brolgus tattersali</i>	88	117	66	26	8
Pilumnidae	<i>Heteropilumnus fimbriatus</i>	1	2	2		
	<i>Pilumnus serratifrons</i>	23	31	24		
Podoceridae	Podoceridae spp. (2)	4	11			
Portunidae	Portunidae sp.	3	2			1
Tanaidacea	Tanaidacea	435	77	20	2	
	Apseudidae sp.	234	423	571	6	
Echinodermata						
Amphiuridae	Amphiuridae sp.	3^				
Cidaridae	Cidaridae sp.			1^		
Mollusca						
Acanthochitonidae	Acanthochitonidae spp. (2)	4	1	1		
Arcidae	Arcidae sp.			1^		
	<i>Anadara trapezia</i>		6	1		
	<i>Barbatia pistachia</i>	85	46	30		
Calyptraeidae	<i>Sigapatella</i> spp. (2)				1	2
Cardiidae	<i>Pratulium thetidis</i>					7^
Carditidae	Carditidae sp.				2	1
Cerithiidae	<i>Cacozeliana granaria</i>	5^				
Columbellidae	<i>Mitrella</i> sp.					1^
Haminoeidae	Haminoeidae sp.				1	1
Hiatellidae	Hiatellidae sp.	2	2	1		
Mytilidae	Mytilidae sp.				2^	
	<i>Arcuatuta senhousia</i>				6	4
Nassariidae	<i>Nassarius</i> sp.	1		4		
Ostreidae	<i>Ostrea angasi</i>	44	35	12		
Pectinidae	<i>Pecten fumatus</i>			1^		
Tellinidae	Tellinidae sp.	7	8	2		
	<i>Macomona deltoidalis</i>	1	12	1		
Veneridae	<i>Venerupis</i> sp.				7	2
Tunicata						
Asciadiacea	Asciadiacea	1	1	1		
Didemnidae	<i>Didemnum</i> sp.	2	2			
Holozoidae	<i>Sycozoa cerebriformis</i>	7	7	1		
Pyuridae	<i>Pyura stolonifera</i>	133	47	56		
Other						
Golfingiida	Golfingiida sp.	3	2			1
Damaged polychaete		1	2			
Hydrozoa	Hydrozoa	1^				
Pantopoda	Pantopoda			1^		
Porifera	Porifera	4^				
TOTAL		2409	2562	2603	295	157

Crustaceans were the most dominant taxa making up 75% of the total abundance and 42% of the total number of morphospecies, while annelids made up 17% of the total abundance and 33% of the total number of morphospecies. Molluscs (4% abundance and 10% morphospecies) were somewhat common while rare taxa like brachiopods, Sipuncula, Echinodermata, cnidarians, and porifera together accounted for less than 4% of morphospecies and abundance (Figure 4). Crustaceans and annelids were also the most abundant taxa in the neighbouring sediment and *C. cactoides* habitats contributing to 93% and 87% of the total abundances, respectively (Figure 4).

A



B

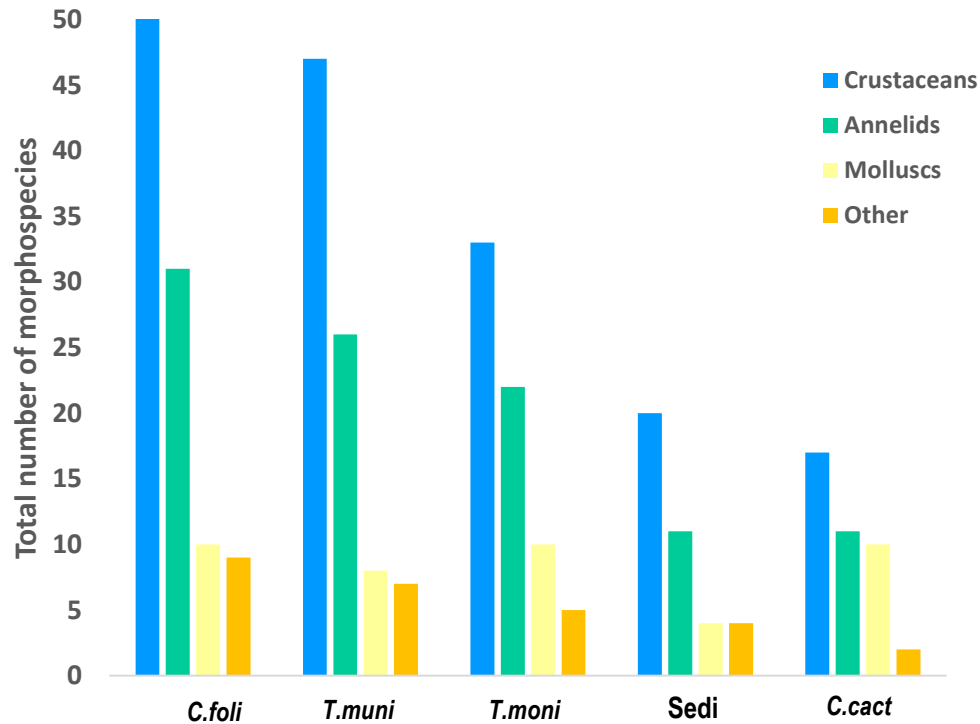


Figure 4. Relative abundance (%) in pooled bryozoans, sediment, and *C. cactoides* habitats (A) and total number of different species found in the three bryozoan species (*C. foliata*, *T. munitum*, and *T. moniliferum*), sediment, and *C. cactoides* habitats (B).

Taxa typically smaller than ~5 mm dominated the matrix fauna contributing to 69% of the total abundance of fauna. Relatively few species provided the majority of individuals with 50% of the total abundance of invertebrates within the bryozoan matrix attributed to four dominant crustacean morphospecies – sea fleas (*Paranebalia tiparra*), Tanaidacea sp.,

Apseudidae sp., and amphipods (Corophiidae sp.), while 114 morphospecies (88% of the total identified) accounted for $\leq 1\%$ each to the total abundance (Table 2).

Within the bryozoan matrix, the family Apseudidae was highly abundant; *C. foliata* ($\bar{x} = 21.27$), *T. munitum* ($\bar{x} = 32.54$), and *T. moniliferum* ($\bar{x} = 51.91$) as was the family Corophiidae in *C. foliata* ($\bar{x} = 29.73$), *T. munitum* ($\bar{x} = 32.46$), and *T. moniliferum* ($\bar{x} = 54.45$). The family Paranebaliidae was abundant in both *Triphyllozoon* species – *T. munitum* ($\bar{x} = 18.08$) and *T. moniliferum* ($\bar{x} = 49$). There were 17 ubiquitous (found in the reef matrix, sediment, and *C. cactoides*) morphospecies including the crustaceans (*Biribius* sp., *Brolgus tattersali*, *Paranebalia tiparra*, *Xenocheira fasciata*, Amaryllididae spp., Anthuriidae sp., Corophiidae spp., Paranthuriidae sp., and Phoxocephalidae spp.), annelids (*Armandia* sp., Capitellidae spp., Goniadidae sp., Lumbrineridae spp., Syllidae spp., and Trichobranchidae spp.), and the brachiopod *Magellania flavescens* (Table 2).

The most common conspicuous taxa (>5 mm) in the bryozoan matrix were banded arks (*Barbatia pistachio* – a species of mollusc), 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) (Table 2).

The mean number of morphospecies observed in the bryozoans was compared to that observed within the neighbouring habitats. One-way ANOVA showed that there was a significantly greater species richness in the pooled bryozoans compared to neighbouring habitats ($F = 30.743$, $df = 89$, $p < 0.001$, Figure 5). Tukey's post hoc analysis showed that the bryozoan matrix harboured a significantly higher number of different species than both

the sediment ($p = <0.001$) and *C. cactoides* ($p = <0.001$) habitats. This was the case for all subsets (Appendix 3.1).

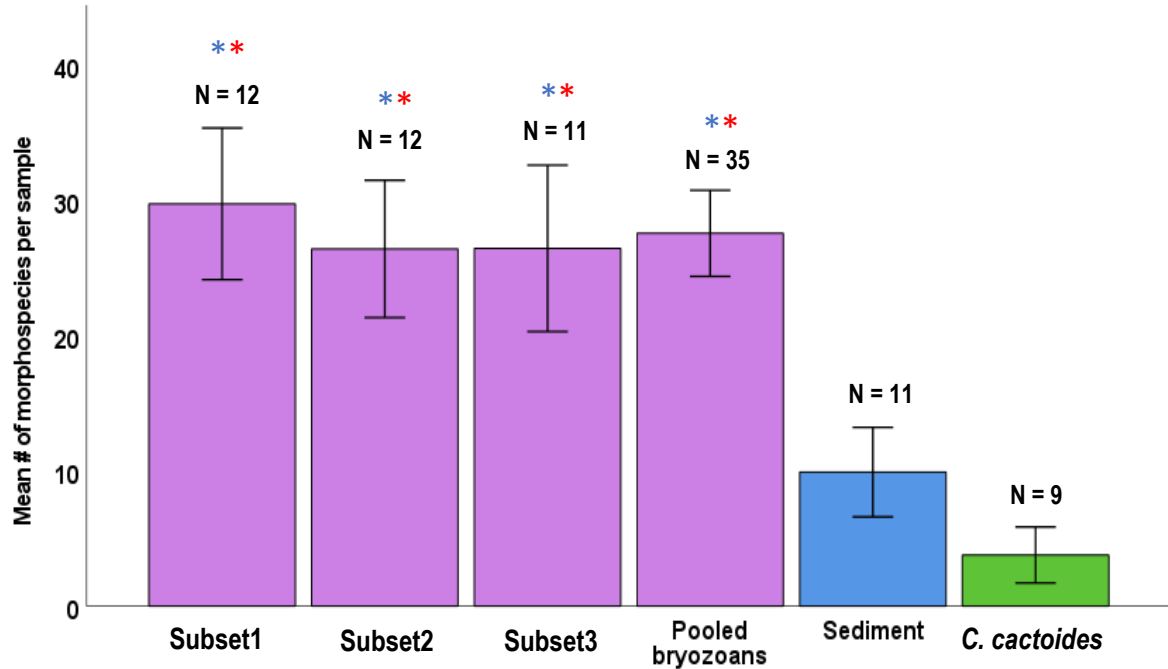
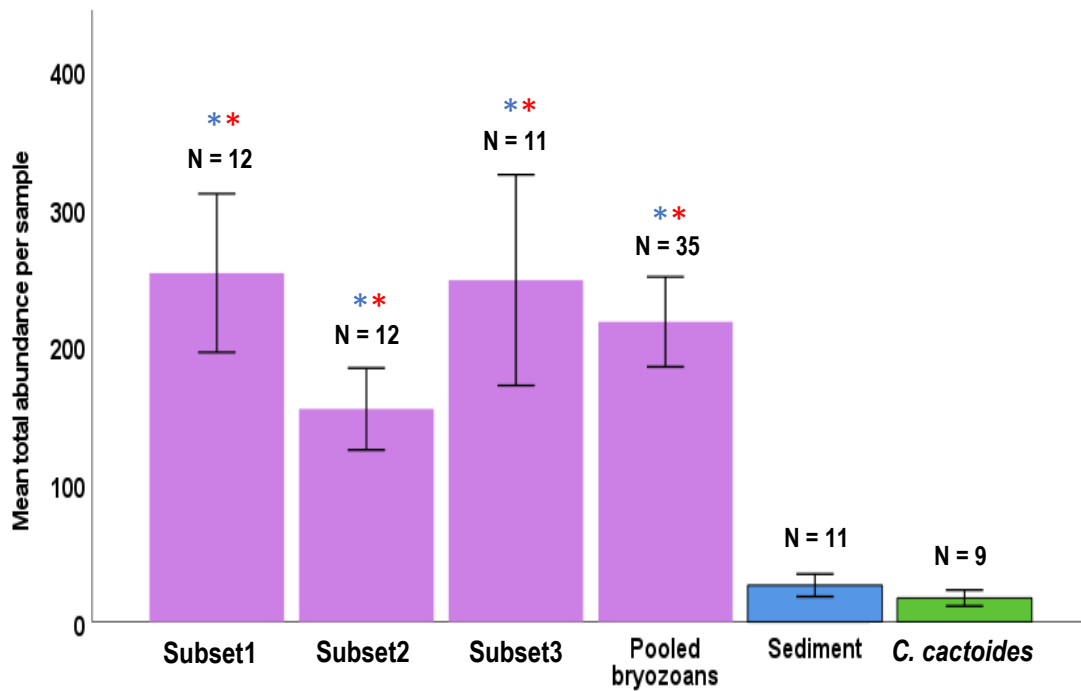


Figure 5. Mean number of morphospecies per sample across habitats. Pooled bryozoans include taxa observed in *C. foliata* ($n = 11$), *T. munita* ($n = 13$), and *T. moniliferum* ($n = 11$). Subset 1 – 3 are random subsets from the pooled bryozoans. Blue asterisks represent a significantly greater number than sediment and red asterisks represent a significantly greater number than *C. cactoides*, Error bars represent ± 1 standard error.

The mean total abundance of taxa observed in the bryozoans was compared to that observed within the neighbouring habitats. One-way ANOVA showed that there was a significantly greater abundance of invertebrates in the pooled bryozoans compared to neighbouring habitats ($F = 10.688$, $df = 89$, $p < 0.001$, Figure 6). Tukey's post hoc analysis showed that the bryozoan matrix harboured a significantly higher abundance than both the sediment ($p = < 0.001$) and *C. cactoides* ($p = 0.001$) habitats. This was the case for all subsets (Appendix 3.2).

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Figure 6. Mean total abundance per sample across habitats. Pooled bryozoans include taxa observed in *C. foliata* (n = 11), *T. munita* (n = 13), and *T. moniliferum* (n = 11). Subset 1 – 3 are random subsets from the pooled bryozoans. Blue asterisks represent a significantly greater number than sediment and red asterisks represent a significantly greater number than *C. cactoides*. Error bars represent ± 1 standard error.

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Given they were the most common, the number of annelids, crustacean, and mollusc morphospecies observed in the bryozoan reefs were compared to those found in the neighbouring habitats. There was a significantly greater number of annelid morphospecies in the bryozoans than both sediment ($p = <0.001$) and *C. cactoides* ($p = 0.006$) and a significantly greater number of crustacean morphospecies in the bryozoans than both sediment ($p = <0.001$) and *C. cactoides* ($p = <0.001$). One-way ANOVA showed a significant difference in the number of molluscan morphospecies between the habitats ($F = 6.02$, $df = 89$, $p = <0.001$), however, out of the three bryozoan subsets, only Subset3 was different to sediment ($p = <0.001$) and *C. cactoides* ($p = 0.004$) (Appendix 3.3). Therefore,

there was considered to be no difference in the number of molluscan morphospecies between habitats.

The total abundance of annelids, crustaceans, and molluscs observed in the bryozoan reefs were compared to that found in the neighbouring habitats. There were no significant differences in annelid abundance amongst the habitats ($F = 2.121$, $df = 89$, $p = 0.071$) and although one-way ANOVA showed a significant difference in mollusc abundance ($F = 4.19$, $df = 89$, $p = 0.002$), there was only one subset (Subset1) that was different to sediment ($p = 0.034$) and *C. cactoides* ($p = 0.029$), and therefore deemed to be not significant (Appendix 3.3). The total abundance of crustaceans was significantly different between habitats ($F = 17.294$, $df = 89$, $p = <0.001$). Pooled bryozoans had a significantly greater abundance of crustaceans compared to both sediment ($p = 0.001$) and *C. cactoides* ($p = <0.001$) and this was supported by all subsets (Appendix 3.3).

Species richness and abundance of taxa observed in each bryozoan species as separate entities were compared. One-way ANOVA showed that there was no significant difference in the mean number of morphospecies ($F = 1.057$, $df = 34$, $p = 0.359$, Figure 7A) or mean abundance of taxa ($F = 0.77$, $df = 34$, $p = 0.838$, Figure 7B) per sample between the three bryozoan species.

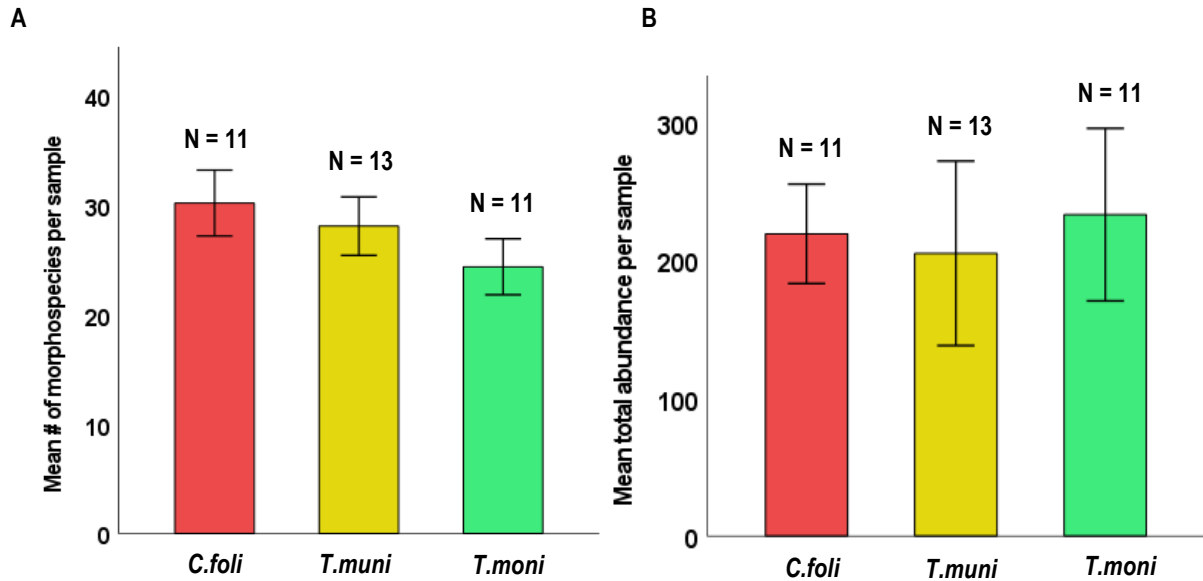


Figure 7. Mean number of morphospecies per sample found in the three dominant species of bryozoan. Error bars represent ± 1 standard error. (A) Mean total abundance of taxa per sample found in the three dominant species of bryozoan (B). Error bars represent ± 1 standard error.

There were no significant differences between the bryozoan species in terms of crustacean abundance ($F = 0.403$, $df = 34$, $p = 0.672$) or morphospecies ($F = 0.304$, $df = 34$, $p = 0.74$). Annelid abundance was not significantly different between the bryozoan species ($F = 2.399$, $df = 34$, $p = 0.107$), though the number of annelid morphospecies was significantly higher in *C. foliata* than *T. moniliferum* ($p = 0.031$), which was somewhat attributed to a marked difference in the distribution of Eunicid worms among the bryozoan species. Six Eunicid morphospecies presented in the bryozoan matrix; all 6 were found in *C. foliata* (292 individuals, $\bar{x} = 26.54$), 4 in *T. munitum* (9 individuals), two morphospecies in *T. moniliferum*. The number of molluscan morphospecies did not differ significantly amongst the bryozoan species, however, the abundance of molluscs was greater in *C. foliata* than both *T. munitum* ($p = 0.048$) and *T. moniliferum* ($p = 0.002$). The abundance of taxa was not significantly different between the sediment and *C. cactoides* habitats ($p = 0.998$), however, species richness was higher in *C. cactoides* ($p = 0.022$) (Appendix 3.3).

Shannon-Weiner Diversity Index (H') was used to compare the levels of biodiversity observed in each habitat using a single factor that considers both species richness and abundance (Table 1 and Figure 8). One-way ANOVA showed a significant difference in H' between habitats ($F = 13.752$, $df = 54$, $p = <0.001$). There were no differences between the three bryozoan species or between the two neighbouring habitats (Appendix 3.4). *T. munitum* had a significantly higher H' than both sediment ($p = <0.001$) and *C. cactoides* ($p = <0.001$) as did *C. foliata*. *T. moniliferum* on the other hand had a greater H' than *C. cactoides* ($p = 0.002$) but not sediment ($p = 0.098$) (Appendix 3.4).

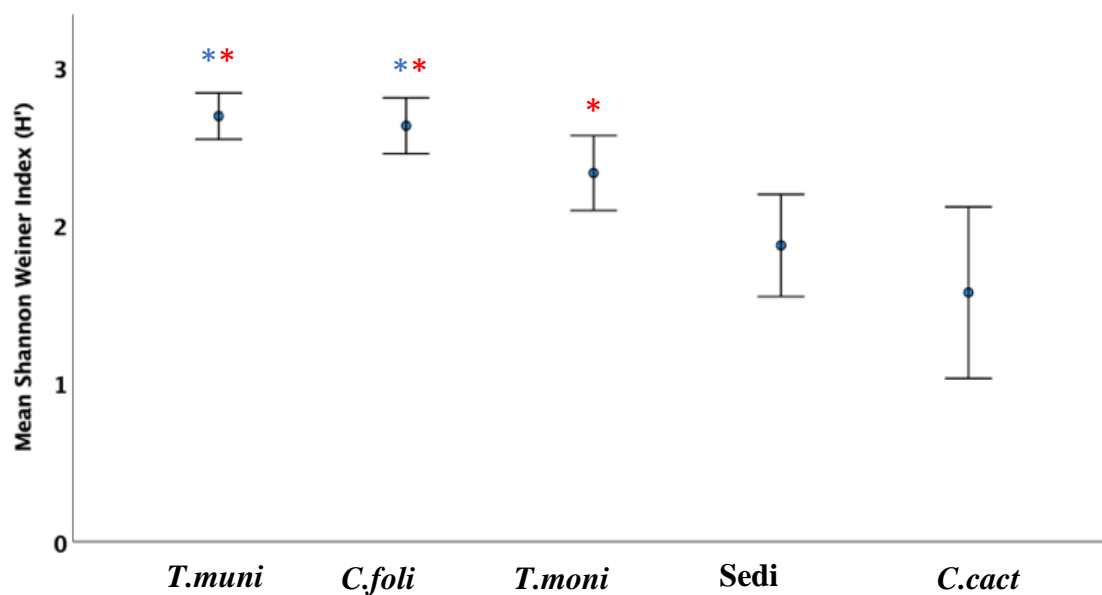


Figure 8. Mean Shannon-Weiner Diversity Index (H') for each of the bryozoan species (*T. munitum*, *T. moniliferum*, and *C. foliata*), sediment, and *C. cactoides*. Blue asterisks represent a significantly greater H' than sediment and red asterisks represent a significantly greater H' than *C. cactoides*. Error bars represent a 95% confidence level.

A *non-metric* MDS (nMDS) based on square root transformed Bray-Curtis similarities of assemblages between the three bryozoan species and neighbouring habitats was created to illustrate how dis/similar each sample (55 in total) was to all others (Figure 9). The bryozoan

reef matrix has a markedly different assemblage compared to the neighbouring habitats. There is a large spread across axis 2 and overlapping of points for the non-bryozoan habitats illustrating that the composition of the samples within those habitats were relatively dissimilar to each other, and that the two sediment habitats share some similarities in composition. There is considerable overlap of points among the bryozoan habitats indicating similarities in assemblages especially between the *Triphyllozoon* species. There is some overlap between *C.foliata* and the other bryozoan species, however, the spreading out of the points demonstrates that the samples were more different to the *Triphyllozoon* samples than they were to each other.

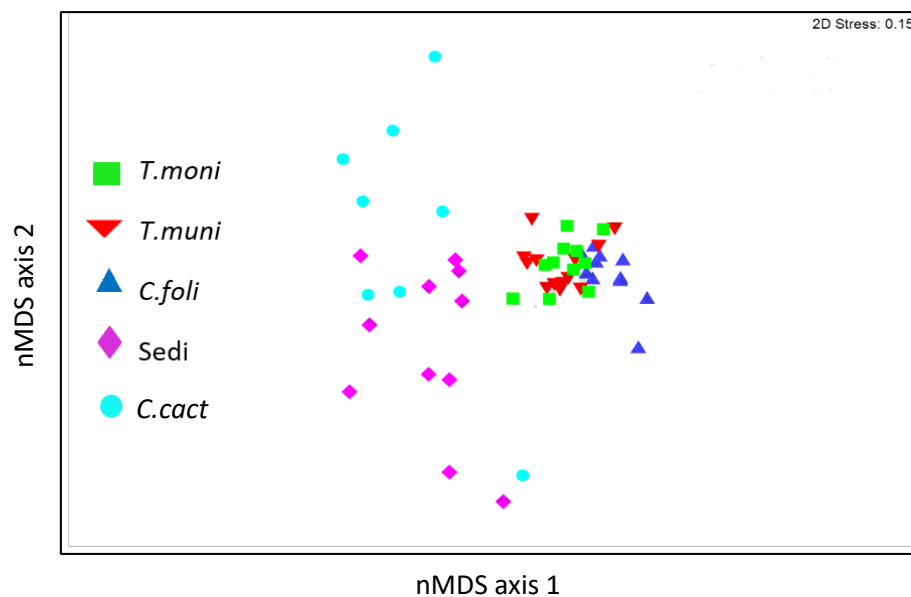


Figure 9. Non-metric MDS showing the invertebrate composition similarities between *C. foliata*, *T. munitum*, *T. moniliferum*, *C. cactoides*, and sediment habitats. Each marker represents a sample from the associated habitat. Values are based on square root transformed Bray-Curtis similarities.

Eighty-six morphospecies were found in the bryozoan matrix that were not observed in either of the neighbouring habitats. Both neighbouring habitats had ≤ 10 unique morphospecies (Figure 10B). Thirty-eight percent of all morphospecies species observed in

the bryozoan matrix were found in all three bryozoan species. The *Triphyllozoon* species had 11 and 12 morphospecies unique to their assemblage, while there were 24 (23.5%) morphospecies unique to *C. foliata* (Figure 10A).

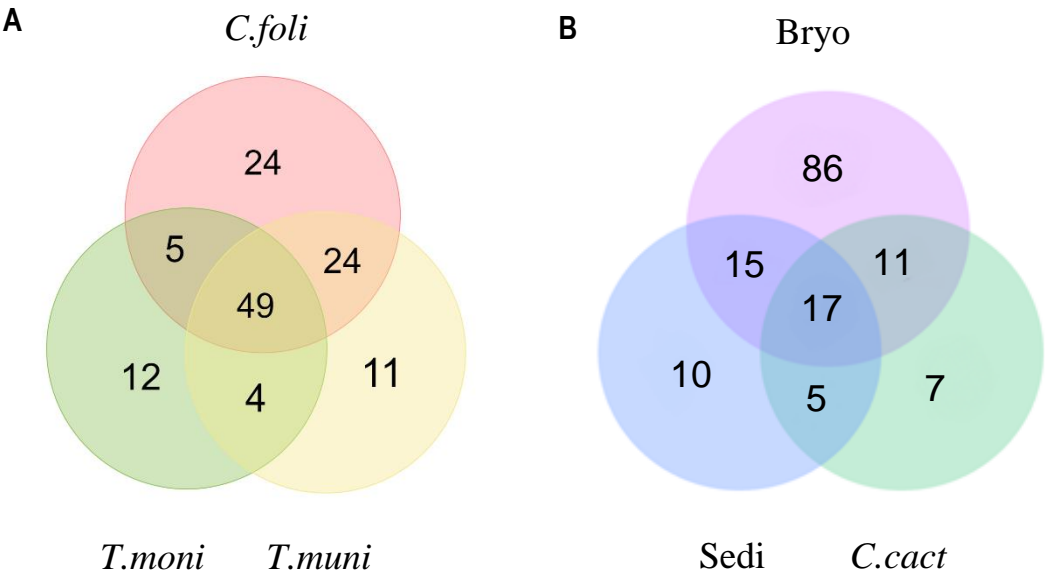


Figure 10. Venn diagram illustrating the number of similar and dissimilar morphospecies observed in each of the bryozoan species (A). Venn diagram illustrating the number of similar and dissimilar morphospecies observed in the bryozoan reef, sediment, and *C. cactoides* (B).

Data from external sources was used to create a presence/absence table to visually display how the macroinvertebrate assemblages observed on the bryozoan reef compares to that observed in other habitats nearby (WP seagrass, WP unvegetated sediment, WP rhodoliths, and PPB mud and sand). The families listed represent the twenty most abundant observed in each study (Table 3). It appears that the bryozoan matrix fauna is a distinctly different community with high crustacean diversity, but low annelid and molluscan diversity compared to the other habitats.

Table 3. Presence/absence of the 20 most abundant families observed in each of; the Western Port bryozoan reefs from the present study and data sourced from previous studies; Western Port (WPBR), Western Port seagrass (WPSG1) (Watson et al. 1984), Western Port seagrass (WPSG2) (Edgar et al. 1994), Western Port unvegetated sediment (Edgar et al. 1994), Port Phillip Bay mud (PPBM) (Wilson et al. 1998), Port Phillip Bay sand (PPBS) (Wilson et al. 1998), and Western Port Rhodoliths (WPRL) (Harvey & Bird 2008).

	WPBR	WPSG1	WPSG2	WPUV	PPBM	PPBS	WPRL		WPBR	WPSG1	WPSG2	WPUV	PPBM	PPBS
Annelida								Crustacea						
Ampharetidae						Red		Alpheidae	Purple	Blue				
Amphinomidae							Pink	Ampeliscaidae				Yellow	Orange	Red
Capitellidae		Blue	Green	Yellow	Orange	Red		Apseudidae	Purple					
Chaetopteridae					Orange	Red		Bodotriidae	Purple					
Cirratulidae		Blue	Green	Yellow	Orange			Callianassidae		Blue		Yellow		
Ctenodrilidae							Pink	Corophiidae	Purple					
Dorvilleidae								Dexaminidae			Green			
Eunicidae	Purple	Blue					Pink	Diastylidae					Orange	Red
Flabelligeridae	Purple		Green		Orange			Gammaridea		Blue				
Glyceridae		Blue						Goneplacidae		Blue				
Hesionidae							Pink	Gynodiastylidae						Red
Lumbrineridae	Purple		Green	Yellow	Orange	Red	Pink	Hymenosomatidae		Blue	Green			
Magelonidae						Red		Imphimediidae	Purple					
Maldanidae					Orange			Joeropsididae	Purple					
Melinnidae				Yellow				Leptanthuridae						Red
Nephtyidae		Blue	Green	Yellow			Pink	Leptocheliidae			Green			
Nereididae	Purple	Blue					Pink	Liljeborgiidae	Purple					
Opheliidae	Purple	Blue		Yellow				Mysidae	Purple					
Orbiniidae		Blue		Yellow	Orange	Red		Ocypodidae		Blue				
Paraonidae		Blue			Orange	Red		Paranebaliidae	Purple					
Pilargidae							Pink	Phoxocephalidae	Purple					Red
Phyllodocidae		Blue		Yellow			Pink	Pilumnidae	Purple					
Polynoidae			Green	Yellow	Orange		Pink	Pontogeneiidae			Green			
Sabellidae					Orange	Red		Tanaidae		Blue				
Spionidae		Blue	Green	Yellow	Orange			Urohaustoriidae				Yellow		
Syllidae	Purple						Pink	Mollusca						
Terebellidae		Blue			Orange	Red	Pink	Arcidae	Purple					
Trichobranchidae			Green		Orange	Red		Corbulidae					Orange	Red
Echinodermata								Dialidae			Green			
Amphiuridae					Orange			Haminoeidae						Red
Chiridotidae					Orange			Lasaeidae				Yellow		
Cnidaria								Litiopidae			Green			
Edwardsiidae					Orange			Mactridae				Yellow		
Tunicata								Nassaridae			Green	Yellow		
Pyuridae	Purple							Ostreidae	Purple					
								Pectinidae			Green			
								Pholadidae				Yellow		
								Pteriidae						Red
								Rissoidae			Green	Yellow		
								Semelidae					Orange	Red
								Tellinidae		Blue	Green	Yellow		
								Trochidae			Green			Red
								Vitrinellidae			Green	Yellow		

Discussion

Bryozoan reef biodiversity compared to neighbouring habitats

The reefs exhibited high species richness, abundance, and diversity (H') compared to both the sediment and *C. cactoides* habitats. These findings are consistent with studies from around the world showing that habitat-forming bryozoan colonies support an elevated faunal diversity compared to neighbouring habitats (Bradstock & Gordon 1983; McKinney & Jaklin 2000; Morgado & Tanaka 2001; Cocito et al. 2002; Jones & Lockhart 2011). Habitat-forming structures are well known to harbour elevated abundances of taxa, compared to less complex surrounding habitats, by providing surfaces with varying orientations and interstitial space sizes (Otero-Ferrer et al. 2019). Habitat heterogeneity is also associated with more diverse faunal assemblages (Gray 1974). The vertical relief and size of bryozoan colonies may also alter currents, affecting the distribution of sediment particle size, and as a result create more heterogenous sediment immediately below colonies (McKinney & Jaklin 2000; Jones 2006).

Beneath both the sediment and *C. cactoides* sites there was predominantly compact dead molluscan shells and fine silt mud, with sparse patches of *C. cactoides* fronds interspersed throughout the latter. The invertebrate assemblages observed are consistent with other vegetated and unvegetated sediment studies from WP (Coleman et al. 1978; Edgar et al. 1994). Soft sediments (that offer little in the way of habitat heterogeneity) are the prevailing habitat of WP, covering approximately two thirds of the bay (Harvey & Bird 2008). It is essential that the faunal assemblages of the more complex habitats, such as bryozoans, of the bay are more extensively researched. It is known that there is a positive correlation between habitat complexity and ecosystem production (Barnard & Drummond 1978), thus

making it likely that these rigid, elevated, biogenic structures play a larger role in ecosystem services than the homogenous non-complex sediment surrounding them.

Bryozoan reef assemblage

In this study, 127 morphospecies were found within a single patch of bryozoan reef comprising three dominant bryozoan species. This is remarkably consistent with the bryozoan associated invertebrate community on the Otago Shelf, NZ, where 138 invertebrate species were associated with three habitat-forming bryozoan species (Wood 2005; Wood & Probert 2013). The most abundant group were deposit and suspension feeding crustaceans, followed by annelids. This is in accord with bryozoan biodiversity studies from New Zealand (Wood & Probert 2013) and elsewhere (Ferdeghini & Cocito 1999; Morgado & Tanaka 2001) that have demonstrated that crustacean and annelid dominated assemblages are typical of habitat-forming bryozoans. The neighbouring habitats were dominated by these two phyla also, however, the number of crustaceans in terms of both species richness and abundance was significantly greater in the bryozoan reefs, as was annelid species richness, but not annelid abundance. The annelids that were abundant in the sediment and *C. cactoides* sites included the families; Capitellidae, Lumbrineridae, and Opheliidae, which are also abundant in other soft sediments in WP (Coleman et al. 1978; Edgar et al. 1994; Butler & Bird 2010). The dominance of crustaceans, annelids, and molluscs appears to not only be characteristic of bryozoan dominated habitat, but also a bay-wide pattern in WP. For instance, an extensive quantitative survey of the macroinvertebrates of WP bay 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 characterized. Edgar et al. (1994) 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.

In contrast, the somewhat nearby (San Remo) rhodolith beds (biogenic bed formed by free-living calcified coralline red algae) were found to be dominated by polychaete worms, both in abundance (89% of the total assemblage) and number of morphospecies with family Terebellidae comprising 53% of the annelid community (Harvey & 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 & Bird 2008). In general, biodiversity in rhodolith beds has proven to be remarkably higher than in surrounding habitats (Foster 2001). Consistent with the finding of this current study, the shallow biogenic rhodolith beds in WP display high levels of biodiversity compared to soft sediment communities elsewhere in the bay (Harvey & Bird 2008).

The order Amphipoda were also well represented in the bryozoan reefs with at least 14 different families observed. They are a group that is diverse throughout WP, which is suggestive that they may have undergone adaptive radiation despite WP only being formed approximately 10,000 years ago; a relatively short period in terms of evolutionary processes (Shapiro 1975; Barnard & Drummond 1978). Small crustaceans, such as amphipods, which made up approximately 70% of the total abundance of invertebrates collected from the reefs, are important dietary items for many demersal (bottom-dwelling) fish (Edgar & Shaw, 1995b) and other taxa. Analysis of gut contents of 91 fish species from WP by Edgar & 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 ingesting amphipods in particular. Therefore, the bryozoan reefs represent areas of enhanced prey abundance for fish species preferentially targeting crustacea. This concept is re-visited in depth in Chapter 3. of this thesis that focuses on the seasonal fluctuations in invertebrate diversity.

It was noted by Probert et al. (1979) on the Otago shelf and more recently by Fathom Pacific (2020) in the WP 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. As expected, the epifaunal assemblage found in the WP bryozoan matrix was more diverse than the surrounding sediment and *C. cactoides* bed, even at the level of phylum. Many motile taxa observed here are not strictly infaunal or epifaunal within a phylum (e.g., annelids, crustaceans, and molluscs), however, the absence of sessile sponges, ascidians, and brachiopods in the neighbouring habitats that were observed in the bryozoan matrix demonstrates that the reefs provide attachment opportunities not otherwise available. 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. Often what was collected in the cylinder was a few small heads and these were counted as a single colony (1 individual). The Western Port Bryozoan Reefs Research Project examined the larger epifauna on the reef using exploratory ROV footage from December 2017, and underwater imagery still photographs from diver exploration surveys between February 2018 – January 2020 (Fathom Pacific 2020). *Sycozoa cerebriformis* was in the top five most

abundant species detected and this is evident in photographs of the reef and from hand samples taken during field sampling for the present study. Our counts, therefore, may underestimate the occurrence of this species.

The mud oyster (*O. angasi*) occurred frequently in the bryozoan matrix and appears to be associated mainly with *C. foliata*. The WP dredge fishery began targeting oysters in the bay (and in the location of the bryozoan reefs) from the 1820's but it was overfished and eventually closed in the 1920's (Hannan & Bennett 2010). The occurrence of mud oysters in the WP bryozoan reefs adds to the habitat-forming structure and conservation significance of the biotope (Flynn et al. 2019). Additionally, mud oysters might play an important role in providing suitable substrate for the settlement of bryozoan larvae and the establishment of new colonies.

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. The *non-metric* MDS configuration based on square root transformed Bray-Curtis dis/similarities of assemblages demonstrated through relatively tight clustering that the *Triphyllozoons* have similar invertebrate compositions while some of the *C. foliata* samples were unique. It also shows how markedly different the bryozoan matrix assemblage is to both the *C. cactoides* and sediment habitats. Notwithstanding the morphological differences between the fragile, fenestrate bryozoans (*T. munitum* and *T. moniliferum*) and the more robust, plated *C. foliata*, there was no difference in the mean abundance or mean taxon richness observed between

these species. However, Wood (2005) reported that the distribution of macroinvertebrates differs depending on the form that habitat-forming bryozoans take (e.g., fenestrate, dendroid, encrusting, plated, and foliaceous) (McKinney & 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 protection (Wood 2005). It is unsurprising then that the differences between bryozoan assemblages in this study were not related to mean counts but rather to the distinct macrofauna assemblages of the two genera, illustrated by the Venn diagram. *Celleporaria foliata* only contributes to approximately 5% of the bryozoan cover in the reefs in comparison to the dense coverage (~95%) of the *Triphyllozoons* (Fathom Pacific 2020). Despite this, the plate-like, solid colonies appear to provide opportunities to a larger range of unique taxa than the other genera (see Table 2). Interestingly, during the initial sorting process there was a visually high presence of Eunice worms in *C. foliata* compared to other bryozoan species and neighbouring habitats. The abundance of Eunicids in *C. foliata* (292) in comparison to the *Triphyllozoons* (11) indicates possible stochastic effects coupled with aggregating behaviour. Perhaps the folds of *Triphyllozoons* are too tight for them to move about, especially given the more tightly folded *T. moniliferum* contained only two individuals. No information on associations between bryozoans and Eunicid worms is available. However, a study that quantified interactions between *Eunice norvegica* and cold-water coral species *Lophelia pertusa*, discovered reef aggregating behaviour by the polychaete as well as aggressive territorial behaviour that could protect the coral from predation (Mueller et al. 2013). Further research on the ecological processes of the reefs is needed to ascertain the role that these carnivorous polychaetes play.

Given DNA analysis was not possible in this study and the majority of morphospecies are only identified to family level, it is unknown if any of them are vulnerable. For instance, *Amphiura triscacantha*, a brittle star, listed as threatened under the *Flora and Fauna Guarantee Act (1988)*, has only been observed in Victorian waters in northern WP and Corner Inlet (Butler & Bird 2010). Two brittle star individuals from family Amphiuridae were collected from *C. foliata* samples in the present study. Further identification of these specimens will reveal whether they are individuals from this elusive species.

Other WP habitats

A review by Chidgey et al. (2009) stated that the current understanding of the ecological assets of WP is decades old and that there is little contemporary information on WP ecosystem processes or marine community characteristics. Although the faunal biodiversity of Western Port has been studied for 50+ years, there are many habitats that have not yet been explored. Those that have been are likely to have undergone ecological changes since and there are few studies that have used comparable sampling methods to the present study. It would be ideal to compare the quantitative data collected from the bryozoan reefs to data sets from other WP biodiversity studies; however, sampling methods vary from trawls to diver surveys, with varying sampling efforts, rendering any comparisons unvaluable for the most part. The presence/absence table used in this report simply visually represents the top twenty most abundant species observed in each habitat (except for the rhodolith study where only the annelids observed are listed).

822 This detailed study of the macrofauna biodiversity associated with the newly discovered
823 Western Port biogenic bryozoan reefs have shown that:

- 824 1) They harbour a highly diverse community of macrofauna,
- 825 2) They have significantly high species richness and abundance compared to immediately
826 neighbouring habitats,
- 827 3) These results are consistent with the only other known biogenic habitat in Westernport
828 (the closely situated rhodolith bed)
- 829 4) These results are consistent with a patchy thicket-like bryozoan-dominated habitat on
830 the Otago Shelf, New Zealand (known hotpots for biodiversity), and
- 831 5) More research is required to better understand the complexity of these reefs and provide
832 recommendations on future management or protection.

4 SEASONAL FLUCTUATIONS IN THE INVERTEBRATE BIODIVERSITY AND ABUNDANCE ASSOCIATED WITH THE BRYOZOAN REEFS

Introduction

Shallow marine systems are among the most valuable ecosystems on earth (Constanza et al. 1997), supporting commercial and recreational fisheries around the world by providing a wide range of fish species with spawning habitat (Gray & Miskiewicz 2000; Hamer & Jenkins 2004), food (Begg & Hopper 1997; Jenkins et al. 2013), and nursery grounds (Jenkins et al. 2013; Sheaves et al. 2015). However, due to their location, they are susceptible to environmental changes and are among the most threatened systems (Elliott et al. 2014). Loss or disruption of food web connectivity and densities or composition of assemblages can lead to population collapse and have a cascade effect across trophic levels (Pinnegar et al. 2000; Altieri et al. 2012). Consequently, fish stocks may decline even when fisheries and the key habitats supporting them are well managed (Bostrom et al. 2011; Glaser et al. 2014). The study of temporal changes and fluctuations (seasonal and annual) in populations of invertebrate assemblages help our understanding of ecosystem processes and how biodiversity can be maintained or restored (Barrow & Parr 2008; Weeks & Holtzer 2000).

Seasonality in benthic assemblages depends largely on environmental fluctuations, which can influence community structure from population to ecosystem level (Officer & Parry 1996; Akin et al. 2003; Zhang et al. 2015). In cold temperate waters, food abundance is generally low during the winter because of the inhibition of phytoplankton growth affecting all trophic levels (Coma et al. 2000). Consequently, temperature and food availability are

positively correlated in these ecosystems (Coma et al. 2000). Ectothermic fish and invertebrates in shallow benthic systems are subject to, and rely on, seasonal variations in temperature, photoperiod (changes in light intensity and day length), and food availability to determine their metabolic demands (Ward & Stanford 1982; Brockington & Clarke 2001). Seasonal temperature changes trigger life-history events in many marine organisms (Ward & Stanford 1982). For many species, co-ordination of spawning in a population is maintained by these fundamental environmental cues. In some species, or in some environments, one cue may have a dominant role in this coordination. For example, *Eunice viridis* (Samoan palolo polychaete worm) rely on lunar periodicity (Caspers 1984), whilst salmonids (salmon, trout, graylings and freshwater whitefishes) are thought to depend on photoperiod alone to trigger reproductive behaviours (Pankhurst & Porter 2003). Pheromone induced coordinated spawning has also been observed in a variety of invertebrates, such as the rag worms *Nereid succinea* and *Platynereis dumerilii* (Zeeck et al. 1998) and sea slug *Aplysia* spp. (Painter et al. 1998). Interestingly, it has been demonstrated that some species spawn in response to other species from the same phylum, like synchronous coral spawning (Babcock et al. 1986; Starr et al. 1990; Hardege et al. 1998) or different phyla, as demonstrated by herring and Nereididae (polychaete worms) spawning (Watson et al. 2003). Additionally, a study of the zooplankton in Western Port (WP) and Port Phillip Bay (PPB) by Kimmerer & McKinnon (1985) suggested that the abundance of many of the zooplankton species observed showed a strongly seasonal pattern with abundance at its highest in summer and lowest throughout autumn and winter. Phytoplankton, and in turn, zooplankton, are thought to trigger and co-ordinate spawning in fish populations (Brander 1994; Chambers & Trippel 1997), and invertebrates (Starr et al. 1990). Given that a primary source of food for larval stages of fish and marine invertebrates is plankton, it is understandable that they spawn or release broods in waters rich with this

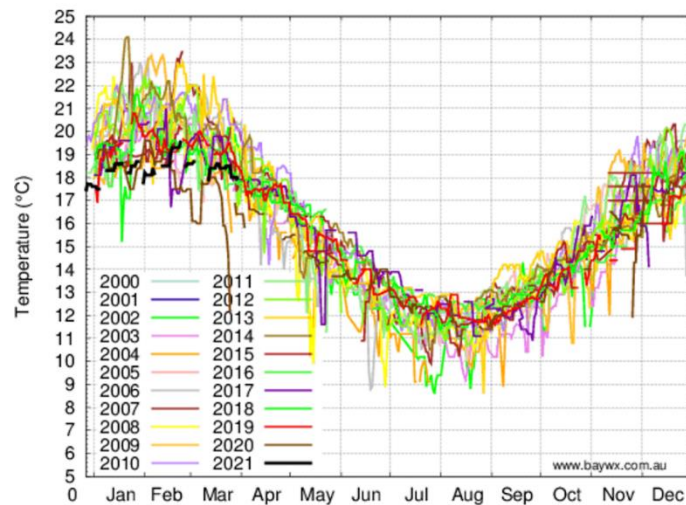
food source. Since larvae are subject to predation, fast growth and development is critical to reduce that risk and this is dependent primarily on the amount of food available (Cushing & Horwood 1994; Watson et al. 2003).

Western Port environment

Embayments support high biomasses of juvenile fauna across a range of phyla that use them for critical growth and development (Fodrie & Herzka 2008). Those juveniles and other small benthic invertebrates often become prey components of predatory fish that migrate inshore to spawn and to access prey-rich coastal areas (Barnett & Semmens 2012). The findings from Chapter 3 indicate that the WP bryozoan reefs support a diverse and abundant assemblage of small prey items. Environmental fluctuations (such as temperature, day length, and salinity) within the bay influence the behaviours of a variety of fauna associated with the bay; many of which only spend part of their lives there or use different parts of the bay during different stages of their life (Hindell & Jenkins 2004). Movements of populations reflects both evolutionary and ecological responses to environmental heterogeneity (Levin 1984).

February is the warmest month with the 10-year average surface temperature at 20.1 °C (min = 18.2 °C, max = 22.8 °C), while August is the coldest at 11.8 °C (min = 10.6 °C, max = 13.4 °C) (Figure 11).

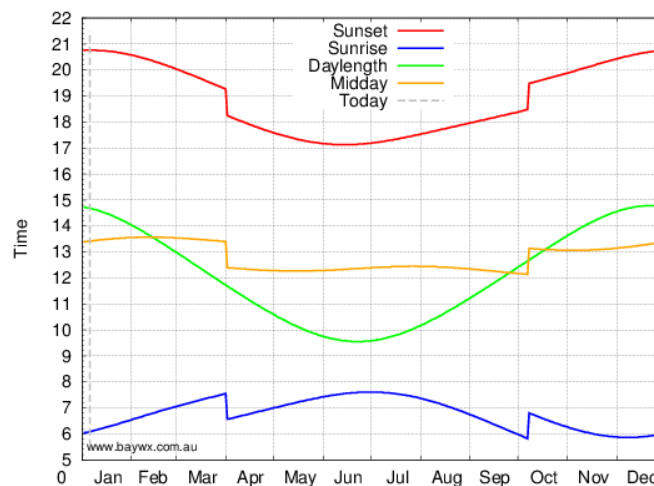
902



903 **Figure 11.** Western Port ocean sea surface temperature from 2000 – present. Sourced from
 904 www.baywx.com.au.

905 Average day length (sunrise to sunset) is lowest in winter (9h 13m) and jumps considerably
 906 by spring (12h 02m) and summer (13h 21m), and then drops again by Autumn (10h 16m)
 907 (Figure 12).

908



909 **Figure 12.** Melbourne 2018 sunrise, sunset, day length and midday. Sourced from
 910 www.baywx.com.au

Sediment load from erosion of the Upper North Arm basin is transported to, and deposited in, the Rhyll and Corinella basins via a net clockwise direction of water flow within the bay (Hancock et al. 2001; Counihan et al. 2003), resulting in high turbidity at the bryozoan reef site. Turbidity can decrease the overall transmittance of light (McFarland 1986) and therefore may impact on the light intensity that the bryozoan reef community encounter. This may indicate that the fauna associated with the reefs does not exhibit photoperiod spawning responses and instead rely on different cues, however, no information on light intensity within the bay could be located and no known studies on invertebrate spawning in the area have been undertaken.

Important fish in Western Port

Most demersal fish species have distinct spawning periods resulting in seasonal patterns of juvenile recruitment and, therefore, seasonal fluctuations in fish community structure (Jenkins et al. 1997). Edgar and Shaw (1995a) observed a strong seasonal pattern in fish abundance in WP with the highest levels in summer and a gradual decline through autumn and winter.

Western Port supports the second largest fishery in Victoria, which in the last 30 years, has seen a large increase in anglers targeting the recreationally and commercially important King George Whiting (*Sillaginodes punctatus*), snapper (*Pagrus auratus*), and gummy shark (*Mustelus antarcticus*). *Pagrus auratus* is a long-lived demersal species found in bays, estuaries, and coastal waters in NZ, Japan, and southern Australia (Tabata and Taniguchi 2000). Studies have indicated that spawning behaviour and egg development are prompted when ambient temperatures exceed 18 °C (Coutin et al. 2003; Fielder & Allan 2003). *Pagrus auratus* typically spawn within large, sheltered bays during seasonal spawning aggregation

events (Fowler & Jennings 2003). Western Port does not appear to be a nursery area for *P. auratus* (Hamer & Jenkins 2004). It appears that *P. auratus* migrates into WP bay after spawning in PPB (Hamer et al. 2011). The larval stages are usually pelagic for up to 4 weeks (Fowler & Jennings 2003) until settlement in the sheltered bay when they reach approximately 12 mm length (Kingsford & Atkinson 1994). *Sillaginodes punctatus* spawn off-shore in winter causing a decline in biomass within the bay, and then enter WP as post-larvae at approximately 3 - 5 months old and 15 – 20 mm in length (Jenkins et al. 2020). They leave the bay for coastal waters at around four years of age (Hamer & Jenkins 2004). Jenkins et al. (2020) estimated hatching dates using otolith microstructure and found that dates ranged from early May to July, with a mean larval duration of 128 days, resulting in the mean arrival date of larvae in WP on October 7 (spring). *Mustelus antarcticus* is very common in the Rhyll segment of WP (Edgar & Shaw 1995a), particularly juveniles, indicating that it is a pupping area (Stevens & West 1997). They have litters during the summer months after an 11 – 12 month gestational period (Walker 2007).

Chapter 3 demonstrated that crustaceans and annelids dominate the bryozoan reef invertebrate macrofauna assemblages. They are important in the marine benthos for numerous reasons, the biggest being contributions to trophic webs (Edgar & Shaw 1995a, 1995b). Gut contents of 91 species of fish in WP revealed most fish fed on crustaceans, with 25% of species feeding on polychaetes (Edgar & Shaw, 1995a, 1995b). Parry et al. (1995) found that crustaceans were also the most abundant prey of snapper in PPB, along with annelids, molluscs, and other fishes. However, there is the potential for a skewing towards taxa that have harder body parts over those that do not (e.g., polychaete worms), particularly if not consumed recently.

It appears that most demersal fishes that reside in the bay are opportunistic feeders rather than specialised feeders (Jenkins et al. 2020). For instance, Robertson (1977) reported that in November, the main food source of juvenile whiting in WP was almost entirely comprised of copepods, gammarid amphipods, and Mysidacea (shrimp-like crustaceans). By December, its major prey items had shifted to the ghost prawn *Callinassa australiensis* as well as the polychaetes *Nephtys australiensis*, *Armandia* sp. and Nereididae spp. This shift is probably correlated with increased body size and mouth gape, as well as spawning times and importantly, the abundance of prey items (Officer & Parry 1996; Karpouzi & Stergiou 2003). Edgar & Shaw (1995a, 1995b) observed an increase in the mortality rate and increase in emigration of fishes occurring concurrently with a decline in crustacean production and cited this as a causal relationship between crustacean production and small fish production. The study found that the production of crustaceans was at its lowest in May (the end of autumn).

Like the demersal fishes associated with WP, seasonal variation in benthic invertebrates is mostly explained by the specific life histories of each species. Many crustaceans undergo strong seasonal periodicity demonstrated by low abundances during the cooler months (Kreiling et al. 2020) and surges in abundances as the ambient water temperature starts to warm (Guerra-García et al. 2011). High fecundity and fast development are features of species with a high risk of mortality (Johnson et al. 2001). Nelson (1980) showed that in Amphipoda, the smaller infaunal haustoriids have a greater brood volume, and therefore greater fecundity, than the larger epifaunal gammarids and ampeliscids. Van Dolah & Bird (1980) argue that short incubation times of small prey species increases the odds of the females surviving to release broods. Annelids respond to environmental cues, such as changes in temperature and day length, by coordinating spawning events and development

of gametes, resulting in all individuals within a population spawning simultaneously (Olive 1984). Some species have sensory structures on their anterior ends that stimulate the endocrine system to produce hormones when they sense changes (Olive 1984).

Aim of this study

Estimates of biodiversity and monitoring of changes over long periods of time require the consideration of seasonal fluctuations and variability. If a snapshot of biodiversity was taken from a single timepoint, it would not be a true reflection of biodiversity (either under or overestimating biodiversity and abundance on a yearly scale). Understanding seasonal patterns of invertebrate biodiversity in an ecosystem allows for good planning around experimental research and taxon-specific surveys, especially when resources are limited. In regard to elucidating the role of the bryozoan reefs in supporting important Victorian fisheries, the current project aims to provide an understanding of seasonal fluctuations in invertebrate fauna in WP. The macrofauna within the matrix of the bryozoan reefs was examined by collecting samples from three dominant bryozoan species across four consecutive seasons. Specifically, the aim was to detect any seasonal fluctuations in species richness and/or abundance of invertebrates in the bryozoan matrix. It was hypothesised that there would be fluctuations in both species richness and abundance across seasons, with a noticeable peak in spring

Results

In total, 35 bryozoan samples were collected: 9 in autumn, winter, and summer as planned, and 8 in spring as one of the samples was lost when the cylinder opened upon resurfacing. The fewest number of morphospecies in a single sample was observed in autumn (11) and the highest number of morphospecies was observed in a spring sample (47). In winter there

1011 was a sample with a mere 28 individuals, while the densest sample, in spring, contained
1012 923. The occurrence and abundance of morphospecies observed each season are listed in
1013 Table 4.

1014
1015
1016

Table 4. Occurrence and abundance of macroinvertebrate taxa ≥ 0.5 mm in the bryozoan reef matrix in Western Port across four consecutive seasons in 2019 – 2020. The numbers in brackets represent the number of morphospecies. Morphospecies unique to a habitat are denoted by a ^.

	Taxon	Autumn	Winter	Spring	Summer
Annelida					
Ampharetidae	<i>Melinninas</i> sp.	1^			
Capitellidae	Capitellidae spp. (2)	2		42^	
Cirratulidae	Cirratulidae sp.			3	1
Eunicidae	Eunicidae spp. (2)	1	28	3	3^
	<i>Eunice</i> spp. (3)	66	92	27	76
	<i>Lysidice</i> sp.	3^			
Flabelligeridae	<i>Pherusa</i> sp.	25	25	117	19
Glyceridae	Glyceridae sp.			1^	
Goniadidae	Goniadidae sp.		3	1	1
Lumbrineridae	Lumbrineridae spp. (3)	2	28	35^	15
Nephtyidae	Nephtyidae sp.			1^	
Nereididae	Nereididae spp. (6)	14^	39	34	15^
	<i>Australonereis</i> sp.			10^	
	<i>Simplisetia</i> sp.	6		19	2
Opheliidae	<i>Armandia</i> sp.	41	62	52	2
Orbiniidae	Orbiniidae sp.	1		1	2
Phyllodocida	Phyllodocida			1^	
Polynoidae	Polynoidae spp. (4)	2	2^	15^	10
Sigalionidae	Sigalionidae sp.		1^		
Syllidae	Syllidae spp. (3)	27	34	232^	42
Terebellidae	Terebellidae sp.			1^	
Trichobranchidae	Trichobranchidae spp. (2)	5	2	15	4^
Brachiopoda					
Terebratulidae	<i>Magellania flavescens</i>	12	2		12
Crustacea					
Alpheidae	Alpheidae spp. (2)		1^	2	1
	<i>Alpheus</i> spp. (2)	3^			1^
	<i>Alpheus villosus</i>		1^		
	<i>Alpheus astrinx</i>	1			1
	<i>Synalpheus tumidomanus</i>	38	40	83	41
Amaryllididae	Amaryllididae spp. (5)			31^^	7^
	<i>Amaryllis</i> sp.	1^			
Ampeliscidae	Ampeliscidae sp.		1^		
Amphilocidae	Amphilocidae spp. (3)		4	1	6
Amphipoda	Amphipoda		2^		
Anthuriidae	Anthuriidae sp.	5	20	3	7
	<i>Mesanthura</i> sp.				1^
Bodotriidae	Bodotriidae sp.	14	12	25	18
Callianassidae	Callianassidae spp. (2)	1		2^	
Caprellidae	Caprellidae sp.			17^	
Colomastigidae	Colomastigidae sp.			5	4
	<i>Colomastix</i> sp.		2	27	5
Corophiidae	Corophiidae spp. (2)	327	235	506	126
	<i>Monocorophium insidiosum</i>		6	15	7
	<i>Xenoecheira fasciata</i>	54	33	19	28
Cyclopidae	Cyclopidae sp.				2^

Table 4 continued.

	Taxon	Autumn	Winter	Spring	Summer
Cylindroleberididae	Cylindroleberididae sp.			7	3
Galatheidae	Galatheidae spp. (3)			5^^	1^
	<i>Galathea australiensis</i>	1	2		
Hyperiididae	Hyperiididae sp.			5^	
Imphimediidae	Imphimediidae sp.	3	7	23	6
Joeropsidae	Joeropsidae sp.	23	21	72	41
Leucothoidae	Leucothoidae sp.		4	27	14
Liljebergiidae	Liljebergiidae sp.	19	52	6	12
Lysianassidae	Lysianassidae sp.		3	7	1
Maeridae	Maeridae sp.	1	3	4	19
Munididae	Munididae sp.		2		2
Mysidae	Mysidae sp.	60	58	94	107
Paranebaliidae	Paranebaliidae sp.			10^	
	<i>Levinebalia</i> sp.	2	2	61	2
	<i>Paranebalia tiparra</i>	109	210	348	134
Paranthuridae	Paranthuridae sp.	3	1		19
Phoxocephalidae	Phoxocephalidae spp. (5)		3^	28^^	7^
	<i>Birubius</i> sp.	5	12	7	39
	<i>Brolgus tattersali</i>	20	53	54	144
	<i>Heteropilumnus fimbriatus</i>		2	2	1
Pilumnidae	<i>Pilumnus serratifrons</i>	23	16	20	19
Podoceridae	Podoceridae spp. (2)			12	3
Portunidae	Portunidae sp.			2	3
Tanaidacea	Tanaidacea	85	108	83	256
	Apseudidae sp.	107	262	595	264
Echinodermata					
Amphiuridae	Amphiuridae sp.		1		2
Cidaridae	Cidaridae sp.			1^	
Mollusca					
Acanthochitonidae	Acanthochitonidae spp. (2)		2	2	2
Arcidae	Arcidae sp.				1^
	<i>Anadara trapezia</i>			2	5
	<i>Barbatia pistachia</i>	42	40	41	38
	<i>Cacozeliana granaria</i>	5^			
Cerithiidae	Cerithiidae sp.			4	1
Hiatellidae	Hiatellidae sp.			2	2
Nassariidae	<i>Nassarius</i> sp.		2	33	19
Ostreidae	<i>Ostrea angasi</i>	16	23		
Pectinidae	<i>Pecten fumatus</i>		1^		
Tellinidae	Tellinidae sp.	4	6	1	6
	<i>Macomona deltoidalis</i>	1	12		1
Tunicata					
Ascidacea	Ascidacea	2	1		
Didemnidae	<i>Didemnum</i> sp.			2	2
Holozoidae	<i>Sycozoa cerebriformis</i>	2	3	5	5
Pyuridae	<i>Pyura stolonifera</i>	55	76	36	69
Other					
Golfingiida	Golfingiida sp.		3	1	1
Damaged polychaete					3^
Hydrozoa	Hydrozoa	1^			
Pantopoda	Pantopoda			1^	
Porifera	Porifera	1	3		
TOTAL		1243	1669	2949	1713

The number of morphospecies observed each season was compared using one-way ANOVA and pairwise comparisons (Appendix 4.1). There was a significant difference among seasons ($F = 10.755$, $df = 34$, $p = <0.001$) with spring being more species rich than autumn ($p = <0.001$), winter ($p = 0.001$), and summer ($p = 0.004$) (Figure 13). Given that there was a large range in the number of morphospecies in the spring samples, a two-way ANOVA confirmed that this was not explained by habitat type.

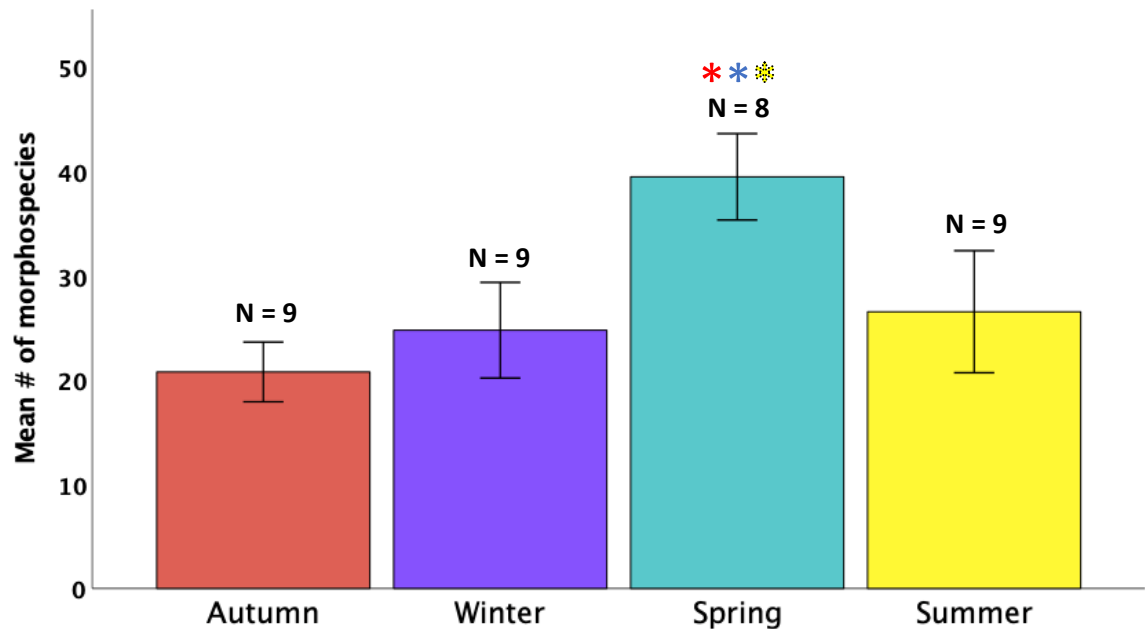


Figure 13. Mean number of morphospecies per sample across seasons. Red asterisk = significantly higher than autumn. Blue asterisk = significantly higher than winter. Yellow asterisk = significantly higher than summer. Error bars represent ± 1 standard error.

The number of morphospecies from the three most dominant phyla (crustaceans, annelids, and molluscs) were compared across seasons using one-way ANOVA and pairwise comparisons (Appendix 4.2, 4.3, 4.4). There was a significant difference in crustacean species richness across the seasons ($F = 12.159$, $df = 34$, $p = <0.001$). The number of morphospecies was significantly higher in spring than in autumn ($p = <0.001$), winter ($p =$

0.001), and summer ($p = 0.008$). The number of annelid morphospecies was also significantly different across seasons ($F = 8.359$, $df = 34$, $p = <0.001$), with higher species richness recorded in spring compared to autumn ($p = 0.001$), winter ($p = 0.004$), and summer ($p = <0.001$) (Figure 14). The number of molluscan morphospecies, however, was not significantly different across seasons ($F = 0.918$, $df = 34$, $p = 0.444$) (Figure 14). All other paired comparisons were not significant.

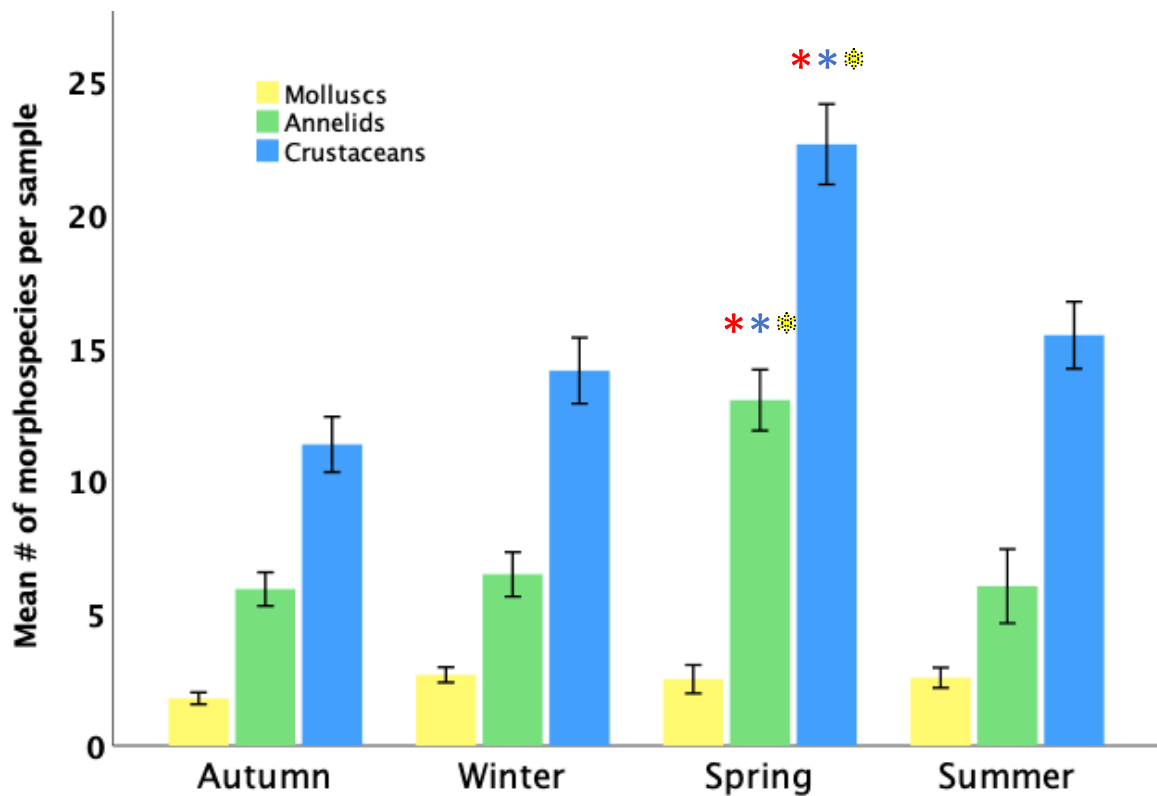


Figure 14. Mean number of morphospecies per sample from the most dominant phyla in the reefs (crustaceans, annelids, and molluscs) across the seasons. Red asterisks = significantly higher than autumn. Blue asterisks = significantly higher than winter. Yellow asterisks = significantly higher than summer. Error bars represent ± 1 standard error.

Thirty-three morphospecies were ubiquitous (appeared in all seasons). Autumn had the fewest number of morphospecies (57) and shared 74% of its assemblage with winter. Summer shared 70% of its assemblage with spring (Figure 15).

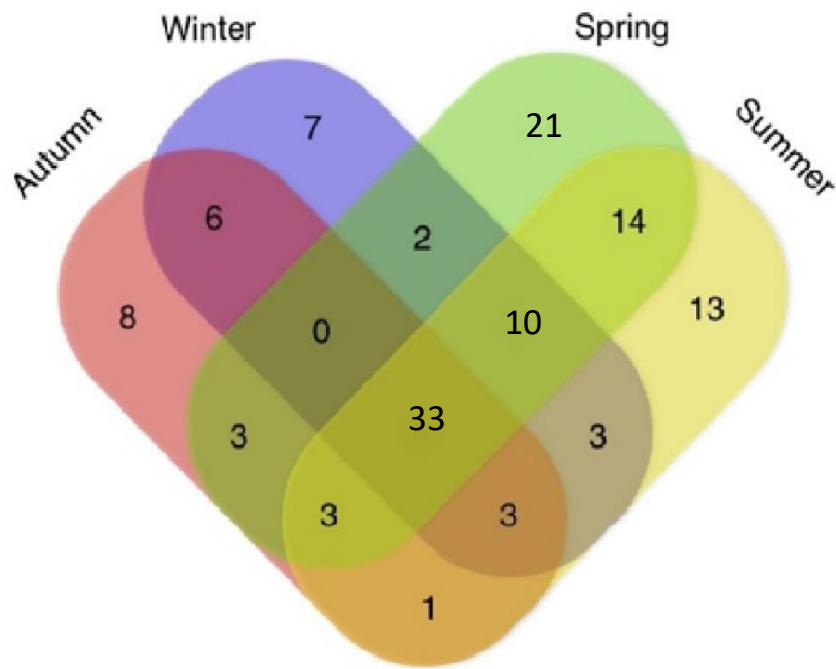


Figure 15. Venn diagram showing the number of unique and shared morphospecies observed each season. The number of unique species present during each season is indicated in the non-overlapping outer segments.

Spring had the most unique assemblage. It had the greatest number of total morphospecies (86) as well as the highest number of unique morphospecies (21) (species that were found in that season only). When considering the number of unique species in autumn (8) as 100% (as it was the first season sampled), the number of unique species surged by almost 270% in spring (Figure 16).

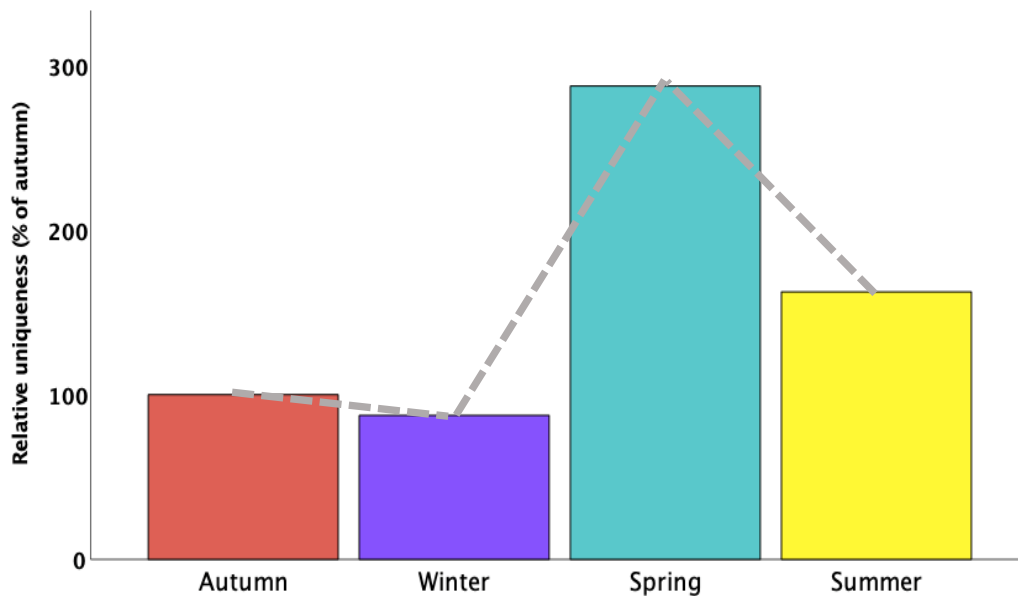


Figure 16. Relative uniqueness of assemblages within each season as a function of the number of unique species found in autumn (100%). Dashed grey line highlights approximately 3-fold change.

The mean abundances of taxa were compared across seasons using one-way ANOVA and pairwise comparisons (Appendix 4.1). Abundance was significantly different across seasons ($F = 3.158$, $df = 34$, $p = 0.038$) with spring having more individuals than autumn ($p = 0.033$), but not winter or summer (Figure 17). Given that there was a large range in abundance values in the spring samples, a two-way ANOVA was used to confirm that could not be explained by habitat type. All other paired comparisons were not significant.

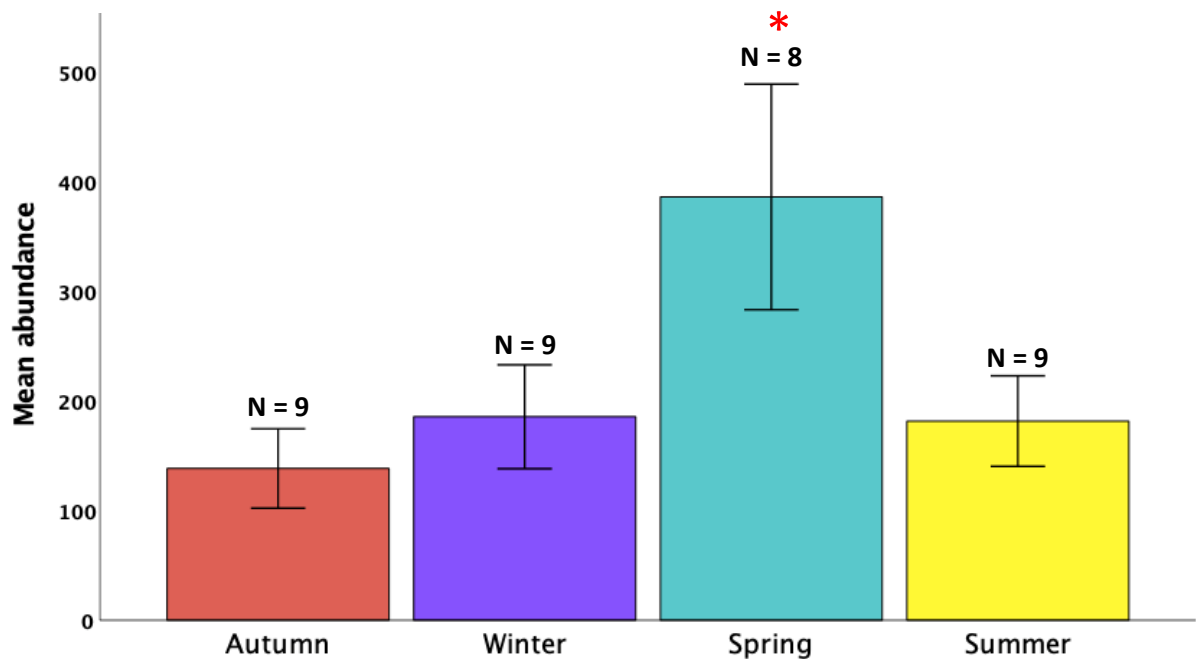
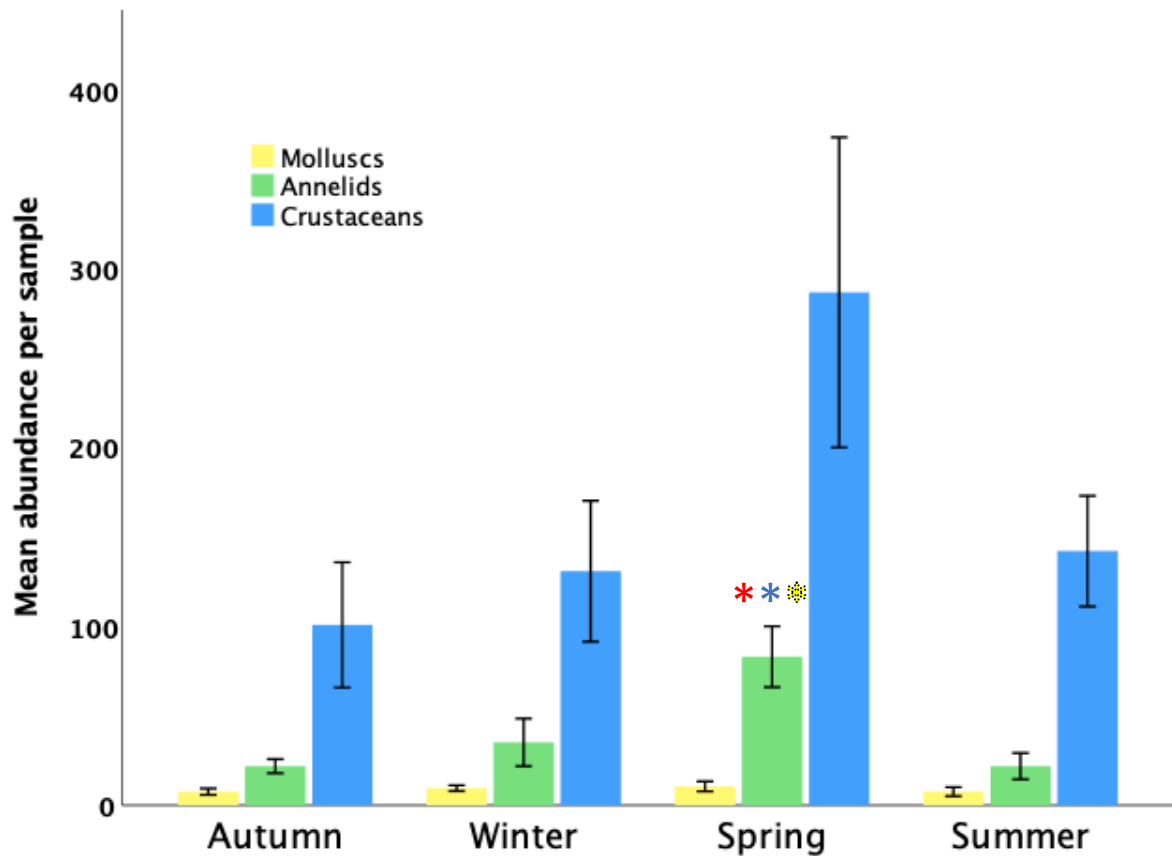


Figure 17. Mean abundance of taxa per sample across seasons. Red asterisk = significantly higher than autumn. Error bars represent ± 1 standard error.

The abundances of taxa from the three most dominant phyla (crustaceans, annelids, and molluscs) were compared across seasons using one-way ANOVA and pairwise comparisons (Appendix 4.2, 4.3, 4.4). There was no difference in crustacean abundance ($F = 2.539$, $df = 34$, $p = 0.075$) or mollusc abundance ($F = 0.4$, $df = 34$, $p = 0.754$) across the seasons. There was a significant difference in annelid abundance across seasons ($F = 7.684$, $df = 34$, $p = <0.001$). Annelid abundance was significantly higher in spring compared to autumn ($p = <0.001$), winter ($p = 0.001$), and summer ($p = 0.008$) (Figure 18). All other paired comparisons were not significant.

1074



1075 **Figure 18.** Mean abundance of taxa per sample from the most dominant phyla in the reefs
1076 (crustaceans, annelids, and molluscs) across the seasons. Red asterisks = significantly higher than
1077 autumn. Blue asterisks = significantly higher than winter. Yellow asterisks = significantly higher
1078 than summer. Error bars represent ± 1 standard error.

1079 The families responsible for differences among seasons were revealed using one-way
1080 ANOVA and pairwise comparisons (Appendix 4.6). Three families (Corophiidae and
1081 Phoxocephalidae- amphipods, and Joeropsidae- isopods) and one order (Tanaidacea) of
1082 crustacean, and four annelid families (Flabelligeridae, Lumbrineridae, Opheliidae, and
1083 Syllidae) explain the differences in abundances across the seasons. The annelid
1084 Flabelligeridae was much more abundant in spring than all other seasons ($F = 15.854$, $df =$
1085 34 , $p = <0.001$). Spring exhibited a greater abundance of Joeropsidae ($p = 0.016$),
1086 Phoxocephalidae ($p = 0.048$), Tanaidacea ($p = 0.016$), Lumbrineridae ($p = <0.001$), and
1087 Syllidae ($p = 0.014$) than autumn, a greater number of Joeropsidae ($p = 0.029$), Tanaidacea

($p = 0.029$) and Syllidae ($p = 0.049$) than winter, and a greater number of Corophiidae ($p = 0.02$), Lumbrineridae ($p = 0.009$), and Opheliidae ($p = <0.001$) compared to summer (Figure 19). All other paired comparisons were not significant.

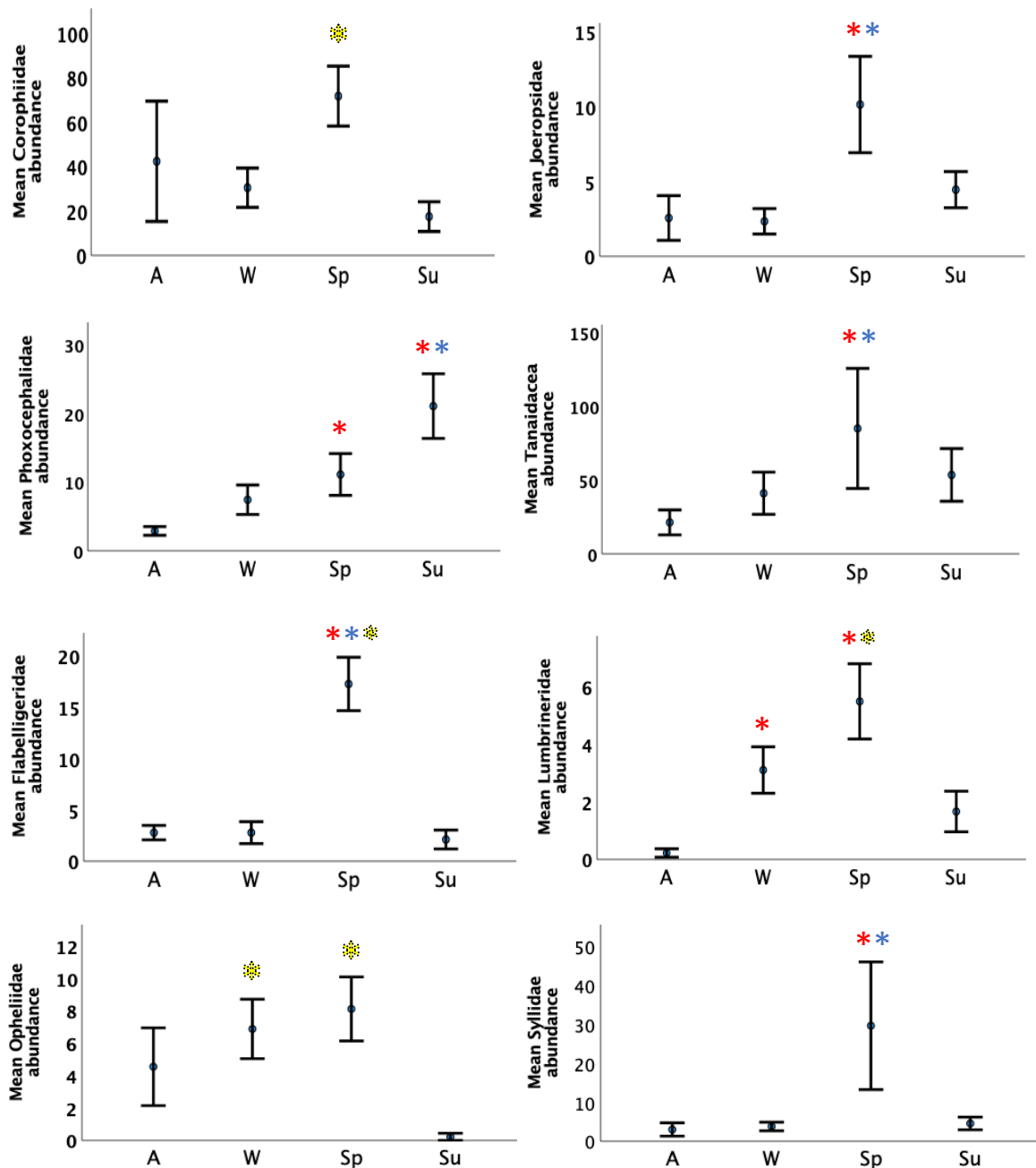


Figure 19. Mean abundance of the crustacean and annelid families responsible for differences across seasons. A = autumn, W = winter, Sp = spring, and Su = summer. Red asterisks = significantly higher than autumn. Blue asterisks = significantly higher than winter. Yellow asterisks = significantly higher than summer. Error bars represent ± 1 standard error.

Discussion

Crustaceans and annelids were not only the most diverse and abundant taxa in the bryozoan reef matrix, but they also explained the fluctuations, particularly the boom in spring, across the four consecutive seasons sampled. Supporting these findings, seasonal fluctuations in species richness and abundance of dominant invertebrate taxa have been demonstrated around the world in temperate marine systems (Watling 1975; Bauer 1985; Beermann 2014; Saulnier et al. 2019). Molluscs showed no significant change to either richness (Figure 14) or abundance (Figure 18). Little fluctuation, however, was expected as the majority were sessile bivalves which are typically long-lived (Montero-Serra et al. 2018).

Spring displayed enhanced crustacean and annelid diversity compared to all other seasons, but only annelid abundance was greater in spring than other seasons. Spring did see a surge in the mean abundance of crustaceans, however, as the range was so high across the spring samples (a minimum of 51 and a maximum of 693 crustaceans), the standard deviation was also very high, resulting in non-significance. By summer, there had been a decrease of 39% of the crustacean abundance observed in spring (2208 individuals).

Spring had the most unique invertebrate assemblage with 17% of the morphospecies observed in that season only. It could be inferred that some of those unique morphospecies have migrated in or experienced reproductive events triggered by the increase in ambient water temperature. The compositions of winter and autumn, and spring and summer, were more similar to each other than any other combination of seasons. This signifies a discrimination in assemblages between warmer and cooler periods. Autumn and winter had relatively few unique species with their assemblages comprised predominantly of ubiquitous morphospecies.

All the crustaceans that had a significantly enhanced abundance in spring belong to the superorder Peracarida (including orders Amphipoda, Isopoda, and Tanaidacea) (WoRMS Editorial Board 2021). Peracarids are among the most abundant and diverse taxa of benthic fauna around the world (Dauby et al. 2001; Lourido et al. 2008) and among the smallest of the benthic macrofauna (Blazewicz-Paszkowycz et al. 2012). They typically live strictly benthic life cycles and have low dispersion rates (Blazewicz-Paszkowycz et al. 2012). A positive relationship between increased temperature and increased abundance of tanaids has been noted (Mendoza 1982; Kneib 1992). Moreover, reproduction in amphipods, isopods and mysids is known to be influenced by increases in temperatures, promoting juvenile growth and sexual maturation (McKenney & Celestial 1995; Focke et al. 2005; Hosono 2011). These small crustaceans are likely the primary food source for juvenile *P. auratus* (among other teleosts), which are known to reside in the bryozoan reef region after migrating in from the spawning site in PPB. Jenkins et al. (2020) analysed data from the Victorian Fisheries Recreational Survey (Ryan & Conron 2019) that was based on interviews with boat-based fishers in WP from 1998 to 2013. Large *P. auratus* were most frequently caught in depths of 7 – 18 m in deep reef habitat where there are habitat-forming bryozoans, sponges, and other sessile invertebrates (Blake et al. 2013). Undersized *P. auratus* were typically caught in shallower water across a range of different habitats and were most abundant in the Rhyll Segment. Australian salmon (*Arripis truttaceus*) (Robertson 1982) as well as *M. antarcticus* likely feed on this crustacean assemblage as well. Additionally, gummy sharks have litters in the Rhyll segment in summer and the juveniles feed on amphipods (Edgar & Shaw 1995a; Stevens & West 1997). The decline in crustacean richness and abundance by the end of summer might be indicative of predation on both adults and larvae alike, as well as the natural die-off of the adults following brooding.

High densities of polychaetes are often attributed to low dispersal ability, a prolonged reproductive season, and a rapid development rate (Glasby 2000). Given that most annelids in temperate benthic habitats display synchronous spawning when ambient temperatures increase (Olive 1984; Wilson 1991), it is reasonable to deduce that not much dispersal had occurred between the beginning of spring when a mass spawning event likely took place, and the end of spring when sampling was undertaken. The annelids that were responsible for an increase in abundance in spring display a range of life history strategies. For example, Lumbrineridae were found to reach reproductive age at ~ 4 years of age and live for ~ 10 years which is among the longest life histories in polychaetes (Glasby 2000), while Syllidae reach reproductive age around 7 months of age and only live for a year and a half (McHugh & Fong 2002). By December, *S. punctatus* are believed to have shifted their diet from small crustaceans to annelids (Robertson 1977), including Opheliidae, which was one of 4 annelid families that contributed to the increase in faunal abundance in spring in this study.

Mean species richness and abundance respectively were almost identical in winter ($\bar{x} = 25, 185$) and summer ($\bar{x} = 27, 181$) which really highlights the surge that occurred in spring ($\bar{x} = 39, 385$). These findings highlight the importance of sampling across seasons to ensure a true measure of biodiversity. It was not possible for the current study to assess biodiversity over multiple years due to time limitations of the Masters candidature, but it is likely that a similar pattern occurs most years when there are no abrupt environmental or weather conditions that may alter it.

Given that the changes in diversity across seasons were explicable by a few annelid and crustacean families that are known to feature in the diet of commercially and recreationally

1169 important fish species in the bay, it can be argued that the WP bryozoan reefs support and
1170 provide for important Victorian fisheries. Conserving, restoring, or replacing lost biogenic
1171 reefs in WP, is therefore considered to be beneficial to maintaining and enhancing
1172 recreational fishing opportunities as well as general biodiversity. It is possible that
1173 detrimental impacts to the bryozoan reefs could result in reduced fish biomass.

5 FUTURE STUDIES AND CONCLUSIONS

Future studies

Identifying the taxa observed in this study to a lower classification using DNA analysis could possibly reveal undescribed or unique species associated with the bryozoan reefs. Additionally, it may also reduce the possibility that the biodiversity of this current study is underestimated. It would then be an easier task to place each morphospecies into a functional guild to further our understanding of how the bryozoan reef community functions as an ecosystem. The present study did attempt this, however, due to the cryptic nature of many of the crustaceans and annelids and the range of feeding habitats among species, DNA analysis is required to positively identify each down to at least genus level to place them into their correct functional guild.

Additionally, highly mobile, and large macrofauna will need to be targeted specifically in an intensive way. Apart from the obvious physical exclusion of large invertebrates and fish from the small corer, poor visibility limits the techniques that can be utilised to accurately record fish biodiversity in the area. Two of the most common methods utilized such as 1) BRUVs (Baited Remote Underwater Vehicles), and 2) fine mesh netting and poisoning of a patch of reef – are either only possible with excellent visibility or not an acceptable option for the purposes of this study. Line fishing is an option but may miss many species owing to restrictions in their diet, size, and competitive exclusion by other species. The more practical approach will be to extensively survey the bryozoan reef with sophisticated bioacoustics sonar at various stages of tide, on multiple days and during all seasons, however this method too also has limitations (size and burrowing species). This would be a large undertaking in itself and beyond the scope of this current project.

The most comprehensive study on the diets of fish in WP was 25 years ago by Edgar and Shaw (1995a, 1995b). To fully understand and appreciate the extent of support that the bryozoan reefs currently provide to important fish species within the bay, it would be helpful to undertake a gut analysis of the three key fisheries species (*P. auratus*, *S. punctatus*, and *M. antarcticus*) in the Rhyll segment of WP.

This study is a discrete unit contributing to a much larger over-arching project and sought to establish the reefs' conservation value to support potential listing of the bryozoan community under the *Flora and Fauna Guarantee (FFG) Act*. In the near future aspects of its conservation value will become clearer by 1) identifying associated taxa to lower classification to potentially reveal unique species, 2) placing species into functional guilds to examine ecosystem function of the reef, 3) surveying associated large macrofauna (i.e. fish), 5) comprehensively mapping the extent of the reefs in fine scale using bioacoustics sonar, 6) identifying and assessing potential threats, and 7) educating and creating partnerships with the various stakeholders.

Conclusions

This study of the biodiversity associated with the recently discovered WP bryozoan biogenic reefs demonstrates a wide range of taxa rely on these reefs. After 30 years of protection, the bryozoan reefs on the Otago Shelf have not recovered from the damage sustained from oyster dredging and the WP bryozoan reefs may also be under threat from anthropogenic activities. Understanding the role of these reef communities in ecosystems is essential for making informed management and conservation decisions. The results of this study will provide crucial knowledge about their associated biodiversity and contribute to future studies that will highlight their significance and possible future protection (i.e. either spatial or temporal restrictions). There are, however, still many unanswered questions that need to

1225 be addressed to establish the full extent of the conservation value of these unique reefs and
1226 to prevent these reefs from suffering the same fate as those of the Otago Shelf.

1227

1228 Future research is needed to determine their full extent, any co-occurring biodiversity, and
1229 elucidate the threatening processes of the WP bryozoan reefs, as they are expected to be
1230 ecologically important. There are no other known occurrences of *Triphyllozoon*-dominant
1231 biogenic bryozoan reefs of this kind in the world and it is therefore likely that they are
1232 globally significant and requiring protection of some kind. Virtually nothing is known about
1233 this newly discovered biotope and it could be lost if its significance is not understood or
1234 highlighted, and appropriate protection is not considered.

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APPENDICES

1698 Appendix 1. Occurrence and abundance of macroinvertebrates taxa ≥ 0.5 mm found in
1699 fine silt sediment immediately between rows of bryozoan reef mounds in Western Port.
1700 Three samples of sediment were taken in May 2019.
1701

Family		Proximal sediment
Annelida		
Capitellidae	Capitellidae sp.	1
Orbiniidae	Orbiniidae sp.	2
Sigalionidae	Sigalionidae sp.	2
Trichobranchidae	Trichobranchidae sp.	8
Cnidaria		
Hydrozoa		1
Crustacea		
Bodotriidae	Bodotriidae sp.	1
Callianassidae	Callianassidae sp.	3
Phoxocephalidae	Phoxocephalidae sp.	3
Mollusca		
Carditidae	Carditidae sp.	1
Nassariidae	Nassariidae sp.	2
Tellinidae	Tellinidae sp.	3
Veneridae	Veneridae sp.	1
Total		28

Appendix 2. Number of morphospecies identified to each taxonomic level. The numbers in brackets represent the percentage of morphospecies it represents in that phyla.

Taxonomic level	Species	Genus	Family	Higher level	No.species
Annelida	0 (0)	10 (22)	31 (67)	5 (11)	46
Crustacea	13 (18)	10 (14)	48 (65)	3 (4)	74
Mollusca	7 (33)	5 (24)	9 (43)	0 (0)	21
Tunicata	2 (67)	1 (33)	0 (0)	0 (0)	3
Other	1 (14)	0 (0)	2 (29)	4 (57)	7
Total	23 (15)	26 (17)	90 (60)	12 (8)	151

Appendix 3.

Appendix 3.1. Statistical results of the one-way ANOVA used to test the difference between the mean number of species sampled in the bryozoan matrix and neighbouring sediment and *C. cactoides* habitats. Tukey's post hoc comparisons were used for pairwise comparison. Significant results are given in bold.

1710
1711

Mean no. species	F	df	P
Between all habitats	30.743	89	<0.001
Between bryozoan species	1.057	34	0.359
Pairwise comparisons			
Pooled bryozoans vs sediment			<0.001
Pooled bryozoans vs <i>C. cactoides</i>			<0.001
Subset 1 vs sediment			<0.001
Subset 2 vs sediment			<0.001
Subset 3 vs sediment			<0.001
Subset 1 vs <i>C. cactoides</i>			<0.001
Subset 2 vs <i>C. cactoides</i>			<0.001
Subset 3 vs <i>C. cactoides</i>			<0.001
<i>C. foliata</i> vs <i>T. munitum</i>			0.876
<i>C. foliata</i> vs <i>T. moniliferum</i>			0.341
<i>T. munitum</i> vs <i>T. moniliferum</i>			0.588

1712 Appendix 3.2. Statistical results of the one-way ANOVA used to test the difference between
1713 the mean abundance of taxa sampled in the bryozoan matrix and neighbouring sediment and
1714 *C. cactoides* habitats. Tukey's post hoc comparisons were used for pairwise comparison.
1715 Significant results are given in bold.
1716

Mean abundance of taxa	F	df	P
Between habitats	10.688	89	<0.001
Between bryozoan species	0.77	34	0.838
Pairwise comparisons			
Pooled bryozoans vs sediment			<0.001
Pooled bryozoans vs <i>C. cactoides</i>			<0.001
Subset 1 vs sediment			<0.001
Subset 2 vs sediment			0.014
Subset 3 vs sediment			<0.001
Subset 1 vs <i>C. cactoides</i>			<0.001
Subset 2 vs <i>C. cactoides</i>			0.006
Subset 3 vs <i>C. cactoides</i>			<0.001
<i>C. foliata</i> vs <i>T. munitum</i>			0.851
<i>C. foliata</i> vs <i>T. moniliferum</i>			0.997
<i>T. munitum</i> vs <i>T. moniliferum</i>			0.887

1717 Appendix 3.3. Statistical results of one-way ANOVA's used to test the difference between
1718 the mean no. of species and mean abundance of the most dominant phyla (crustaceans,
1719 annelids, and molluscs) sampled in the bryozoan matrix and neighbouring sediment and *C.*
1720 *cactoides* habitats. Tukey's post hoc comparisons were used for pairwise comparison.
1721 Significant results are given in bold.

Crustaceans - Mean no. species	F	df	P
Between habitats	14.962	89	<0.001
Between bryozoan species	0.304	34	0.74
Pairwise comparisons			
Pooled bryozoans vs sediment			<0.001
Pooled bryozoans vs <i>C. cactoides</i>			<0.001
Subset 1 vs sediment			<0.001
Subset 2 vs sediment			0.001
Subset 3 vs sediment			<0.001
Subset 1 vs <i>C. cactoides</i>			<0.001
Subset 2 vs <i>C. cactoides</i>			<0.001
Subset 3 vs <i>C. cactoides</i>			<0.001
Crustaceans - abundance			
Between habitats	17.294	89	<0.001
Between bryozoan species	0.403	34	0.672
Pairwise comparisons			
Pooled bryozoans vs sediment			<0.001
Pooled bryozoans vs <i>C. cactoides</i>			<0.001
Subset 1 vs sediment			<0.001
Subset 2 vs sediment			<0.001
Subset 3 vs sediment			<0.001
Subset 1 vs <i>C. cactoides</i>			<0.001
Subset 2 vs <i>C. cactoides</i>			<0.001
Subset 3 vs <i>C. cactoides</i>			<0.001
Annelids - Mean no. species			
Between habitats	6.564	89	<0.001
Between bryozoan species	3.994	34	0.028
Pairwise comparisons			
Pooled bryozoans vs sediment			<0.001
Pooled bryozoans vs <i>C. cactoides</i>			0.006
Subset 1 vs sediment			0.002
Subset 2 vs sediment			0.028
Subset 3 vs sediment			0.009
Subset 1 vs <i>C. cactoides</i>			0.01
Subset 2 vs <i>C. cactoides</i>			0.089
Subset 3 vs <i>C. cactoides</i>			0.033
<i>C. foliata</i> vs <i>T. munitum</i>			0.072
<i>C. foliata</i> vs <i>T. moniliferum</i>			0.031
<i>T. munitum</i> vs <i>T. moniliferum</i>			0.921
Annelids – abundance	F	df	p
Between habitats	2.121	89	0.071
Between bryozoan species	2.399	34	0.107
Molluscs- Mean no. species			

Between habitats	6.02	89	<0.001
Between bryozoan species	3.443	34	0.044
Pairwise comparisons			
Pooled bryozoans vs sediment			0.002
Pooled bryozoans vs <i>C. cactoides</i>			0.055
Subset 1 vs sediment			0.108
Subset 2 vs sediment			0.108
Subset 3 vs sediment			<0.001
Subset 1 vs <i>C. cactoides</i>			0.467
Subset 2 vs <i>C. cactoides</i>			0.467
Subset 3 vs <i>C. cactoides</i>			0.004
<i>C. foliata</i> vs <i>T. munitum</i>			0.1
<i>C. foliata</i> vs <i>T. moniliferum</i>			0.055
<i>T. munitum</i> vs <i>T. moniliferum</i>			0.921
Molluscs - abundance			
Between habitats	4.19	89	0.002
Between bryozoan species	7.459	34	0.002
Pairwise comparisons			
Pooled bryozoans vs sediment			0.019
Pooled bryozoans vs <i>C. cactoides</i>			0.029
Subset 1 vs sediment			0.034
Subset 2 vs sediment			0.115
Subset 3 vs sediment			0.6
Subset 1 vs <i>C. cactoides</i>			0.043
Subset 2 vs <i>C. cactoides</i>			0.135
Subset 3 vs <i>C. cactoides</i>			0.73
<i>C. foliata</i> vs <i>T. munitum</i>			0.048
<i>C. foliata</i> vs <i>T. moniliferum</i>			0.002
<i>T. munitum</i> vs <i>T. moniliferum</i>			0.304

1722 Appendix 3.4. Statistical results of a one-way ANOVA's used to test the difference
 1723 between the Shannon-Weiner Diversity Index (H') of the three bryozoan species and
 1724 neighbouring sediment and *C. cactoides* habitats. Tukey's post hoc comparisons were used
 1725 for pairwise comparison. Significant results are given in bold.

Shannon Weiner	F	df	P
Between habitats	13.752	54	<0.001
Pairwise comparisons			
<i>T. munitum</i> vs <i>C. foliata</i>			0.997
<i>T. munitum</i> vs <i>T. moniliferum</i>			0.246
<i>T. moniliferum</i> vs <i>C. foliata</i>			0.469
<i>T. munitum</i> vs sediment			<0.001
<i>T. munitum</i> vs <i>C. cactoides</i>			<0.001
<i>C. foliata</i> vs sediment			0.001
<i>C. foliata</i> vs <i>C. cactoides</i>			<0.001
<i>T. moniliferum</i> vs sediment			0.098
<i>T. moniliferum</i> vs <i>C. cactoides</i>			0.002
Sediment vs <i>C. cactoides</i>			0.524

Appendix 4.

1727 Appendix 4.1. Statistical results of one-way ANOVA's used to test the difference between
 1728 the mean no. of species and mean abundance of taxa across four consecutive seasons.
 1729 Tukey's post hoc comparisons were used for pairwise comparison. Significant results are
 1730 given in bold.
 1731

Mean no. species	F	df	P
Across seasons	10.755	34	<0.001
Pairwise comparisons			
Spring vs Autumn			<0.001
Spring vs Winter			0.001
Spring vs Summer			0.004
Mean abundance of taxa	3.158	34	0.038
Across seasons			
Pairwise comparisons			
Spring vs Autumn			0.033
Spring vs Winter			0.118
Spring vs Summer			0.144

1732 Appendix 4.2. Statistical results of one-way ANOVA's used to test the difference between
 1733 the mean no. of species and mean abundance of crustacean taxa across four consecutive
 1734 seasons. Tukey's post hoc comparisons were used for pairwise comparison. Significant
 1735 results are given in bold.
 1736

Mean no. crustacean species	F	df	P
Across seasons	12.159	34	<0.001
Pairwise comparisons			
Spring vs Autumn			<0.001
Spring vs Winter			0.001
Spring vs Summer			0.008
Mean abundance of crustaceans			
Across seasons	2.539	34	0.075
Pairwise comparisons			
Spring vs Autumn			0.061
Spring vs Winter			0.173
Spring vs Summer			0.342

Appendix 4.3. Statistical results of one-way ANOVA's used to test the difference between the mean no. of species and mean abundance of annelid taxa across four consecutive seasons. Tukey's post hoc comparisons were used for pairwise comparison. Significant results are given in bold.

Mean no. annelid species	F	df	P
Across seasons	8.359	34	<0.001
Pairwise comparisons			
Spring vs Autumn			0.001
Spring vs Winter			0.004
Spring vs Summer			<0.001
Mean abundance of annelids			
Across seasons	7.684	34	<0.001
Pairwise comparisons			
Spring vs Autumn			0.002
Spring vs Winter			0.015
Spring vs Summer			<0.001

Appendix 4.4. Statistical results of one-way ANOVA's used to test the difference between the mean no. of species and mean abundance of molluscan taxa across four consecutive seasons. Tukey's post hoc comparisons were used for pairwise comparison. Significant results are given in bold.

Mean no. mollusc species	F	df	P
Across seasons	0.918	34	0.444
Mean abundance of molluscs			
Across seasons	0.4	34	0.754

Appendix 4.5. Statistical results of one-way ANOVA's used to test the difference between the mean no. of annelid and crustacean families across four consecutive seasons. Tukey's post hoc comparisons were used for pairwise comparison. Significant results are given in bold.

Mean no. annelid families	F	df	P
Across seasons	7.879	34	<0.001
Pairwise comparisons			
Spring vs Autumn			0.001
Spring vs Winter			0.01
Spring vs Summer			<0.001
Mean no. crustacean families			
Across seasons	7.195	34	<0.001
Pairwise comparisons			
Spring vs Autumn			<0.001
Spring vs Winter			0.022
Summer vs Autumn			0.045

Appendix 4.6. Statistical results of one-way ANOVA's used to test the difference between the mean abundance of annelid and crustacean families across four consecutive seasons. Tukey's post hoc comparisons were used for pairwise comparison. Significant results are given in bold.

Mean abundance	F	df	P
Crustaceans			
Corophiidae	3.396	34	0.03
Joeropsidae	4.307	34	0.012
Phoxocephalidae	8.725	34	<0.001
Tanaidacea	4.307	34	0.012
Annelids			
Flabelligeridae	15.854	34	<0.001
Lumbrineridae	10.305	34	<0.001
Opheliidae	8.754	34	<0.001
Syllidae	4.119	34	0.014
Pairwise comparisons			
Spring			
Crustaceans			
vs Summer Corophiidae			0.02
vs Autumn Joeropsidae			0.016
vs Winter Joeropsidae			0.029
vs Autumn Phoxocephalidae			0.048
vs Autumn Tanaidacea			0.016
vs Winter Tanaidacea			0.029
Annelids			
vs Autumn Flabelligeridae			<0.001
vs Winter Flabelligeridae			<0.001
vs Summer Flabelligeridae			<0.001
vs Autumn Lumbrineridae			<0.001
vs Summer Lumbrineridae			0.009
vs Summer Opheliidae			<0.001
vs Autumn Syllidae			0.014
vs Winter Syllidae			0.049
Summer			
vs Autumn Phoxocephalidae			<0.001
vs Winter Phoxocephalidae			0.013
Winter			
vs Autumn Lumbrineridae			0.004
vs Summer Opheliidae			0.001

