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Journal

Frontiers of Biogeography, 15(2)

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Publication Date

2023

DOI

10.21425/F5FBG57954

Supplemental Material

<https://escholarship.org/uc/item/6pc1d40w#supplemental>

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Intertidal macroalgal and epiphytic polychaete distributions strengthen marine ecoregions of Western Australia

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Abstract

The Marine Ecoregions of the World system separates the oceans into 232 ecoregions based on coastal and shelf-water species distributions. We tested the separation of those ecoregions and delineated subcoregions within Western Australian waters using intertidal macroalgal and epiphytic polychaete distributions. Environmental predictors of those assemblages were also determined. We collected macroalgae and polychaetes on 38 rocky intertidal shores within four marine ecoregions from 18°S to 34°S: (1) Exmouth to Broome, (2) Ningaloo, (3) Houtman, and (4) Leeuwin. We evaluated differences in species composition of macroalgae and polychaetes among those ecoregions using pairwise permutational multivariate analysis of variance and delineated subcoregions within each ecoregion using hierarchical cluster analysis. Multivariate relationships between environmental variables and assemblages were determined using distance-based linear models. The species composition of macroalgae and polychaetes significantly differed among ecoregions, with dissimilarity of 78-96% for macroalgae and 62-75% for polychaetes. We identified three subcoregions within Exmouth to Broome and Ningaloo and two subcoregions within Houtman and Leeuwin based on macroalgal distribution. We also found two subcoregions within Houtman and no subcoregion within Exmouth to Broome, Ningaloo, and Leeuwin based on polychaete distribution. Environmental predictors could explain 51% of the total variation of macroalgae and 41% of the total variation of polychaetes. The top two predictors explaining a high proportion of assemblage distribution were sea surface temperature (15% for macroalgae and 12% for polychaetes) and tidal amplitude (10% for macroalgae and 6% for polychaetes). These ecoregions and subcoregions can be used as an alternative spatial framework for classifying rocky intertidal habitats for designing marine protected area networks within Western Australian waters.

Highlights

- We analysed differences in species composition of intertidal macroalgae and epiphytic polychaetes among four marine ecoregions of Western Australia (Exmouth to Broome, Ningaloo, Houtman, and Leeuwin) and refined those ecoregions into subcoregions.
- We found significant differences in species composition between ecoregions.
- We identified ten subcoregions based on macroalgal distribution and two subcoregions based on polychaete distribution.
- Sea surface temperature and tidal amplitude were the environmental factors that explained the greatest portion of the variability in macroalgal and polychaete distributions.

Keywords: biogeographical distribution, environmental drivers, sea surface temperature, species composition, subcoregions, tidal amplitude

Introduction

Understanding large-scale distribution patterns of marine assemblages (i.e., regional to global variations) and processes that cause these patterns (e.g., geological events and environmental drivers) is a grand challenge in marine biogeography (Jenkins and Ricklefs 2011, Hortal et al. 2012, Dawson et al. 2013). Previous studies have delineated the global distribution of marine species into realms (large regions) and provinces (medium-sized regions) based on expert knowledge (Forbes 1856, Ekman 1953, Briggs 1995, Bailey 1998, Sherman and Duda 1999, Hayden et al. 2009) or statistical analyses (Adey and Steneck 2001, Kulbicki et al. 2014, Costello et al. 2017). Spalding et al. (2007) proposed the Marine Ecoregions of the World (MEOW) to refine marine realms and provinces into 232 ecoregions based on expert knowledge of coastal and shelf-water species distributions. These ecoregions represent areas of similar species composition (Spalding et al. 2007) and are often used as a spatial basis to evaluate the biogeographic representativeness of Marine Protected Areas (MPAs) in protecting marine biodiversity and ecosystem services (Lindegren et al. 2018, Gownaris et al. 2019, Sala et al. 2021).

Rocky intertidal shores are a heterogeneous marine environment with habitat structures including rock cliffs, platforms, rock pools, and boulder fields. Marine assemblages on rocky intertidal shores are influenced by both local (e.g., substrate profiles) (Meager et al. 2011, Bessey et al. 2019, Hadiyanto et al. 2020) and regional environmental factors (e.g., physio-chemical parameters of surface water and hydrodynamics) (Schoch et al. 2006, Fenberg et al. 2015, Ibanez-Erquiaga et al. 2018) and they often show variability from small (metres) to large scales (hundreds of kilometres) (Liuzzi and López Gappa 2008, Martins et al. 2008). The variability of rocky intertidal assemblages at small scales tends to be larger than that at large scales, often driven by habitat complexity resulting in small-scale patchiness. However, scaling up these effects does not always explain the variability at large scales (Fraschetti et al. 2005). Due to the uniqueness of these patterns, the MEOW system is not always appropriate to represent the large-scale distribution of rocky intertidal assemblages. The MEOW system has been found to be suitable for describing the distribution of some temperate rocky intertidal assemblages, including the coast of southern Africa (Bustamante and Branch 1996), Iberian Peninsula (Izquierdo and Guerra-García 2011), northeastern Pacific Ocean (Fenberg et al. 2015), and south-east Australia (Lathlean et al. 2015), but the system was inadequate in many other widespread locations, e.g., the coast of KwaZulu-Natal (Sink et al. 2005), Angola (Anderson et al. 2012), Ireland (Merder et al. 2016), Portugal (Pereira et al. 2006), Mediterranean Sea (Sales et al. 2012), Japan (Nakaoka et al. 2006), North America (Blanchette et al. 2008), Chile (Thiel 2002), Argentina (Wieters et al. 2012), and Peru (Ibanez-Erquiaga et al. 2018).

Some studies have used a broad range of taxonomic or functional groups to analyse the general patterns

of rocky intertidal assemblages (Bustamante and Branch 1996, Sink et al. 2005, Nakaoka et al. 2006, Blanchette et al. 2008, Sales et al. 2012, Wieters et al. 2012, Fenberg et al. 2015, Lathlean et al. 2015, Ibanez-Erquiaga et al. 2018). However, other studies have selected macroalgae as an assemblage surrogate (Bolton et al. 2004, Shears et al. 2008, Anderson et al. 2012). Macroalgae (i.e., Chlorophyta, Rhodophyta, and Ochrophyta) can be used as a biogeographical indicator on rocky intertidal shores because the group encompasses different evolutionary processes (McCoy et al. 2020, Vieira et al. 2021), distribution ranges (Kerswell 2006), and ecologies across the sessile and dominant groups on rocky intertidal shores (Anderson et al. 2012). Shears et al. (2008) found that assemblage matrices based on macroalgal data delineate clearer and more regions than those derived from invertebrate data.

Small invertebrates (<10 mm), predominantly polychaetes, are often associated with macroalgae on rocky intertidal shores (Liuzzi and López Gappa 2008, Cacabelos et al. 2010, Gestoso et al. 2012, Torres et al. 2015, Gallucci et al. 2020). Polychaetes (Annelida) are an important taxon that shows differences in epiphytic assemblages between rocky intertidal provinces (~1000 km) (Liuzzi and López Gappa, 2008), yet the biogeographical distribution and environmental drivers of this taxon on rocky intertidal shores are rarely studied (Benedetti-Cecchi et al. 2010). The assemblage structure of epiphytic polychaetes at local scales is determined by the density, heterogeneity, and complexity of macroalgae (Torres et al. 2015, Gan et al. 2019, Mikac et al. 2020). At large spatial scales, the biogeographical distribution of epiphytic crustaceans has been found to correlate with geographical changes in macroalgal assemblages in the Bay of Biscay (Arrontes and Anadón, 1990). However, there are some inconsistencies as there was no correlation in the Portuguese coast (Pereira et al. 2006). It remains unknown whether the distribution of epiphytic polychaetes on rocky intertidal shores at large scales is correlated with the macroalgal distribution.

Western Australia is recognised as one of the marine biodiversity hotspots (Ramírez et al. 2017) and multitaxon centres of endemism in the world (Roberts et al. 2002), especially for benthic marine algae (Phillips 2001, Kerswell 2006, Vieira et al. 2021). The MEOW system delineates Western Australian waters into six ecoregions: Bonaparte Coast, Exmouth to Broome, Ningaloo, Shark Bay, Houtman, and Leeuwin (Spalding et al. 2007). Rocky intertidal shores constitute about 19% of the Western Australia coastline, extending from tropical to temperate regions (Edyvane 2005), and are home to diverse and endemic species (Huisman and Borowitzka 2003, Slack-Smith and Bryce 2004, Kendrick and Rule 2014). However, distribution patterns and environmental drivers of rocky intertidal assemblages within these waters have been mostly studied at local scales (Wells 1977, Black et al. 1979, Scheibling 1994, Bessey et al. 2019). Hence, analysis of the large-scale distribution of macroalgae and epiphytic polychaetes on rocky

intertidal shores of Western Australia will facilitate the evaluation of the MEOW system.

The present study aims to test the separation of marine ecoregions within Western Australian waters using intertidal macroalgal and epiphytic polychaete distributions and delineate new subecoregions within those ecoregions. We also evaluate the multivariate relationships between those assemblages and environmental variables. At the practical level, this study will address a marine ecological research priority for MPAs within Western Australian waters as identified by Kendrick et al. (2016) and provide new measures for establishing MPAs within those waters as called for by Roberts et al. (2018).

Materials & Methods

Study area

The coastline of Western Australia extends 20,781 km from the Northern Territory in the north to the border with South Australia in the south (~34.8% of the total coastline of Australia) (Edyvane 2005). A major current (i.e., the Leeuwin Current) and four seasonal current systems (i.e., the Holloway Current, the Ningaloo Current, the Shark Bay Outflow, and the Capes Current) flow along the coast of the Indian Ocean of Western Australia (Pattiaratchi 2006, D’Adamo et al. 2009). At Point Cloates (22.7°S 113.7°E), the Ningaloo Current recirculates in an anticlockwise direction in response to the westward extension of the coastline and the southward flowing Leeuwin Current (Woo et al. 2006) (Fig. 1).

The coast of Western Australia is macrotidal from 14°S to 20°S and microtidal towards high latitudes, with a range in tidal amplitude from around 8 m in the north to less than 1 m in the south (Harker et al. 2019). Significant wave height is low (~1 m) from the northern parts to the latitude of 20°S and increases (up to 4 m) towards the southern parts, especially between 30°S and 60°S (Bosselle et al. 2012). The wave height is often higher during winter, particularly in July, when storms are more frequent and intense (Lemm et al. 1999). The coast shows a great difference in sea surface temperature (~10°C) between the northernmost and southernmost boundaries of Western Australia (Wijffels et al. 2018). The coast is also oligotrophic due to the combined effect of the Leeuwin Current that delivers low nutrient waters and little riverine inflow (Lourey et al. 2006, Hanson et al. 2007, Molony et al. 2011, McLaughlin et al. 2019).

Rocky intertidal shores stretch from tropical to temperate regions (Edyvane 2005) and are interspersed by sandy beaches or mangals (Wilson 2013). Those shores are karstified Pleistocene limestone with different profiles and erosional features depending on the coastal orientation to wind and waves, climates, and riverine influx (Semeniuk and Johnson 1985). Some rocky intertidal shores are located inside MPAs with different protection levels (Grech et al. 2014).

Sampling

Macroalgal and polychaete samples were collected from 14 localities throughout four marine ecoregions of Western Australia (Exmouth to Broome, Ningaloo,

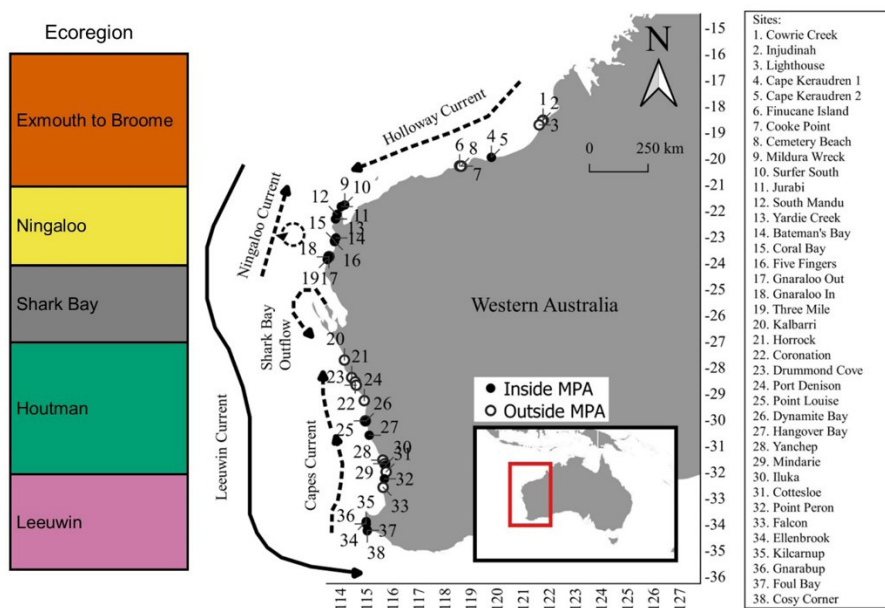


Figure 1. Sampling sites and the latitudinal range of the Marine Ecoregions of the World (Spalding et al. 2007) within Western Australian waters from 18°S to 34°S. A solid arrow represents the main current, and dashed arrows represent seasonal currents (Pattiaratchi 2006, D’Adamo et al. 2009). The map was projected on the World Geodetic System (WGS) 84 datum

Houtman, and Leeuwin), from 18°S to 23°S and 27°S to 34°S, keeping 1° of latitudinal distance between localities (Fig. 1, Table S1). Rocky intertidal shores between 23°S and 27°S (Shark Bay) are inaccessible due to high rock cliffs and remoteness. Thus, this ecoregion was not examined in the present study. There were 38 sites (i.e., beaches with horizontal rock platforms) across the 14 localities. The number of sites in each locality and the distance between them varied depending on the availability and accessibility of rock platforms.

Macroalgal and polychaete samples were collected during low tide from September 2020 (spring) to January 2021 (summer). At each site, three line transects, separated by up to 50 m depending on the length of the rock platforms, were placed perpendicular to the shoreline. At each transect, three quadrats of 1 m x 1 m (with four grids of 0.5 m x 0.5 m in each quadrat) were haphazardly placed at the inner (nearest to the waterline), middle, and outer of the rock platform to determine rock platform profiles. A smaller quadrat (0.2 m x 0.2 m) was placed on the densest patch of macroalgae within the grid of 0.5 m x 0.5 m for quantifying macroalgae and polychaetes. The same size, number, and placement of quadrats have previously been used to capture the diversity and density of macroalgae and macroinvertebrates (Pereira et al. 2006, Wieters et al. 2012, Lathlean et al. 2015). Sampling at the Cosy Corner site (34°S) was only conducted at the inner and middle of the rock platform due to the difficulty of getting to the outer platform.

Macroalgae inside the 0.2 m x 0.2 m quadrats were scraped from the rock and washed gently using fresh seawater to detach epiphytic fauna. Macroalgae were preserved in 95% ethanol in the field. In the laboratory, macroalgae were identified to species level following Open Nomenclature qualifiers (e.g., sp. 1, sp. 2, etc.) for unknown species names (Sigovini et al. 2016) and categorised into seven functional groups (i.e., filamentous algae, foliose algae, corticated foliose algae, corticated macrophytes, leathery macrophytes, articulated calcareous algae, and crustose algae) (Steneck and Dethier 1994). Simpson's reciprocal index of the functional group of macroalgae was calculated to determine the heterogeneity of macroalgae. We also measured fractal dimensions based on the area and perimeter of each taxon (as a whole plant) to quantify the structural complexity of macroalgae. The fractal dimensions were calculated by photographing each taxon and transferring the photo to black-and white image to produce binary data. ImageJ software was then used to analyse the fractal structure of each image (McAbendroth et al., 2015). The mean fractal dimensions for each taxon were used to calculate complexity indices for the entire macroalgal samples. The calculations were weighted based on the proportion of macroalgal biomass contributed by each taxon within a sample (McAbendroth et al. 2005, Torres et al. 2015).

The seawater used to wash macroalgae was sieved through 0.5 mm mesh to retain epiphytic polychaetes. The same mesh size has also been

used to retain polychaetes for ecological analyses (Benedetti-Cecchi et al. 2010, Hartwell and Fukuyama 2015). The retained polychaetes were preserved in 95% ethanol in the field. In the laboratory, the polychaetes (i.e., non-clitellate annelids excluding sipunculans and echiurans) were identified to species level, either using Linnean names for existing species or Open Nomenclature qualifiers for unknown species (Sigovini et al. 2016); species were then categorised into functional groups based on feeding guilds (Jumars et al. 2015) and counted individually.

Environmental variables

Environmental variables consisted of rock platform profiles and sea surface physico-chemical parameters (Table S2). Rock platform profiles included the proportion of structural components (i.e., macroalgae, barnacles, boulders, rubble, crevices, seagrass, pits, sand, and bare), heterogeneity, and complexity. The proportion of structural components within 1 m x 1 m quadrats was estimated individually (i.e., the total percentage within a quadrat was 100%). Simpson's reciprocal index of structural components was calculated to determine the heterogeneity of rock platforms (Meager et al. 2011). The rugosity of rock platforms (i.e., the length of the actual surface of the rock platform within 1 m x 1 m quadrats) was measured using a metal chain to determine the complexity of rock platforms. A longer actual surface indicates a more complex rock platform (Risk 1972).

Physico-chemical parameters included wave height, tidal amplitude, current velocity, sea surface temperature, photosynthetically active radiation, salinity, dissolved oxygen, pH, nitrate, and particulate organic carbon. Mean wave height was downloaded from Copernicus Marine Service at the resolution of ~9.2 km (<https://marine.copernicus.eu/>); mean tidal amplitude was downloaded from Global Marine Environment Datasets at the resolution of ~9.2 km (<http://gmed.auckland.ac.nz>); mean sea surface temperature and salinity were downloaded from MARSPEC at the resolution of ~1 km (Sbrocco and Barber 2013); mean surface current velocity, dissolved oxygen, and nitrate were downloaded from Bio-ORACLE at the resolution of ~9.2 km (Tyberghien et al. 2012); mean photosynthetically active radiation and particulate organic carbon were downloaded from the Aqua MODIS satellite at the resolution of ~4 km (<http://oceancolor.gsfc.nasa.gov>). Coordinates of sites were matched to the closest available physico-chemical data.

Data analysis

Assemblage data were aggregated into sites to capture the local diversity of macroalgae and polychaetes. This included the Cosy Corner site despite it missing the data from the outer platform. The data matrix of species biomass or abundance was Hellinger transformed to reduce the contribution of very abundant species (Legendre and Gallagher 2001). A dissimilarity matrix was constructed using the Bray-Curtis dissimilarity index as it is the most robust abundance-based index for minimising taxonomic,

numerical, and geographic sampling error (Schroeder and Jenkins 2018). A Mantel test was used to analyse the correlation between macroalgal and polychaete dissimilarity matrices (Legendre and Legendre 1998).

Assemblage patterns of macroalgae and polychaetes among ecoregions were visualised using non-metric multidimensional scaling (NMDS) (Legendre and Legendre 1998). Spearman's rank-order correlation analysis was performed to evaluate correlations between Hellinger-transformed species biomass/abundance data and NMDS scores. Species that showed high ($|r_s| > 0.5$) and significant correlations ($p < 0.05$) were selected to determine which species that significantly contributed to structuring assemblages among ecoregions.

To evaluate the separation of ecoregions, differences in macroalgal and polychaete assemblages among those ecoregions were tested using pairwise permutational multivariate analysis of variance (PERMANOVA) (Anderson 2001) with false discovery rate adjusted p value (Benjamini and Hochberg 1995) and their dissimilarity percentages were determined using similarity percentages (SIMPER) (Clarke 1993). PERMANOVA and SIMPER were analysed based on Bray-Curtis dissimilarity for Hellinger-transformed assemblage data with 999 permutations. Ecoregions that were significantly different ($p < 0.05$) were assigned as distinct ecoregions, while ecoregions that were not significantly different ($p > 0.05$) were assigned as similar ecoregions and combined into a single larger ecoregion (Waters et al. 2010, Boonzaaier-Davids et al. 2020, Hadiyanto et al. 2021). Subcoregions within distinct ecoregions were delineated using hierarchical cluster analysis based on Bray-Curtis dissimilarity using the unweighted pair-group method with arithmetic averages (UPGMA). The grouping of sites was determined using silhouettes (Rousseeuw 1987), and those groups were assigned as subcoregions. Borders between subcoregions were approximated based on the latitude of sites. To examine the effect of different identification approaches, we conducted the same analyses at higher taxonomic levels (i.e., genus and family) and functional groups as supplementary analyses (Fig. S1-S2).

Environmental data (i.e., sea surface physico-chemical parameters, rock platform profiles, and morphological profiles of macroalgae) were z-score standardised to account for different measurement units. Spearman's rank-order correlation analysis was conducted to evaluate the collinearity among environmental parameters. Environmental parameters that are ecologically important for macroalgae and epiphytic fauna were used as proxies for other parameters that were highly correlated ($|r_s| > 0.80$).

Multivariate relationships between assemblages and environmental variables were analysed using distance-based linear models (distLMs) with 999 permutations based on Bray-Curtis dissimilarity for Hellinger-transformed abundance data and standardised environmental data (Legendre and Anderson 1999). The model was selected using automatic forward stepwise iteration based on Akaike's

information criterion (AIC). The most parsimonious model should have the lowest AIC (Burnham and Anderson 2004). As a supplement, we did the same analysis at higher taxonomic levels (genus and family) and using functional groups.

Data analysis and visualisation were performed using R software (<https://www.r-project.org/>) with the following packages: 'vegan' (Oksanen et al. 2016), 'RVAideMemoire' (Hervé 2019), 'optpart' (Roberts 2020), 'ggplot2' (Wickham 2009), and 'ggVennDiagram' (Gao et al. 2021). The map of biogeographical zonation of macroalgae and polychaetes was created based on the World Geodetic System (WGS) 84 datum using QGIS version 3.16.

Results

Evaluating marine ecoregions

A total of 187 macroalgal species were identified (Chlorophyta: 43 species, Ochrophyta: 61 species, Rhodophyta: 83 species). Between 12 and 20% of total species were unique for a particular ecoregion (i.e., species present in only one ecoregion) (Fig. 2a). Epiphytic polychaetes consisted of 126 species and two multispecies groups (Nereididae spp and Syllinae spp). The top three most diverse families were Syllidae (25 species), Nereididae (15 species), and Eunicidae (12 species). The proportion of unique species within ecoregions was 8-12% of total species (Fig. 2b). The multispecies groups of polychaetes were not included in multivariate analyses to minimise the distortion of analyses. The Mantel test showed a significant but low correlation between macroalgal and polychaete dissimilarity matrices ($r = 0.47$, $p < 0.01$).

Non-Multimetric Dimensional Scaling 3D plots showed clear separations between northern (i.e., Exmouth to Broome and Ningaloo) and southern ecoregions (i.e., Houtman and Leeuwin) for both macroalgae (stress = 0.10) (Fig. 3a) and polychaetes (stress = 0.15) (Fig. 3b). Pairwise PERMANOVA showed that those assemblages also significantly differed among ecoregions ($p < 0.05$), with the dissimilarity percentages of 77.72-95.52% for macroalgae and 62.12-75.32% for polychaetes (Table S3). Thus, we assigned Exmouth to Broome, Ningaloo, Houtman, and Leeuwin as distinct ecoregions. Each distinct ecoregion was refined into smaller regions. Sites within each ecoregion were clustered into two to five groups based on macroalgal assemblages and two groups based on polychaete assemblages (Fig. S1-S2). Based on the grouping of sites with the consideration of site continuity and latitudes, we assigned the distribution of macroalgae into ten subcoregions: three subcoregions within each of Exmouth to Broome and Ningaloo and two subcoregions within each of Houtman and Leeuwin. The distribution of polychaetes was delineated into two subcoregions within Houtman and no subcoregion within Exmouth to Broome, Ningaloo, and Leeuwin (Fig. 4).

Supplementary analyses showed that the separation of ecoregions and subcoregions could also be identified based on the distribution of macroalgae at

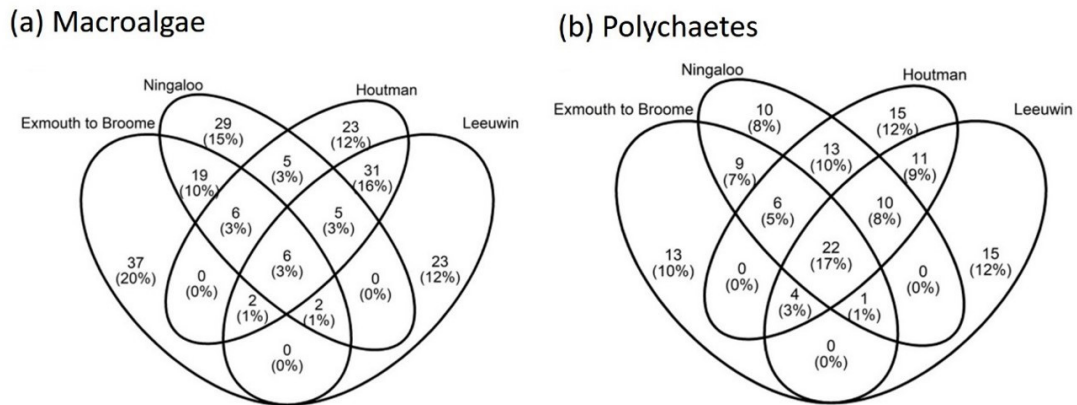


Figure 2. The number of unique and shared species of (a) macroalgae and (b) polychaetes within marine ecoregions of Western Australia. Unique species are species found in only one ecoregion, and shared species are species found in at least two ecoregions

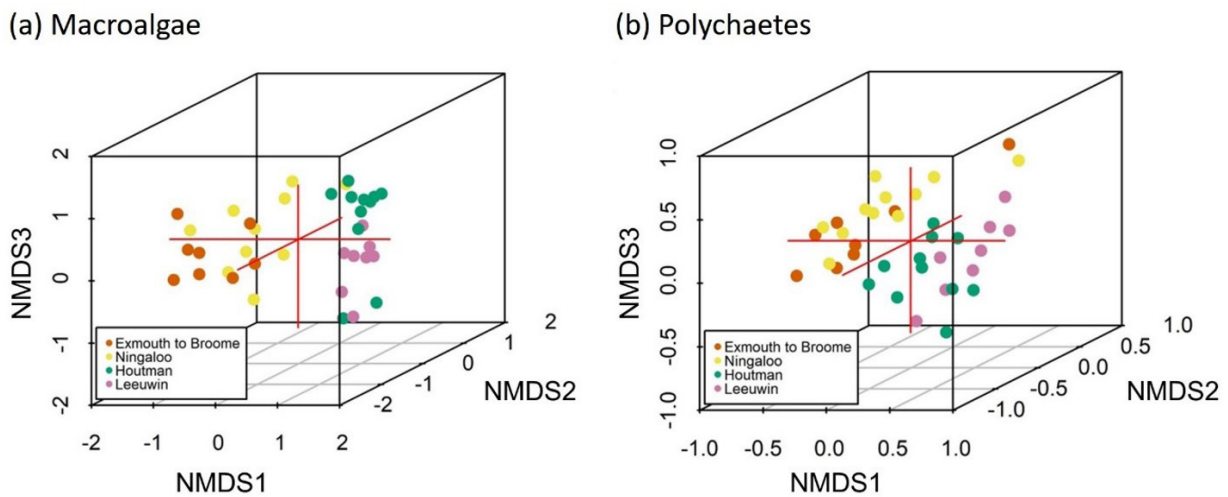


Figure 3. 3-D non-metric multidimensional scaling of (a) macroalgae and (b) polychaetes within marine ecoregions of Western Australia based on Bray-Curtis dissimilarity for Hellinger-transformed species biomass/density data. Stress was 0.10 for macroalgae and 0.15 for polychaetes

genus level but not at family level and functional group. Analysing the distribution of polychaetes at higher taxonomic levels (genus and family) and functional group failed to differentiate those ecoregions and subcoregions (Table S3, Fig. S1-S2).

Twenty-two macroalgal and 14 polychaete species had high ($|r_s| > 0.5$) and significant correlations ($p < 0.05$) with the underlying sample distributions, indicating they provided significant contributions in structuring assemblages along marine ecoregions and subcoregions. Most of them were found within one subcoregion (e.g., *Caulocystis cephalornithos* (Labillardière) J.E. Areschoug, 1854), or one (e.g., *Laurencia* sp.1) or two ecoregions (e.g., *Hormophysa cuneiformis* (J.F. Gmelin) P.C. Silva, 1987). Two macroalgal species, *Hypnea valentiae* (Turner)

Montagne, 1841 and *Sirophysalis trinodis* (Forsskål) Kützing, 1849, showed increases in biomass towards southern ecoregions. The density of two polychaete species (*Branchiomma* sp. and *Timarete* sp.1) increased towards southern ecoregions, but that of *Eunice* sp.1, *Platynereis* sp. and *Polyopthalmus* sp. showed a reverse trend (Fig. 5).

Relationships between assemblages and environmental variables

Significant wave height, tidal amplitude, sea surface temperature, and particulate organic carbon showed obvious latitudinal gradients along the marine ecoregions. Other physico-chemical factors did not have clear patterns but tended to vary spatially among

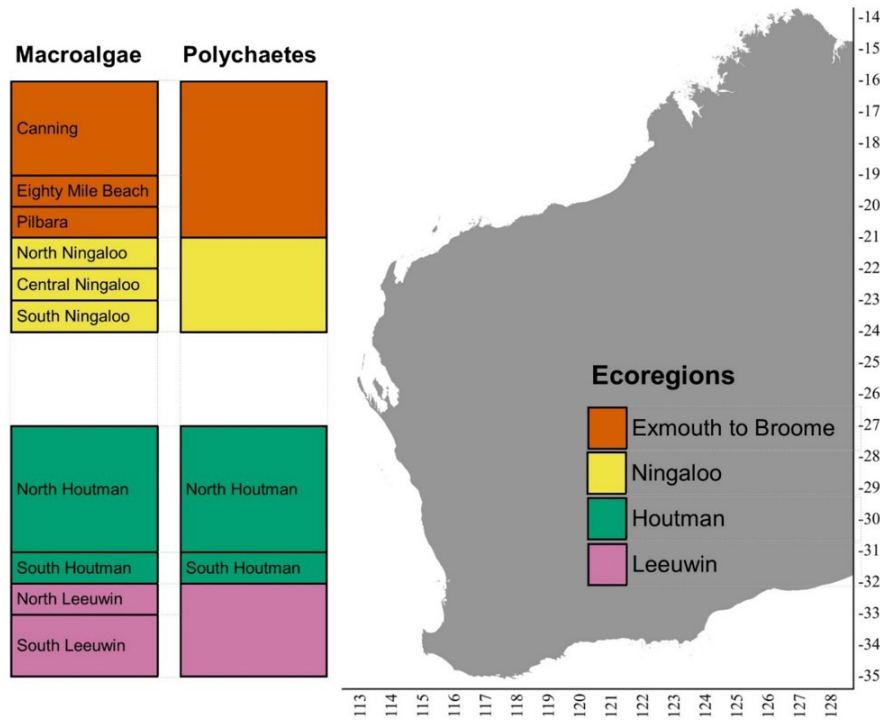


Figure 4. The latitudinal range of marine ecoregions (coloured) and subcoregions (labelled for macroalgae and polychaetes) within Western Australian waters from 18°S to 34°S. The map was projected on the World Geodetic System (WGS) 84 datum

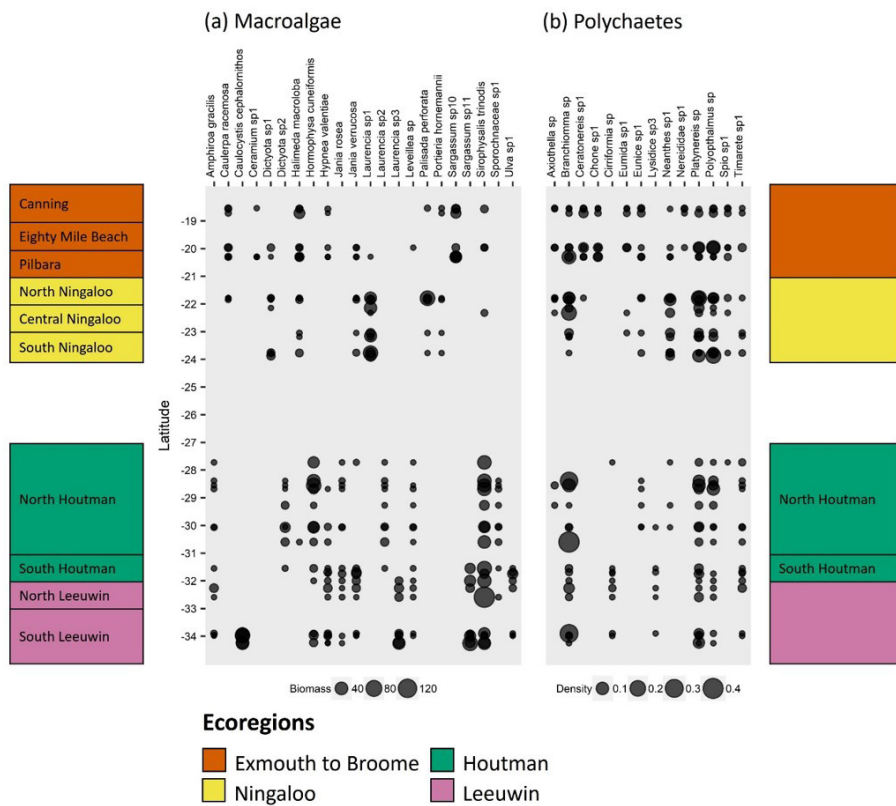


Figure 5. Latitudinal changes in (a) the biomass of macroalgae (g per 0.04 m²) and (b) the abundance of polychaetes (individuals per 1 g of macroalgae) within marine ecoregions (coloured) and subcoregions (labelled) of Western Australia. Species were selected based on significant ($p < 0.05$) and high ($|r_s| > 0.5$) correlations between Hellinger-transformed species biomass/abundance data and NMDS scores.

ecoregions. Spatial variations were also observed for rock platform profiles and macroalgal heterogeneity and complexity (Table S2). Photosynthetically active radiation, dissolved oxygen, and salinity were highly correlated with sea surface temperature, and thus the former variables were excluded in the analysis of distLMs. Fractal dimension based on the perimeter was also excluded because it was highly correlated with fractal dimension based on area (Table S4).

The marginal tests of distLMs showed that each predictor explained less than 4% of the total variation of macroalgal and polychaete assemblages (Table S5). The most parsimonious distLM showed that the combination of nine predictors (sea surface temperature, tidal amplitude, pH, nitrate, bare coverage, current velocity, particulate organic carbon, wave height, and boulder coverage) could explain 51.29% of the total variation of macroalgal assemblages (AIC = 87.29). The combination of eight predictors (sea surface temperature, tidal amplitude, pit coverage, current velocity, nitrate, bare coverage, fractal dimension based on area, and the biomass of filamentous algae) was the best distLM for polychaete assemblage (variation explained = 41.05%, AIC = 73.97) (Table S6). Sea surface temperature and tidal amplitude were the top two predictors explaining a high proportion of the distribution of macroalgae (sea surface temperature = 14.59% and tidal amplitude = 10.42%) and polychaetes (sea surface temperature = 11.58% and tidal amplitude = 6.44%) (Fig. 6). Supplementary analyses showed that those predictors also best explained the distribution of assemblages at higher taxonomic levels (genus and family) for both macroalgae and polychaetes and at functional group level for macroalgae (Table S7).

Discussion

The Marine Ecoregions of the World (MEOW) system separates the oceans into 232 ecoregions based on the distribution of coastal and shelf-water assemblages (Spalding et al. 2007), yet separation of those ecoregions is not always suitable to represent the broad scale distribution of rocky intertidal assemblages (Bustamante and Branch 1996, Thiel 2002, Sink et al. 2005, Nakaoka et al. 2006, Pereira et al. 2006, Blanchette et al. 2008, Izquierdo and Guerra-García 2011, Anderson et al. 2012, Sales et al. 2012, Wieters et al. 2012, Fenberg et al. 2015, Lathlean et al. 2015, Merder et al. 2016, Ibanez-Erquiaga et al. 2018). Here, we show that the distribution of intertidal macroalgae and epiphytic polychaetes supports the characterisation of marine ecoregions of the MEOW system within Western Australian waters (i.e., Exmouth to Broome, Ningaloo, Houtman, and Leeuwin). Nevertheless, those ecoregions can be refined into ten subecoregions based on macroalgal distribution and two subecoregions based on polychaete distribution. Our study also reveals that sea surface temperature and tidal amplitude are two main environmental drivers of those assemblages.

We found apparent separations between northern and southern ecoregions of Western Australian waters

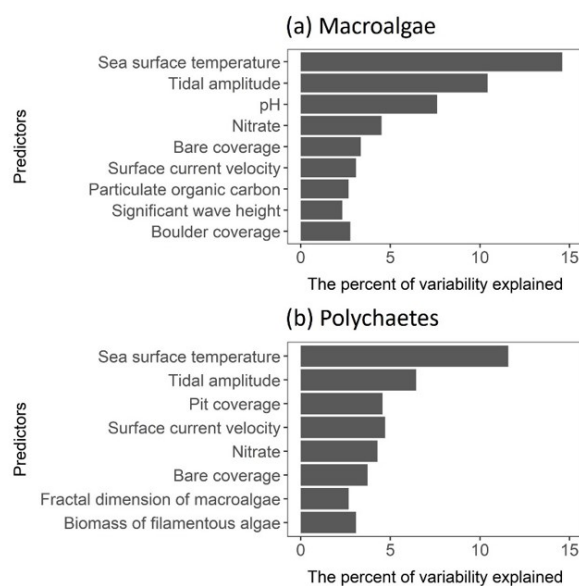


Figure 6. The percent of variability explained by each predictor based on the most parsimonious distance-based linear model (distLM) for (a) macroalgae and (b) polychaetes. The distLM was done based on Bray-Curtis dissimilarity with Hellinger-transformed species biomass/abundance data and standardised environmental data. The most parsimonious model was determined using automatic forward stepwise iteration with the Akaike's information criterion. The predictor axis within plots was arranged based on the predictor order of the most parsimonious distLM

for both macroalgal and polychaete distributions. These separations are matched to two marine realms: North-West (tropical realm) and South-West Australia (temperate realm) (Forbes 1856, Ekman 1953, Briggs 1995, Bailey 1998, Sherman and Duda 1999, Adey and Steneck 2001, Spalding et al. 2007, Hayden et al. 2009, Costello et al. 2017). Differences in the distribution patterns of marine assemblages between those realms are also found for other groups, e.g., coastal zooplankton (McCosker et al. 2020), shallow-water barnacles (Jones 2003), and fishes (Alan et al. 2001, Fox and Beckley 2005, Last et al. 2011), and seem to be stable across geological times (Cowman et al. 2017, Kocsis et al. 2018).

Further, the distribution of intertidal macroalgae and epiphytic polychaetes supports the delineation of marine ecoregions. Hence, we agree with the application of the MEOW system to represent the biogeographical distribution of rocky intertidal assemblages as has been done in previous studies (Bustamante and Branch 1996, Izquierdo and Guerra-García 2011, Fenberg et al. 2015, Lathlean et al. 2015). However, we also found smaller regions within those ecoregions that can be assigned as subecoregions. Unlike deep-sea assemblages (Costello and Chaudhary 2017), the spatial variation of rocky intertidal assemblages can be detected within small scales (metres) (Liuzzi and López Gappa 2008,

Martins et al. 2008). Thus, we were able to refine the marine ecoregions of the MEOW system as has also been done in previous studies (Thiel 2002, Sink et al. 2005, Nakaoka et al. 2006, Pereira et al. 2006, Blanchette et al. 2008, Anderson et al. 2012, Sales et al. 2012, Wieters et al. 2012, Merder et al. 2016, Ibanez-Erquiaga et al. 2018). We suggest that future bioregionalisation systems should delineate the oceans into depth strata, namely intertidal, subtidal, and deep-sea ecoregions, due to the influence of different environmental drivers explaining distribution patterns (Watling et al. 2013, Douglass et al. 2014).

Marine ecoregions of Western Australia are characterised by different macroalgal and polychaete distributions. The proportion of unique species within ecoregions was up to 15% for polychaetes and 20% for macroalgae, slightly lower than that for multi marine assemblages (up to 25%) (Hadiyanto et al. 2021). The proportion of unique species may indicate the endemism of marine ecoregions. However, the endemic status of those species needs to be confirmed to calculate the threshold of species endemism for an ecoregion. Currently, the threshold of species endemism is only available for a marine realm (42%) (Costello et al. 2017) and province (10%) (Briggs and Bowen 2012).

Species density is also an important component in separating marine ecoregions and subecoregions. Some species showed differences in density between ecoregions (e.g., *S. trinodis* and *H. cuneiformis*) and subecoregions (e.g., *C. cephalornithos*). This suggests that anthropogenic impacts on macroalgal density may influence ecological characteristics and delineation of those ecoregions and subecoregions. The density of large canopy performing species (kelps, Order Laminariales) within marine ecoregions has declined over the last five decades due to climate change, overfishing, and direct harvest (Krumhansl et al. 2016), but they are subtidal species that do not occur on intertidal habitats.

Physico-chemical water and substrate profiles partially explained the distribution of intertidal macroalgae and epiphytic polychaetes. Oceanographic processes, such as ocean currents, may partly explain the residuals as have been observed on New Zealand coasts (Menge et al. 2003), the U.S. Oregon coast (Dudas et al. 2008), the Southern California Bright (Watson et al. 2011), the West Indian Ocean (Tsang et al. 2012), and Mediterranean coasts (Rattray et al. 2016). In our study, the ecoregion boundaries of macroalgae and polychaetes coincide with seasonal currents (i.e., Holloway Current, Ningaloo Current, and Capes Current) (Pattiaratchi 2006, D'Adamo et al. 2009). These currents could limit propagule and larval dispersal, which in turn influences the dissimilarity of adult assemblages between ecoregions.

Sea surface temperature and tidal amplitude appear to be primary environmental drivers of macroalgal and polychaete distributions on rocky intertidal shores. Sea surface temperature limits tropical (warm) macroalgae and polychaetes to occupy high latitudinal waters and replace them with temperate

(cold) macroalgae and polychaetes at higher latitudes. Sea surface temperature also influences the density of widespread macroalgae and polychaetes. Thus, our data support the finding that sea surface temperature is a main environmental driver of latitudinal patterns of rocky intertidal assemblages (Blanchette et al. 2008, Anderson et al. 2012, Fenberg et al. 2015, Ibanez-Erquiaga et al. 2018). The tidal amplitude is probably more responsible for structuring macroalgae and polychaetes in macrotidal waters. Tidal cycles may challenge the ability of rocky intertidal species to deal with physical (e.g., desiccation) and biological pressures (e.g., predation) (Kunze et al. 2021). The role of tidal range in determining the distribution of rocky intertidal assemblages has also been recorded in the California Current region (Schoch et al. 2006), the tropical eastern Pacific coast of Colombia (Castellanos-Galindo et al. 2010), and the Brazilian coast (Andrades et al. 2018).

Other variables, including pH, nutrients, surface current velocity, and substrate profiles, are probably secondary environmental drivers of rocky intertidal assemblages. These variables are more important in determining the distribution of rocky intertidal assemblages within longitudinal (Merder et al. 2016, Puente et al. 2016, Ramos et al. 2016) or local ranges (Arevalo et al. 2007, Piazzini et al. 2011, Bessey et al. 2019, Hadiyanto et al. 2020). In addition to these drivers, the complexity of macroalgae and the biomass of filamentous algae are probably secondary environmental drivers for epiphytic polychaete distributions. The complexity of macroalgae represents the availability of space and the variety of resources, and thus it often determines the assemblage structure of epiphytic invertebrates (Veiga et al. 2014, Torres et al. 2015, Gan et al. 2019, Mikac et al. 2020). At small to moderate amounts, filamentous algae provide alternative habitats (Arroyo and Bonsdorff 2017) and food for herbivorous or omnivorous polychaetes, e.g., Syllidae, Nereididae, and Eunicidae (Jumars et al. 2015), which are diverse families on rocky shores (Giangrande et al. 2003; Antoniadou et al. 2004; Parapar et al. 2009).

Temporal variation was not accounted for in our analyses due to logistic limitations given the large-scale study area and the difficulty of sampling in winter. The diversity and density of rocky intertidal assemblages show seasonal variations and peak between spring and summer (Scheibling 1994, Prince 1995, Bellgrove et al. 2004). Hence, our study probably shows the main distribution patterns in these assemblages. The coast of South-West Australia experiences strong and high waves during winter (Lemm et al. 1999). Thus, it is not easy to collect samples during this season, especially those from the outer sections of the rock platforms. The large-scale distribution of rocky intertidal assemblages is often studied during low-spring or low-summer tides to minimise the effect of hydrodynamics on the quality of samples (Nakaoka et al. 2006, Izquierdo and Guerra-García 2011, Anderson et al. 2012, Sales et al. 2012, Ibanez-Erquiaga et al. 2018).

Macroalgae should be the first group to be analysed in the evaluation of marine ecoregion systems in representing the distribution of rocky intertidal assemblages. Macroalgae are a foundation assemblage on rocky shores (Graham et al. 2016) and often show clearer and more regions than invertebrates (Shears et al. 2008). Indeed, in our analyses, macroalgae showed higher dissimilarity percentages among ecoregions and identified more subcoregions than polychaetes did. However, the combination of macroalgae and other assemblages (e.g., epiphytic and benthic invertebrates) is probably better than single taxon for yielding more general results in testing and refining marine ecoregion systems. This is because the large-scale distribution of epiphytic invertebrates can be independent of changes in the biogeographical distribution of macroalgae as has also been found on the Portuguese coast (Pereira et al. 2006).

Regardless of these limitations, we have examined the suitability of the MEOW system in describing the distribution of rocky intertidal assemblages and refined this system into subcoregions. The MEOW system is often used as a spatial basis for marine conservation and management around the world (Lindegren et al. 2018, Gownaris et al. 2019, Sala et al. 2021). However, this system can be improved by the inclusion of subcoregions to be a more suitable tool for protecting and managing rocky intertidal assemblages. Therefore, we suggest that subcoregions are the smallest spatial units where MPAs should be established. Sea surface temperature and tidal amplitude appear to be main environmental drivers of the distribution of rocky intertidal assemblages and can be important predictors to model the present and future distribution of these assemblages.

Acknowledgements

This paper is a part of PhD study of the first author at the University of Western Australia. The study was sponsored by Indonesia Endowment Fund for Education (*Lembaga Pengelola Dana Pendidikan*), the Ministry of Finance, Republic of Indonesia, and the period of 2019-2023 (No. 201901220213791). The authors would like to thank: the Department of Biodiversity, Conservation and Attractions (DBCA) and the Department of Primary Industries and Regional Development (DPIRD) of Western Australia for permits of macroalgal and polychaete collection (Regulation 4 No. CE006192, Regulation 25 No. FO25000309, Regulation 61 No. FT61000627, and Exemption Number 3547); Karajarri Rangers for the permit and help while collecting samples in Bidyadanga; and volunteers (Matilda Murley, Jessi Walker, Andri Irawan, Ni Made Indira Santi, Ni Luh Gede Rai Ayu Saraswati, and Putriana Indah Lestari) for the help during the fieldwork.

Author Contributions

HH, JP, RKH, and CJG conceived the ideas; HH, JP, and RKH collected the samples; HH identified macroalgae

and polychaetes; HH analysed the data with significant suggestions from JP and RKH; HH led the writing with assistance from JP, RKH, and CJG; HH, JP, RKH, and CJG reviewed and edited.

Data Accessibility

Macroalgal, polychaete, and substrate data are available in figshare (<https://doi.org/10.6084/m9.figshare.21875346.v1>). Mean significant wave height at the resolution of ~9.2 km is available in the Copernicus Marine Service (<https://marine.copernicus.eu/>). The average of maximum tidal amplitude at the resolution of ~9.2 km is available at the Global Marine Environment Datasets (<http://gmed.auckland.ac.nz/>). Mean sea surface temperature and sea surface salinity at the resolution of ~1 km are available at the MARSPEC (<http://marspec.weebly.com/modern-data.html>). Mean surface current velocity, dissolved oxygen, and nitrate at the resolution of ~9.2 km are available at the Bio-ORACLE (<https://www.bio-oracle.org/>). Mean photosynthetically available radiation and particulate organic carbon POC at the resolution of ~4 km are available in the Aqua MODIS satellite (<http://oceancolor.gsfc.nasa.gov>).

Supplementary Material

The following materials are available as part of the online article at <https://escholarship.org/uc/fb>.

Figure S1. The hierarchical cluster analyses of macroalgae for each of distinct marine ecoregions of Western Australia

Figure S2. The hierarchical cluster analyses of polychaetes for each of distinct marine ecoregions of Western Australia

Table S1. Coordinates of sampling sites within rocky intertidal shores of Western Australia

Table S2. Summary of environmental parameters within marine ecoregions of Western Australia

Table S3. The dissimilarity percentages of macroalgal and polychaete assemblages between marine ecoregions of Western Australia based on taxa and functional group compositions

Table S4. Spearman's rank-order correlation coefficients among environmental variables within rocky intertidal shores of Western Australia

Table S5. The percentage of variability explained each predictor based on marginal tests of distance-based linear models (distLMs) between rocky intertidal assemblages (macroalgae and polychaetes) and environmental variables.

Table S6. Automatic forward stepwise iteration of distance-based linear models (distLMs) for intertidal macroalgae and epifaunal polychaetes within Western Australian waters based on the Akaike's information criterion (AIC).

Table S7. The percent of variability explained by each predictor based on the most parsimonious distance-based linear model (distLM) for intertidal macroalgae and epiphytic polychaetes at different identification levels.

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- Submitted: 4 July 2022
First decision: 1 October 2022
Accepted: 11 January 2023
- Edited by Cascade Sorte and Janet Franklin