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Substrate Preferences and Interspecific Affinities of Antarctic Macroalgae: Insights from Maxwell Bay, King George Island

Young Wook Ko [1], Kwon Mo Yang [2] and Han-Gu Choi [1,*]

[1] Division of Life Sciences, Korea Polar Research Institute, Incheon 21990, Republic of Korea; ywko@kopri.re.kr
[2] Department of Biological Sciences, Sungkyunkwan University, Suwon 16419, Republic of Korea; outro@skku.edu
* Correspondence: hchoi82@kopri.re.kr; Tel.: +82-32-760-5511

Abstract: This study investigates the diversity and ecological dynamics of macroalgae in Maxwell Bay, King George Island, Antarctica, focusing on species distribution, substrate composition, and interspecific interactions. Across nine survey sites, 31 macroalgal species were recorded, with 12 species identified as significant due to their considerable relative frequency, coverage, and biomass. *Palmaria decipiens* was the most dominant species in terms of frequency and coverage, while *Desmarestia anceps* had the highest biomass. The study revealed distinct substrate preferences, with *P. decipiens* favoring cobble and mud substrates, and *Himantothallus grandifolius* associating predominantly with pebble substrates. A core group of species, including *Plocamium* sp., *H. grandifolius*, *Picconiella plumosa*, *Iridaea* sp., and *Trematocarpus antarcticus*, exhibited strong ecological interactions characterized by high substrate similarity and mutual affinity. In contrast, pioneer species like *P. decipiens* and *Monostroma hariotii* showed lower affinity with other species, reflecting their early successional roles. These findings enhance our understanding of the complex interspecific relationships within Antarctic macroalgal assemblage and provide valuable baseline data for future ecological studies in the region.

Keywords: species distribution; substrate composition; interspecific interactions; macroalgal assemblage; Antarctica

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1. Introduction

Macroalgae exhibit a high degree of environmental variance in their habitats, thriving in a range of conditions such as intertidal zones exposed to air with extreme fluctuations in temperature and salinity (even enduring desiccation stress), tide pools, shallow subtidal zones subject to intense physical disturbance from wave action, and deep waters with very low light intensity. Most macroalgae are benthic, originally requiring an attachment point, but some of them are known to have thalli that propagate asexually by fragmentation, after which the detached clones become pelagic, such as in some *Sargassum* spp. and *Ulva* spp. [1–3] Consequently, benthic macroalgae necessitate a hard substratum, but they are not limited to well-developed rocky substrates; they also colonize hard substrata of varying sizes, such as boulders, cobbles, and pebbles [4–6], and even attach to bivalve shells [2,3]. Sometimes, they may colonize sand grains [7] or grow epiphytically on other macroalgal fronds [8]. The colonization of these diverse substrata by macroalgae often results from chance settlement during the propagule stage. However, subsequent growth into the sporophyte stage is influenced by biological (e.g., competition, herbivory) and abiotic (e.g., light utilization, tidal action, wave amplitude) factors that lead to selective survival [6,9,10]. Despite the broad potential for macroalgae to inhabit various substrates, species-specific substrate preferences are observed. For example, the Antarctic brown macroalga *Himantothallus grandifolius* is commonly found on substrates developed from pebbles rather than well-developed rock substrata, while *Desmarestia* species are associated with sandy substrates [4,5,11]. Although the substrate preferences and underlying reasons for such preferences in macroalgae are intriguing, research on the substrate composition of various macroalgal habitats remains limited. While some studies have reported on macroalgae associated with different substrate types [6,12–14], discussions on substrate type preferences at the species level are notably lacking.

When conducting classical studies on the distribution, composition, and diversity of macroalgae in the field, it is frequently observed that certain species tend to co-occur with high regularity. For instance, in the intertidal zones along the Korean coast, *Sargassum fusiformis* and *S. thunbergii* are commonly found with high frequency [15]. Similarly, in the Antarctic intertidal zones, *Iridaea* sp. [16] (*Iridaea cordata* by [8]) and *Phaeurus antarcticus* often appear together [17], while in the subtidal zones, *Himantothallus grandifolius* and *Plocamium* sp. [18] (as *Plocamium cartilagineum*, *P. hookeri*, and *P. secundatum* by [8]) are frequently found in association [19]. These examples involve dominant species within their respective environments, which researchers can readily identify during field surveys without the need for extensive data processing. However, in assemblage studies, the relationships between these species are often given relatively limited attention, with the focus predominantly placed on spatio-temporal variations within community analyses. This approach tends to highlight the species contributing to differences between assemblages, thereby attributing significance and ecological value to these species [15,17,19,20]. Consequently, the interactions among other significant species are frequently overlooked apart from the prominent examples mentioned. While it is challenging to infer the nature of species interactions—whether they are competitive, symbiotic, or coincidental—without controlled experimental conditions, assemblage studies still have the potential to offer foundational data on interspecific relationships. Nonetheless, such examples are rare. Research on interspecific interactions among macroalgae has largely focused on competition and co-occurrence [21–25], as well as interactions with other taxa, such as herbivory, symbiosis, and spatial competition with corals [26–29]. Furthermore, there has been considerable research on the interactions between invasive and endemic species [22,30,31]. Despite this, as mentioned earlier, a notable paucity of foundational data could serve as a basis for understanding the correlations between species, essential for initiating more in-depth studies of these interactions.

Approximately 120 macroalgal species inhabit the Antarctic region, with the majority distributed along the western Antarctic Peninsula [32]. In the Ross Sea, located in East Antarctica above 76° latitude, a few species highly adapted to low-light conditions, such as *Iridaea* sp., *Phyllophora antarctica*, *Phycodrys antarctica*, *Hildenbrandia lecannellieri*, *Monostroma hariotii*, and *Desmarestia menziesii*, have been documented [8]. Consequently, most research has primarily been conducted in the western Antarctic Peninsula and the South Shetland Islands. Despite the region's limited accessibility and the challenging weather conditions that are not conducive to research activities, there has been considerable progress in foundational studies on the taxonomic diversity, distribution, and life cycles of Antarctic macroalgae [5,8,12,33–36]. Moreover, extensive research has been conducted on the physiological responses of these algae to environmental conditions such as temperature [37,38], light [39,40], and salinity [41]. Additionally, various ecological studies have addressed aspects such as biomass [12,42,43], grazing [44,45], and succession [46]. Despite the breadth of these studies, research on the habitat substrates of *Desmarestia* species and *Himantothallus grandifolius* has been relatively limited to interpretations of these large brown algae, which are known to contribute the highest biomass in Antarctic marine ecosystems [4,5,12]. Moreover, studies on interspecific interactions have predominantly focused on the relationships between *Desmarestia* species and *H. grandifolius* [4,5]. These two large brown algae are canopy-forming species interacting with various smaller macroalgae, including understory species, forming complex assemblages. However, very few studies have attempted to explore the fundamental relationships among these diverse species.

The purpose of this study is to investigate the diversity of macroalgae inhabiting Maxwell Bay by examining the density, coverage, frequency, and biomass of these species. Additionally, the study aims to analyze the substrate composition of the macroalgal habitats and explore the relationship between substrate composition and macroalgal distribution. It includes identifying the substrate preferences of significant species and examining the affinity and interactions among them, thereby providing insights into the ecological dynamics of these macroalgal assemblage.

2. Materials and Methods

2.1. Study Area and Samplings

This study was conducted in Maxwell Bay, located on King George Island in the South Shetland Islands, 120 km from the Antarctic Peninsula. Of the nine study sites, six are located in Marian Cove, while the remaining three sites are situated in other areas within Maxwell Bay (Figure 1). Surveys were carried out during the austral summers of January and February in 2019 and 2024. Detailed information about each study site is well-documented in Ko et al. (2023) [19]. At each site, macroalgal assemblages were examined at depths of 5, 15, and 25 m via SCUBA diving. Data collection employed non-destructive methods, with five quadrats in 2019 and seven quadrats in 2024 photographed using an underwater camera (DSC-RX100M5A, Sony Corporation, Tokyo, Japan) at each depth (5, 15, and 25 m). To identify rare species and measure biomass, some destructive sampling was necessary, involving the removal of specimens from one of the five or seven quadrats. Easily identifiable species were identified directly from the photographs, while rare or difficult-to-identify species were collected and turned into specimens for identification in the laboratory. All macroalgae were classified to the lowest possible taxonomic level based on the taxonomy provided by the AlgaeBase database [47]. However, crustose coralline algae were categorized at the subfamily level (Melobesioideae) instead.

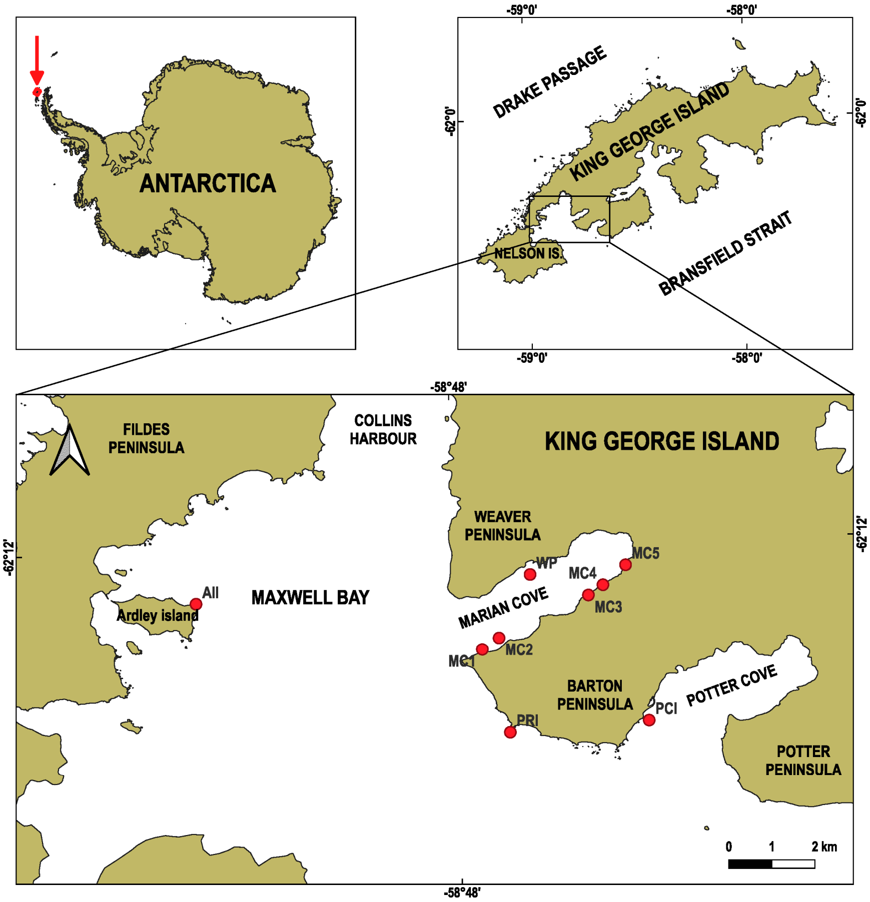


Figure 1. The nine survey sites in Maxwell Bay, King George Island, Antarctica. The red arrow indicates King George Island in the South Shetland Islands, located at the tip of the Antarctic Peninsula,

representing the area in the upper right map section. The map was created using a basemap provided by the British Antarctic Survey Geophysics Data Portal (BAS−GDP; http://geoportal.nerc-bas.ac.uk/GDP; accessed on 8 August 2024) and utilizing QGIS version 3.24 (https://qgis.org/; accessed on 8 August 2024).

2.2. Data Processing and Analysis

2.2.1. Macroalgal Assemblage and Significant Species

The coverage of each macroalgal species and substrate type within the quadrats was visually quantified to determine the macroalgal assemblage and substrate composition in the study area. When calculating the coverage for each substrate type, areas obscured by the macroalgal canopy in the photographs were marked as N.I. (not identified). The coverage of identified substrate types was then converted to percentages, resulting in relative coverage values. Substrate types were classified based on a modified version of Wentworth [48] grain size classification: rock (whole hard bottom), boulder (>256 mm), cobble (64–256 mm), pebble (4–64 mm), granule (2–4 mm), sand (0.0625–2 mm), and mud (<62.5 µm). The habitat substrate for the macroalgae investigated in this study is clearly a hard substrate, with at least sand serving as the attachment point. The classification of mud as a substrate was to reflect the high turbidity of the environment and does not imply that macroalgae directly attach to and inhabit the mud. Both the coverage and relative frequency of each macroalgal species were calculated, and biomass was measured in the laboratory by determining the wet weight of each species. A table was created to present the relative frequency, coverage, and biomass of all identified species. The 12 species with a 5% or more relative frequency were designated as significant species and used for the practical affinity analysis.

2.2.2. Variability of Substrate Composition by Significant Species

The average substrate type of the macroalgal habitat in Maxwell Bay was determined by calculating the mean relative coverage of each substrate type. The relative coverage of each substrate type at each site was computed to assess the variability of substrate composition across different sites. A resemblance matrix was created to compare the similarity of substrate compositions between sites, evaluating all possible site combinations. This matrix was then used to perform non-metric multidimensional scaling (nMDS) analysis, which included a substrate correlation vector plot. For each significant species, the average relative coverage of substrate types within the quadrats where the species were present was calculated to understand their substrate composition. Using these values, a resemblance matrix was developed to compare the substrate compositions for all combinations of significant species, including the average substrate cover (ASC). This matrix facilitated nMDS analysis to visually represent the similarity of substrate compositions among the significant species. Clustering was performed based on the similarity between significant species and their ASC, and this clustering was illustrated along with substrate-type correlations in a substrate vector plot. The similarity of substrate composition between species was categorized into four levels: the 100–75 percentile was labeled as "++", the 75–50 percentile as "+", the 50–25 percentile as "-", the and 25–0 percentile as "--".

2.2.3. Affinity from the Synchronous Occurrence of Macroalgae

To determine the affinity among 12 significant species, each species is treated as a host while the remaining species are considered neighbors. The affinity between the host species and each of the 11 neighbor species is calculated based on the relative frequency of the neighbors when the host is present. This process is repeated for all 12 significant species, and the affinity for each host–neighbor pair is defined as "1/relative frequency for host species". These affinity values are compiled into a matrix, resulting in 132 (12 × 11) pairs. The affinity values are visualized using polar graphs. Each of the three polar plots illustrate the affinity of neighbor species for one of the 12 significant species. The polar plots are divided into four arcs at 90-degree intervals, with each arc representing the affinity of 11 neighbor species for one host species. Higher affinity is indicated closer to the center of the polar plot, while lower affinity is further from the center. Radial scaling is expressed in natural logarithms to facilitate affinity comparisons among species. Due to the significant variation in occurrence frequencies among significant species, the relative distances indicated on the affinity scale can be distorted. Therefore, the occurrence frequency of each species is regarded as the expected frequency, and interspecific affinity values are compared and categorized into four levels:

- High affinity (++): greater than twice the expected frequency;
- Medium affinity (+): greater than the expected frequency;
- Low affinity (-): less than the expected frequency;
- Very low affinity (--): less than half the expected frequency.

2.2.4. The Combination of Substrate Composition Similarity and Affinity

To simultaneously interpret substrate composition and affinity among significant species, we constructed a substrate–affinity matrix by combining the four levels of substrate composition similarity and the four levels of affinity described in the previous section. This matrix consists of 16 cells formed by pairing substrate similarity levels ("--", "-", "+", "++") with affinity levels ("--", "-", "+", "++"). Out of the 132 possible host–neighbor pairs (12 hosts × 11 neighbors), four species—*Desmarestia anceps*, *Sarcopeltis antarctica* [49] (as *Gigartina skottsbergii* by [8]), *Trematocarpus antarcticus*, and *Pantoneura plocamioides*—did not co-occur with *Monostroma hariotii* as either a host or a neighbor, resulting in a total of 124 actual host–neighbor pairs. In the matrix, a double arrow indicates a two-way match between the substrate–affinity interaction for both species, while a single arrow indicates a one-way match, with the species at the head of the arrow being the host and the species at the tail being the neighbor.

The nMDS analysis used in this study was conducted with PRIMER 7 software (PRIMER-E, Ltd., Auckland, New Zealand). The data underwent standardization and square root transformation as a pre-treatment process before the analysis. The grouping overlaid on the nMDS plots reflects the results of the CLUSTER analysis based on the resemblance matrix.

3. Results

3.1. Macroalgal Assemblage and Habitat Structure

Thirty-one macroalgal species were recorded at the nine sites in the study area: 2 green algae, 10 brown algae, and 19 red algae (Table 1). Based on the relative frequency and coverage, the dominant species was *Palmaria decipiens*, while *Desmarestia anceps* had the highest biomass. Twelve species with a relative frequency of 5% or more were identified as significant species for this study. Following *P. decipiens*, *D. anceps* and *Himantothallus grandifolius* showed high coverage, likely due to the morphological characteristics of large brown algae. Additionally, *D. anceps* and *H. grandifolius* ranked first and second in biomass. The cumulative coverage of the 12 significant species (*P. decipiens*, Crustose coralline algae, *Plocamium* sp., *H. grandifolius*, *D. anceps*, *Picconiella plumosa*, *Desmarestia menziesii*, *Iridaea* sp., *Sarcopeltis antarctica*, *Monostroma hariotii*, *Trematocarpus antarcticus*, and *Pantoneura plocamioides*) was approximately 57%, covering 95% of the total coverage of about 60%, and the cumulative biomass amounted to 98% of the total biomass (or 2.48 kg out of 2.5 kg). This indicates that the significant species selected based on relative frequency sufficiently represent the macroalgal assemblage in the study area.

Based on the average substrate composition across nine sites in the study area, an nMDS analysis revealed six groups (MC3-MC4, MC1-MC2, PRI-PCI, MC5, WP, and AII) with a similarity level of 80% (Figure S1). This clustering indicates that within Marian Cove, the substrate composition at the sites is associated with mud and rock types. The site closest to the glacial retreat area, MC5, showed a predominance of mud, whereas rock became more dominant further from the glacier. The three sites near the glacial retreat area—MC3, MC4, and MC5—exhibited a development of mud substrates influenced by the high turbidity typical of glacial retreat regions, with MC5 being distinguished by a particularly high turbidity compared to MC3 and MC4. In contrast, the outermost sites in Marian Cove, MC1 and MC2, were associated with rock substrates and shared over 70% similarity in substrate composition with sites PRI and PCI located around Barton Peninsula. The site AII, located on the western side of Maxwell Bay, was associated with sand and granules and exhibited a distinct substrate composition compared to the sites near Barton Peninsula.

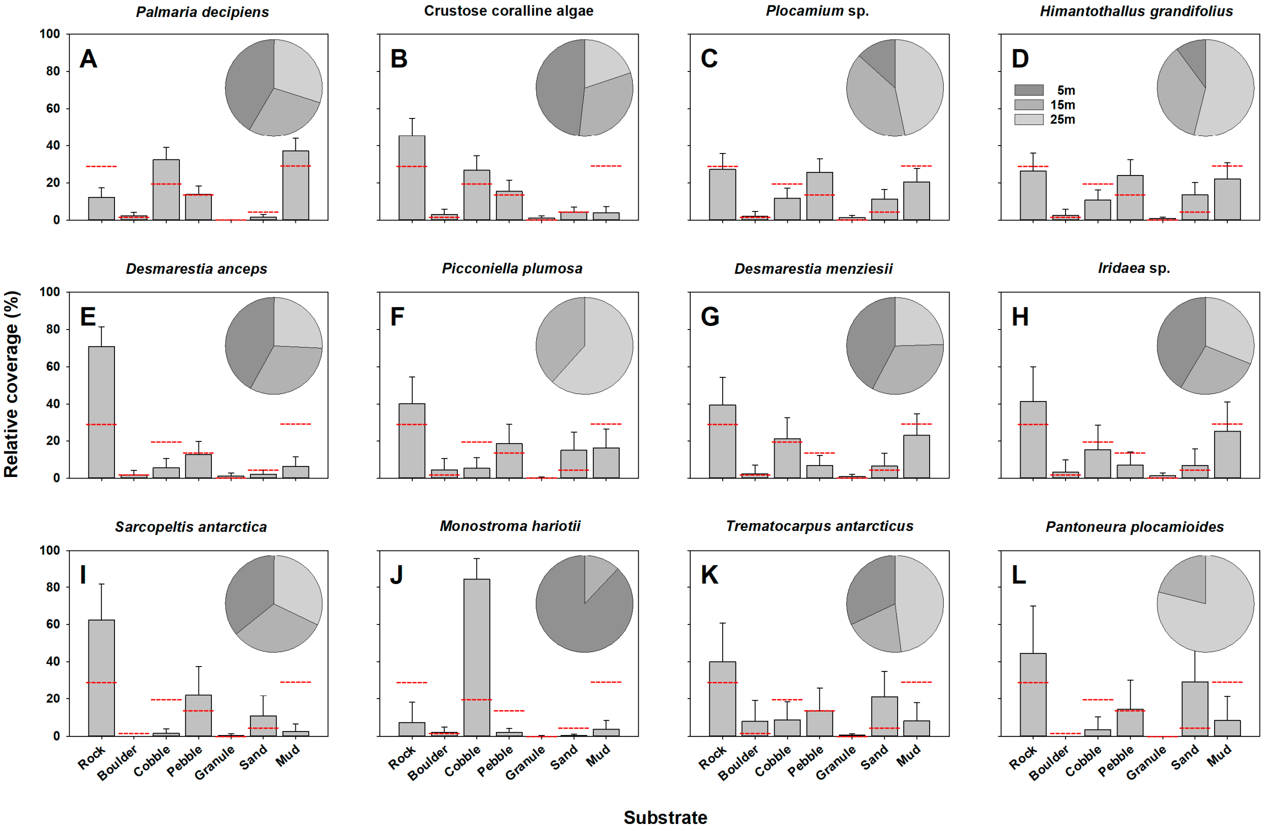
Table 1. Relative frequency, coverage, and biomass of macroalgal species on Maxwell Bay, King George Island, Antarctica.

Group	Species	Relative Frequency	Coverage (%)		Biomass (Wet wt. g m^{-2})	
			Mean	S.E.	Mean	S.E.
Red	*Palmaria decipiens*	50.62%	13.70	1.31	327.59	83.64
Red	Crustose coralline algae	32.72%	3.11	0.44	-	-
Red	*Plocamium* sp.	32.72%	7.46	1.00	146.69	51.51
Brown	*Himantothallus grandifolius*	27.47%	11.06	1.33	612.22	179.75
Brown	*Desmarestia anceps*	22.84%	12.77	1.67	1230.32	508.66
Red	*Picconiella plumosa*	14.51%	2.12	0.45	11.10	5.62
Brown	*Desmarestia menziesii*	13.89%	3.44	0.85	0.93	0.85
Red	*Iridaea* sp.	8.95%	0.52	0.17	55.44	28.15
Red	*Sarcopeltis antarctica*	8.64%	1.75	0.49	55.33	25.73
Green	*Monostroma hariotii*	7.72%	0.30	0.11	0.59	0.32
Red	*Trematocarpus antarcticus*	7.72%	0.57	0.18	25.28	20.81
Red	*Pantoneura plocamioides*	5.86%	0.44	0.12	13.89	6.84
Brown	*Desmarestia antarctica*	3.70%	0.80	0.31	14.46	9.94
Red	*Phycodrys antarctica*	2.78%	0.11	0.04	2.91	1.74
Green	*Ulva hookeriana*	2.78%	0.03	0.01	0.12	0.12
Brown	*Phaeurus antarcticus*	2.16%	0.03	0.02	1.63	1.32
Brown	*Ascoseira mirabilis*	1.85%	0.48	0.25	-	-
Brown	*Cystosphaera jacquinotii*	1.54%	0.32	0.19	-	-
Red	*Myriogramme manginii*	1.54%	0.07	0.04	0.14	0.14
Red	*Meridionella antarctica* *	1.23%	0.27	0.14	-	-
Red	*Ahnfeltia plicata*	1.23%	0.07	0.04	1.16	1.13
Brown	*Halopteris obovata*	1.23%	0.08	0.04	1.39	1.17
Brown	*Petroderma maculiforme*	0.93%	0.17	0.13	-	-
Red	*Ballia callitricha*	0.62%	0.10	0.07	-	-
Red	*Delisea pulchra*	0.62%	0.01	0.01	-	-
Red	*Georgiella confluens*	0.62%	0.04	0.03	3.27	2.74
Red	*Notophycus fimbriatus*	0.62%	0.05	0.05	-	-
Brown	*Adenocystis utricularis*	0.31%	0.00	0.00	0.02	0.02
Brown	*Desmarestia* spp. **	0.31%	0.01	0.01	0.11	0.08
Red	*Myriogramme smithii*	0.31%	0.01	0.01	2.42	2.42
Red	*Neuroglossum ligulatum*	0.31%	0.00	0.00	-	-

* Meridionella antarctica [50] (as Acanthococcus antarcticus by [8]). ** Unidentifying between *D. anceps* and *D. menziesii* from photo.

3.2. Substrate Composition Characteristics by Significant Species

The relative coverage of substrate types for significant species and the depth distribution of significant species are shown in Figure 2. Additionally, the results of the nMDS analysis based on the substrate composition of significant species are presented in Figure 3. *Palmaria decipiens* showed higher relative coverage of cobbles and mud compared to the average substrate cover. In comparison, its coverage of rock was lower than that (Figure 2A). Crustose coralline algae were predominantly found on hard substrates, resulting in a higher rock cover than the average substrate cover and a lower mud cover, with a notable presence at shallower depths (Figure 2B). *Plocamium* sp. and *Himantothallus grandifolius* exhibited a higher relative coverage of pebbles than the average substrate cover and had a prominent distribution at a depth of 25 m. The substrate composition of these two species was over 90% similar (Figures 2C,D and 3). *Desmarestia anceps* showed a strong preference for rock compared to its congener *Desmarestia menziesii*, with a notable avoidance of mud (Figure 2E). *Picconiella plumosa* and *Trematocarpus antarcticus* demonstrated a substrate composition similarity of over 90% and showed a distinct preference for sand. Notably, *P. plumosa* was found to inhabit relatively deeper waters (Figures 2F,K and 3). *Desmarestia menziesii* and *Iridaea* sp. showed similar substrate distributions with over 90% similarity, indicating a widespread and even distribution across Maxwell Bay (Figures 2G,H and 3). *Sarcopeltis antarctica* showed a high affinity for rock similar to *D. anceps*, while *Monostroma hariotii* showed a strong preference for cobbles (Figure 2I,J). *Pantoneura plocamioides*, like *P. plumosa* and *T. antarcticus*, showed a significant preference for sand, but the similarity in substrate composition between these two species was not high (Figures 2L and 3).



Palmaria decipiens

Crustose coralline algae

Plocamium sp.

Himantothallus grandifolius

Desmarestia anceps

Picconiella plumosa

Desmarestia menziesii

Iridaea sp.

Sarcopeltis antarctica

Monostroma hariotii

Trematocarpus antarcticus

Pantoneura plocamioides

Figure 2. Relative substrate coverage and species occurrence by depth for significant species. Subfigures (**A**–**L**) represent the significant species individually (**A**) *Palmaria decipiens*; (**B**) Crustose coralline algae; (**C**) *Plocamium* sp.; (**D**) *Himantothallus grandifolius*; (**E**) *Desmarestia anceps*; (**F**) *Picconiella plumosa*; (**G**) Desmarestia menziesii; (**H**) *Iridaea* sp.; (**I**) *Sarcopeltis antarctica*; (**J**) *Monostroma hariotii*; (**K**) *Trematocarpus anstarcticus*; (**L**) *Pantoneura plocamioides*. The bar charts show the relative coverage of each substrate (mean ± S.E.), while the pie charts depict the relative occurrence frequency of each species by water depth. The red dotted line overlaid on the bar charts represents the average substrate cover across the entire study area.

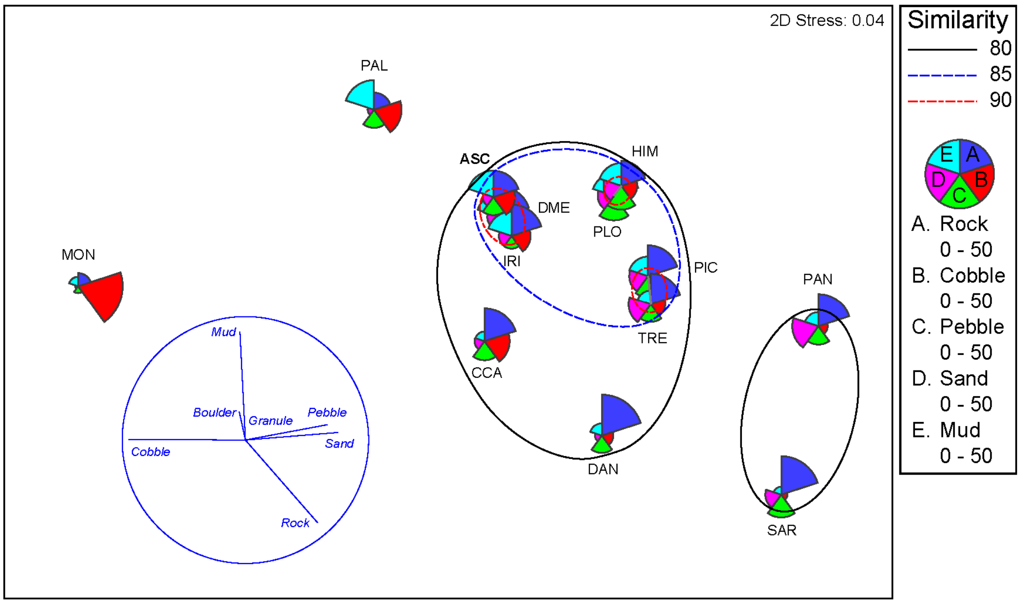


Figure 3. Segmented bubble plot for nMDS with superimposed vector plot showing correlation with substrate. ASC: average substrate cover; PAL: *Palmaria decipiens*; CCA: Crustose coralline algae; PLO: *Plocamium* sp.; HIM: *Himantothallus grandifolius*; DAN: *Desmarestia anceps*; PIC: *Picconiella plumosa*; DME: *Desmarestia menziesii*; IRI: *Iridaea* sp.; SAR: *Sarcopeltis antarctica*; MON: *Monostroma hariotii*; TRE: *Trematocarpus antarcticus*; PAN: *Pantoneura plocamioides*.

3.3. *Affinity among Significant Species*

The affinity between significant species, defined as the reciprocal of the frequency of neighbor species occurring in the presence of the host species, is illustrated in Figure 4. In the polar plots, the affinity between host and neighbor species is indicated by the proximity of scatter circle dots to the center of the plot, with dots closer to the center representing higher affinity and those further away indicating lower affinity. It should be noted that differences in species occurrence frequencies may distort the affinity depicted in the polar plot. For instance, since *Palmaria decipiens* has a relative frequency exceeding 50% (Table 1), it inevitably shows high affinity when *P. decipiens* are neighbors. To correct for this distortion, affinity values are compared to the expected frequency (Table 1; relative frequency). If the host–neighbor affinity exceeds the expected frequency, it is interpreted as genuinely high, whereas values below the expected frequency are considered genuinely low. Consequently, affinity was categorized into four levels based on comparison with the species-specific expected frequency (see Section 2.2.3).

The host–neighbor affinity analyzed using this method reveals that *Plocamium* sp., *Himantothallus grandifolius*, *Picconiella plumosa*, *Iridaea* sp., and *Pantoneura plocamioides* exhibit mutual high affinity, suggesting that these species co-occur in the study area (Figure 4C,D,F,H,L). Conversely, *Palmaria decipiens* and *Monostroma hariotii* show very low affinity (Figure 4A,J). Notably, despite having the highest relative frequency (Table 1), *P. decipiens* tends to inhabit environments with lower richness, alone or with very few other species. Similarly, *M. hariotii* is predominantly found at shallower depths (Figure 2J) and is less likely to co-occur with other species due to lower richness in these shallow zones. Crustose coralline algae and *Sarcopeltis antarctica* displayed medium levels of affinity, showing no strong associations with any particular species (Figure 4B,I). The two species within the genus *Desmarestia* exhibited very low affinity (Figure 4E,G). The low similarity in the composition of habitat substrates (Figures 2E,G and 3) indicates that this is a result of differences in habitat preference. Most host–neighbor affinities were bidirectional; however, *P. decipiens* (host) and *D. menziesii* (neighbor), *Trematocarpus antarcticus* (host) and *D. anceps* (neighbor), and *Pantoneura plocamioides* (host) and *S. antarctica* (neighbor) demonstrated high affinity when the relationship was in one direction, but did not show high affinity when reversed, indicating one-way interactions (Figure 4A,K,L).

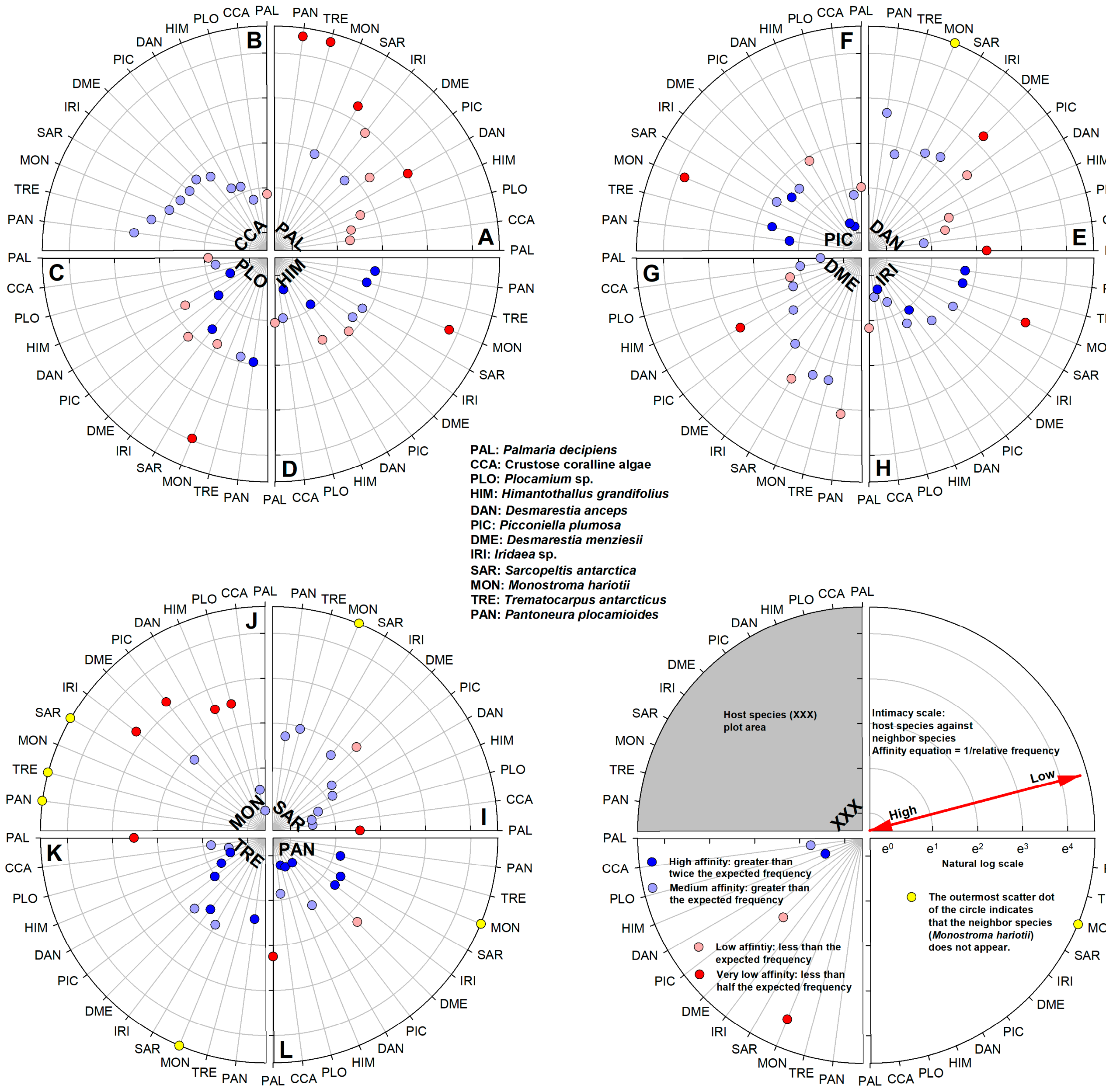


Figure 4. Polar plots of interspecies affinity based on neighbor species occurrence frequency in the presence of host species. High affinity (blue circle): greater than twice the expected frequency; Medium affinity (light blue circle): greater than the expected frequency; Low affinity (light red circle): less than the expected frequency; Very low affinity (red circle): less than half the expected frequency. (**A**) PAL (*Palmaria decipiens*); (**B**) CCA (Crustose coralline algae); (**C**) PLO (*Plocamium* sp.); (**D**) HIM (*Himantothallus grandifolius*); (**E**) DAN (*Desmarestia anceps*); (**F**) PIC (*Picconiella plumosa*); (**G**) DME (*Desmarestia menziesii*); (**H**) IRI (*Iridaea* sp.); (**I**) SAR (*Sarcopeltis antarctica*); (**J**) MON (*Monostroma hariotii*); (**K**) TRE (*Trematocarpus antarcticus*); (**L**) PAN (*Pantoneura plocamioides*).

3.4. The Combination of Substrate Composition Similarity and Affinity

In this study, we created a substrate–affinity matrix to simultaneously analyze substrate composition and affinity among significant species that were previously examined independently (Figure 5). Out of 124 pairwise comparisons, 61 pairs (about 50%) were categorized into four cells: "--/--", "-/-", "+/+", and "++/++", reflecting changes in affinity corresponding to substrate similarity. This shows that affinity and substrate similarity are positively correlated for half of the species pairs. Pairs with high substrate similarity and high affinity ("++/++") include *Plocamium* sp., *Picconiella plumosa*, *Himantothallus grandifolius*, *Iridaea* sp., and *Trematocarpus antarcticus*. These species prefer similar substrates (Figures 2 and 3) and co-occur (Figure 4). Conversely, pairs with very low substrate similarity and very low affinity ("--/--") involve *Palmaria decipiens* and *Monostroma hariotii* with other species, indicating these species have distinct habitat preferences and weak interactions with others. No pairs were found with very high substrate similarity and very low affinity ("--/++") or very low substrate similarity and very high affinity ("++/--"). However, pairs such as *Iridaea* sp.–*Sarcopeltis antarctica*, Crustose coralline algae–*M. hariotii*, and *Desmarestia menziesii*–*M. hariotii*, which show very low substrate similarity but medium affinity ("+/--"), suggest clear interactions independent of substrate similarity. Similarly, pairs like *Plocamium* sp.–*H. grandifolius* and *Iridaea* sp.–*Pantoneura plocamioides*, with low substrate similarity but very high affinity ("++/-"), also indicate significant interactions beyond substrate effects. The pair *Plocamium* sp.–*D. menziesii*, showing high substrate similarity but low affinity ("-/++"), and *D. anceps*–*Plocamium* sp., with high substrate similarity but low affinity ("-/+"), suggest that interactions between *Desmarestia* spp. and *Plocamium* sp. may be influenced more by biological factors than by substrate similarity. Interactions involving crustose coralline algae show a wide range of substrate similarity and affinity levels, indicating weaker interactions with other species. This suggests that environmental factors such as turbidity and depth (Figure 2), particularly light availability, are crucial in shaping the habitat of this species.

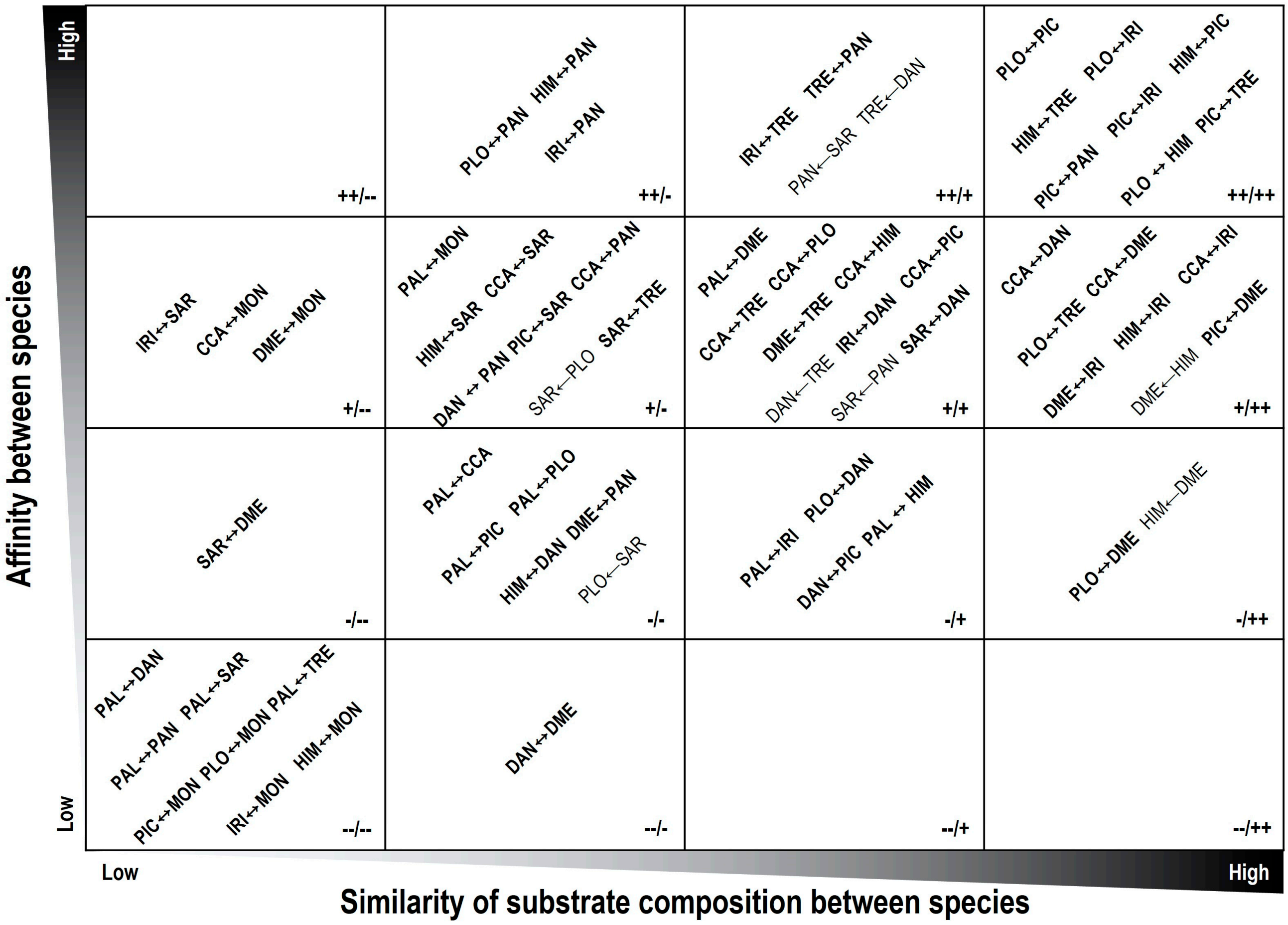


Figure 5. Substrate—affinity matrix for interaction between all combinations of significant species. The double arrow indicates a two-way interaction where both species act as host and neighbor, while

the single arrow represents a one-way interaction where the species at the head of the arrow is the host and the species at the tail is the neighbor. Only the two-way interaction is highlighted in bold. PAL: *Palmaria decipiens*; CCA: Crustose coralline algae; PLO: *Plocamium* sp.; HIM: *Himantothallus grandifolius*; DAN: *Desmarestia anceps*; PIC: *Picconiella plumosa*; DME: *Desmarestia menziesii*; IRI: *Iridaea* sp.; SAR: *Sarcopeltis antarctica*; MON: *Monostroma hariotii*; TRE: *Trematocarpus antarcticus*; PAN: *Pantoneura plocamioides*.

4. Discussion

4.1. Habitat Characteristics and Affinity of Pioneer Species: Palmaria decipiens and Monostroma hariotii

Palmaria decipiens is a species commonly found throughout Antarctica, including the Ross Sea, and is known as the most dominant species in terms of density [8,11,51]. In this study, it was also identified as the most dominant species based on frequency and coverage, ranking high in biomass as well (Table 1). This species is a pioneer; it is the first to colonize newly exposed hard substrates in glacial retreat areas [52] and it thrives in the most disturbed sites [42]. Additionally, *P. decipiens* is a euryhaline species and is highly adapted to shaded environments [51,53]. These ecological characteristics enable it to survive in the harshest conditions of glacial retreat areas in Antarctica and to adapt well to the extreme environmental changes of the intertidal zone [17,19]. Interestingly, despite being highly abundant—appearing in 50% of all quadrats surveyed—*P. decipiens* exhibited low affinity with other significant species except for *Monostroma hariotii* and *Desmarestia menziesii* (Figure 4A). This result is attributed to the high relative frequency of *P. decipiens*, as 80 of the 324 quadrats analyzed contained only one species, 51 of which were solely *P. decipiens* (Figure S2). Although *P. decipiens* is the most frequently occurring species in Maxwell Bay, it primarily inhabits sites at an early successional stage, where the macroalgal assemblage is not yet fully developed (e.g., near the glacier in Marian Cove). Consequently, despite its dominance, interactions with other species were limited. In fact, of the 161 quadrats where *P. decipiens* was found, it appeared alone in 51 (about 31%). Therefore, the low affinity of *P. decipiens* with other species in Maxwell Bay can be attributed to the ecological characteristics of its habitat. As the macroalgal assemblage in this region progresses to more developed successional stages, it is likely that the dominance of *P. decipiens* will decrease, and species with higher interspecific affinity, such as *Plocamium* sp., *Himantothallus grandifolius*, *Picconiella plumosa*, *Iridaea* sp., *Trematocarpus antarcticus*, and *Pantoneura plocamioides*, will expand their presence.

Monostroma hariotii, like *Palmaria decipiens*, is a well-known pioneer species that inhabits the most disturbed sites in Antarctica [8,42]. It is a representative non-endemic species in the region, colonizing barren stones in the early stages of succession, particularly favoring rocky substrates with sand-filled crevices [5,52]. In this study, *M. hariotii* was frequently found on cobbles, which differs from the previously known habitat preferences [5]. The characteristic of colonizing the most denuded areas, as reported in previous studies [5], supports the observed low affinity with species like *Sarcopeltis antarctica*, *Trematocarpus antarcticus*, and *Pantoneura plocamioides*, with which it does not co-occur (Figure 4J).

Both *Palmaria decipiens* and *Monostroma hariotii* are involved in species pairs that exhibit very low substrate composition similarity and very low affinity (Figure 5, “--/--”). While this can be interpreted as a result of differences in their habitat substrates, it may also reflect their similar ecological traits as pioneer species, such as opportunistic colonization and competitive disadvantage with other species. Particularly *P. decipiens*, which, despite being a pioneer species and the dominant species, presents an intriguing and somewhat paradoxical case of showing low interaction with other species.

4.2. Interconnected Core Group within Significant Species

Plocamium sp., *Himantothallus grandifolius*, *Picconiella plumosa*, *Iridaea* sp., and *Trematocarpus antarcticus* form a highly interconnected species group characterized by both high substrate composition similarity and high affinity (Figure 5; "++/++"). The high mutual affinity and strong interspecific interactions among these five substrate composition species, which share over 85% similarity with the average substrate cover (Figure 3), indicate that they form a core group of significant species within the study area, Maxwell Bay. The substrate composition among these core group species exceeds 85%, demonstrating their presence in the typical substrate composition of the study area. Additionally, these species are representative shade-adapted species [8], primarily found at mid-depths (below 15 m) (Figure 2). Notably, *Himantothallus grandifoliusis* one of the largest canopy-forming species in Antarctica and, along with *Desmarestia* species, represents a dominant component of the region's biomass [32,42]. In our study, *H. grandifolius* recorded the second-highest biomass, following *Desmarestia anceps*, with a value of 612.22 g wet wt. m^{-2} (Table 1). Previous studies have reported biomass values ranging from 1250 to 10,336 g wet wt. m^{-2} [12,43], which are more than double the levels observed in our study. In areas where *H. grandifolius* dominates, it forms a dense canopy, but species such as *Plocamium* sp. and *P. plumosa*, which are strongly shade-adapted, thrive in the understory beneath this canopy. This relationship is reflected in the high affinity observed between these species (Figure 4D). The coverage of the core group species is approximately 36%, exceeding that of *Desmarestia* species, which is approximately 28%. In terms of biomass, the core group accounts for around 34%, while *Desmarestia* species contribute 50%. These findings suggest that both the core group and *Desmarestia* species are key to understanding the macroalgal assemblage in Maxwell Bay.

4.3. Desmarestia spp.: Similar but Not Together

Three species of the genus *Desmarestia*—*D. anceps*, *D. menziesii*, and *D. antarctica*—were observed in the study area (Table 1). While *D. antarctic*a is morphologically distinct and likely an annual, *D. anceps* and *D. menziesii* share morphological similarities that make them difficult to distinguish, particularly in their juvenile stages [54]. When comparing the habitats of these two species, our study found that *D. anceps* tends to develop more on rocky substrates and is more prevalent in environments with lower mud content (and thus lower turbidity) compared to *D. menziesii* (Figure 2E,G). Additionally, the affinity between these two species was very low (Figure 4E,G). This relationship can be characterized by both low substrate composition similarity and low affinity (Figure 5). Previous studies have also noted distinct habitats for these two species. For instance, Klöser et al. (1996) [5] reported that *D. anceps* and *D. menziesii* occupy clearly distinct habitats, a conclusion supported by Quartino et al. (2001) [11]. While our findings align with these earlier results, it's important to note that previous interpretations were primarily based on species profiling according to depth and substrate type. In contrast, our study compared species affinity and substrate composition based on frequency, offering a new perspective. Before the study by Klöser et al. (1996) [5], environments dominated by *D. menziesii* with *D. anceps* intermixed had been reported [12,55]. However, studies by Klöser et al. (1996) [5] and Quartino et al. (2001) [11] have suggested that *D. anceps* inhabit relatively deeper waters (mid-depth) and is more abundant in low-turbulence environments compared to *D. menziesii*. Our findings indicate little difference in the depth distribution between these two species (Figure 2E,G), which diverges somewhat from the previous results. In particular, a study conducted in Potter Cove, not far from the PCI site, found that *D. anceps* was more prevalent on sandy substrates, whereas *D. menziesii* favored boulder-dominated substrates [11], which also contrasts with our results. These differences in findings may reflect the broader range of habitats covered in our study, suggesting that site variation could account for the discrepancies. Furthermore, while Küpper et al. (2019) [54] noted that distinguishing between *D. anceps* and *D. menziesii* using keys is challenging, it is possible to differentiate the two in adults based on holdfast structure—*D. anceps* having a hapteroid holdfast and *D. menziesii* a discoid holdfast [8]. Although this structural difference in holdfasts could influence substrate preferences, it is beyond the scope of this study to establish a causal relationship. However, the prevalence of *D. anceps* on sandy substrates [11], where a hapteroid holdfast would struggle to attach, might be best interpreted as a site-specific outcome.

4.4. What Can Be Discerned from Substrate Composition Similarity and Affinity?

In this study, we aimed to provide insights into the relationships among species by interpreting the substrate preferences and affinity levels between the significant species comprising the macroalgal assemblage in Antarctica. Notably, our study did not observe cases where the substrate composition, which was expected to be the most significant factor in species interactions, was highly similar with low affinity or, conversely, highly dissimilar with high affinity (Figure 5). However, we identified intriguing interspecific correlations, such as the strong affinity observed between *Pantoneura plocamioides* and each of *Plocamium* sp., *Himantothallus grandifolius*, and *Iridaea* sp., despite their dissimilar substrate compositions. Another notable relationship was found between *Monostroma hariotii* and crustose coralline algae, as well as between *Desmarestia menziesii* and the *Iridaea* sp.–*Sarcopeltis antarctica* pair, where the substrate compositions were also dissimilar, but the affinity levels were moderate. *Pantoneura plocamioides*, which ranked high among significant species in terms of frequency, coverage, and even biomass, exhibited a strong correlation with *Plocamium* sp. and *H. grandifolius*, regardless of niche similarity. This suggests a significant association between these species, with *P. plocamioides* likely fluctuating in response to the population dynamics of these two dominant species.

Research on the interactions among species within macroalgal assemblages has traditionally focused on competition-based studies [21,22,56,57]. Recently, various studies have explored the interactions between invasive and endemic species from a competitive perspective [30,31]. Additionally, there has been considerable research on the relationships between macroalgae and other taxonomic groups, such as coral [28,29], epiphytic bacteria [58,59], and fauna [60]. However, studies focusing on the interrelationships among macroalgae themselves have primarily employed removal experiments to elucidate competitive and symbiotic relationships among a few conspicuous species within an assemblage [23,61,62]. Reports specifically addressing the interactions among species within the assemblage, without interpreting these relationships, remain scarce.

4.5. Additional Considerations

In the South Orkney Islands, *Himantothallus grandifolius* is known to inhabit deeper areas than *Desmarestia* species, with a notable preference for substrates composed of sand and smaller-sized pebbles [4]. Similar observations have been made near Potter Peninsula on King George Island, where differences in the depth preferences of these two species were reported. *Desmarestia* species showed a strong affinity for solid substrata, while *H. grandifolius* preferred smaller-grained substrates [5]. Studies conducted in Potter Cove further highlighted the spatial separation of these two species, noting that *Desmarestia* species are more dominant in these areas [11]. The ecological characteristics of these kelp-like brown algae, as demonstrated by the differences in substrate composition, affinity, and depth between *H. grandifolius* and *Desmarestia anceps*/*Desmarestia menziesii*, strongly support previous research findings (Figure 2D,E,G and Figure 4D,E,G). In particular, the interpretation of spatial separation is well-explained by the low affinity between those species observed in our study.

One of the intriguing findings of our study is that most species interactions (affinity) were bidirectional. Specifically, 94% of the possible species pairs among the significant species (116 out of 124 pairs) exhibited high affinity in both directions; if one species served as the host and showed high affinity with its neighbor, the relationship remained strong when the roles were reversed. For example, *Himantothallus grandifolius* and *Plocamium* sp. displayed high affinity regardless of which species acted as the host (Figure 4C,D). This indicates that most interspecific interactions are not one-sided but rather are mutual. However, we identified four species pairs—*Desmarestia menziesii* and *Himantothallus grandifolius*; *Desmarestia anceps* and *Trematocarpus antarcticus*; *Sarcopeltis antarctica* and *Plocamium* sp.; and *Sarcopeltis antarctica* and *Pantoneura plocamioides*—that exhibited one-way interactions (Figure 5; resulting in eight host–neighbor combinations). Our findings suggest that these one-way interactions may be attributed to differences in substrate composition. Although our study does not provide a direct ecological interpretation of these one-way interactions, it raises the possibility that various factors, including abiotic elements, may play a role in these species' relationships.

The ecological question of how biological interactions shape communities has been a long-standing topic of inquiry. Deriving general principles from the interpretation of these interactions is both challenging and complex. Community structure is determined by factors such as competition, predation, colonization, and chance events, and various interpretations have been proposed to understand these factors [63]. In 1975, Jared Diamond introduced the concept of "assembly rules" to describe species distribution patterns within different communities, using absent–present data to interpret these patterns [64]. Since Diamond suggested that species distributions within communities are determined by competition, debates have persisted for decades regarding the roles of chance, evolutionary perspectives, and other factors [65–67]. In our study, we aimed to provide foundational data for interpreting the interrelationships among species that compose Antarctic macroalgal assemblages. We focused on simple relationships between species—such as the frequent co-occurrence of *Himantothallus grandifolius* and *Plocamium* sp., in contrast to *Monostroma hariotii*, which is rarely observed with other species—to explore the interactions that constitute assembly rules. To achieve this, we reinterpreted the concept of affinity among species pairs by using the relative frequency of neighboring species, similar to the absent–present data used in assembly rules. This approach allows for a straightforward graphical representation of species relationships by translating these into a relative distance—although this distance does not have an absolute meaning—making the interactions easier to comprehend. The method proposed in our study is not only useful for interpreting macroalgal assemblages as it also possesses versatility, making it applicable to any research involving quadrats. While this approach may not provide deep insights into the specifics of species interactions, it offers various perspectives on the relationships between species, potentially laying the groundwork for future research.

5. Conclusions

In this study, we have delved into the complex interactions and substrate preferences of Antarctic macroalgae, revealing significant insights into their ecological dynamics. Our research highlights the dominance of *Palmaria decipiens* in terms of frequency and coverage, as well as the unique substrate associations of species like *Desmarestia anceps* and *Himantothallus grandifolius*. These findings underscore the intricate interspecific relationships within this fragile ecosystem, where substrate similarity and species affinity often align to form tightly interconnected communities. However, notable exceptions exist, such as the low affinity of pioneer species like *P. decipiens* and *Monostroma hariotii*, which thrive in more isolated conditions, reflecting their early successional roles. This study not only enriches our understanding of Antarctic marine ecosystems but also sets the stage for future research into the mechanisms driving these interactions, offering a valuable baseline for ecological monitoring efforts in this rapidly changing environment.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d16100628/s1, Figure S1: The non-metric multidimensional scaling (nMDS) plot based on site-specific substrate composition; Figure S2: Frequency graph of the number of species observed per quadrat and stacked bar chart of single-species occurrences.

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writing—review and editing, Y.W.K., K.M.Y. and H.-G.C.; visualization, Y.W.K.; supervision, H.-G.C.; project administration, H.-G.C.; funding acquisition, H.-G.C. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement: The data utilized in this study have been processed into a primary form and uploaded to the Korea Polar Data Center (KPDC) (https://kpdc.kopri.re.kr/; accessed on 8 August 2024). Macroalgal samples collected during this research have been prepared as specimens and are registered and managed in the KOPRI Virtual Herbarium (KVH) (https://kvh.kopri.re.kr/; accessed on 8 August 2024). Further data will be made available upon request.

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