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# The Roles of Alpha, Beta, and Functional Diversity Indices in the Ecological Connectivity between Two Sub-Antarctic Macrobenthic Assemblages

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**Abstract:** The study of ecological connectivity is a global priority due to the important role it plays in the conservation of diversity. However, few studies in this context have focused on marine benthic ecosystems. To address this issue, the present work determines the ecological connectivity between two sub-Antarctic macrobenthic assemblages through assessment of the α-, β-, and functional diversity indices. Samples were collected using a van Veen grab at stations located in Bahia Inútil and Seno Almirantazgo. The ecological analysis was based on a total of 113 invertebrate taxa. The mean abundance values were lower in Bahia Inútil (888.9 ± 26.8 ind $m^{-2}$) than in Seno Almirantazgo (1358.6 ± 43.4 ind $m^{-2}$). While the mean α-diversity values showed significant differences between assemblages, β- and functional diversity indices presented no significant differences. These results indicate that, despite the distance (56 km) separating the two basins from each other, there is a high degree of connectivity at the functional level between the assemblages due to the high number of shared species and their functional traits. The species most responsible for this observation were the polychaetes *Capitela capitata* and *Aricidia* (*Acmira*) *finitima*, as well as the bivalves *Nucula pisum* and *Yoldiella* sp. 1. In terms of functional biodiversity, species characterized as omnivorous and with lecithotrophic larval development were mostly responsible for connectivity between assemblages. These results suggest the importance of including β- and functional diversity indices as criteria in the future planning of marine protected areas for the maintenance of marine ecosystem integrity.

**Keywords:** Tierra del Fuego; species richness; species abundance; taxonomic composition; feeding mode

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## 1. Introduction

Ecological connectivity (EC) is widely recognized by the scientific community and decision-makers as a global priority for preserving ecosystem diversity and functionality [1,2]. Furthermore, it is a fundamental component for the regulation of ecological processes [3,4], landscape resilience, and the provision of general ecosystem services [5–7]. However, EC studies are poorly developed with regard to marine ecosystem investigations [8].

Although EC is a concept widely used in the context of terrestrial ecosystem studies, no scientific consensus has been reached regarding the understanding of the EC concept for marine ecosystems. For instance, there are numerous associated definitions, leading to considerable scientific debate [9]. In fact, the definition of EC may change depending on whether the study is at the population, community, or ecosystem level, and it can also change depending on the geographic area where the research is conducted [10,11]. For example, Endo et al. [12] defined EC as the simple exchange of individuals within assemblages of coral reef communities. In contrast, Nagelkerken [13] focused the definition on interactions between ecosystems through the movement of species and the exchange of both nutrients and organic matter, which are part of the ecological processes occurring in tropical coral reefs, mangroves, and seagrasses. Thrush et al. [14] defined it as the ability to transport organic matter and species between communities in Antarctic areas. In a more global context, Balbar and Metaxas [15] defined EC as a link developed through the exchange of genes, organisms, and energy between populations, communities, or ecosystems. The lack of a unified definition of EC makes its determination and study difficult. In our study, EC is defined as the linkage between assemblages through the turnover levels of the species (e.g., shared species among assemblages versus exclusive species of each assemblage) and/or their ecological attributes; depending on these, EC among assemblages may show a high or low linkage.

Several methods exist for measuring EC in benthic marine ecosystems, which broadly fall into two categories. The first category of measurements examines EC among benthic assemblages by calculating the β-diversity [14,16], which describes species turnover among assemblages in terms of species composition [17]. β-diversity is assessed according to qualitative indices (presence/absence) [18,19] or quantitative similarity analysis (abundance) [2,19], which have also been used as measures of EC. Consequently, we use both approaches as a suitable framework for connectivity assessments among benthic assemblages. The second category of measurements involves determining the degree of connectivity through quantifying larval dispersal [20–23]. However, this category is hardly applied to benthic assemblages because it is difficult to determine the source area of the larval pool as well as the linkage between a meroplankton larva and the corresponding benthic adult organism [21,24–26]. These factors make the reliable measurement of connectivity between benthic assemblages complex. However, these limitations can be solved through the application of functional diversity, which encompasses functional traits of species such as the type of larval development, trophic mode, and mobility, among others [27]. In recent decades, studies using functional diversity have undergone significant development in marine research, from populations to ecosystems [28–31]. Despite these advances, there remain few empirical studies that have considered functional diversity as a part of EC between benthic assemblages [32]. Therefore, studies that investigate functional relationships with EC are highly required, by both the scientific community and relevant authorities, for the development of marine protected area (MPA) management plans [9,33,34].

The Patagonian marine ecosystem constitutes the most important area of fjords and channels in the southern hemisphere and is one of the most extensive on the planet, together with similar ecosystems in Scandinavia, Iceland, Norway, Greenland, and Alaska [35,36]. Regarding this ecosystem, the presence of hundreds of channels and fjords builds up an enormous oceanographic web, where the channels play a role as natural corridors, interconnecting marine communities that inhabit this ecosystem. Additionally, the Patagonian region is one of the most pristine areas worldwide [37]. Consequently, there are eleven marine protection areas comprising 41% of the total region [38]. In this ecosystem, there have been numerous investigations focused on determining the traditional α-diversity for sublittoral soft-bottom benthic assemblages [39–46]. However, studies using the β-diversity index are scarce. In fact, Villalobos et al. [47] determined the β-diversity for benthic communities, and their results highlighted an important percentage of species (48%) turnover in an environmental gradient along the Comau fjord (Norther Patagonian). In contrast, research conducted on the benthic community of central Patagonia has described a β-diversity along a bathymetric gradient. However, the existing literature lacks analyses of β-diversity as a component of connectivity. Nevertheless, knowledge of the EC among benthic communities of MPA and their surrounding areas is essential. In the Patagonia ecosystem, this knowledge is missing.

From a theoretical point of view, β-diversity has a converse relationship with EC [48]. In this context, our working hypothesis is that there will be low β-diversity values between two comparable benthic assemblages; consequently, they will have a high EC. This emergent characteristic will be a consequence of the high shared species numbers with omnivorous and lecithotrophic larval development. Therefore, the objective of this work was to determine the ecological connectivity between two benthic assemblages, one located in Bahía Inútil and the other in Seno Almirantazgo (Isla Grande de Tierra del Fuego), considering the evaluation of the α-, β-, and functional diversity indices as factors reflecting the connectivity between the assemblages of the two marine basins.

## 2. Materials and Methods

### *2.1. Study Area*

The study area is located in two basins on the northwestern coast of the Isla Grande de Tierra del Fuego—Bahía Inútil (BI; 53°30′ S–69°30′ W) and Seno Almirantazgo (SA; 54°21′ S–69°21′ W)—which are linked only by Canal Whiteside (56 km long, 16 km wide, and 500 m in depth; Figure 1). The area of BI (4776 km$^2$) is larger than that of SA (1150 km$^2$). The maximum depths of BI and SA are 200 and 300 m, respectively [49] (Figure 1). At present, BI is a free-harvesting area, while SA was declared an MPA in 2018, allowing sustainable anthropogenic activities in the area.

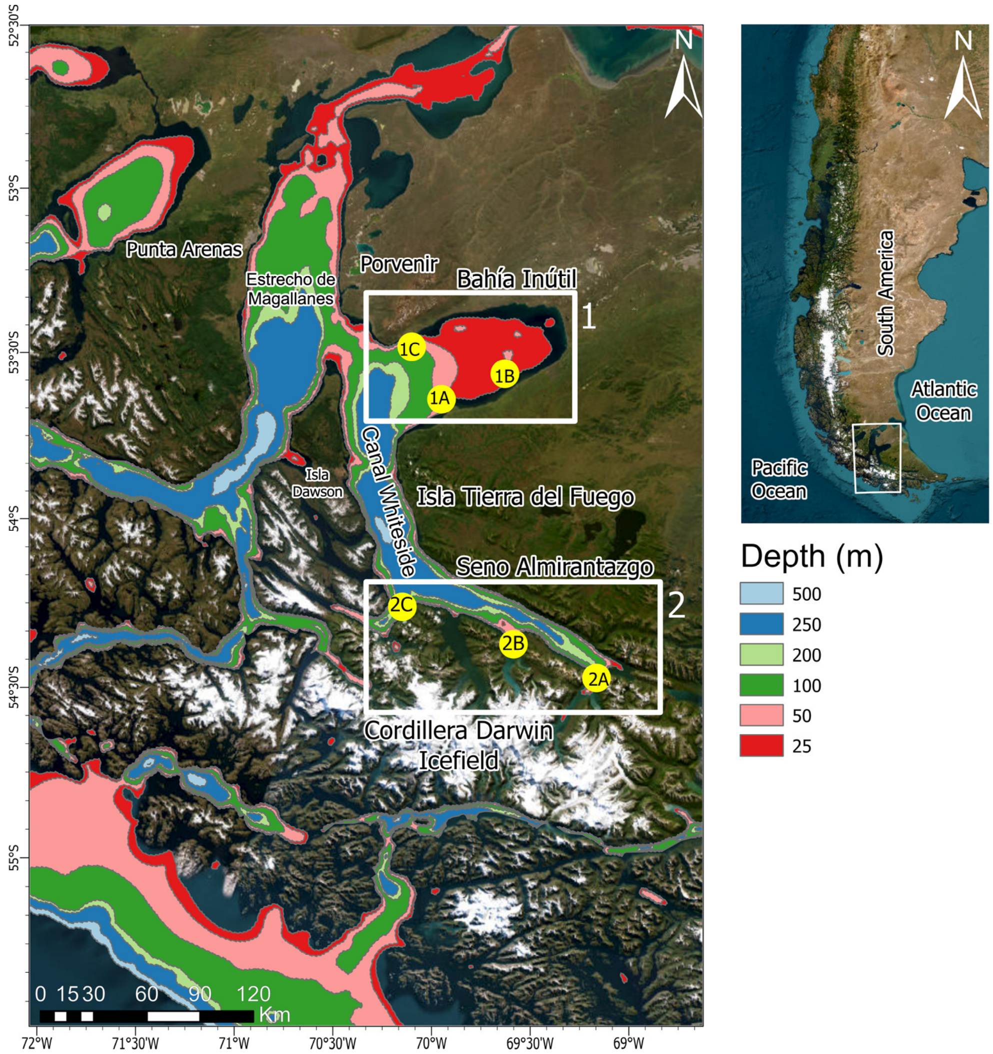

**Figure 1.** Study area, Magallanes region. Square 1 indicates the location of the Bahía Inútil sampling area and Square 2 indicates the location of the Seno Almirantazgo sampling area. The sampled stations (1A–1C and 2A–2C) indicated with yellow dots. The color shades indicate the bathymetry of the area [49].

The oceanographic characteristics indicate the influence of glaciers coming from the Cordillera Darwin Icefield, which affected both the formation of estuarine water masses and the development of marked oceanographic gradients [50]. Aracena et al. [51] included BI within the central microbasin, which is part of the central area of the Estrecho de Magallanes and Canal Whiteside. This microbasin is characterized by a less-stratified water column than that of SA, with intermediate temperature and salinity values compared with the previous layers (7 and 8 °C; 30 and 31 psu, respectively). Meanwhile, SA is included in the southeastern microbasin, which is characterized by estuarine conditions with a cold surface layer (<7 °C) and low salinity (<28 psu). This is due to the fact that the southeastern part of SA is located between important glaciers that are part of the Cordillera Darwin Icefield [50,51]. Concerning the soft sediment at the bottom, the BI area is characterized as having sand on both the north and east coasts. Meanwhile, on the south coast, the presence of sand and mud at a depth between 32 and 135 m has been reported. At the bottom of the SA, mud is the dominant-type sediment at a depth between 135 and 290 m [52,53].

### *2.2. Sample Design*

#### 2.2.1. Field Work

The sediment samples were collected during the Rio Seco Natural History Museum scientific expedition in November 2018 [54]. Six stations were selected: three stations in BI and three in SA, respectively. At each station, one sample with two replicates (N = 18) was collected by means of a van Veen grab (0.15 $m^2$). In order to achieve the aim of the study, our design allowed the comparison of two benthic assemblages in the most similar field conditions. Therefore, we collected the samples in a narrow range between 30 and 48 m depth ($\overline{X}$ 36.2 ± 7.6; Table 1). Consequently, the depth was relatively constant and should not have affected further comparative analysis. All the sediment samples were washed on a board using 0.5 mm mesh-size sieves. Subsequently, all the sediment retained in the sieve was preserved in a solution of formalin with seawater (10%) and buffered with borax for further analysis in the laboratory.

**Table 1.** Geographic location and characteristics of stations sampled during the first Rio Seco Natural History Museum scientific expedition in 2018. Sampling stations at Bahía Inútil and Seno Almirantazgo (in bold) in Isla Grande de Tierra del Fuego.

| Station N° (N° Samples) | Date (November 2018) | Depth ($\overline{X}$) | Lat (°S) | Long (°W) |
|---|---|---|---|---|
| 1A (3) | 20 | 30 | 53°39′00″ | 69°56.3′ |
| 1B (3) | 20 | 30 | 53°35′00″ | 69°36.1′ |
| 1C (3) | 20 | 30 | 53°28′00″ | 70°07.0′ |
| **2A (3)** | **21** | **36** | **54°33′00″** | **69°10.7′** |
| **2B (3)** | **23** | **45** | **54°23′33″** | **69°37.7′** |
| **2C (3)** | **24** | **48** | **54°23′00″** | **70°12.9′** |

#### 2.2.2. Laboratory Work

All the benthic organisms were sorted from the sediment using a stereomicroscope. Subsequently, specimens were identified to the lowest taxonomic level possible. The following literature was used for taxonomic identification: for the taxon Polychaeta, Böggemann [55], Hartman [56,57], Hartmann-Schröder [58,59], Kornicker [60], Orensanz [61], Schüller [62] and Rozbaczylo [63]; for Mollusca, Linse [64,65], Reid and Osorio [66], and Zelaya [67]; and for Arthropoda, Menzies [68] and Retamal [69]. Other invertebrates were determined according to Häussermann and Försterra [70] and Zagal and Hermosilla [71].

### *2.3. Statistical Analysis*

#### 2.3.1. General Characteristics of Benthic Assemblages

Abundance was calculated by standardizing the number of individuals to one square meter (Ind $m^{-2}$). These values were represented geographically using a graduated colors map based on BI and SA data concentrations. The map was constructed using the ArcGIS Pro version 2.7.7 software. In addition, the taxonomic composition was described based on the abundance data of the assemblages, presented as a box plot using the BoxPlotR program [72].

#### 2.3.2. Analysis of α-Diversity

Rarefaction–extrapolation curves were calculated relative to the number of individuals collected in each area, with a 95% confidence interval equal to 2500 individuals [73]. The first and second orders of diversity, corresponding to Shannon–Wiener ($H'$: q = 1) and Simpson's diversity ($\lambda$: q = 2), were calculated. This analysis was performed with the iNEXT package (online program) [74] following the parameters established by Chao et al. [73]. For comparative purposes with previous work in the study area, Shannon–Wiener ($H'$) and Simpson ($\lambda$) indices were calculated. To determine the presence of significant differences between these indices, the diversity permutation test described by Hammer et al. [75] was used.

#### 2.3.3. Ecological Connectivity between BI and SA Assemblages

In order to determine connectivity between BI and SA assemblages, the β-, and functional diversity indices were calculated as measures of connectivity.

(*a*) *β-Diversity Analysis*

(*i*) *Quantitative Data*

β-diversity was calculated from the quantitative data (abundance; ind $m^{-2}$) using the Bray and Curtis index ($\beta_{BC}$), as indicated by Baselga [76]. Previously, the abundance values were transformed to the fourth root. To determine significant differences between the sampling areas, a one-way permutational multivariate analysis of variance (PERMANOVA) was performed [77].

(*ii*) *Qualitative Data*

To obtain the β-diversity based on the qualitative data, the abundance values were transformed into presence/absence and the Whittaker index ($\beta_W = S/\alpha - 1$), where S is the number of species recorded in a set of samples and α is the mean number of species in the samples was calculated. We followed the recommendation of Magurran [78], who indicated the Whittaker index over other indices and described that the minimum value for the $\beta_W$-diversity is 0, while 1 is the maximum value.

(*iii*) *Functional Diversity Analysis*

Functional diversity was calculated using three approaches. In the first approach, each species was categorized according to the nomenclature described by Koleff et al. [18], which describes the relationship between components *A*, *B*, and *C*, expressed as proportions ($A + B + C = 100\%$) where *A* is the number of species present exclusively in BI, *B* is the number of species present exclusively in SA, and *C* is the number of species shared or present in both BI and SA [79]. This relationship is presented by means of a ternary plot using abundance and species richness data.

The second approach used to calculate functional diversity among the benthic assemblages of the considered basins was through classifying species according to their diet, according to Macdonald et al. [80]. Species were categorized into carnivores, herbivores, and omnivores. This relationship is presented by means of ternary diagrams and principal component analysis (PCA). Subsequently, the $H'$ diversity was calculated using the diversity permutation test to evaluate differences between the assembles.

Finally, the third approach was the classification of species according to their larval development. According to the database (https://niwa.co.nz/coasts-and-estuaries/research-projects/NZTD, accessed on 22 January 2024), each species was categorized into larvae classified as planktotrophic, lecithotrophic, or other types of larvae (benthic and direct development). This relationship is presented by means of ternary diagrams and their PCA. Subsequently, the $H'$ diversity was calculated using the diversity permutation test to evaluate differences between the assembles.

The PERMANOVA and permutation test hypotheses were as follows: the presence of significant differences means that there is no EC, while the absence of significant differences indicates that there exists connectivity between BI and SA. Additionally, for both quantitative and qualitative β-diversity analyses, it was interpreted that β-diversity and dissimilarity present a converse relationship with connectivity. This means that higher β-diversity indicates lower connectivity or higher dissimilarity. Reciprocally, the lower the β-diversity, the higher the connectivity and the lower the dissimilarity.

All analyses, including ternary plots, were performed using the Paleontological Statistic (PAST) software version 4.16 [75].

## 3. Results

### *3.1. General Structure of the BI and SA Assemblages*

#### 3.1.1. Abundance

From the total of 3076 individuals collected, 113 taxa and 8 phyla were determined (Supplementary Table S1). A total of 55% of the taxa were determined at the species level, 20.4% at the genus level, and 23% at the family level, with the remaining 1.6% corresponding to taxa at the phylum level.

In terms of abundance, the BI assemblage obtained a lower abundance than the SA assemblage (Figure 2). In BI, the mean abundance value was 888.9 (±S.D. 26.8), whereas the mean abundance value of SA was 1358.6 (±43.4).

#### 3.1.2. Taxonomic Composition

Figure 3 shows the three most abundant phyla and their respective class-level details for the BI and SA areas. In addition, this figure includes other groups whose taxa have lower abundances.

The abundance of the phylum Annelida was higher in SA, with a mean of 655.1 ± 266.7, than in BI, with a mean of 446.7 ± 83.77 (see Figure 3A). The mean abundance values of Polychaeta were $\overline{X}$BI = 440.0 ± 89.0 and $\overline{X}$SA = 652.1 ± 270.8, and the most abundant species were *Capitella capitata* and *Aricidia* (*Acmira*) *finitima*, with 574 and 373 ind $m^{-2}$, respectively. Meanwhile, for Sipunculidae, the abundance was relatively higher in BI than in SA ($\overline{X}$BI = 6.7 ± 9.7 and $\overline{X}$SA = 3.0 ± 5.2) (see Figure 3B).

The second most important phylum was Arthropoda, whose abundance values were higher in SA (mean of 96.9 ± 65.7) than in BI (mean of 93.8 ± 75.4) (see Figure 3C). On one hand, the taxa following the previously described pattern were Cumacea ($\overline{X}$BI = 6.7 ± 5.9 and $\overline{X}$SA = 46.2 ± 31.4), Balanomorpha, Pycnogonida, and Tanaideacea ($\overline{X}$BI = 3.0 ± 5.2 and $\overline{X}$SA = 17.9 ± 11.6). On the other hand, for Amphipoda ($\overline{X}$BI = 56.6 ± 54.8 and $\overline{X}$SA = 30.5 ± 25.9) and Isopoda ($\overline{X}$BI = 10.4 ± 8.5 and $\overline{X}$SA = 2.2 ± 2.2), the abundance in SA was lower than that in BI (Figure 3D). Meanwhile, Decapoda was present in BI only ($\overline{X}$BI = 18.6± 11.2). In terms of species, the most abundant taxa were Amphipoda spp., *Pagurus villosus*, and Sphaeromatidae spp., with 203.2, 24.6 and 17.9 ind $m^{-2}$, respectively.

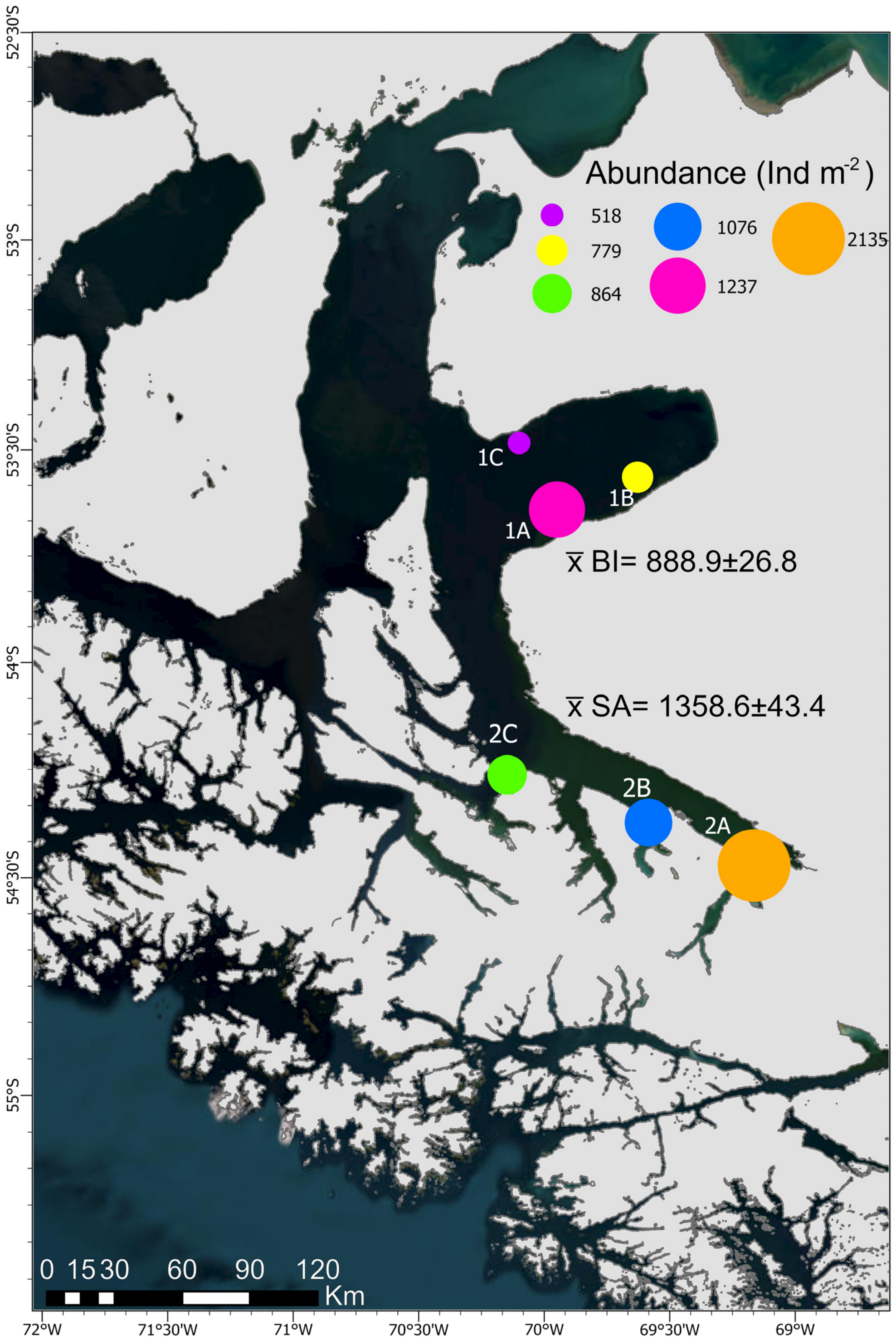

**Figure 2.** Graduated colors map of the abundance distribution pattern (Ind $m^{-2}$) of the Bahía Inútil (BI) and Seno Almirantazgo (SA) assemblages, including the mean ($\overline{X}$) and their standard deviation (±S.D.).

The third most abundant phylum was Mollusca, with abundance values higher in SA (mean of $\overline{X}$SA = 468.3 ± 463.9) than in BI (mean of $\overline{X}$BI = 243.4 ± 304.7) (see Figure 3E). The only taxon that followed the pattern was Bivalvia ($\overline{X}$BI = 225.6 ± 292.5 and $\overline{X}$SA = 466.0 ± 461.9). For Gastropoda ($\overline{X}$BI = 14.1 ± 15.2 and $\overline{X}$SA 2.2 ± 2.2), the abundance in SA was lower than that in BI, whereas Polyplacophora ($\overline{X}$BI = 3.7 ± 4.6, see Figure 3F) was present in BI only. In terms of species, the most abundant species were *Nucula pisum* and *Yoldiella* sp. 1, with 846.4 and 507.0 ind $m^{-2}$, respectively.

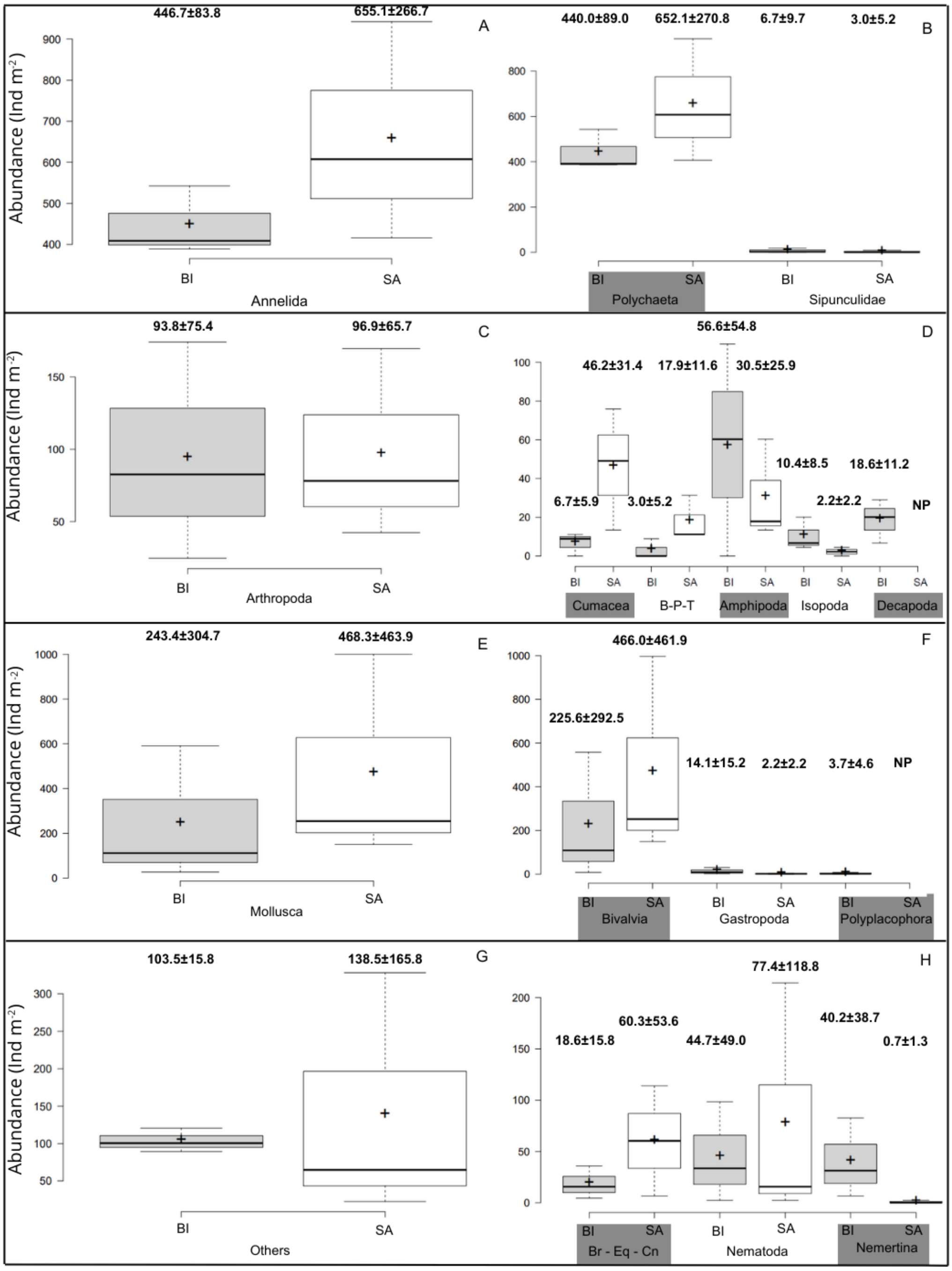

**Figure 3.** Box plot showing the abundance values (Ind $m^{-2}$) between Bahía Inútil (BI; in grey) and Seno Almirantazgo (SA; in white), including mean values (($\overline{X}$) ± S.D.) in bold, located at the top of each box plot. (**A**) = phylum Annelida; (**B**) = class Polychaeta and family Sipunculidae; (**C**) = phylum Arthropoda; (**D**) = class Cumacea, order Balanomorpha (B), class Pycnogonida (P), orders Tanaideacea (T), Amphipoda, Isopoda, and Decapoda; (**E**) = phylum Mollusca; (**F**) = classes Bivalvia, Gastropoda, and Polyplacophora; (**G**) = others group, (**H**) = consisting of phylum Brachiopoda (Br), Echinodermata (Eq) and Cnidaria (Cn), and Nematoda and Nemertina. Center lines show medians; box boundaries indicate the 25th and 75th percentiles, as determined using BoxPlotR program [72] whiskers extend 1.5 times the interquartile range from the 25th and 75th percentiles; outliers are represented by dots; NP: Not present.

Finally, the group "others" had higher abundance in SA (mean of $\overline{X}$SA = 103.5 ± 15.8) than in BI (mean of $\overline{X}$BI = 138.5 ± 165.8; Figure 3G) and included Brachiopoda (*Magellania venosa*, with 509 ind $m^{-2}$), Echinodermata, Cnidaria ($\overline{X}$BI = 18.6 ± 15.8 and $\overline{X}$SA = 60.3 ± 53.6), and Nematoda ($\overline{X}$BI = 44.7 ± 49.0 and $\overline{X}$SA = 77.4 ± 118.8). By contrast, the Nemertina abundance values were higher in BI than in SA ($\overline{X}$BI = 40.2 ± 38.7 and $\overline{X}$SA = 0.7 ± 1.3; Figure 3H).

### 3.1.3. Pattern of α-Diversity

The rarefaction curves indicated that the species diversity for BI was higher than that for SA (Figure 4A,B). The difference between these two values was supported through the evaluation of the 95% confidence intervals, indicating statistically significant differences between the two assembles. The extrapolated data in both assemblages indicated an asymptotic trend (Figure 4). In terms of the observed species richness between the assemblages, BI was slightly higher than SA. BI recorded a total of 82 species with a mean of 46 (±1.7), while SA recorded a total of 72 species with a mean of 47 (±5.3). The diversity indices $H'$ and $\lambda$ followed the pattern of species richness and the rarefaction curves, where BI ($H' = 3.402$ and $\lambda = 0.946$) was higher than SA ($H' = 3.215$ and $\lambda = 0.937$). When comparing the two indices ($H'$ and $\lambda$) through the diversity permutation test, both indices showed significant differences ($p < 0.05$).

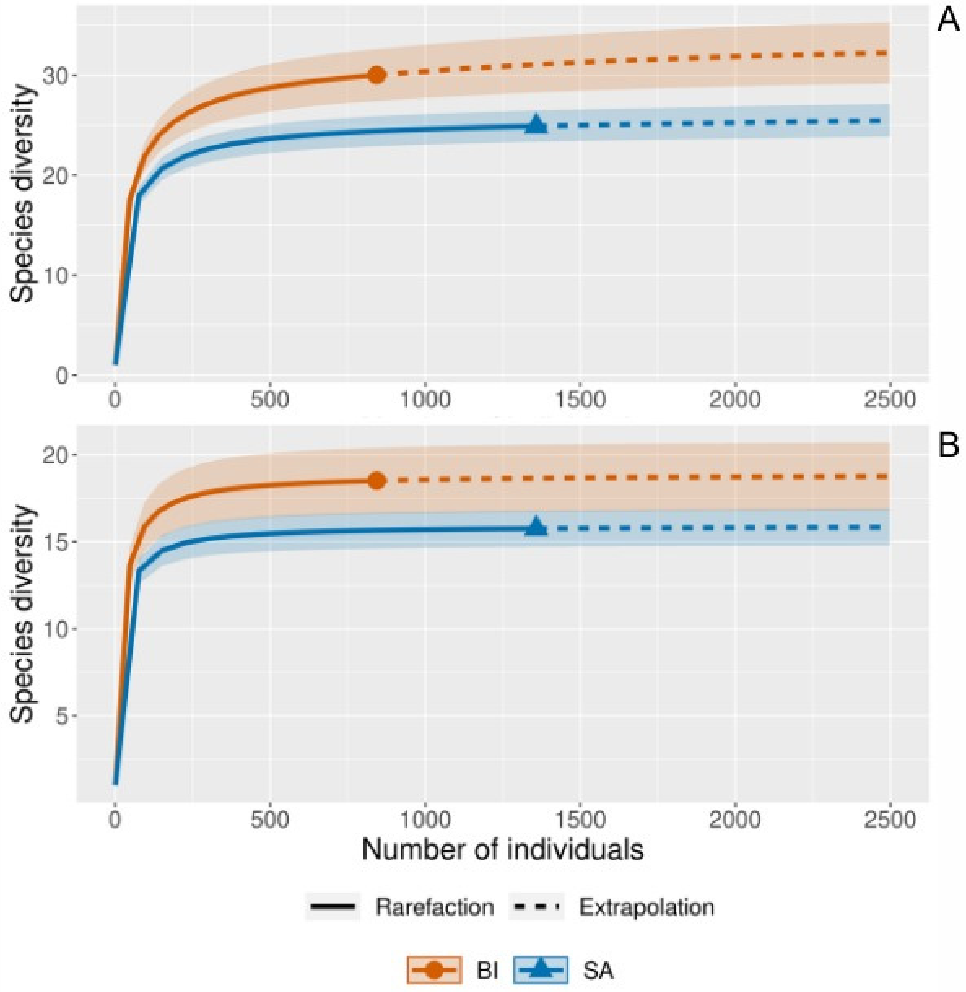

**Figure 4.** Rarefaction–extrapolation curves of the Bahía Inútil (BI) and Seno Almirantazgo (SA) assemblages. The solid line indicates interpolation (rarefaction) and the dashed line indicates extrapolation to 2500 individuals. The bands correspond to the 95% confidence interval for each site. Shannon–Wiener (**A**) and Simpson (**B**) indices.

### *3.2. Ecological Connectivity between BI and SA Assemblages*

(*a*) *Pattern of β-Diversity*

The EC calculated based on the $\beta_{BC}$ index between the BI and SA assemblages was 36.4%. Among the areas studied, no significant differences were found according to the PERMANOVA results (F = 1.519; $p > 0.05$). Indeed, analysis of the β-diversity using the qualitative data indicated that the $\beta_w$ index value was 0.51 between the areas.

(*b*) *Functional Diversity Pattern*

A total of 41 shared species were identified between the assemblages of both basins, corresponding to 36.28% of the total species identified. Annelida represented 60.97% (25 spp.), followed by Mollusca with 17.07% (7 spp.), while Arthropoda and Echinodermata reached 12.36% (5 spp.) and 4.87% (2 spp.), respectively, and Nematoda and Nemertina reached only 4.87% (2 spp.) each.

Table 2 shows the shared species that contributed most to connectivity between the assemblages. The phylum Annelida is represented by the species *Capitella capitata*, *Aricidia* (*Acmira*) *finitima*, *Aphelochaeta* sp. 1, *Lumbrineris* sp., *Notomastus latericeus*, and *Spiophanes* sp. These species contributed the most to connectivity, with abundance values varying between 446.65 and 104.97 ind $m^{-2}$. These were followed by the species *Cirriformia nasuta*, *Prionospio patagonica*, *Monticenlina* sp., *Hemipodia* sp., and *Caulleriella* sp., with values ranging from 96.03 to 46.90 ind $m^{-2}$. Finally, the species Sipunculida indet., *Cistenides ehlersi*, *Melinna cristata*, *Eteone aurantiaca*, *Eulalia subulifera*, *Brania* sp., *Nicon maculata*, *Magelona* sp., *Harmothoe ciliata*, *Augeneria tentaculata*, *Trichobranchus glacialis*, *Harmothoe* spp., *Hauchiella* sp., and *Paraninoe* sp. Had values ranging from 20.10 to 4.47 ind $m^{-2}$.

**Table 2.** PERMANOVA values.

| | |
|---|---|
| Permutation N | 9999 |
| Total sum of squares: | 1.321 |
| Within-group sum of squares: | 0.9573 |
| F: | 1.519 |
| p (same): | 0.1976 |

For the phylum Mollusca, the species that contributed most to connectivity were *Nucula pisum* and *Yoldiella* sp. 1, with 491.33 and 504.73 ind $m^{-2}$, respectively. These were followed by Bivalvia indet. 1, *Neilonella sulculata*, *Xymenopsis muriciformis*, *Tawera elliptica*, and *Pareuthria atrata*, ranging between 158.57 and 4.47 ind $m^{-2}$ (Table 3).

In relation to the phylum Arthropoda, the taxa that contributed most to connectivity were Cumacea spp. and Amphipoda spp., with 138.53 and 129.53 ind $m^{-2}$, respectively, followed by Tanaidacea spp., Epimeriidae spp., and Isopoda spp., with values varying between 51.37 and 4.47 ind $m^{-2}$. Contributing to a lesser extent, the phylum Echinodermata, Ophiuroidea indet., and Holothuroidea indet. had values between 15.63 and 4.47 ind $m^{-2}$. Finally, Nemertina indet. and Nematoda indet. had values of 232.27 and 120.60 ind $m^{-2}$, respectively (Table 3).

In terms of abundance per station, shared species reached 81.15%, while the species present exclusively in BI and SA were 6.23 and 12.62%, respectively. The abundance values of shared species by station ranged from 1233 to 5132 ind $m^{-2}$. The abundance values of exclusive species in BI by station ranged between 201.50 and 569.50 ind $m^{-2}$, while those for SA ranged between 428.80 and 1273 ind $m^{-2}$ (Figure 5A).

**Table 3.** Mean abundance values of species shared between Bahía Inútil (BI) and Seno Almirantazgo (SA). An = Annelida, Mo = Mollusca, Ar = Arthropoda, Ec = Echinodermata, Ne = Nematoda, Na = Nemertina.

| No | Share Species | Phylum | Spp. BI | Spp. SA |
|---|---|---|---|---|
| 1 | *Capitella capitata* | An | 127.30 | 446.65 |
| 2 | *Aricidia* (*Acmira*) *finitima* | An | 67.00 | 305.97 |
| 3 | *Aphelochaeta* sp. 1 | An | 238.97 | 67.00 |
| 4 | *Lumbrineris* sp. | An | 127.30 | 178.67 |
| 5 | *Notomastus latericeus* | An | 122.83 | 2.23 |
| 6 | *Spiophanes* sp. | An | 11.17 | 104.97 |
| 7 | *Cirriformia nasuta* | An | 60.30 | 96.03 |
| 8 | *Prionospio patagonica* | An | 6.70 | 87.10 |
| 9 | *Monticellina* sp. | An | 80.40 | 75.93 |
| 10 | *Hemipodia* sp. | An | 67.00 | 6.70 |
| 11 | *Caulleriella* sp. | An | 46.90 | 2.23 |
| 12 | Sipunculida indet. | An | 20.10 | 8.93 |
| 13 | *Cistenides ehlersi* | An | 20.10 | 2.23 |
| 14 | *Melinna cristata* | An | 2.23 | 20.10 |
| 15 | *Eteone aurantiaca* | An | 6.70 | 15.63 |
| 16 | *Eulalia subulifera* | An | 6.70 | 15.63 |
| 17 | *Brania* sp. | An | 2.23 | 11.17 |
| 18 | *Nicon maculata* | An | 2.23 | 8.93 |
| 19 | *Magelona* sp. | An | 8.93 | 2.23 |
| 20 | *Harmothoe ciliata* | An | 2.23 | 8.93 |
| 21 | *Augeneria tentaculata* | An | 4.47 | 6.70 |
| 22 | *Trichobranchus glacialis* | An | 6.70 | 2.23 |
| 23 | *Harmothoe* spp. | An | 4.47 | 6.70 |
| 24 | *Hauchiella* sp. | An | 6.70 | 2.23 |
| 25 | *Paraninoe* sp. | An | 4.47 | 4.47 |
| 26 | *Nucula pisum* | Mo | 335.10 | 491.33 |
| 27 | *Yoldiella* sp. 1 | Mo | 2.23 | 504.73 |
| 28 | Bivalvia indet. 1 | Mo | 158.57 | 20.10 |
| 29 | *Neilonella sulculata* | Mo | 53.60 | 93.80 |
| 30 | *Xymenopsis muriciformis* | Mo | 24.57 | 2.23 |
| 31 | *Tawera elliptica* | Mo | 8.93 | 2.23 |
| 32 | *Pareuthria atrata* | Mo | 4.47 | 4.47 |
| 33 | Cumacea spp. | Ar | 17.87 | 138.47 |
| 34 | Amphipoda spp. | Ar | 129.53 | 73.70 |
| 35 | Tanaidacea spp. | Ar | 4.47 | 51.37 |
| 36 | Epimeriidae spp. | Ar | 20.10 | 17.87 |
| 37 | Isopoda spp. | Ar | 4.47 | 6.70 |
| 38 | Ophiuroidea indet. | Ec | 15.63 | 4.47 |
| 39 | Holothuroidea indet. | Ec | 13.40 | 4.47 |
| 40 | Nemertina indet. | Na | 134.00 | 232.27 |
| 41 | Nematoda indet. | Ne | 120.60 | 2.23 |

In relation to species richness by station, shared species reached 63.0%, while the species present exclusively in BI and SA were 19.05 and 17.95%, respectively. The shared species richness values by station ranged from 16 to 20 species. The species richness values for species shared exclusively in BI by station ranged from 14 to 21 species, while those for SA ranged from 24 to 34 species (Figure 5B).

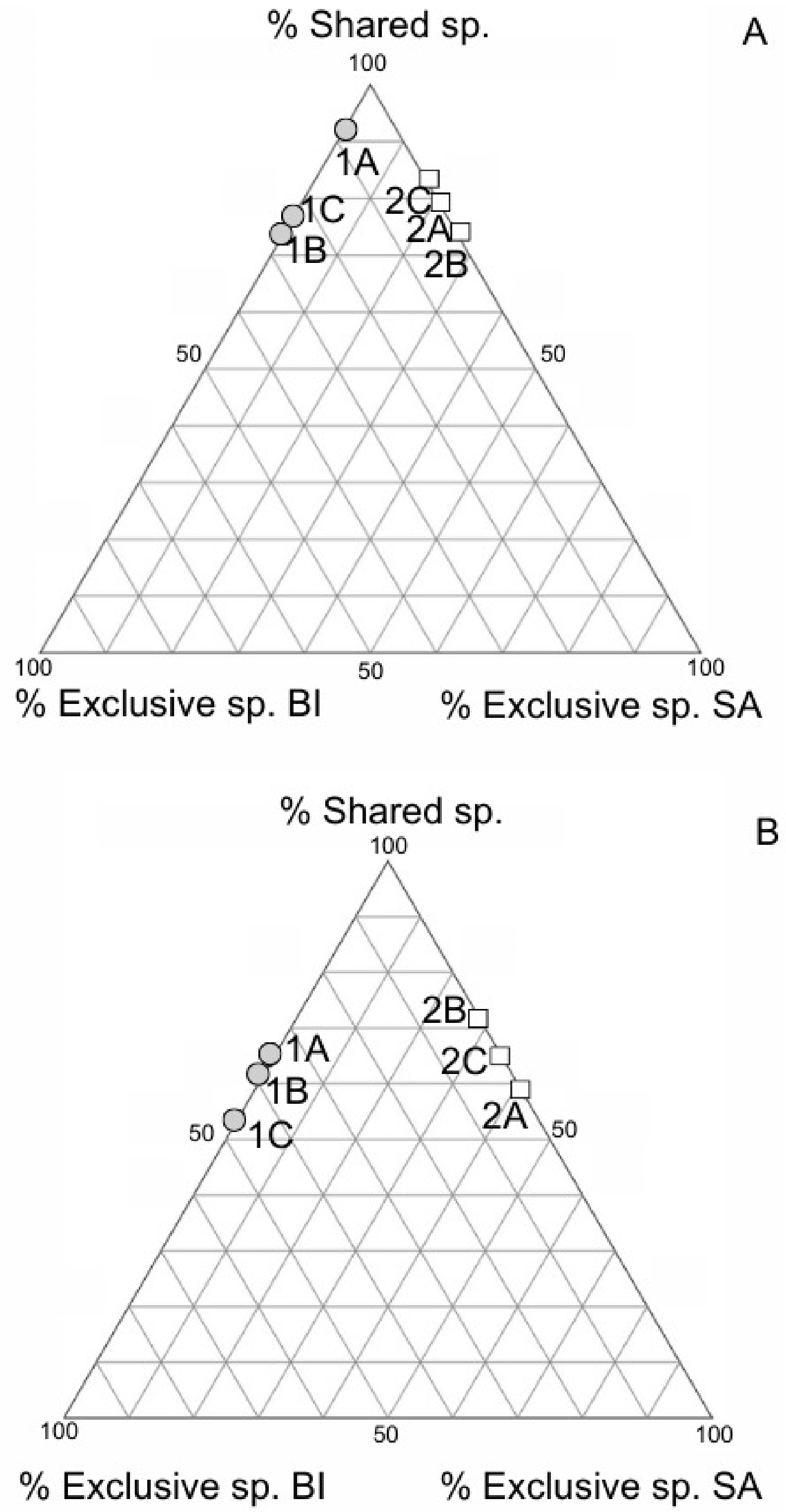

**Figure 5.** Ternary diagram of the assemblages of Bahía Inútil (BI and sampling stations 1A–1C), Seno Almirantazgo (SA sampling stations 2A–2C), and the degree of species connectivity between the two areas (Shared Species). (**A**) = abundance (Ind $m^{-2}$) and (**B**) = species richness. Grey circles indicate BI stations and white squares indicate SA stations. Grey lines represent 20% increments of the components.

The results for functional diversity based on the diet of organisms in both areas indicated that 65.49% of the species were categorized as omnivorous, 26.55% as carnivorous, and only 7.96% as herbivorous.

The distribution of the sampling stations in Figure 6A was shown to be grouped, indicating a high connectivity between the assemblages of both areas. Regarding abundance values, the BI group of stations had values between 352.9 and 1056.4 ind $m^{-2}$ for omnivores, 180.9 and 192.1 ind $m^{-2}$ for carnivores, and 4.5 and 26.8 ind $m^{-2}$ for herbivores; meanwhile, in the SA group of stations, the abundance values ranged from 739.2 to 1929.6 ind $m^{-2}$ for omnivores, 116.1 to 201.0 ind $m^{-2}$ for carnivores, and 4.5 to 13.4 ind $m^{-2}$ for herbivores (Figure 6A). The PCA explained 96.9% of the variance, with PC1 explaining 63.5% and PC2 explaining 33.4%. For PC1, the omnivorous diet species group was the most correlated factor (eigenvector = 0.7), while for PC2, it was the carnivorous species group (eigenvector = 0.8) (see Figure 6B).

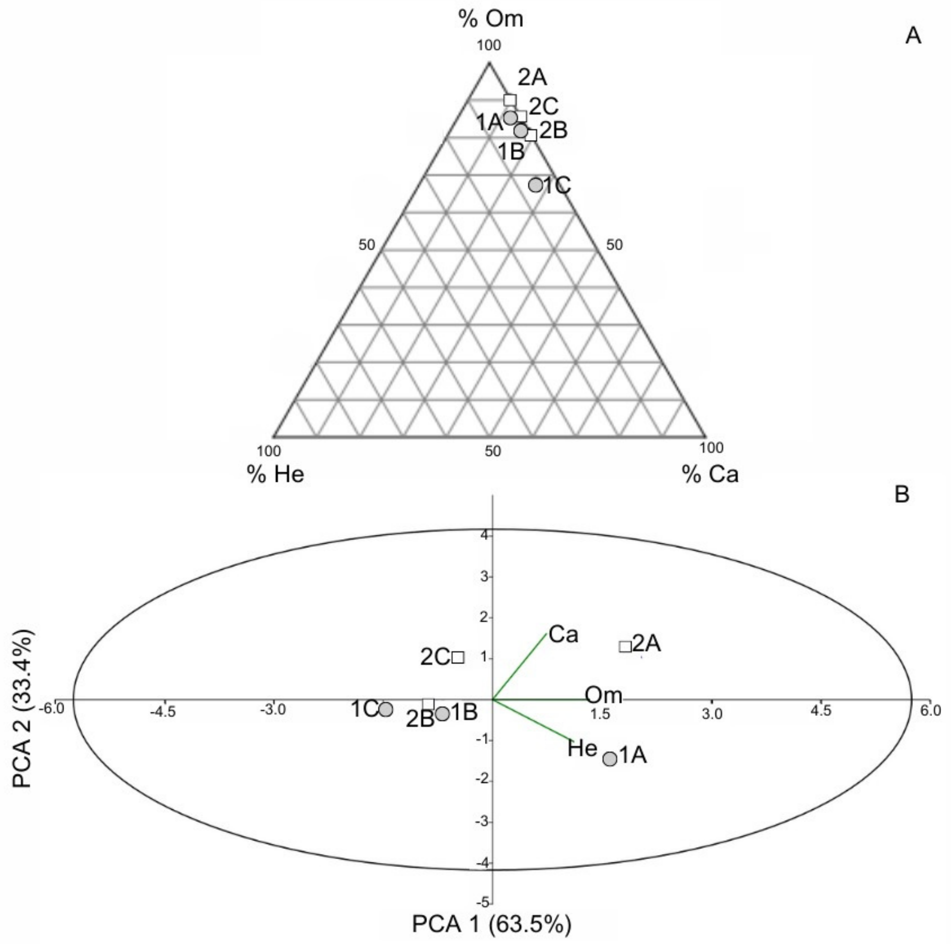

**Figure 6.** Ternary diagram (**A**) and principal component analysis (PCA); the ellipse represents the 95% confidence (**B**) of the species shared among the assemblages. He = Herbivores, Om = Omnivores, Ca = Carnivores. Grey circles indicate stations in Bahía Inútil (BI) and white squares indicate stations in Seno Almirantazgo (SA). Grey lines represent 20% increments in the components. Grey circle indicates the sampling stations in BI (1A–1C) and white square indicates the sampling stations in SA (2A–2C).

With respect to the results of diet diversity, the *H′* diversity index indicated no significant differences ($p > 0.05$) in any of the pairwise tests between Herbivores BI (1.718) and SA (1.248), Omnivores BI (3.147) and SA (2.954), and Carnivores BI (2.083) and SA (2.248) (Table 4), thus confirming the high functional connectivity. With respect to the analysis of functional diversity based on the larval development of organisms by station, it was found that 40.7% of the species recorded in this study were categorized as species with lecithotrophic larval development and 39.8% as species with planktotrophic larval development, while other types of larvae (benthic and direct development) had a value of 19.0%.

The distribution of the sampling stations was clustered, indicating a high connectivity of species with lecithotrophic and planktotrophic larval development between the BI and SA assemblages. Regarding abundance values, the BI group of stations had between values of 332.7 and 911.2 ind $m^{-2}$ for species with lecithotrophic larval development and 134.0 and 685.6 ind $m^{-2}$ for species with planktotrophic larval development, with other types of development reaching values between 31.2 and 82.6 ind $m^{-2}$. Meanwhile, in the SA group of stations, the abundance values ranged from 442.2 to 1252.9 ind $m^{-2}$ for species with lecithotrophic larval development and 442.2 to 1252.9 ind $m^{-2}$ for species with planktotrophic larval development, with other types of development reaching values between 6.7 and 67.0 ind $m^{-2}$ (Figure 7A). The PCA explained 97% of the variance, where PC1 explained 71.7% and PC2 explained 25.5%. For PC1, the lecithotrophic larval species group was the best-correlated factor (eigenvector = 0.7), while for PC2, it was the planktotrophic larval species group (eigenvector = 0.8) (see Figure 7B).

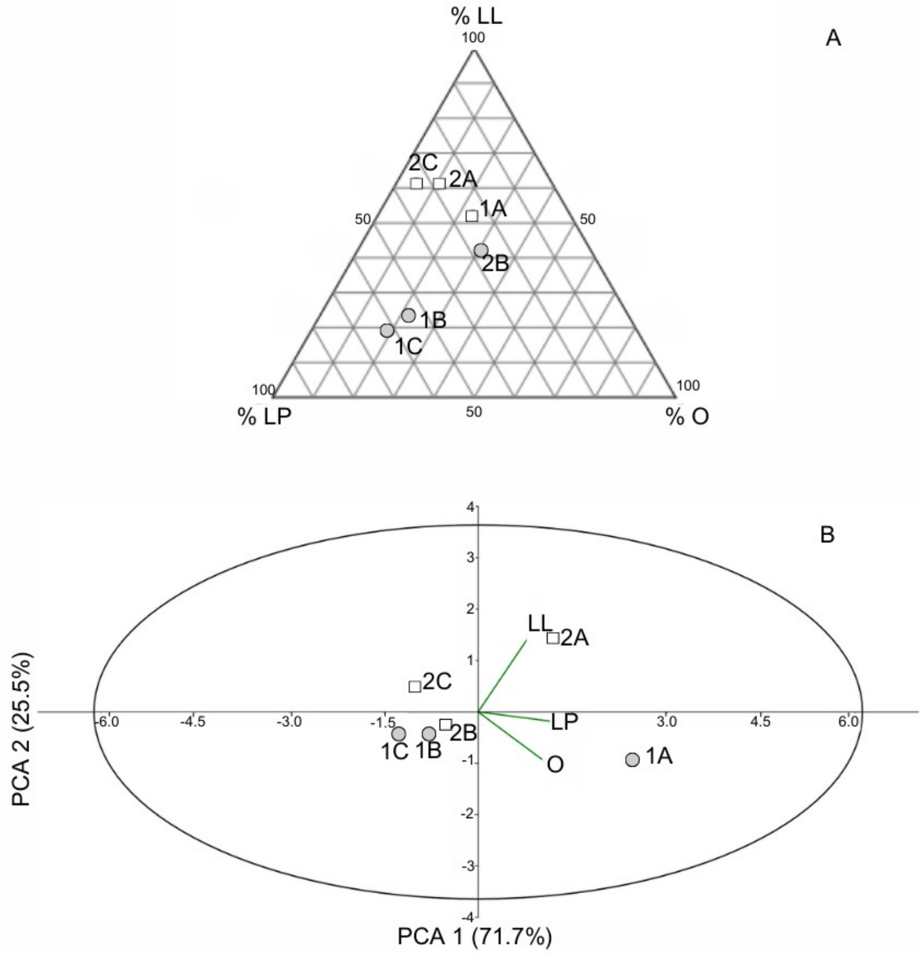

**Figure 7.** Ternary diagram (**A**) and principal component analysis (PCA); the ellipse represents the 95% confidence (**B**) of the species shared among the assemblages. PL = planktotrophic larvae, LL = lecithotrophic larvae, O = other types of larvae (benthic and direct development). Grey circles indicate stations in Bahía Inútil (BI) and white squares indicate stations in Seno Almirantazgo (SA). Grey lines represent 20% increments in the components. Grey circle indicates the sampling stations in BI (1A–1C) and white square indicates the sampling stations in SA (2A–2C).

**Table 4.** Simpson diversity index between Bahía Inútil (BI) and Seno Almirantazgo (SA). Ca = Carnivores; Om = Omnivores, He = Herbivores; LL = lecithotrophic larvae; PL = planktotrophic larvae; O = other types of larvae (benthic and direct development) (in bold—significant difference ($p \leq 0.001$)).

| | **BI** | **SA** |
|---|---|---|
| Diet type | | |
| $H'$ He | 1.718 | 1.248 |
| $H'$ Om | 3.147 | 2.954 |
| $H'$ Ca | 2.083 | 2.248 |
| Larval development | | |
| $H'$ PL | 2.322 | 2.304 |
| $H'$ LL | 2.585 | 2.508 |
| $H'$ **O** | **2.231** | **1.745** |

Regarding the functional diversity results, the $H'$ diversity index indicated no significant difference ($p > 0.001$) between pairwise Planktotrophic larvae of BI (2.322) and SA (2.304), lecithotrophic larvae of BI (2.585) and SA (2.508), whereas the pairwise between BI (2.231) and SA (1.745) based on the group "other types of larvae" showed significant differences only (Table 4).

## 4. Discussion

The present work determined the EC between two sublittoral benthic assemblages based on an assessment of the β- and functional diversity indices. The Patagonian fjords and channels are a high-latitude and geomorphologic heterogeneous ecosystem, where research on the soft-bottom benthic ecosystem has mainly focused on local and exploration studies. Therefore, our study is the first to address the issue of connectivity as a key component for understanding this complex benthic southern sub-Antarctic ecosystem. In particular, our results are key to understanding the functioning between marine protected areas and their adjacent areas with open access for fisheries harvesting.

It is worth noting the scarcity of information on biodiversity for soft-bottom communities in both areas, which, including the present work, has only two investigations. Nevertheless, with our research, the taxonomic inventory increased by 17.1% for BI and 18% for SA. Thus, the taxonomic inventory for soft-bottom assemblages has reached 48 species for BI and 43 species for SA.

### *4.1. Abundance, Species Richness, and α-Diversity Patterns*

Concerning the patterns of abundance and species richness, our results clearly showed that the mean abundance increased from BI to SA. Meanwhile, the species richness showed a decrease from BI to SA. Similar results have been described by Thatje and Brown [44], but with lower abundance and species richness values. In fact, Thatje and Brown [44] determined, for BI and SA, mean abundance values of 67 and 114.0 ind $m^{-2}$, respectively—an order of magnitude lower than the values obtained in the present study. Likewise, the mean richness was also higher, which reached 41 species in BI and 39 species in SA [41]. These patterns may be explained by differences in the sampling equipment used. A van Veen grab was used in the present study, whereas in the study of Thatje and Brown [44], the samples were collected using a Reineck box corer. Additionally, the studies had different sampling designs; in our study, the samples were collected until a 40 m depth, while in Thatje and Brown [44], the sampling depth range was below 100 m.

The α-diversity pattern of macrobenthic assemblages described in the present study is high compared to those in other studies conducted in adjacent areas [42,43]. The rarefaction curves reach the asymptotic level, indicating that both areas have been well sampled. α-Diversity analyses ($H'$ and rarefaction curves) showed high differences between the two assemblages. These patterns may be a consequence of the environmental conditions at the sampling locations. Meanwhile, the samples obtained in SA were located on the southeast coast of the basin, which is under strong influence from the numerous calving glaciers from the Cordillera Darwin Icefield, while the BI is a wide bay without glacier influence. Therefore, glacial influence is described as the most important drive for the distribution pattern of benthic assemblages in the Magellan region because of the runoff of freshwater and sediment discharge from the glaciers [81,82]. In fact, the presence of glaciers on the coast of the Cordillera Darwin Icefield produces a different type of sediment. Sand with mud dominated seafloor sediments on the south coast of SA, whereas sand-type sediments dominated on the north and east coasts of BI [52].

### *4.2. Ecological Connectivity among Macrobenthic Assemblages*

EC has a converse relationship with β-diversity, and the analysis considered these important ecological relationships between the assemblages. In the present study, the β-diversity values indicate an intermediate connectivity between BI and SA assemblages, according to the scale presented by Magurran [78]. These results indicate that the compositions of macrobenthic communities among the different basins are relatively similar. This emerging pattern of β-diversity agrees with the existence of an environmental gradient. In fact, the study area is within an oceanographic gradient, where the estuarine circulation allows the outflow of fresh and cold water and the inflow of seawater and relatively warmer water [50,51]. A similar situation was observed in the research conducted by Thurst [83], where the factors of distance, habitat heterogeneity, and productivity influenced species composition. However, it also depends on the dispersal ability of individuals. Some larvae may be retained very close to their source area [84] or travel long distances [85].

Concerning the pattern of functional diversity, our results revealed a high functional connectivity between the two assemblages. In fact, the percentage of shared species reached 36.3%, and, in terms of abundance, they concentrated at 81% of the total mean abundance. When contrasting the diversity of diets and the reproductive development of the species of both assemblages, no significant differences were obtained (except for the group of other larvae types). Similar results have been described for polychaete assemblages in the Magallanes region, where omnivorous predators and species with pelagic larvae were dominant [81]. According to Villéger et al. [86], two communities can be very different in terms of species composition but very similar in biological and trophic traits. The presence of an environmental gradient may cause a response in the diet of organisms that affects the trophic structure of benthic communities [87]. Likewise, 80% of the species (mainly polychaete species) have a planktonic larval stage in their life cycle, providing the main way of population dispersal [21,88,89]. In a study of the meroplankton community in a sub-Antarctic proglacial area, polychaete larvae dominated in number but showed low abundances [26], which confirms our finding using functional traits of benthic species.

The analysis of α-diversity is insufficient to describe connectivity between the macrobenthic assemblages of BI and SA, while the analysis of β- and functional diversities contrarily revealed connectivity between the studied assemblages. This paradox was previously described by Villéger et al. [86], who described that taxonomy is insufficient to understand the structure of species assemblages, as species' diversity indices treat all species identically, whereas functional diversity indices do not. Therefore, it is reasonable to expect that functional diversity is more ecologically relevant as species differ from each other in functionally important aspects [27]. The functional diversity of a community has emerged as a facet of biodiversity, which quantifies the value and variety of traits of organisms that influence their performance and, thus, the functioning of the ecosystem [90].

In summary, most studies using only α- diversity analysis focused on describing the differences between assemblages, which neglects the description of the degree of ecological connectivity, which the comparable assemblages undoubtedly have. Therefore, the presence of differences as well as connectivity among the studied assemblages are not contradictory; rather, α-, β-, and functional diversity analyses are complementary and not mutually exclusive.

### *4.3. Ecological Connectivity and the Marine Protected Areas*

Balbar and Metaxas [15] analyzed 746 MPAs, of which only 11% considered connectivity as an ecological criterion for the design and location of the protected areas. Our analysis shows EC between marine protected areas and the adjacent bay. Therefore, our determination of EC may be very useful for conservation and management planning. Shanks et al. [91] suggest an optimal size for MPAs (4–6 km) and spacing (20 km apart) to ensure connectivity between MPAs and adjacent areas. Indeed, integrating EC is an important element for establishing MPAs and for the design of MPA networks, being a fundamental aspect during strategic decision-making or for the design of a network of MPAs. The present study lays the foundation for future research that seeks to preserve the ecological integrity of Patagonian fjords and channels, recognizing the importance of maintaining and protecting the connectivity between their different benthic assemblages.

## 5. Conclusions

The results of this research represent a first approach in evidencing ecological connectivity between two soft-bottom assemblages. In particular, the benthic assemblages of BI and SA are functionally linked by Canal Whiteside, serving as a natural corridor for the exchange of taxa via larvae.

Based on the assessment of the three approaches used to determine the EC between the BI and SA assemblages, functional diversity was found to be the most informative index, where the diet of the taxa and their reproductive development were the characteristics that best represented EC.

**Supplementary Materials:** The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d16070430/s1. Table S1: Full taxonomic list of taxa presents in Bahía Inútil and Seno Almirantazgo.

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