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Traveling Seaweeds—Seasonal and Latitudinal Diversity of Epiphytic Seaweeds on Stranded Rafts of the Floating Seaweed *Durvillaea incurvata* Along the Chilean Coast

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Abstract

Floating seaweeds can be an effective dispersal vector for non-buoyant seaweeds. An under-explored aspect is the examination of seaweed rafts and their non-buoyant seaweed community after the floating journey ends. In this study, we analyzed 476 entire stranded specimens of the floating seaweed *Durvillaea incurvata* and their associated epiphytes, which were collected during winters and summers of 2023–2025 at four sites along the continental coast of Chile (between 31° S and 41° S). A total of 57 species of epiphytic seaweeds were found, with a higher predominance of Rhodophyta (71.9%). The most representative morpho-functional group was coarsely branched (29.1%). The species *Lessonia spicata*, *Antithamnionella ternifolia*, *Corallina chilensis*, *Gelidium rex*, *G. chilense*, and *G. lingulatum* were found frequently, and 67% of all epiphyte specimens found were reproductive. A higher taxonomic richness of epiphytes was observed at the southern-central sites compared to the northern site, being higher in summer than in winter. These results confirm that epiphytes associated with floating seaweeds are common and that many of these have reproductive structures. Co-occurrence analysis suggests that interactions among morpho-functional groups of epiphytes facilitate long-distance dispersal events. Future studies should assess the physiological viability and ability to reproduce of epiphytes after extensive floating journeys. This would contribute to understanding the effectiveness of rafting dispersal by floating seaweeds on the connectivity of raft-associated algal populations.

Keywords: co-occurrence species; epiphytic seaweeds; floating seaweeds; morpho-functional groups; strandings; Chile

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1. Introduction

Rafting dispersal by floating seaweeds promotes genetic connectivity and structuring of geographic ranges among seaweed populations [1–7], and their associated epibionts [8–17]. Several studies have shown the importance of rafting dispersal as passive transport for seaweed populations [18–23], while in the case of the raft-associated species, they have focused mainly on invertebrates that use the rafts as shelter or food [24,25]. Epibionts attached to floating seaweeds have been shown to disperse beyond their known geographic ranges. However, their dispersal capacity can be influenced by factors such as the availability and persistence of the rafts, and biotic interactions between the epibiont species [10].

Several genetic studies have shown that non-buoyant seaweeds can effectively disperse and connect distant populations (i.e., transport from the origin site, settlement in a new area, and post-recruitment survival and reproduction), presumably through rafting material and floating seaweeds [26,27]. However, ecological approaches that address this topic are scarce [10]. Moreover, rafting dispersal of non-buoyant seaweeds associated with these seaweed rafts (henceforth called "epiphytic seaweeds") has received little attention. In general, seaweed spores have a very low autonomous dispersal capacity (<1 km, [28]), and thus rafting dispersal can play an important role in the genetic connectivity of seaweed populations.

The structures used by many seaweeds to attach to rocks have intricate spaces that serve as habitat and protection for a large number of small species, both invertebrates and other seaweeds [29]. After detachment from the primary substratum, seaweeds with positive buoyancy (mainly brown algae) and their raft-associated community can remain afloat for extended periods [9]. However, their persistence at the sea surface is constrained by abiotic factors, such as temperature and solar radiation [19,30]. For example, Tala et al. [31] reported surface water temperatures between 14 and 20 °C and solar radiation of 1000–1200 µmol photons m^{-2} s^{-1} in coastal areas of northern and central Chile (30° S–36° S), mainly in summer, whereas in the south (53° S), these values drop drastically to 6–10 °C and 200–400 µmol photons m^{-2} s^{-1}, respectively. In *Sargassum horneri*, photo-acclimation is crucial for its rapid accumulation and long floating periods at the sea surface [32,33]. In northern Chile, seasonal environmental stress reduces growth and enhances the degradation of floating kelps, particularly during spring and summer [19,34]. Additionally, biotic factors such as herbivory by raft-associated species [19] and epibiont loading [35] can accelerate the sinking of seaweed rafts.

Depending on currents and winds, a fraction of the floating seaweed rafts can return to shore, resulting in strandings along beaches over space and time [36–40]. These stranded seaweeds constitute trophic subsidies in low primary productivity environments, being important in several ecological processes, such as feeding areas for birds and invertebrates, tissue degradation by providing nutrients, habitat supply, and biogeochemical processing [41–45]. Beach-cast seaweeds and their associated epiphytic seaweeds (non-buoyant species) can serve as a proxy for the potential arrival of floating individuals in coastal areas [37,38]. While seaweeds stranded on sandy beaches have no chance to recolonize benthic habitats, they are a reflection of the broader-scale arrival of rafting seaweeds that could colonize adjacent rocky shore habitats [38]. In particular, it allows us to examine the spatial and temporal variability of the abundances of non-buoyant seaweeds attached to beach-rafts, and their possible biological interactions. Additionally, verifying the reproductive status of the specimens after these dispersal events allows us to assess their viability and potential for colonizing new habitats. Furthermore, examining the morpho-functional groups of epiphytic seaweeds present in these beach-cast rafts could provide insights into algal assemblages that are better suited for long-distance dispersal events [46–48]. Moreover, climate change is altering the availability and permanence of these seaweed rafts

and their hitchhikers, which highlights the importance of analyzing these interactions [49]. Recently, using hydrodynamic and individual- based models, Thompson-Saud et al. [50] indicated that El Niño-Southern Oscillation (ENSO) influenced the dispersal distance of *Macrocystis pyrifera* floating fragments in the southeast Pacific, increasing these dispersal distances during El Niño phases.

In the southern hemisphere, one of the main floating seaweeds belongs to the genus *Durvillaea* [12,18,51–53]. Recent genetic studies have shown that what was considered *D. antarctica* comprises two species separated genetically and geographically [18]. Consequently, the species found along the continental coast of Chile between 30° S and 43° S has been renamed *D. incurvata* (Suhr) Macaya 2019. Meanwhile, *D. antarctica* (Chamisso) Hariot 1892 is restricted to the Chilean coast from 43° S to 56° S (Magellan), as well as the coast of New Zealand, and subantarctic islands [1,2].

The 'southern bull kelp' *Durvillaea incurvata* is growing in areas exposed or semi-exposed to waves and rocky substrata [54,55], typically found in the lower intertidal and subtidal zones, reaching depths of up to 10 m [56,57]. In its benthic populations, it is common to observe several species of seaweeds and invertebrates associated with its holdfast [54]. Many of these species are also observed in floating individuals [9], which have the ability to stay afloat for long periods at high latitudes, especially during winter, while at lower latitudes their buoyancy is significantly reduced, mainly due to the loss of frond biomass [31].

Previous studies have investigated stranding patterns of *D. incurvata* and their associated epibiont community. In general, the stranded biomass of *D. incurvata* is high in the summer and autumn months, but decreases during the spring (September-December) [37], which coincides with the annual growth of its benthic populations [55]. Also, latitudinal patterns have been observed, with higher stranded biomasses between 30° S and 33° S and between 37° S and 42° S, and lower at mid-latitudes (33° S to 37° S) [37,38]. Furthermore, these stranded biomasses have a direct relationship with adjacent benthic populations [57]. In the case of the raft-associated community, the richness of epibiont species tends to increase towards latitudes higher than 33° S, being also higher in summer than in winter [10]. Moreover, phylogeographic studies of benthic populations of seaweeds (*Gelidium* spp., [58]), invertebrates [10] and algal pathogens [59,60], frequently found on holdfasts and fronds of stranded *D. incurvata* specimens, suggest that these organisms are dispersed over long distances by rafting along the Chilean coast.

Therefore, this study aimed to evaluate the epiphytic seaweed communities associated with the holdfasts of beach-cast rafts of *D. incurvata* on four beaches along the continental coast of Chile (31° S–41° S) during the winter and summer seasons of two consecutive years (2023/24 and 2024/25). To assess their dispersal potential in the natural environment, we quantified the seasonal and latitudinal variability in species diversity and morpho-functional groups, morphometric characteristics, reproductive stages, and co-occurrences of non-buoyant seaweeds. This study contributes to a better understanding of the rafting dispersal of non-buoyant seaweeds by floating seaweeds.

2. Materials and Methods

2.1. Study Area

The southern-central coastline of Chile (between 31° S and 42° S) is marked by a linear topography and the absence of geographic barriers to marine species dispersal [61,62]. This region exhibits a pronounced latitudinal variation in sea surface temperature as part of the Humboldt Current System [61].

The research was carried out on four beaches, Fundo Agua Dulce (FAD, 31° S), Rumena (RUM, 37° S), Playa Brava (BRA, 41° S), and Playa Chauman (CHAU, 41° S) across the

benthic distribution of *D. incurvata* (Figure 1). The lengths of the surveyed sections on each beach varied from 1.2 to 5.5 km, depending on the overall beach size and quantity of beach-cast bull kelps. Beaches were distributed across the three biogeographic districts located in the Intermediate Area, based on Camus [62] and previous studies on *D. incurvata* strandings [37,38]: Septentrional District (SED), 30° S–33° S; Mediterranean District (MED), 33° S–37° S; Meridional District (MD), 37° S–42° S (Figure 1 and Table S1). López et al. [38] showed that the stranding patterns of *D. incurvata* exhibit significant variation across these biogeographic districts, as well as the diversity of epibionts associated with stranded bull kelp rafts [10]. In addition, the genetic structure of *D. incurvata* in this area [18] indicates that the connectivity of *D. incurvata* populations varies between these districts.

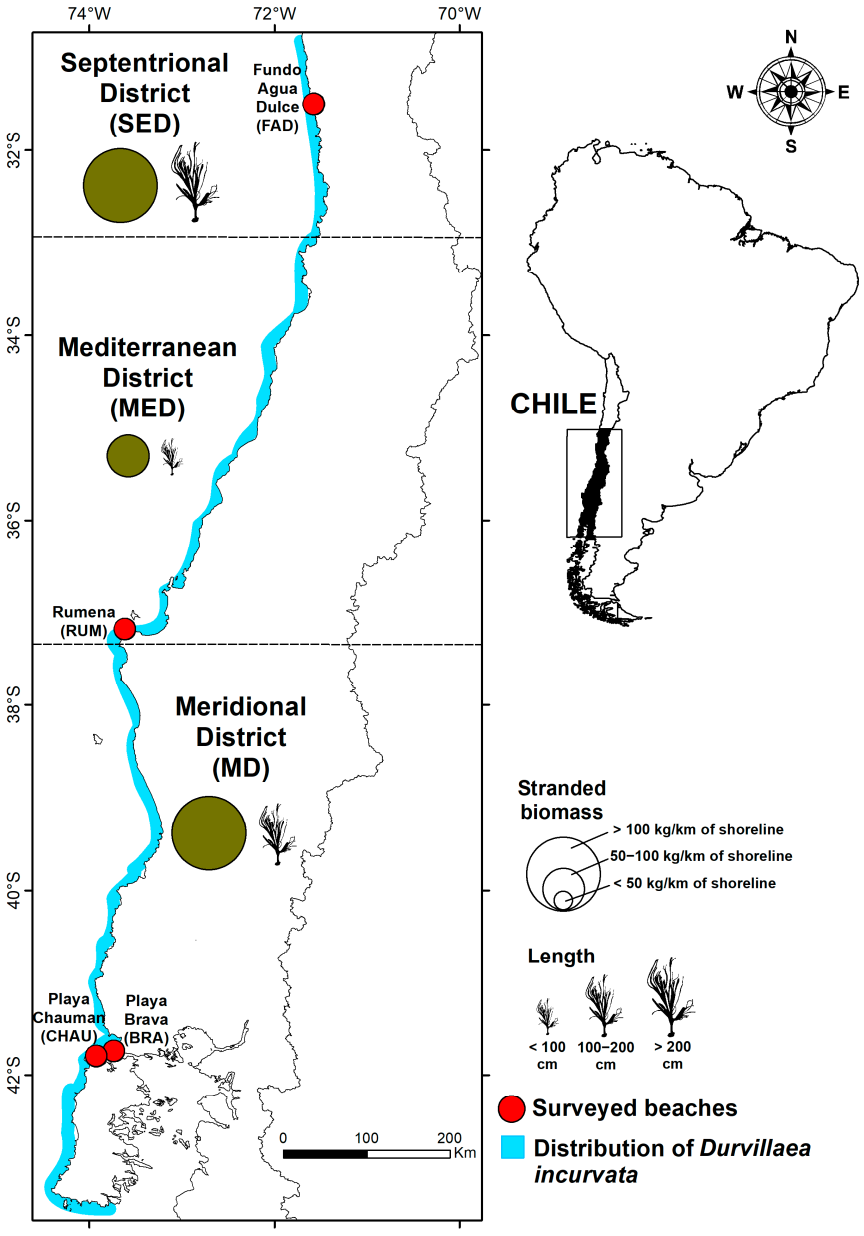


Figure 1. Geographic distribution of surveyed beaches in this study and biogeographic districts (Septentrional District: 30° S–33° S, Mediterranean District: 33° S–37° S, Meridional District: 37° S–42° S) of the Intermediate Area described for the coast of Chile by Camus [62]. The geographic distribution of *Durvillaea incurvata* within the study area is also indicated. For each biogeographic district, the patterns of stranded biomass (represented by green circles) and the sizes of *D. incurvata*, as documented in previous studies [37,38], are depicted.

2.2. Sampling of Stranded Durvillaea incurvata and Its Non-Buoyant Seaweed Community

The methodological protocols outlined below follow the procedures of previous studies on stranded *D. incurvata* specimens conducted in the same study area [37,38,63]. During the austral winters (July) and summers (January) of two consecutive years (2023/24 and 2024/25), recently beach-cast rafts of *D. incurvata* (i.e., only kelps with greenish or dark-brown color that maintained some flexibility and moisture, indicative of freshness) were collected from each beach (Figure 2A). Seasonal surveys (with a 10-day gap between beaches) were conducted on foot along the shoreline, gathering entire specimens (including blades, stipes, and holdfasts) of beached *D. incurvata* from the latest flotsam lines (marked by debris from floating objects, seaweed wracks, and foam). Similarly, because *D. incurvata* can have holdfasts with several stipes (each stipe represents a separate individual, [64]), for practical purposes hereafter, a beach-cast raft (with single or multiple stipes) will be referred to as a "plant". Measurements were only made on entire specimens that had seaweed epibionts attached to their holdfasts and/or with the presence of *Lepas* spp. individuals (Figure 2B). In any case, within the stretches on each beach, the total number of entire *D. incurvata* specimens observed (with and without epiphytes) was quantified to establish the percentage of specimens with non-buoyant seaweeds.

For each sampling, the total distance covered on each beach was calculated using the Google Earth 7.3.7 tool. This enabled accurate distance estimates by accounting for the beach curvature (Table S1). The stranded *D. incurvata* biomass per beach (kg wet weight per km of shoreline) for each season and year was determined based on the total mass of specimens found on a beach and the distance of the examined shoreline (see below).

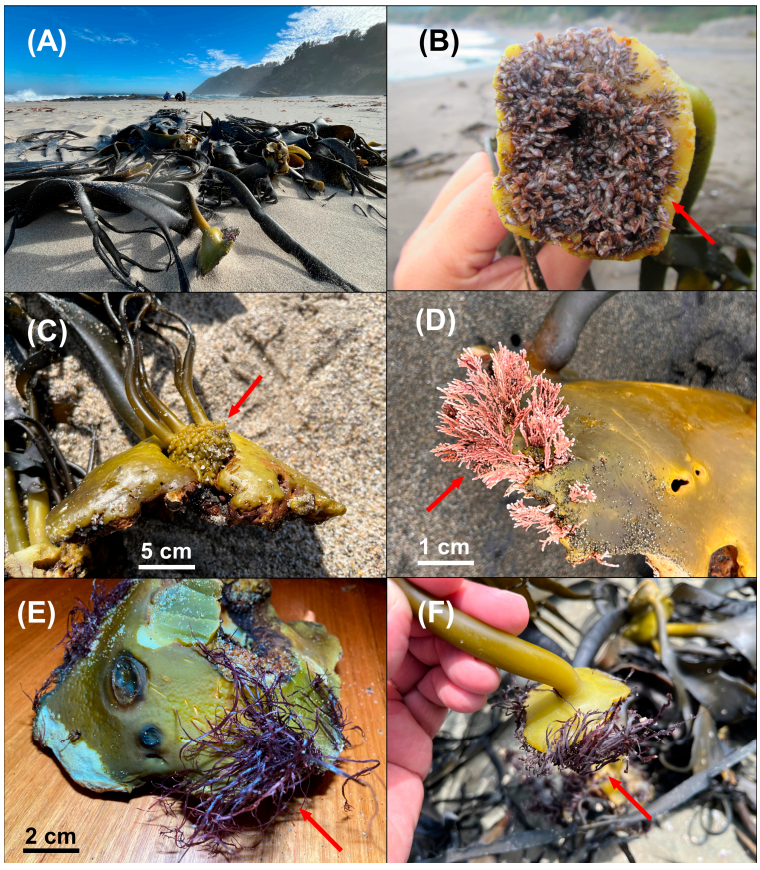


Figure 2. Stranded *D. incurvata* individuals, the most frequent epiphytes, and stalked barnacles (red arrow) attached to their holdfasts throughout the study. (**A**) Stranded bull keps on Rumena beach (RUM) during a summer survey, (**B**) *Lepas* spp. specimens, (**C**) *Lessonia spicata* specimens, (**D**) *Corallina chilensis* ramets, (**E**) *Gelidium rex* ramets, (**F**) *Gelidium lingulatum* ramets.

2.2.1. Measurements on *Durvillaea incurvata* Specimens

A total of 476 complete specimens were analyzed in this study. Entire bull kelp individuals were measured and weighed on the beach. Only the holdfast, representative reproductive tissue samples, and stalked barnacle specimens (*Lepas* spp.) attached to stranded *D. incurvata* were taken to the laboratory for further analyses (see below). The following variables were recorded for each complete *D. incurvata* plant:

(a) Total length: the measurement in centimeters was taken as the straight-line distance from the base of the holdfast to the tip of the longest frond.
(b) Biomass: the individual wet weights of the fronds, stipes, and holdfast of an entire plant were measured separately using a portable electronic hanging digital scale (1 g accuracy). The overall biomass of the plant was determined by adding the weights of the fronds, stipes, and holdfast.
(c) Holdfast diameter: the diameter was determined by measuring the straight-line distance in centimeters along the concave side across the maximum axis of the holdfast.
(d) Number of stipes: the total number of stipes on each plant was counted.
(e) Reproductive stage: tissue samples were collected from the longer fronds of each plant to assess the reproductive stage. Two samples were collected, one from the middle part and one from the apical part of the frond. These samples were then placed in Ziploc bags and frozen at 18 °C to maintain the integrity of the reproductive tissues [38]. The samples were subsequently analyzed in the laboratory after 2–4 weeks. No decalcification or staining methods were used for this purpose.
(f) Floating time: we assessed each plant to determine if it had been colonized by stalked barnacles (*Lepas* spp.) The majority of plants were colonized by *L. australis* Darwin, 1851, which is prevalent in southern Chile (38° S–42° S), and *L. anatifera* Linnaeus, 1758, which is more common in the northern section of the study area (31° S–32° S) [65] (Figure 2B). Given that these two species exhibit similar sizes and growth rates [65], we refer to them as *Lepas* spp. If the plants were found to have only cyprids (newly settled larvae) of *Lepas*, this was noted on site, but no samples were collected from these plants. However, if the plants contained *Lepas* individuals that had already metamorphosed, we collected samples of the 10–20 largest individuals to measure their sizes, which is indicative of floating time [38,65]. Each *Lepas* specimen was measured using scaled images with Image Pro Plus v6 software (Media Cybernetics Inc., Silver Spring, MD, USA). For each survey, the percentage of *D. incurvata* individuals with *Lepas* spp. was determined, as well as the size of the attached specimens [37,38]. As reported by Goehlich et al. [65], the growth rates for *L. anatifera* and *L. australis* vary between 0.21 and 0.47 mm per day at a temperature of 14 °C. Consequently, *D. incurvata* individuals with *Lepas* measuring over 5 mm correspond to more than 10 days of floating time [38]. This threshold value of *Lepas* size (5 mm) has been used in several studies in the same area [10,37,38]. This difference in the floating time of seaweed rafts allows us to infer possible long-distance dispersal events from others at shorter distances.

Analysis of Reproductive Stage

Durvillaea incurvata is a species with separate male and female individuals, and its sex and reproductive stages can only be identified through histological examination [66]. In the laboratory, after the samples were thawed and rehydrated with seawater, thin cross-sections of each tissue sample were sliced and examined under a microscope to identify sex and maturity. In this analysis, 30 conceptacles per sample were examined following the protocols outlined by Collantes et al. [66]. For further analysis, we classified tissue maturity into two stages: “vegetative” and “reproductive”, according to the protocols described in detail by López et al. [38].

An individual was considered reproductive when at least half of the conceptacles examined (considering both samples) were mature. Subsequently, the percentage of reproductive individuals by sex was determined for each beach based on the total number of sampled specimens.

2.2.2. Measurements of Epiphytic Seaweeds

The methodological protocols outlined below follow the procedures of a prior study on epibionts of stranded *D. incurvata* specimens conducted in the same study area [10]. For each beach-cast bull kelp, the presence of non-buoyant seaweed species on the holdfasts was noted by checking the convex top of each holdfast (Figure 2C–F). All seaweed species (usually clumps or ramets connected at their basal structures) were carefully removed from the holdfast. In cases (n = 3) where two or more clumps of the same epiphyte species were found in different positions on the same holdfast, the clumps were collected separately but treated as one for subsequent analyses (see Section 2.3 below). All manipulation and cleaning of epiphytes were carried out without the use of freshwater to avoid affecting the taxonomic identification of key morphological structures and the reproductive status of the specimens. All seaweed species were taken to the laboratory for detailed species identification and reproductive status. The individual weights and lengths of each epiphyte (i.e., ramets or clumps) were also recorded. Length was measured as the rectilinear distance from the basal structure to the tip of the longest ramet or frond. The wet weight of the entire clumps or ramets was measured using a portable electronic digital scale (0.1 g accuracy). Because we documented numerous taxa at different levels of detail (such as species, genus, and order), we use the term "taxonomic richness" to denote the presumed species richness. For each *D. incurvata* specimen, the total number of non-buoyant seaweed taxa was calculated and considered as the taxonomic richness at the plant level. Mean and standard deviation values of taxonomic richness for total epiphytic seaweeds were calculated according to beach, year, and season using PRIMER v7 software [67]. Because of the way epiphytes are attached and the *D. incurvata* holdfast shape, it is difficult to perform any coverage analysis that would allow for abundance assessment. For this reason, other diversity indices were not calculated because of the use of presence/absence values for each epiphyte. Epiphytes were also classified according to the morpho-functional groups of Chilean intertidal seaweeds [47] for further analyses (see Section 2.2.3 below).

To account for the possibility that the taxonomic richness of epiphytic seaweeds may be affected by the sampling effort and the number of stranded bull kelps on each beach, taxonomic richness was also calculated for each beach using the Chao 2 index, referred to as "accumulated taxonomic richness." [10,68], calculating a value for each beach, year, and season, using the 'vegan' package [69] in R 4.4.2 [70]. Additionally, a rarefaction curve was calculated to verify the sampling effort per beach and season using the 'vegan' package [69] in R 4.4.2 [70].

In the same way as in the case of *D. incurvata*, the reproductive status of epiphytes was examined by beach, season and year, looking at the presence of reproductive structures under a stereoscopic magnifying glass with seawater. Considering the differences in life cycles and phases among all the epiphytes found, they were classified into three categories based on the qualitative criteria: (a) vegetative: without the presence of developed reproductive structures, (b) reproductive: with the presence of reproductive structures, and (c) indeterminate: differentiation is not possible due to the deteriorated state of the tissue (mainly due to decay), presence of calcareous structures. The lack of information in the literature for some species made it difficult to identify their reproductive status, and they were considered in this latter category. Likewise, in the specific case of Florideophyceae in Rhodophyta seaweeds (given their high presence and diversity, see Results), the state of the life cycle

was established, classifying it into three categories: (a) vegetative (non-reproductive thalli), (b) cystocarpic (bearing cystocarps), and (c) tetrasporic (bearing tetrasporangia) [71,72].

To examine differences in morphometric characteristics (length and weight) of the epiphytes attached to the stranded *D. incurvata* holdfasts between beaches, years, and seasons, a subset of six species was chosen, considering their high frequencies within the entire study and belonging to different morpho-functional groups: (a) *Lessonia spicata*, (b) *Antithamnionella ternifolia*, (c) *Corallina chilensis*, (d) *Gelidium rex*, (e) *G. chilense*, and (f) *G. lingulatum* (see Section 3 below). In the case of holdfasts with more than one clump or ramet of the same epiphyte, the weight and length values for the same holdfast were added. For these analyses, only descriptive values (mean and standard deviation) of weights and lengths for beaches, years, and seasons were calculated because of the zero frequency of epiphyte species in some beaches or seasons, which did not allow orthogonal factor analyses to be performed (see Section 2.3 below).

The reproductive status of the six epiphytic seaweeds described above was examined by counting the number of clumps (or individuals for *Lessonia spicata*) that presented reproductive structures [71,72]. For holdfasts (n = 2) with several specimens of the same epiphyte, the data were treated as a whole. The percentage of reproductive clumps (or individuals for *L. spicata*) was calculated for each species by beach, season, and year. Due to the absence of specimens on some beaches and during some seasons, only descriptive results were reported (see Section 2.3 below).

2.2.3. Co-Ocurrences of Epiphytic Seaweed Species

To examine the co-occurrence of epiphyte species within a single holdfast of beach-cast *D. incurvata* individuals, we focused on a subset of 25 species that had at least four records across all holdfasts collected during the study [10]. Using these data, matrices indicating the presence or absence of epiphyte species were constructed. Of the 300 pair combinations initially considered, 63 pairs (21%) were excluded from the analysis because their expected co-occurrence was less than 1, leaving 237 pairs for examination. In the case of morpho-functional groups of epiphytes, this subset was classified into seven groups: (a) filamentous, (b) sheet-like/foliose, (c) sheet-like/tubular, (d) thick leathery, (e) coarsely branched, (f) articulate calcareous, and (g) crustose [47]. In this case, of the 21 pair combinations evaluated, one pair (4.8%) was excluded from the analysis due to an expected co-occurrence of less than 1, leaving 20 pairs for examination. False positives were managed by using null models (i.e., maintaining fixed matrix row/column sums) to check if observed co-occurrence patterns were significantly different from random, reducing spurious associations. The co-occurrence matrices for species and morpho-functional groups were calculated, revealing positive co-occurrences (indicating species that tend to be found together), negative co-occurrences (indicating species that hinder the presence of others), and random co-occurrences (indicating species that are unrelated) [10,73], using the 'cooccur' package [74] in R 4.4.2 [70].

2.3. Statistical Analyses

For each beach surveyed, year, and season, we calculated the following dependent variables for *D. incurvata*: (a) total stranded wet biomass per km of shoreline, (b) number of stranded entire individuals per km of shoreline, (c) percentage of stranded *D. incurvata* with epiphytic seaweeds, (d) percentage of stranded *D. incurvata* according to reproductive stages, (e) mean length, (f) mean wet weight, and (g) mean stipes of stranded *D. incurvata*, (h) percentage of individuals with *Lepas* spp., and (i) size (capitular length) of *Lepas* spp. specimens. Owing to the low frequency of stranded *D. incurvata* with *Lepas* spp. During the

study, only descriptive statistics (mean and standard deviation) were determined for the percentage of stranded individuals with *Lepas* spp. and the size of *Lepas* spp. specimens.

To determine whether the aforementioned response variables differed based on the surveyed beach, year, and season, we conducted generalized linear models (GLM) with a normal (Gaussian) distribution [75]. A Gaussian fit was chosen with a preliminary check using the "fitdistrplus" package in R 4.4.2 [76]. Additionally, the residual analysis of the models indicated that the error distribution was more closely aligned with a Gaussian distribution. Separate three-way GLM analyses were conducted to evaluate the stranded biomass and number of stranded entire individuals, according to beach (fixed factor: four levels, FAD, RUM, BRA, and CHAU), year (fixed factor: two levels, 2023/24 and 2024/25), and season (fixed factor: two levels, winter and summer) as factors. For these analyses, the stranded biomass and number of stranded entire individuals were transformed using a logarithm x + 1. We employed a variant of a three-factor analysis without replication to test the hypotheses [77].

Full three-way GLMs were conducted for the length and wet weight of stranded *D. incurvata*, considering the same factors mentioned above. The goodness of fit of these fixed-factor models was estimated using pseudo-R^2 for GLM [78]. Wald test analyses of variance (ANOVA) were used to evaluate the statistical significance of each factor and its interactions. If there were significant effects ($p < 0.05$), the differences between the categories of factors were examined using Tukey's HSD tests [79]. These statistical analyses were conducted using the "lme4", "MuMIn", and "multcomp" packages in R 4.4.2 [70].

To assess the frequency of stranded *D. incurvata* individuals with epiphytic seaweeds according to beach, year, and season, analyses were performed with GLMs using the Poisson distribution, offset by the natural log of the total number of sampled *D. incurvata* individuals for beach and season. The model used was: model = glm (count of stranded individuals with epiphytes ~ beach × year × season + offset (log(total individuals per beach)), family = poisson (link = "log"), data = data). This statistical analysis was performed using the "MASS" and "vigreg" packages in R 4.4.2 [70].

In the case of epiphytes, only species with more than one occurrence on all the stranded *D. incurvata* examined during the study were considered [10]. Three-way ANCOVA was conducted to assess the taxonomic richness of epiphytes, considering beach, year, and season as factors, following the analysis of slope homogeneity and square root x + 1 transformation of the dependent variable [79]. Because epibiont taxonomic richness is strongly related to kelp holdfast size [10], the relationships between taxonomic richness and two holdfast morphometric variables, (a) wet weight and (b) diameter, were determined using the Pearson correlation coefficient and linear regression analysis [79]. The variable with the strongest relationship was incorporated as a covariate in the analysis of the taxonomic richness of epiphyte species. If significant effects were observed ($p < 0.05$), the differences among the factor categories were analyzed using Tukey's HSD test [79]. All statistical analyses of taxonomic richness were conducted using the "lme4" and "multcomp" packages in R 4.4.2 [70].

To assess whether the proportion of male, female, and vegetative individuals of *D. incurvata* varied across the four beaches, two years, and two seasons, a four-level contingency table ($3 \times 2 \times 2 \times 4$) was constructed. The chi-square test of independence was used to identify any significant differences [79]. A similar test ($3 \times 2 \times 2 \times 4$ three-level contingency table) was conducted to examine the proportion of reproductive status (i.e., vegetative, reproductive and indeterminate) of epiphytes. In the case of Florideophyceae (red seaweeds), the proportion of phase status (i.e., vegetative, cystocarpic, and tetrasporic) according to beach, year, and season was also analyzed using a chi-square test of independence [79].

3. Results

3.1. Stranded Biomasses and Morphometric Characteristics of D. incurvata

Stranded biomasses of *D. incurvata* varied according to the surveyed beach (pseudo-R^2 = 0.653, Table 1). Higher levels of stranded biomass were observed at the northern beach FAD than at RUM, BRA, and CHAU (Figure 3A–C, $p < 0.05$). There were significant interactions between beach and season, and among the three factors (Table 1). The seasonal pattern varied according to the beaches, being higher in winter (e.g., FAD), while at RUM it was higher in summer; a pattern that varied the following year (Figure 3A–C, $p < 0.05$). The number of stranded *D. incurvata* individuals also varied among beaches (pseudo-R^2 = 0.706, Table 1). More stranded individuals per km of shoreline were observed at RUM than at the other beaches (Figure 3B–E, $p < 0.05$). There was significant interaction among the three factors (Table 1). During the first year, the number of stranded individuals was higher at FAD and RUM in summer, and higher at BRA and CHAU in winter. An inverse pattern to the one described above was observed in the second year between beaches and seasons (Figure 3B–E, $p < 0.05$).

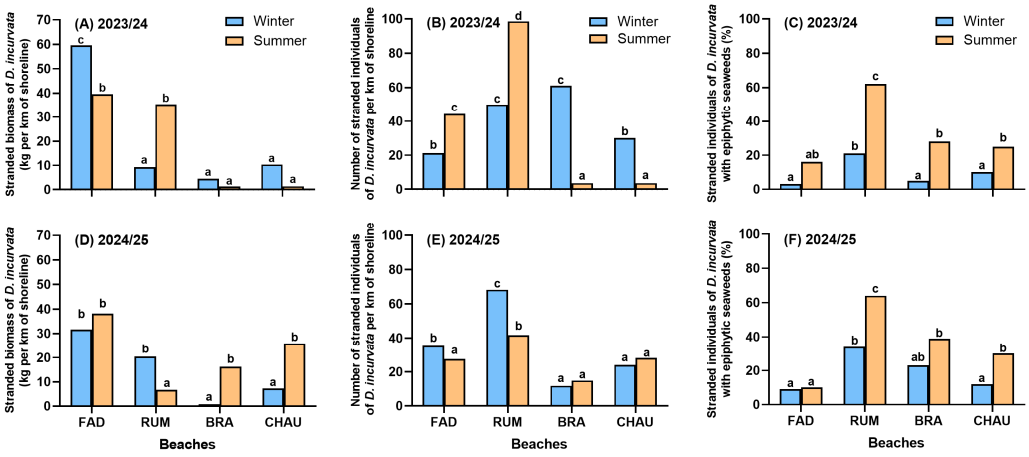


Figure 3. Stranded biomass, number of stranded entire plants, and percent of individuals of *Durvillaea incurvata* with epiphytic seaweeds on four beaches (FAD, RUM, BRA, and CHAU) from the continental coast of Chile (31° S–41° S), during two years (2023/24 and 2024/25), and two seasons (winter and summer). (**A**,**D**): Stranded biomass, (**B**,**E**): Number of stranded individuals, (**C**,**F**): Percent of stranded individuals with epiphytic seaweeds. Different letters above each column indicate significant differences among categories ($p < 0.05$). The sampled *D. incurvata* specimens (with and without epiphytes attached to the holdfast) for each beach and season are listed in Table S1.

There were statistical differences in the percentages of stranded *D. incurvata* individuals with epiphytes on their holdfasts among the sampled beaches and seasons (pseudo-R^2 = 0.571, Table 1). Higher percentages of individuals with epiphytes attached were observed at RUM compared to the other sites (Figure 3C–F; $p < 0.05$). Additionally, higher percentages were observed in summer than in winter ($p < 0.05$). No significant differences were observed between years or interactions between factors ($p > 0.05$, Table 1).

Significant differences in the lengths of stranded *D. incurvata* specimens were observed between beaches, years, seasons, and the interaction between year and season (pseudo-R^2 = 0.414, Table 2). Longer specimens were observed at FAD, intermediate sizes on the southern beaches (CHAU), and smaller individuals at RUM and BRA (Figure S1A–D, $p < 0.05$). In general, *D. incurvata* specimens were larger in winter, especially the first year of survey, while the second year, the stranded kelps tended to be larger in summer (Figure S1A–D, $p < 0.05$). On the other hand, wet weights varied according to beaches, years, and seasons (pseudo-R^2 = 0.694, Table 2). The wet weights of the stranded *D. incurvata*

specimens were higher on the beaches at FAD and CHAU compared to the other two beaches (Figure S1B–E, $p < 0.05$). Also, higher wet weights were observed in winter than summer of the first year, while in the second year, higher weights were observed in summer at most beaches (Figure S1B–E, $p < 0.05$). The number of stipes of stranded *D. incurvata* specimens varied between 1 and 14 (with most individuals having 1 to 5 stipes), and there were no significant differences between beaches, years, seasons or interactions among factors (pseudo-$R^2 = 0.528$, Figure S1C–F, $p > 0.05$).

Table 1. Summary of GLM (three factor analysis without replication) for stranded biomass, number of stranded entire individuals, and percentage of stranded *Durvillaea incurvata* with epiphytic seaweeds on beaches from the continental coast of Chile (31° S–41° S), according to beach (FAD, RUM, BRA, and CHAU), year (2023/24 and 2024/25), and season (winter and summer). Significant values ($p < 0.05$) are shown in bold.

	Stranded Biomass			Number of Stranded Entire Individuals			Percentage of Stranded Individuals with Epiphytic Seaweeds		
Source of Variation	**df**	**F**	***p*-Value**	**df**	**F**	***p*-Value**	**df**	**F**	***p*-Value**
Beach, (B)	3;16	7.41	**<0.01**	3;16	3.74	**<0.05**	3;16	6.38	**<0.01**
Year, (Y)	1;16	1.09	0.311	1;16	0.58	0.457	1;16	2.06	0.170
Season, (S)	1;16	1.19	0.291	1;16	0.22	0.645	1;16	4.78	**<0.05**
B × Y	3;16	1.97	0.159	3;16	1.17	0.352	3;16	2.37	0.108
B × S	3;16	6.68	**<0.01**	3;16	7.13	**<0.01**	3;16	1.04	0.401
Y × S	1;16	1.58	0.226	1;16	1.89	0.188	1;16	1.82	0.196
B × Y × S	3;16	5.12	**<0.05**	3;16	5.84	**<0.01**	3;16	1.39	0.281

Table 2. Summary of GLM (full three factor analysis) for length, wet weight, number of stipes of stranded *Durvillaea incurvata* individuals on beaches from the continental coast of Chile (31° S–41° S), according to beach (FAD, RUM, BRA, and CHAU), year (2023/24 and 2024/25), and season (winter and summer). Significant values ($p < 0.05$) are shown in bold.

	Length			Wet Weight			Number of Stipes		
Source of Variation	**df**	**F**	***p*-Value**	**df**	**F**	***p*-Value**	**df**	**F**	***p*-Value**
Beach, (B)	3;460	10.34	**<0.001**	3;460	5.89	**<0.001**	3;460	1.34	0.260
Year, (Y)	1;460	4.11	**<0.05**	1; 460	4.96	**<0.05**	1; 460	1.21	0.271
Season, (S)	1;460	4.23	**<0.05**	1; 460	4.21	**<0.05**	1; 460	0.94	0.332
B × Y	3;460	2.27	0.081	3; 460	1.67	0.172	3; 460	1.97	0.117
B × S	3;460	1.88	0.132	3;460	1.38	0.248	3;460	0.68	0.564
Y × S	1;460	5.11	**<0.05**	3;460	6.19	**<0.01**	1;460	2.19	0.088
B × Y × S	3;460	1.17	0.320	3;460	0.73	0.534	3;460	1.75	0.155

Stranded *D. incurvata* specimens with *Lepas* spp. (mainly *L. australis*) were only observed at the southern-central sites (RUM, BRA, and CHAU), with frequencies of occurrence ranging from 3% to 34%, being more frequent in winter than in summer (Figure S2A–C). The average sizes of the *Lepas* spp. specimens attached to the holdfasts did not exceed 6 mm in capitular length (mean = 4.7 ± 0.9 mm), particularly on the southern beaches. In addition, the observed sizes of *Lepas* spp. were similar across years and seasons (Figure S2B–D).

The reproductive status of stranded *Durvillaea incurvata* specimens fluctuated between seasons ($\chi^2_6 = 13.58$; $p < 0.05$). Mature specimens (males and females) were more frequent in winter (60–70%) than in summer (<40%), although some mature specimens were also observed during summer (mainly on the southern beaches BRA–CHAU, Figure 4A–D). The proportion of male and female specimens varied between seasons and beaches ($\chi^2_6 = 12.78$;

$p < 0.05$), with a higher presence of female specimens in winter (40–50%) than in summer (<30%) and no clear pattern in male specimens (Figure 4A–D).

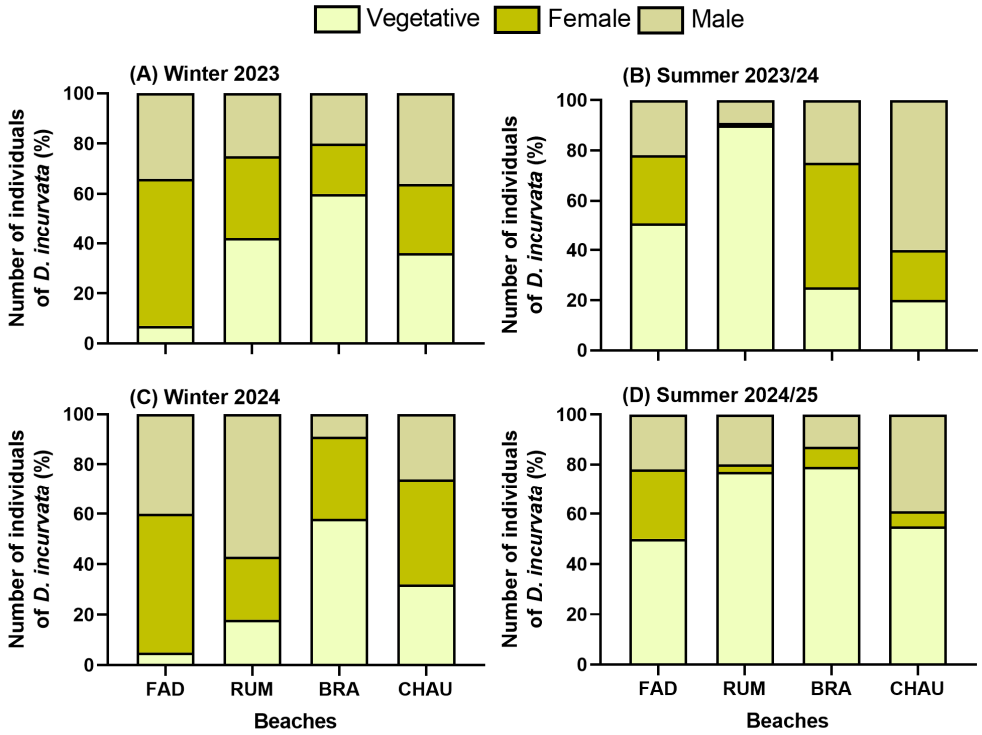


Figure 4. Percentage of stranded individuals of *Durvillaea incurvata* on four beaches (FAD, RUM, BRA, and CHAU) from the continental coast of Chile (31° S–41° S), during two years (2023/24 and 2024/25), and two seasons (winter and summer), according to three categories of reproductive status (vegetative, female, and male). (**A**) Winter 2023, (**B**) Summer 2023/24, (**C**) Winter 2024, (**D**) Summer 2024/25.

3.2. Taxonomic Richness and Reproductive Status of Epiphytic Seaweeds

A total of 57 epiphytic seaweed taxa were recorded on holdfasts of stranded *D. incurvata*. Of the species found, 71.9% were Rhodophyta, 19.3% Phaeophyceae, and 8.8% Chlorophyta (Figure 5A and Table 3). The species of seaweeds most frequently found were articulated coralline algae (31.7%), *Lessonia spicata* (14.9%), *Antithamnionella ternifolia* (9.6%), *Gelidium chilense* (6.5%), *Polysiphonia* sp. (6.1%), *G. rex* (5.9%), and *G. lingulatum* (5.8%) (Table 3). Of the total species found, 19 species were reported from a single stranded specimen throughout the study (Table 3). Also, these epiphytes belong to eight functional groups (Figure 5B and Table 3). The most representative morpho-functional groups on the stranded holdfasts were coarsely branched (29.1%), filamentous (27.3%), and thick leathery seaweeds (25.5%) (Figure 5B and Table 3).

There was a significant relationship between taxonomic richness of epiphytic seaweeds with holdfast diameter ($R^2 = 0.15$, $F_{1;339} = 61.4$, $p < 0.001$), unlike holdfast wet weight ($R^2 = 0.003$, $F_{1;339} = 0.11$, $p = 0.737$) (Figure S3). The taxonomic richness of epiphytes varied according to beaches and seasons (Table 4). Higher taxonomic richness was observed on the southern-central beaches of the study area compared to the northern beach (FAD) (Figure 6A–C, $p < 005$). Likewise, taxonomic richness was higher in summer than in winter (Figure 6A–C, $p < 0.05$). There were no significant differences between years or interactions among factors (Table 4). On the other hand, accumulated taxonomic richness (Chao2 index) varied across beaches, years, and seasons (Table 4). In general, there was higher accumulated taxonomic richness on the southern-central beaches (mainly at RUM and CHAU) than on the northern beach (FAD), although this pattern varied between both sampling years

(Figure 6B–D, $p < 0.05$). Moreover, there was higher accumulated taxonomic richness in summer than in winter, albeit this pattern was more evident in the second year of study (Figure 6B–D, $p < 0.05$). A similar pattern to that described was observed in taxonomic richness according to the sampling effort between beaches and seasons (Figure S4).

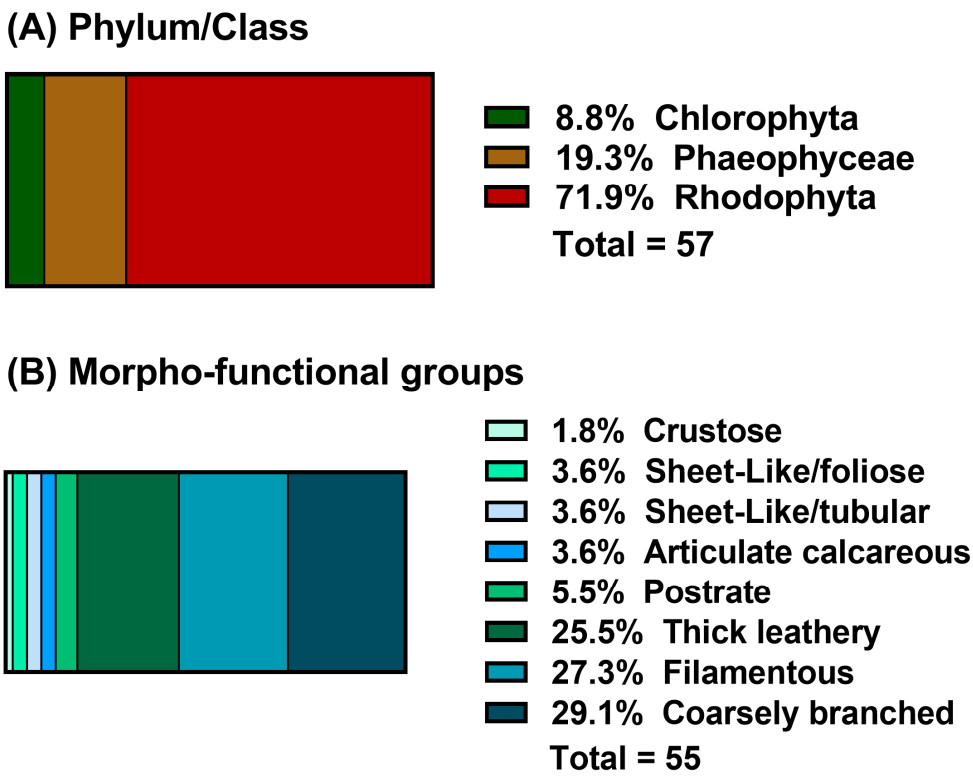


Figure 5. Percent of occurrence of epiphytic seaweeds on stranded *D. incurvata* holdfasts on four beaches (FAD, RUM, BRA, and CHAU) from the continental coast of Chile (31° S–41° S), during two years (2023/24 and 2024/25), and two seasons (winter and summer), according to (**A**) Taxonomic classifications, and (**B**) Morpho-functional groups. A complete list of the epiphytic seaweed species is presented in Table 3.

Table 3. Epiphytic seaweed species found on holdfasts of stranded bull kelp *Durvillaea incurvata* on four sandy beaches from the continental coast of Chile (31° S–41° S) during winters and summers 2023/24 and 2024/25. The percentage is based on a total of 476 stranded individuals of *D. incurvata*. The morpho-functional group for each registered species is also indicated, according to Gómez and Huovinen [47]. Only species with more than one record were included in statistical analyses. (*) Species that were incorporated in the co-occurrence analysis. The unidentified species corresponded to individuals that, due to their small size, absence of reproductive structures and/or tissue deterioration, it was not possible to reach a more specific taxonomic level.

		Presence		
Species	**Morpho-Functional Group**	**Total Number of Stranded Individuals**	**Percentage**	**Number of Stranded Individual per Beach (FAD/RUM/BRA/CHAU)**
Chlorophyta				
Cladophora sp.	Filamentous	2	<0.5	(0/0/2/0)
Codium bernabei	Postrate	2	<0.5	(1/0/0/1)
Codium dimorphum	Postrate	1	<0.5	(1/0/0/0)
Ulva intestinalis (*)	Sheet-like/tubular	8	1.6	(0/2/0/6)
Ulva sp. (*)	Sheet-like/foliose	12	2.5	(0/8/3/1)

Table 3. *Cont.*

Species	Morpho-Functional Group	Presence		
		Total Number of Stranded Individuals	Percentage	Number of Stranded Individual per Beach (FAD/RUM/BRA/CHAU)
Phaeophyceae				
Desmarestia sp.	Thick leathery	1	<0.5	(0/0/0/1)
Dictyota kunthii	Coarsely branched	1	<0.5	(0/1/0/0)
Ectocarpaceae unidentified	Filamentous	1	<0.5	(0/1/0/0)
Ectocarpus sp. (*)	Filamentous	29	6.1	(0/7/9/13)
Hincksia sp.	Filamentous	1	<0.5	(0/0/0/1)
Lessonia spicata (*)	Thick leathery	71	14.9	(22/42/5/2)
Macrocystis pyrifera	Thick leathery	2	<0.5	(0/0/0/1)
Petalonia fascia	Thick leathery	2	<0.5	(0/1/1/0)
Planosiphon gracilis (*)	Sheet-like/tubular	4	0.8	(0/1/1/2)
Pylaiella littoralis (*)	Filamentous	16	3.4	(0/7/4/5)
Unidentified species		1	<0.5	(0/0/0/1)
Rhodophyta				
Acrochaetium sp.	Filamentous	1	<0.5	(0/0/1/0)
Anisocladella pacifica	Thick leathery	1	<0.5	(0/1/0/0)
Antithamnion densum	Filamentous	3	0.6	(0/1/1/1)
Antithamnionella ternifolia (*)	Filamentous	46	9.6	(0/33/5/8)
Asterfilopsis disciplinalis (*)	Coarsely branched	4	0.8	(0/4/0/0)
Ballia callitricha (*)	Filamentous	7	1.5	(0/7/0/0)
Bossiella sp.	Articulate calcareous	2	<0.5	(0/2/0/0)
Branchioglossum bipinnatifidum	Thick leathery	1	<0.5	(0/1/0/0)
Camontagnea oxyclada (*)	Filamentous	4	0.8	(0/0/1/3)
Capreolia implexa	Coarsely branched	2	<0.5	(0/2/0/0)
Catenella fusiformis	Coarsely branched	1	<0.5	(0/0/0/1)
Ceramium sp. (*)	Filamentous	4	0.8	(0/2/1/1)
Chondria secundata (*)	Coarsely branched	21	4.4	(8/6/1/6)
Corallina chilensis (*)	Articulate calcareous	151	31.7	(11/77/27/36)
Corallina crustose (*)	Crustose	97	20.3	(0/42/19/36)
Delessereaceae unidentified	Thick leathery	1	<0.5	(0/1/0/0)
Gelidiales unidentified	Coarsely branched	2	<0.5	(0/1/0/1)
Gelidium chilense (*)	Coarsely branched	31	6.5	(0/14/3/14)
Gelidium lingulatum (*)	Coarsely branched	25	5.8	(0/7/6/12)
Gelidium rex (*)	Coarsely branched	28	5.9	(28/0/0/0)
Gigartinales unidentified		6	1.3	(0/3/2/1)
Griffithsia chilensis (*)	Filamentous	4	0.8	(0/0/0/4)
Gymnogongrus durvillei (*)	Coarsely branched	4	0.8	(0/4/0/0)
Mazzaella laminarioides	Thick leathery	1	<0.5	(0/0/0/1)
Mazzaella membranacea	Thick leathery	1	<0.5	(0/1/0/0)
Non-calcareous crustose unidentified	Postrate	1	<0.5	(0/0/0/1)
Paraglossum crassinervium	Thick leathery	2	<0.5	(0/2/0/0)
Phyllophoraceae unidentified	Coarsely branched	1	<0.5	(0/0/0/1)
Plocamium cartilagineum (*)	Thick leathery	4	0.8	(0/2/0/2)
Polysiphonia mollis	Filamentous	1	<0.5	(0/0/1/0)
Polysiphonia sp. (*)	Filamentous	29	6.1	(0/20/5/4)
Pyropia sp. (*)	Sheet-like/foliose	4	0.8	(0/1/1/1)
Rhodymenaceae 1	Coarsely branched	1	<0.5	(0/1/0/0)
Rhodymenaceae 2	Coarsely branched	1	<0.5	(0/1/0/0)
Rhodymenia skottsbergii (*)	Coarsely branched	4	0.8	(0/1/1/1)
Rhodymeniales unidentified	Coarsely branched	2	<0.5	(0/1/0/1)
Sarcothalia crispata (*)	Thick leathery	11	2.3	(0/5/4/2)
Schimmelmannia plumosa	Thick leathery	2	<0.5	(0/1/0/1)
Schottera nicaeensis (*)	Coarsely branched	15	3.1	(8/6/0/1)
Symphyocladia dendroidea	Filamentous	1	< 0.5	(0/0/0/1)
Unidentified species		9	1.8	(4/3/1/1)

Table 4. Summary of three-way ANCOVA for taxonomic richness of epiphytes attached on stranded individuals of *Durvillaea incurvata* on beaches from the continental coast of Chile (31° S–41°S), according to beach (FAD, RUM, BRA, and CHAU), year (2023/24 and 2024/25), season (winter and summer) and holdfast diameter (HD) as covariate. Significant values ($p < 0.05$) are shown in bold.

	Taxonomic Richness			Accumulated Taxonomic Richness		
Source of Variation	**df**	**F**	***p*-Value**	**df**	**F**	***p*-Value**
Beach, (B)	3;390	8.39	**<0.001**	3;390	4.74	**<0.01**
Year, (Y)	1;390	1.42	0.234	1;390	3.88	**<0.05**
Season, (S)	1;390	7.35	**<0.01**	1;390	4.22	**<0.05**
Holdfast Diameter, (HD)	1;390	61.4	**<0.001**	1;390	55.9	**<0.001**
B × Y	3;390	2.03	0.109	3;390	1.17	0.320
B × S	3;390	1.48	0.219	3;390	1.53	0.206
Y × S	1;390	1.28	0.258	1;390	3.89	**<0.05**
B × HD	3;390	2.04	0.107	3;390	1.41	0.239
Y × HD	1;390	1.58	0.209	1;390	1.11	0.293
S × HD	1;390	1.22	0.370	1;390	0.19	0.663
B × Y × S	3;390	1.19	0.312	3;390	0.22	0.882
B × Y × HD	3;390	0.87	0.456	3;390	1.65	0.177
B × S × HD	1;390	0.93	0.335	1;390	1.78	0.182
Y × S × HD	1;390	1.09	0.297	1;390	2.18	0.141
B × Y × S × HD	3;390	1.67	0.173	3;390	1.84	0.139

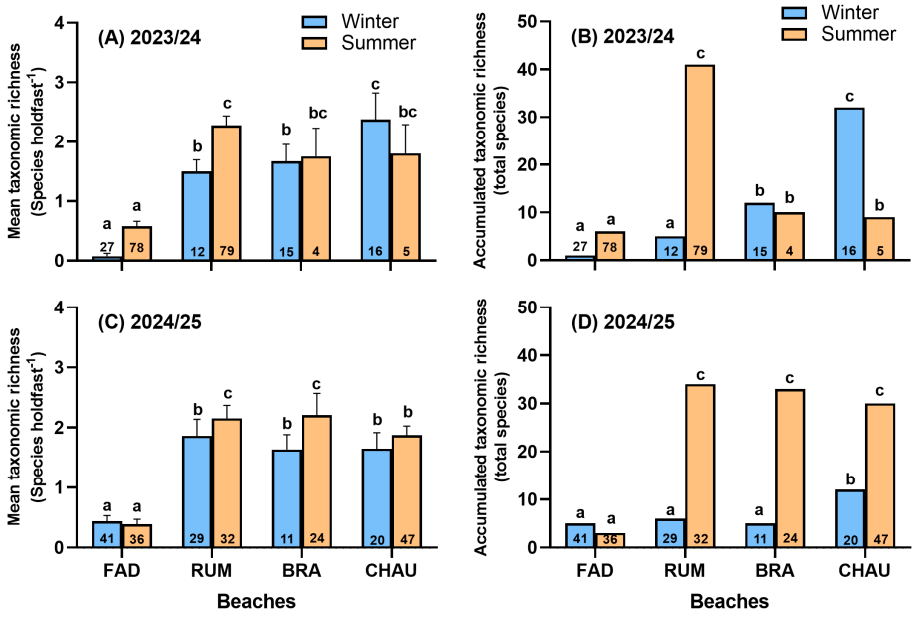


Figure 6. Average (mean + 1 SD) taxonomic richness of epiphytic seaweeds attached on stranded individuals of *Durvillaea incurvata* on four beaches (FAD, RUM, BRA, and CHAU) from the continental coast of Chile (31° S–41° S), during two years (2023/24 and 2024/25), and two seasons (winter and summer). (**A**–**C**) Taxonomic richness at the plant level and (**B**–**D**) accumulated per beach (Chao 2 index). (**A**) Winter 2023, (**B**) Summer 2023/24, (**C**) Winter 2024, (**D**) Summer 2024/25. Letters (a,b,c) above the columns indicate significant differences between beaches and seasons ($p < 0.05$). The number of sampled *D. incurvata* individuals per beach and season is listed at the bottom of each column.

The reproductive status of epiphytic seaweed specimens fluctuated between seasons, with a high variability between beaches ($\chi^2_6 = 15.02$; $p < 0.05$). In general, there was a higher frequency of vegetative specimens on all beaches and seasons, although reproductive specimens were more frequent in winter (40–50%) than in summer (<30%) (Figure 7A–D). There was no clear pattern between beaches, but sites without the presence of mature specimens were observed (e.g., FAD in winter, and CHAU in summer. Figure 7A–D). Regarding the stages of the life cycle of Rhodophyta seaweeds observed on the holdfasts,

there were variations between beaches and seasons ($\chi^2_6 = 13.42$; $p < 0.05$). The vegetative stage was predominant for all beaches and seasons (40–100%, Figure 8A–D). The cystocarpic and tetrasporic stages were frequent (20–60% and 10–30%, respectively) on the southern-central beaches, without showing a clear seasonal pattern (Figure 8A–D).

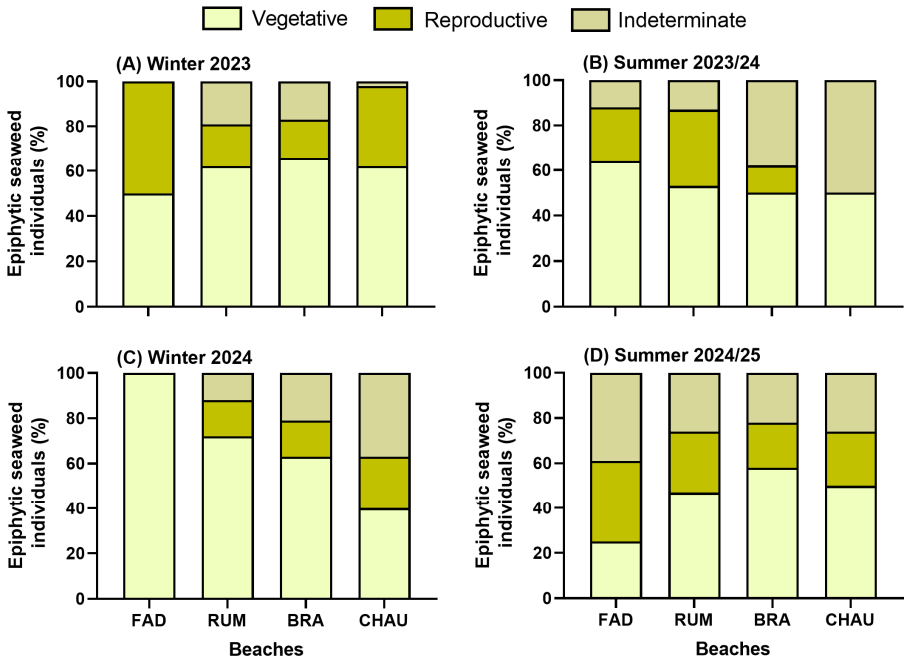


Figure 7. Percentage of epiphytic seaweeds on stranded *Durvillaea incurvata* holdfasts on four beaches (FAD, RUM, BRA, and CHAU) from the continental coast of Chile (31° S–41° S), during two years (2023/24 and 2024/25), and two seasons (winter and summer), according to three categories of reproductive status (vegetative, reproductive, and indeterminate). (**A**) Winter 2023, (**B**) Summer 2023/24, (**C**) Winter 2024, (**D**) Summer 2024/25.

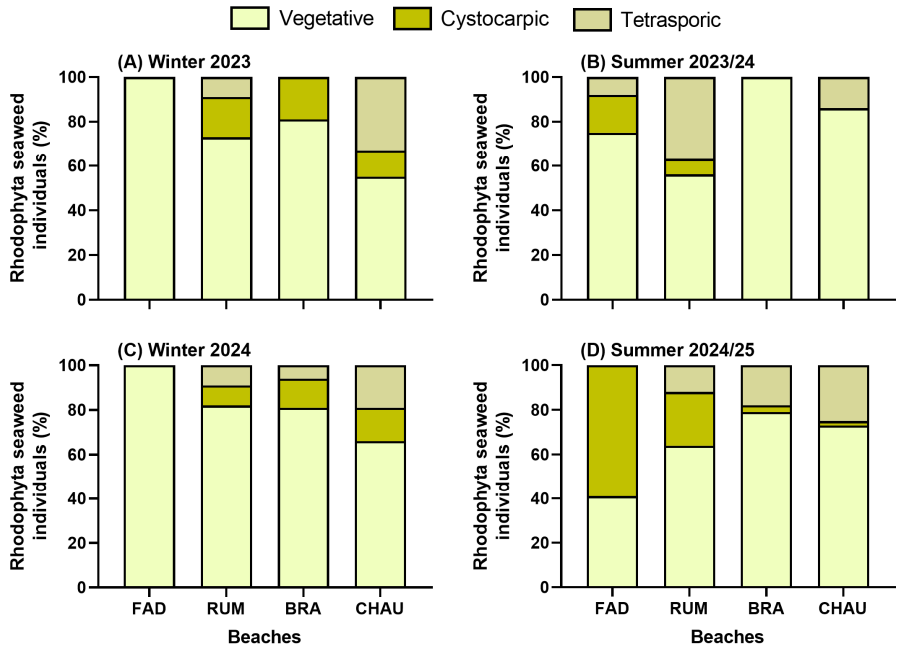


Figure 8. Percentage of Rhodophyta seaweeds from the class Floridophyceae on stranded *Durvillaea incurvata* holdfasts on four beaches (FAD, RUM, BRA, and CHAU) from the continental coast of Chile (31° S–41° S), during two years (2023/24 and 2024/25), and two seasons (winter and summer), according to three life cycle stages (vegetative, cystocarpic, and tetrasporic). (**A**) Winter 2023, (**B**) Summer 2023/24, (**C**) Winter 2024, (**D**) Summer 2024/25.

3.3. Morphometric Characteristics and Reproductive Status of Frequent Epiphytic Seaweeds

The brown seaweed *Lessonia spicata* appeared on all beaches and seasons, although it tended to be more frequent in winter than in summer (Figure S5A–D). The mean lengths of *L. spicata* specimens were higher in winter than in summer, mainly on the beaches of RUM (214.8 ± 27.7 mm) and CHAU (234.7 mm), while in summer the specimens did not exceed 70 mm in length (Figure S5A–C). The maximum wet weights of attached specimens fluctuated between 60 g and 90 g in winter at RUM, while in summer, they did not exceed 15 g on average in the same beach (Figure S5B–D). No statistical comparisons were performed due to many zero values; see also Section 2.

The red seaweed *Antithamnionella ternifolia* was common on the southern-central beaches of the study area, with higher presence in summer than in winter (Figure S6A–D). Mean lengths of specimens ranged from 1.8 to 6.2 mm on most beaches, with a maximum observed at RUM (10.3 ± 1.6 mm), and decreasing towards the southern beaches (Figure S6A–C). On the other hand, wet weights of *A. ternifolia* specimens did not exceed 0.1 g, except for RUM (0.25 ± 0.03 g) (Figure S6B–D).

In the case of seaweed *Corallina chilensis,* it was found along all surveyed beaches and seasons (Figure S7A–D). Larger *C. chilensis* specimens were observed in summer than in winter, mainly in the first year, while in the second year, the specimens did not exceed 20 mm (Figure S7A–C). The wet weights of specimens tended to be higher at RUM (1.18 ± 0.17 g) and BRA (2.43 ± 0.75 g) in summer, while the specimens did not exceed 1 g in the remaining beaches and seasons (Figure S7B–D).

Red seaweed species of the genus *Gelidium* had differential patterns. *Gelidum rex* was only observed in FAD, while *G. chilense* and *G. lingulatum* were observed on the southern-central beaches, but not on the northern beach (Figures S8 and S9). In case of *G. rex*, specimens were longer in winter (7.6 ± 1.0 mm) than in summer (4.9 ± 1.3 mm) (Figure S8A–C). The lengths of *G. chilense* specimens did not show a clear pattern between beaches and seasons (Figure S9A–C). On the contrary, lengths of *G. lingulatum* were higher in summer (36.0 ± 4.3 mm) than in winter (17.6 ± 3.8 mm), with a high variability between the southern-central beaches (Figure S10A–C). On the other hand, wet weights of *G. rex* were higher in summer (1.2 ± 0.2 g) than in winter (0.2 ± 0.1 g) (Figure S8B–D). A similar pattern of wet weights was observed in summer for *G. chilense* during the first year, with a maximum value at CHAU (1.3 ± 0.3), while during the second year, they did not exceed 0.7 g, irrespective of beach (Figure S9B–D). In *G. lingulatum*, wet weights showed a slight tendency to increase towards the southern beaches, without showing a clear seasonal pattern (Figure S10B–D).

A low frequency (< 10%) of reproductive specimens of *Lessonia spicata* was found on all beaches and seasons (Figure S11A–D). Reproductive clumps of *Antithamnionella ternifolia* were mainly observed in summer at RUM and BRA (from 40 to 75%), while in winter, reproductive *A. ternifolia* were only observed at RUM and CHAU (< 45%) (Figure S10B–E). Similarly, a higher frequency of reproductive clumps of *Corallina chilensis* was observed on southern-central beaches in summer (20–70%) than in winter (<20%) (Figure S11C–F). In the case of *Gelidium* spp., only reproductive clumps of *G. rex* were observed at FAD in summer (40%) during the first year (Figure S12A–D). On the other hand, reproductive clumps of *G. chilense* were observed at RUM and CHAU in both seasons (winter: 60–100%, and summer: 30–70%) (Figure S12B–E). Finally, in the case of *G. lingulatum*, reproductive specimens were observed in both seasons (from 40 to 100%) on the southern-central beaches (Figure S12C–F).

3.4. Co-Occurrence of Epiphytic Seaweeds

Among the total 237 combinations analyzed at the species level, 19.2% exhibited non-random co-occurrences. Of these, 9.1% were identified as positive co-occurrences, while

10.1% were negative co-occurrences. The proportion of positive and negative co-occurrences, when considering only non-random interactions, did not differ from expected by chance ($\chi^2 = 1.02$, $p = 0.815$). In particular, species such as *Polysiphonia* sp., *Antithamnionella ternifolia*, and *Ectocarpus* sp. had the highest positive co-occurrences with other epiphyte species on stranded *D. incurvata* individuals (Figure 9A). On the other hand, *Corallina chilensis* and *Corallina* crustose seaweeds had negative co-occurrences with other epiphytes (Figure 9A).

At the morpho-functional group level, 50% of the analyzed pair combinations exhibited non-random co-occurrences, with 15% identified as positive and 35% as negative co-occurrences. The proportion of positive and negative co-occurrences, when considering only non-random interactions, did not differ from what was expected by chance ($\chi^2 = 4.02$, $p < 0.05$). Filamentous seaweeds had positive co-occurrences with sheet-like/foliose and sheet-like/tubular seaweeds (Figure 9B). However, the crustose, articulate calcareous, coarsely branched, and thick leathery seaweed groups had negative co-occurrences with each other and with other groups. Conversely, crustose and articulated calcareous seaweeds had a positive co-occurrence (Figure 9B).

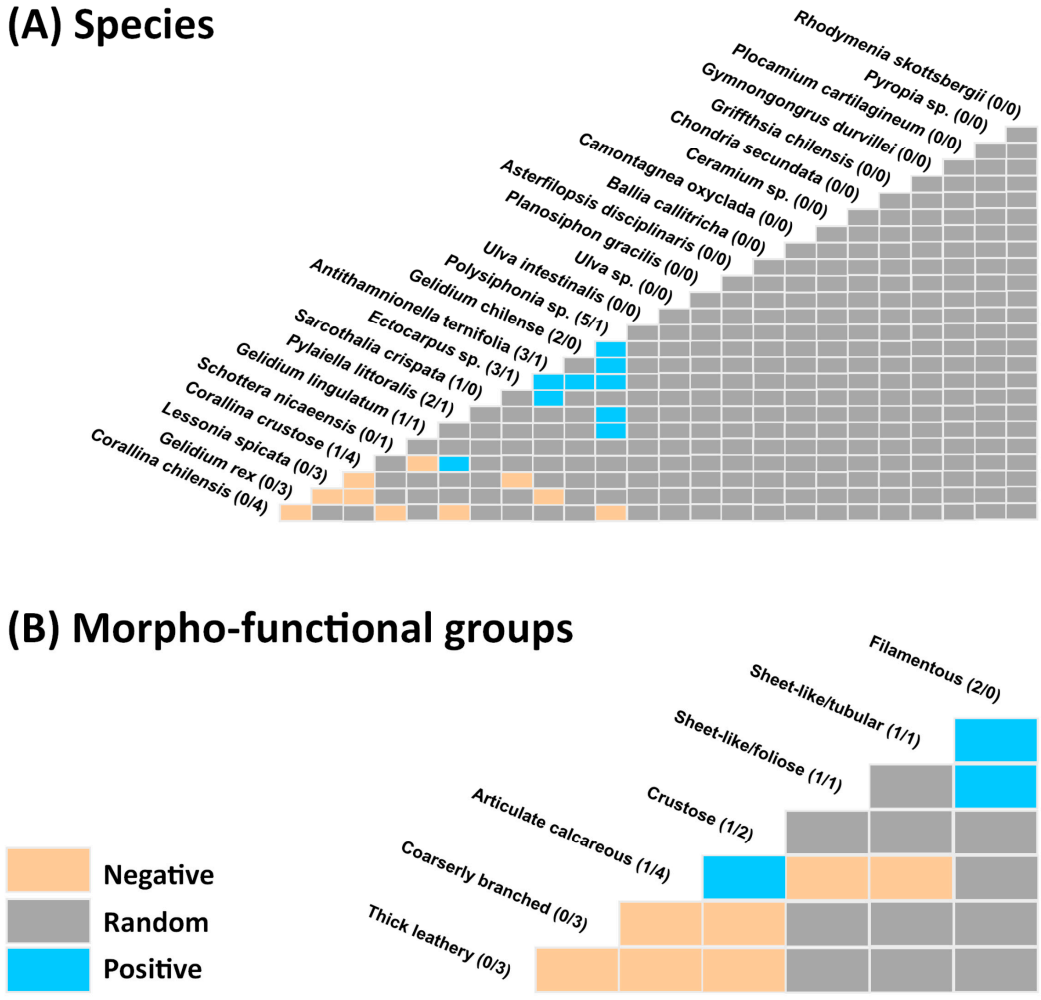


Figure 9. Species co-occurrence matrix of frequent (**A**) epiphytic seaweed species, and (**B**) Morpho-functional seaweed groups attached on stranded individuals of *Durvillaea incurvata* on four beaches (FAD, RUM, BRA, and CHAU) from the continental coast of Chile (31° S–41° S), during two years (2023/24 and 2024/25), and two seasons (winter and summer), according to positive, negative and random species co-occurrences. The number of positive/negative co-occurrences for each species is shown.

4. Discussion

In this study, we identified a distinct seasonal and latitudinal pattern in the strandings and morphometric traits of stranded *D. incurvata* individuals, which partially aligns with previous research [37,38]. The taxonomic richness of epiphytes on holdfasts of stranded *D. incurvata* increased toward the southern-central beaches during summer. Additionally, reproductive stranded specimens were found for both *D. incurvata* and its associated epiphytic seaweeds. This, along with the potential interactions revealed by the co-occurrence outcomes among these epiphytes, highlights the significance of effective transport and rafting dispersal of non-buoyant species by floating seaweeds.

4.1. Seasonal and Spatial Variability of D. incurvata Strandings

Stranded biomasses of *D. incurvata* varied among the surveyed beaches, with the highest biomass found on the northern beach (FAD, 31° S), while the number of stranded specimens was higher at RUM (37° S) compared to the other beaches. This suggests a higher presence of large *D. incurvata* specimens at FAD and smaller ones at RUM, which aligns with the morphometric results observed for stranded individuals on these beaches. These biomass and specimen size values are consistent with *D. incurvata* stranding patterns observed on the continental coast of Chile [37,38]. For instance, at RUM within the Mediterranean Biogeographic District (MED), there is strong extractive pressure from artisanal fishermen and shore gatherers (i.e., 6000 tons per year [80–82]), whereas *D. incurvata* is not commercially harvested at the northern site (FAD). This pressure leads to a reduction in benthic populations and contributes to a phenomenon known as "juvenilization", which in turn affects the frequency of sizes available in benthic populations and thus stranded specimens [63]. In contrast, the southern beaches (BRA and CHAU) exhibited low biomasses and intermediate sizes of stranded specimens, which differ from the high values recorded in previous studies [38,63]. In this area (i.e., Meridional Biogeographic District, MED), benthic populations of *D. incurvata* tend to increase in abundance [57]. However, interannual variations in benthic abundances may also reflect these changes [55]. Similarly, local currents and winds also transport floating specimens toward the coast (particularly into wave-exposed bays), resulting in a high concentration of beach-cast rafts [38,63], which can alter known patterns of *D. incurvata* strandings.

There was a slightly higher stranded biomass in summer than in winter. Other similar studies on stranded *D. incurvata* biomass along the Chilean coast did not reveal seasonal or interannual differences [38,63]. The growth of *D. incurvata* benthic populations varies seasonally, showing peaks during summer and autumn months [54,55], which is reflected in the high levels of stranded individuals observed during summer [37]. Various seasonal factors, particularly coastal oceanographic processes such as fronts and cyclones, play critical roles in hindering the offshore transport of new seaweed rafts to the coast [34,83–88]. Additionally, fluctuations in river discharge, particularly during the winter months (i.e., 1000 $m^3 s^{-1}$ [89]) when rainfall intensifies, significantly impact the movement of propagules and floating objects along the coastline [89,90]. During the winter months, the river plumes are more extensive, which can alter the seasonal abundance of beach-cast rafts.

Reproductive stranded specimens of *D. incurvata* were observed on all beaches throughout the study, mainly during winter. This finding aligns with the established reproductive phenology for this species, which indicates that the maturity stage and the presence of both sexes are most concentrated in winter in benthic [66,91] and floating individuals [30,31]. There was a slightly higher frequency of females than males on the southern beaches, suggesting that females could be more susceptible to elevated temperatures and increased solar radiation. This trend has also been observed in summer on northern beaches in previous studies related to ENSO events [38]. Previous studies have shown that repro-

ductive status is maintained during short periods of floating (i.e., <14 days [30]). However, during long periods (>30 days), tissue disintegration increases and affects reproductive capacity, mainly at lower latitudes [31]. Furthermore, it is unknown whether both sexes (or between vegetative and reproductive individuals) could have differential floating or permanence capacities [92] that could explain the spatio-temporal pattern observed in this study.

Stranded *D. incurvata* specimens with *Lepas* spp. were only found on the southern beaches of the study area, although their percentages were low (<40% of all stranded kelps). Additionally, capitular length of *Lepas* individuals was small (<6 mm), suggesting that their floating times were less than 10 days [65]. This pattern partially coincides with previous studies in the same areas [37,38,63]. High presence and sizes of *Lepas* spp. attached to beach-cast rafts had been observed on southern beaches (from 38° S to 42° S) related to long floating time [38]. High percentages of *Lepas* spp. had previously also been observed on beaches between 30° S and 33° S [38], but at FAD (31° S), there was no presence of *Lepas*, despite high stranded biomasses. The low presence of *Lepas* sp. during the first year (2023/24), particularly on the southern beaches, contrasts with the second year (2024/25). This difference may be influenced by the El Niño phenomenon in 2023/24, which affects local (onshore/offshore) currents and decreases the dispersal capacity of floating specimens [50,93,94]. These results suggest that the specimens may have come from adjacent benthic populations located less than 10 km away [57]. On the other hand, at RUM, molecular evidence in *D. incurvata* indicates low connectivity between benthic populations in that region (from 33° S to 37° S), suggesting oceanographic or topographic barriers to dispersal by floating specimens [18]. Nonetheless, the use of *Lepas* spp. as an indicator of the floating time of rafts requires careful consideration, because larval supplies and the growth rates of these stalked barnacles can vary by region and season [65].

4.2. Non-Buoyant Seaweeds on Stranded D. incurvata Specimens

Epiphytic red seaweeds were the most abundant on the holdfasts of stranded *D. incurvata*. This finding aligns with previous studies conducted in the same area [9,10]. Non-buoyant seaweeds attached to floating seaweed holdfasts tend to exhibit high species diversity, and being sessile favors their permanence throughout the rafting journey, unlike invertebrates (mainly mobile), which, after seaweeds detach from the rocky substratum, can evacuate the floating rafts [24,25]. Additionally, filamentous, coarsely branched, and thick leathery seaweeds were more frequent. These last two are morpho-functional seaweed groups that are characterized by presenting higher structural complexity (i.e., multi-layered structures with specialized tissues, fractal dimension, degree of branching and larger thalli) [47], which could suggest that structurally more complex seaweeds are better suited for long-distance dispersal events. However, these species are also commonly found in the lower intertidal zone, where they coexist with *D. incurvata*, and generally lack the physiological mechanisms to withstand high levels of radiation and temperature [47,95,96]. Therefore, during longer floating times and at lower latitudes, these species could disappear, and filamentous or laminar species, which are more suited to physiological stress, could increase. This could explain the high presence of epiphytic red seaweeds with these morphologies throughout the study (see Table 3). Also, due to the growth of the *D. incurvata* holdfast by individuals coalescing on the primary substratum [64], small recruits of turf-forming seaweeds are likely incorporated into the growing holdfast. Meanwhile, foliose and encrusting seaweeds may be overgrown, but not incorporated into the holdfast. This could explain their frequencies as epiphytes on the stranded specimens.

At the plant-level, the taxonomic richness of epiphytes was higher on southern-central beaches than on the northern beach, as well as in summer than in winter. This pattern of

taxonomic richness coincides with the percentages of stranded *D. incurvata* individuals with epiphytes observed in this study. In the central-southern areas, both temperature and solar radiation decrease, promoting the persistence of floating seaweeds and their epibionts [10,30,31]. Additionally, during the floating stage, the biogenic holdfast remains submerged due to its weight, unlike the frond, which reduces harsh stress on these epibionts during rafting journeys [19]. On the other hand, recruitment of several intertidal seaweeds increases in summer [97], which explains a higher taxonomic richness in that period. Furthermore, Gutow et al. [24] reported that the abundances of rafting organisms exhibit more pronounced seasonal variations at higher latitudes than at lower latitudes, with an increase in summer relative to winter.

The accumulated taxonomic richness of epiphytic species increases toward the southern-central zone of the study area. This trend aligns with the latitudinal biogeographic pattern of benthic algal species richness found along the Chilean coastline [98]. This would explain the higher diversity of seaweed species on stranded *D. incurvata* holdfasts towards the southern area, particularly at RUM. However, the differential sampling effort could mask the observed values of taxonomic richness of epiphytes. Frequent species (i.e., *Lessonia spicata*, *Antithamnionella ternifolia*, *Corallina chilensis*, and *Gelidium* spp.) are consistent with their known geographic distributions along the Chilean coast [56,97]. Additionally, these species have been frequently documented in previous studies of epibionts on stranded *D. incurvata* specimens [9,10]. For instance, in the case of *Gelidium* spp. there is a clear geographical separation among the three identified species (i.e., *Gelidium rex* is found in the northern regions, while *G. chilense* and *G. lingulatum* are more common in the southern-central areas) [99,100]. Phylogeographic studies suggest that *G. lingulatum* is more effectively dispersed by floating specimens of *D. incurvata* along the Chilean coast compared to *G. rex* [58]. Morphologically, the observed epiphytes are generally small and do not cover a large area on the biogenic *D. incurvata* holdfast. They are probably adult specimens [56,97], which was confirmed by the high frequency of reproductive specimens in most beaches and seasons. However, it is possible to find larger specimens (probably recruits) of *Lessonia spicata* having coalescing holdfasts with those of *D. incurvata* [55,64]. This is confirmed by the absence of reproductive specimens of *L. spicata* throughout the study.

On the other hand, in previous studies, we also found invasive seaweed species described for the Chilean coast in the kelp holdfasts (e.g., *Schimmelmannia plumosa* and *Schottera nicaeensis*), mainly in the southern-central region [10]. This suggests that the recent geographical expansion of these species (37° S–42° S) could have been facilitated by the rafting dispersal by floating seaweeds [101].

Throughout all seasons and beaches, epiphytic seaweed specimens were observed in various reproductive stages. Mature reproductive individuals were most frequently observed in winter, although some were also present in summer, depending on the beach. These findings generally align with the reproductive phenology of many intertidal seaweeds found in Chile [102]. It is significant to find reproductive specimens throughout the study, although the viability of the propagules or gametes remains unknown and ultimately determines the effectiveness of dispersal and connectivity between seaweed populations. The possibility of their attachment, growth, and reproduction in new marine areas will be determined by their tolerance to environmental factors, such as temperature or desiccation [102,103]. Future studies should examine the functional responses and viability of epiphytic seaweed propagules along a latitudinal gradient. Additionally, these studies should incorporate ecophysiological experiments under controlled floating conditions (e.g., mesocosm tanks with variable UV/temperature).

4.3. Co-Occurrences of Non-Buoyant Seaweeds

Several positive and negative co-occurrences among epiphytes on stranded *D. incurvata* holdfasts were noted, although most co-occurrences were random (i.e., neutral). These ecological interactions between benthic seaweeds occur during propagule recruitment on the rocky substratum (e.g., [104,105]). Once detached from the primary substratum, these interactions persist throughout the rafting journeys [10]. In our study, engineering species that create structural complexity and provide shelter, such as turf-forming red seaweeds *Polysiphonia* sp. and *Antithamnionella ternifolia*, exhibited positive co-occurrences with other seaweeds. Turf-forming seaweeds are typically fast-growing species that establish settlement and nursery areas for other organisms, such as small invertebrates [106] and early stages of seaweeds [107]. Additionally, dense turfs often accumulate sediments and nutrients [108–110]. In contrast, articulated calcareous and crustose species, such as *Corallina chilensis* and *Corallina* crusts, had negative co-occurrences. Encrusting and articulated calcareous seaweeds release allelopathic molecules that negatively impact the spore recruitment of other algal species, particularly kelp and canopy-forming seaweeds [104,105,111,112]. These results are also consistent with a previous study by López et al. [10] in the same study area that included invertebrates as rafters on stranded *D. incurvata* specimens. Moreover, these results suggest that positive and negative interactions during rafting journeys could be more complex when considering other functional groups of organisms.

In general, the patterns observed at the species-level were consistent with co-occurrence outcomes at the morpho-functional group-level. Filamentous and sheet-like seaweeds exhibited positive co-occurrences. Conversely, negative co-occurrences at the morpho-functional group-level align with the pattern described, particularly concerning encrusting and articulated calcareous seaweeds in relation to kelps (i.e., thick-leathery seaweeds) [111]. It is important to note that many investigations have assorted seaweeds into morpho-functional groups based solely on qualitative or semi-quantitative characteristics [46,48]. Recent approaches have incorporated additional quantitative morphological indicators, such as surface area to volume ratio, which provide a more accurate means of assessing ecology and physiology of seaweeds (e.g., to better absorb nutrients and other resources necessary for maintaining metabolism) [113,114]. These new morphological indicators may be relevant for studies on raft-associated seaweeds, because previous research on epibionts associated with floating *D. incurvata* specimens indicates that possible interactions between species and the presence of organisms that create new habitats within the biogenic holdfast of floating bull kelps during rafting journeys would extend the geographic ranges of epibiont species [10].

5. Conclusions

Our study is one of the few that focuses on non-buoyant seaweeds being dispersed by floating seaweeds. The results indicate that several seaweed species are transported by floating *D. incurvata* specimens along the continental coast of Chile, particularly in the southern-central zone during the summer months, even though the floating times of the rafts are relatively short. Many of these seaweeds (mainly Rhodophyta) exhibit high structural complexity and possess reproductive structures. Additionally, interactions among epiphytic seaweeds during these rafting journeys and morpho-functional traits can either facilitate or hinder effective dispersal. Our findings suggest that rafting on floating seaweeds may be an additional dispersal mechanism that could affect the population connectivity of these benthic seaweeds, particularly over longer distances beyond the range and lifetime of their autonomous dispersal stages (spores).

Future studies should evaluate the reproductive viability of these seaweeds during rafting journeys. Additionally, complementary genetic studies on stranded epiphytic seaweeds, expanding the spatial and temporal scales, could help to identify coastal areas with high and low dispersal rates and determine the distances these seaweeds travel from their source populations. This information would contribute to our understanding of the effective transport and rafting dispersal of non-buoyant species by floating seaweeds.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/jmse14090781/s1, Figure S1. Average (mean + 1 SD) of morphometric variables of stranded individuals of *Durvillaea incurvata* on four beaches (FAD, RUM, BRA, and CHAU) from the continental coast of Chile (31° S–41° S), during two years (2023/24 and 2024/25), and two seasons (winter and summer). Figure S2. Percentage of stranded individuals of *Durvillaea incurvata* with *Lepas* spp. attached, and sizes (mm of capitular length, mean + 1 SD) of specimens of *Lepas* spp. on four beaches (FAD, RUM, BRA, and CHAU) from the continental coast of Chile (31° S–41° S), during two years (2023/24 and 2024/25), and two seasons (winter and summer). Figure S3. Relationship between taxonomic richness of epiphytes and (A) holdfast wet weight (g), and (B) holdfast diameter (cm) on stranded individuals of *Durvillaea incurvata* on four beaches (FAD, RUM, BRA, and CHAU) from the continental coast of Chile (31° S–41° S), during two years (2023/24 and 2024/25), and two seasons (winter and summer). Figure S4. Rarefaction curves of the taxonomic richness of epiphytes according to the number of stranded *Durvillaea incurvata* specimens on four beaches (FAD, RUM, BRA, and CHAU) from the continental coast of Chile (31° S–41° S), during two years (2023/24 and 2024/25), and two seasons (winter and summer). Figure S5. Average (mean + 1 SD) of morphometric variables of *Lessonia spicata* individuals attached to stranded *Durvillaea incurvata* holdfasts on four beaches (FAD, RUM, BRA, and CHAU) from the continental coast of Chile (31° S–41° S), during two years (2023/24 and 2024/25), and two seasons (winter and summer). Figure S6. Average (mean + 1 SD) of morphometric variables of *Antithamnionella ternifolia* individuals attached on stranded *Durvillaea incurvata* holdfasts on four beaches (FAD, RUM, BRA, and CHAU) from the continental coast of Chile (31° S–41° S), during two years (2023/24 and 2024/25), and two seasons (winter and summer). Figure S7. Average (mean + 1 SD) of morphometric variables of *Corallina chilensis* individuals attached to stranded *Durvillaea incurvata* holdfasts on four beaches (FAD, RUM, BRA, and CHAU) from the continental coast of Chile (31° S–41° S), during two years (2023/24 and 2024/25), and two seasons (winter and summer). Figure S8. Average (mean + 1 SD) of morphometric variables of *Gelidium rex* individuals attached on stranded *Durvillaea incurvata* holdfasts on four beaches (FAD, RUM, BRA, and CHAU) from the continental coast of Chile (31° S–41° S), during two years (2023/24 and 2024/25), and two seasons (winter and summer). Figure S9. Average (mean + 1 SD) of morphometric variables of *Gelidium chilense* individuals attached on stranded *Durvillaea incurvata* holdfasts on four beaches (FAD, RUM, BRA, and CHAU) from the continental coast of Chile (31° S–41° S), during two years (2023/24 and 2024/25), and two seasons (winter and summer). Figure S10. Average (mean + 1 SD) of morphometric variables of *Gelidium lingulatum* individuals attached on stranded *Durvillaea incurvata* holdfasts on four beaches (FAD, RUM, BRA, and CHAU) from the continental coast of Chile (31° S–41° S), during two years (2023/24 and 2024/25), and two seasons (winter and summer). Figure S11. Percentage of reproductive individuals/clumps of epiphytic seaweeds on stranded *Durvillaea incurvata* holdfasts on four beaches (FAD, RUM, BRA, and CHAU) from the continental coast of Chile (31° S–41° S), during two years (2023/24 and 2024/25), and two seasons (winter and summer). Figure S12. Percentage of reproductive clumps of epiphytic *Gelidium* spp. on stranded *Durvillaea incurvata* holdfasts on four beaches (FAD, RUM, BRA, and CHAU) from the continental coast of Chile (31° S–41° S), during two years (2023/24 and 2024/25), and two seasons (winter and summer). Table S1: Beaches sampled in the study, according to biogeographic districts (Septentrional District, SED, Mediterranean District, MED, and Meridional District, MD) along the continental coast of Chile (31° S–41° S).

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