THE VARIABLE ROUTES OF RAFTING: STRANDING DYNAMICS OF FLOATING BULL KELP *DURVILLAEA ANTARCTICA* (FUCALES, PHAEOPHYCEAE) ON BEACHES IN THE SE PACIFIC[1]

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Dispersal on floating seaweeds depends on availability, viability, and trajectories of the rafts. In the southern hemisphere, the bull kelp *Durvillaea antarctica* is one of the most common floating seaweeds, but phylogeographic studies had shown low connectivity between populations from continental Chile, which could be due to limitations in local supply and dispersal of floating kelps. To test this hypothesis, the spatiotemporal dynamics of kelp strandings were examined in four biogeographic districts along the Chilean coast (28°–42°S). We determined the biomass and demography of stranded individuals on 33 beaches for three subsequent years (2013, 2014, 2015) to examine whether rafting is restricted to certain districts and seasons (winter or summer). Stranded kelps were found on all beaches. Most kelps had only one stipe (one individual), although we also frequently found coalesced holdfasts with mature males and females, which would facilitate successful rafting dispersal, gamete release, and reproduction upon arrival. High biomasses of stranded kelps occurred in the northern-central (30°S–33°S) and southernmost districts (37°S–42°S), and lower biomasses in the northernmost (28°S–30°S) and southern-central districts (33°S–37°S). The highest percentages and sizes of epibionts (*Lepas* spp.), indicative of prolonged floating periods, were found on stranded kelps in the northernmost and southernmost districts. Based on these results, we conclude that rafting dispersal can vary regionally, being more common in the northernmost and southernmost districts, depending on intrinsic (seaweed biology) and extrinsic factors (shore morphology and oceanography) that affect local supply of kelps and regional hydrodynamics.

Key index words: floating kelps; marine biogeography; rafting; stalked barnacles; strandings

Abbreviations: ANOVA, analysis of variance; CCD, Coquimbo-Choros District; CSC, Coastal System of Coquimbo; MD, Meridional District; MED,

Mediterranean District; PERMANOVA, permutational multivariate analysis of variance; PERMDISP, permutational analysis of multivariate dispersions; RS, rocky shores; SED, Septentrional District; SS, sandy shores

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In marine environments, floating seaweeds are one of the most common natural substrata that serve as transport vehicle for other organisms (Hobday 2000, Thiel and Gutow 2005a,b, Vandendriessche et al. 2007). Furthermore, they support trophic subsidies and provide spatial refugia for both pelagic and benthic communities (Duarte et al. 2009, Duggins et al. 2016). While the role of floating seaweeds as rafting vehicle for a wide range of organisms has been widely described (Helmuth et al. 1994, Ingólfsson 1995, Thiel 2003a, Nikula et al. 2010, Cumming et al. 2014), the supply, pelagic persistence, and oceanic trajectories have received less attention.

Rafting dispersal of floating seaweeds, which includes traveling, arrival, and establishment in new habitats, depends on intrinsic and extrinsic factors (reviewed in Macaya et al. 2016). Over large scales (>1,000 km), latitudinal gradients of temperature and solar radiation affect buoyancy and survival of seaweed rafts, with higher pelagic persistence at high latitudes (Macaya et al. 2005, Rothäusler et al. 2012, Tala et al. 2016). On smaller, regional scales, the connectivity among benthic populations can be influenced by rafting supplies from adjacent populations (Muhlin et al. 2008, Garden et al. 2011) and local oceanographic factors (Hinojosa et al. 2010, Garden et al. 2014, Rothäusler et al. 2015), but the knowledge of mesoscale (~1,000 km) dynamics of floating seaweeds is limited. For example, Collins et al. (2010) reported that in Canterbury Bight (southern New Zealand), there is a strong influence of the north-flowing Southland Current on the dispersal and local strandings of bull kelp *Durvillaea antarctica* (Chamisso) Hariot 1892. Also, Rothäusler et al. (2015) showed that currents and surface winds in the Northern Baltic Sea affect the seasonal trajectories of floating *Fucus vesiculosus* (Linnaeus 1753), dispersing tens to hundreds of kilometers away from their sources.

Different approaches have been used to infer the sources and sinks of floating seaweeds, including genetic analyses (e.g., Muhlin et al. 2008, Collins et al. 2010, Neiva et al. 2014, Bussolini and Waters 2015), hydrographic modeling (Rothäusler et al. 2015), radio telemetry (Harrold and Lisin 1989), and geomorphological indicators (Garden et al. 2011, Garden and Smith 2015). Using the type of rock attached to holdfasts of beach-cast *D. antarctica* as an indicator of source regions in southern New Zealand, Garden et al. (2011) found that some individuals had traveled over 200 km from the original source regions. Modeling dispersal of floating

F. vesiculosus based on ocean circulation and surface winds, Rothäusler et al. (2015) revealed strong spatial and seasonal variability of trajectories in the Northern Baltic Sea, indicating that some coastal areas were functioning as sources and others as sinks. Genetic studies on floating seaweeds indicate that gene flow between populations varies greatly among locations, suggesting that transport and connectivity via seaweed rafts may be highly effective in some areas and limited in others (Fraser et al. 2010, Guillemin et al. 2016).

While all these methods contribute to our knowledge of seaweed rafting, they provide no information on the quantity and status (reproductive stage, size, sex) of the seaweeds traveling between adjacent or distant beaches. This information, however, is fundamental to determine rafting dynamics, because the likelihood of successful dispersal is greater if the individuals reaching a local shore are (i) reproductive, (ii) of both sexes (in dioecious seaweeds such as some Fucales) or the sporophyte phase that can produce male and female gametophytes (Laminariales), (iii) of large size with high reproductive capacity (for sufficient propagules to be released and settled), and (iv) the new habitat is suitable for colonization. Furthermore, in order to understand mesoscale rafting dynamics, it is fundamental to estimate floating times of rafts as this information allows inferring potential floating distances and source regions. The presence and sizes of lepadid barnacles allow inferring floating times and distances of rafts from different sources (Thiel and Gutow 2005b).

Seaweed strandings are frequent on many coasts, and are particularly important on boulder and sandy beaches (McLachlan and Brown 2006), where the seaweeds represent trophic subsidies to these environments with low primary productivity, driving a number of ecological processes, such as degradation, consumption, habitat supply, and biogeochemical processing (Kirkman and Kendrick 1997, Duarte et al. 2008, 2009, Lastra et al. 2014). These strandings on beaches can also be an indicator for the arrival of floating kelps in a particular area, where some areas appear to receive higher supplies than others (Garden et al. 2011). The amounts of stranded seaweeds may also differ between seasons, due to more storm- and herbivore-induced seaweed detachments during fall and winter (Marsden 1991). Seasonal differences in raft survival and reproductive activity, especially between summer and winter (Graiff et al. 2013, Tala et al. 2013, 2016), might also affect dispersal dynamics and population connectivity.

Herein we used the bull kelp *D. antarctica* as model organism to determine rafting dynamics on the regional scale. *D. antarctica* has a wide distribution in the southern hemisphere, with a predominantly subantarctic distribution (Fraser et al. 2009, 2010, 2011). It is a dioecious species that exhibits

holdfast coalescence joining multiple conspecifics (González et al. 2015). In Chile, benthic populations occur from 30°S, the northern distribution limit (Hoffmann and Santelices 1997, Tala et al. 2013) to the Strait of Magellan (55°S) in the south. Genetic studies indicate that there are two distinct clades of *D. antarctica*, a clade from southern-central Chile that is distributed along the continental coast of Chile (30°S–44°S), which in the following will be called "continental clade", and the subantarctic clade that occurs throughout the entire subantarctic region, including southern Chile (49°S–56°S; Fraser et al. 2009, 2010). The continental clade features distinct genetic differences between adjacent populations, indicating that oceanographic, ecological, or biological factors may suppress rafting dispersal and limit effective connectivity between populations (Fraser et al. 2010, Waters et al. 2013).

Durvillaea antarctica has positive buoyancy, being a common floating kelp along the Chilean coast (Hinojosa et al. 2010, Wichmann et al. 2012) with the potential to travel over distances of thousands of kilometers (Fraser et al. 2011). The morphological, physiological, and reproductive stage of floating individuals varies seasonally (Graiff et al. 2013, Tala et al. 2013, 2016), although there is no evidence for functional differences (i.e., pigment and phlorotannin concentrations) between sexes (Lizée-Prynne et al. 2016). Furthermore, there are abundant strandings of kelp rafts on rocky and sandy beaches of southern-central Chile (~39°S, see also Duarte et al. 2008, 2009). In New Zealand, the stranding dynamics of *D. antarctica* varied throughout the year with a slight tendency of higher biomass of stranded kelps in summer (Marsden 1991). However, in Chile, there is no systematic information on the spatiotemporal dynamics of bull kelp strandings across the extensive distribution of the continental clade of *D. antarctica*. This coastal zone has biogeographic regions and subregions with boundaries based on topographical and oceanographic features (Camus 2001, Hormazábal et al. 2004). Consequently, it is likely that the characteristics and floating times of stranded individuals vary between these regions, affecting the dispersal dynamics of bull kelp rafts.

The current study thus aims to (i) determine the spatiotemporal pattern in the amounts of bull kelp *D. antarctica* strandings along the continental coast of Chile (28°S–42°S), (ii) characterize the status (size, sex, reproductive stage) and floating times (using epibionts *Lepas* spp.) of stranded bull kelps, and (iii) evaluate whether local stranding patterns coincide with the marine biogeographic districts described for the continental coast of Chile.

MATERIAL AND METHODS

Oceanographic and biogeographic characteristics of the study area. The South-East Pacific, particularly the southern-central coast of Chile (from ~28°S to 42°S), is characterized by a linear topography with a north–south orientation, a latitudinal temperature gradient in surface waters, as well as the absence of distinct geographic barriers to dispersal of marine organisms (Thiel et al. 2007). The Humboldt Current System (cold and nutrient-rich waters) influences the coastal area, with extensive upwelling zones affecting coastal communities (Hormazábal et al. 2004, Thiel et al. 2007, Lachkar and Gruber 2012, Aravena et al. 2014).

Based on the contrasting topological and oceanographic characteristics, three major biogeographic regions have been described for the marine biota: a northern area which comprises a warm-temperate biota (Peruvian Province, 18°S–30°S), a southern area with the austral biota (Magellan Province, 42°S–56°S), and a nontransitional, intermediate area (30°S–42°S) including mixed components of biota (Camus 2001). In this intermediate area, Camus (2001) distinguished several subregions (districts) based on local oceanographic features, such as for example differences in freshwater inputs from rivers. Also, the total extent and average length of the sandy shores (SS) tends to be higher in southern-central Chile (Thiel et al. 2007) with a decreasing proportion of rocky shores (RS) in the southern part of the study area (33°S–42°S; Fig. 1).
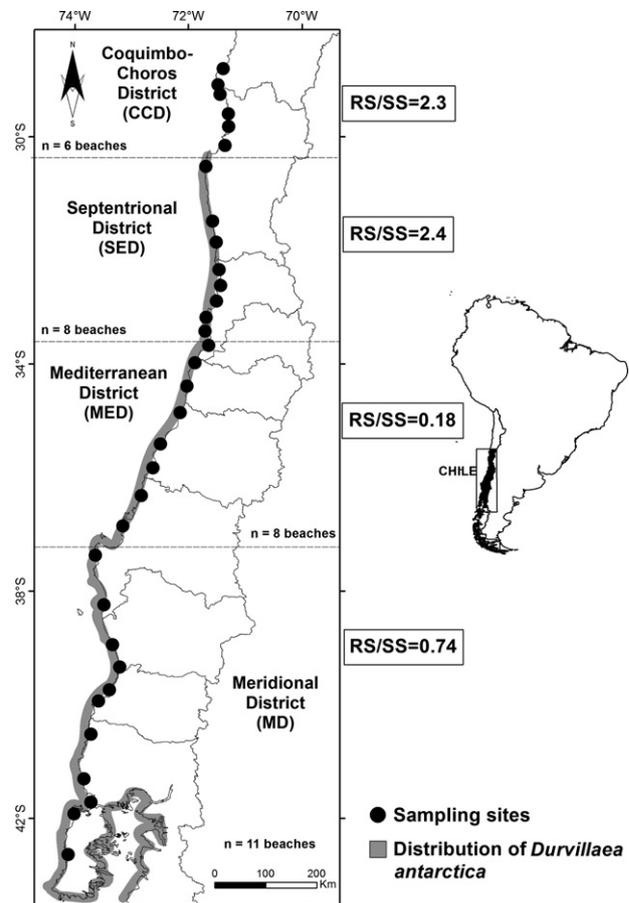

FIG. 1. Geographic distribution of sampling sites and biogeographic districts described for the coast of Chile distinguished in this study (Coquimbo-Choros District: 28°S–30°S, Septentrional District: 30°S–33°S, Mediterranean District: 33°S–37°S, Meridional District: 37°S–42°S). The geographic distribution of *Durvillaea antarctica* within the study area is also indicated. RS/SS = ratio rocky shoreline (km) versus sandy shoreline (km). The number of beaches sampled within each biogeographic district is shown.

This study was conducted on 33 sandy and boulder beaches (28°S–42°S) across the benthic and pelagic geographic range of the continental clade of *D. antarctica* (Fig. 1). The distance between beaches varied from 30 to 100 km and the extension of the stretches that were surveyed on each beach ranged from 0.28 to 11.08 km, depending on beach length and/or amounts of stranded kelps (Table S1 in the Supporting Information). All beaches were delimited by at least one rocky shore and many beaches also contained small, rocky outcrops. While the kelp individuals stranded on sandy beaches have very limited possibilities of colonization, they can be considered representative of stranding dynamics on adjacent rocky shores, the typical habitat of the bull kelp *D. antarctica*.

Beaches were distributed across the four biogeographic districts defined by Camus (2001): the southern edge of the Peruvian Province, 28°S–30°S, hereafter termed Coquimbo-Choros District (CCD); Septentrional District (SED), 30°S–33°S; Mediterranean District (MED), 33°S–37°S; Meridional District (MD), 37°S–42°S (Fig. 1). Another criterion considered for this categorization corresponds to the genetic structure observed for benthic populations of *D. antarctica* (Fraser et al. 2010), which had suggested limited population connectivity and restriction of some haplotypes to particular biogeographic districts, especially between ~33°S and ~37°S.

Sampling of Durvillaea antarctica. Recently stranded individuals of *D. antarctica* were collected on 33 beaches (28°S–42°S) (Fig. 1) during winter and summer in three consecutive years (2013, 2014, 2015). Surveys were made on foot following the coastline, collecting all parts and entire individuals of recently stranded *D. antarctica*, along the most recent flotsam lines (from the last 2–3 high tides). Care was taken to only collect recently stranded kelp parts or plants; during the summer kelps rapidly dried out and only kelps with greenish or dark-brown color that maintained some flexibility (indicative of freshness) were collected. Kelp samples were categorized into plants and fragments. Herein we use the expression "plant" to refer to one or more individuals with intact fronds that are coalesced within a single holdfast, while fragments corresponded to parts of a frond without holdfasts or holdfasts with badly damaged (i.e., non cortical layers) fronds.

On each beach, the start and endpoints of a survey were georeferenced with a portable GPS Garmin eTrex® 20×. For each sampling, the total distance that was surveyed on each beach was determined with the online tool Google Earth, which allowed taking into account the beach curvature for distance estimates. The biomass of stranded *D. antarctica* per beach (kg wet per km of shoreline) at a given sampling date was calculated based on the total weight of plants and fragments found on a beach and the distance surveyed at this beach.

Measurements and samples of complete plants. A total of 7,252 complete plants were measured during the study. For each complete plant of *D. antarctica*, the following variables were measured:

Total length: the length in centimeters was measured as the rectilinear distance from the holdfast to the distal end of the longest frond.
Biomass: the wet weights of the frond, stipes, and holdfast of a plant were measured separately, using a portable electronic hanging digital scale of 1 g accuracy. The total biomass of a plant was calculated by adding the frond, stipes, and holdfast weights.
Number of stipes: the total number of stipes of each plant was counted. It is noteworthy that in the case of *D. antarctica*, each stipe of a holdfast represents a single individual (González et al. 2015).

Reproductive stage: for each plant, tissue samples were taken for analysis of the reproductive stage. If a plant contained more than one stipe, we took one tissue sample per stipe up to a maximum of five stipes per plant (for each case, only the five longest stipes were considered). Each sample was placed in a Ziploc® bag, covered with salt to dehydrate and preserve the reproductive tissues. Depending on the number of complete plants per beach, we took tissue samples from up to 10 plants per beach and survey to determine the reproductive status and sex of stranded kelps.
Floating time: for each plant we determined whether it had been colonized by *Lepas* spp. or not. Most plants were colonized by *L. australis* Darwin, 1851, which dominates in southern Chile (38°S–42°S; Hinojosa et al. 2006), and only relatively few samples in the northernmost district (CCD) contained *L. anatifera* Linnaeus, 1758. As these two species have similar sizes and growth rates (Thiel and Gutow 2005b), we herein consider them as *Lepas* spp. and refer to them in the following simply as *Lepas*. If the plants contained only cyprids (recently settled larvae) of *Lepas* this was recorded in situ but no samples were taken. If a plant contained already metamorphosed individuals of *Lepas*, we took samples of the 10–20 largest individuals in order to measure their sizes, which are indicative of floating time (see below).

Analysis of reproductive stage. *Durvillaea antarctica* is a dioecious species and sex and reproductive stage can only be determined by histological observations (Collantes et al. 2002). In the laboratory, thin transverse sections were cut of each tissue sample and examined microscopically to determine both the sex and maturity. For this, 30 conceptacles per sample were analyzed, considering the protocols described by Collantes et al. (2002). Given the purpose of the study and to simplify subsequent analyses, herein we only distinguished two maturity stages of tissues, namely "vegetative" and "reproductive" (see also Lizée-Prynne et al. 2016):

Vegetative: absence of cellular differentiation or initial differentiation of immature conceptacle between the subcortex and the medulla. In some cases, there may be newly formed conceptacles but, as the gametes are undeveloped and the sex is unidentifiable, these samples were considered as vegetative. Also, any senescent individual (with almost empty conceptacles) was equally categorized as vegetative.
Reproductive: presence of mature conceptacles that are well developed (male or female). These individuals have identifiable sexes where gametes may already be in the process of being released.

An individual was considered reproductive when at least 50% of the examined conceptacles were found to be reproductively mature. Then, the percentage of reproductive individuals was calculated for each beach. In *D. antarctica*, each stipe within a coalesced holdfast represents a single individual (Lizée-Prynne et al. 2016), and therefore the percentage was calculated based on the total number of stipes analyzed for each beach. Also, the number of plants that had stipes at least 50 cm long was quantified, because at this size the individuals start to become sexually mature (Collantes et al. 2002).

Estimates of floating time. Detached seaweeds (and any other objects) that are starting to float in surface waters are immediately colonized by stalked barnacles from the genus *Lepas*. The availability of competent larvae of these stalked barnacles may have some seasonality (i.e., higher in spring), but generally they can be found throughout the year (Anderson 1994). Therefore, the sizes of *Lepas* can be used as a

proxy of floating time because they only adhere to buoyant substrata (Helmuth et al. 1994), and size is a good estimator of the time an item has been afloat (Macaya et al. 2005, Thiel and Gutow 2005b, Fraser et al. 2011).

To evaluate the minimum floating time of stranded bull kelp *D. antarctica*, juvenile or adult *Lepas* were sampled from colonized plants. At the end of each survey day, we took photographs of the 10–20 largest specimens of *Lepas* collected from a plant. The *Lepas* individuals were carefully laid out next to a scale and photographed. Subsequently, the capitular length (rectilinear distance between the distal angle of the carina plate and the beginning of the peduncle) of each specimen was measured, using Image Pro Plus v6 (Media Cybernetics Inc., Rockville, USA).

According to the presence and size of stalked barnacles attached, all the plants of *D. antarctica* were categorized in three groups: (i) short floating time (<2 d) – plants without any *Lepas*; (ii) intermediate floating time (2–10 d) – plants with cyprid recruits or small, juvenile *Lepas* (<5 mm capitular length); and (iii) long floating time (>10 d) – plants with large, adult *Lepas* (≥5 mm capitular length). According to Thiel and Gutow (2005b), the growth rates of *L. anatifera* and *L. australis* range from 0.22 to 0.46 mm · d^{-1}. Therefore, plants of *D. antarctica* with *Lepas* >5 mm are equivalent to more than 10 d of floating times.

Statistical analyses. For each beach, we calculated the following dependent variables: average wet biomass per km of shoreline, percentage of stranded plants with *Lepas*, maximum and mean length of plants, maximum and mean weight of plants, maximum and mean number of stipes per plant and percentage of reproductive plants. In order to examine whether biogeographic district, sampling year, or season had an effect on the dynamics of stranded *D. antarctica*, we conducted permutational multivariate analysis of variance (PERMANOVA; Anderson 2001). The response variables were divided into two 'families' of related dependent variables (Chandler 1995), those associated with (i) stranding dynamics, which included two variables: stranded biomass per km of shoreline and proportion of stranded plants with *Lepas*, and (ii) plant biology, with seven variables that are related to morphometric and phenological characteristics of stranded *D. antarctica* on each beach (mean and maximum length, mean and maximum weight, mean and maximum number of stipes, proportion of reproductive individuals).

Three-way PERMANOVA tests were conducted, considering the factors district (fixed factor: four levels), year (fixed factor: three levels), and season (fixed factor: two levels). Dependent variables such as weight were log+1 transformed, while for those expressed in percent arcsine transformation was used. Data were normalized before Euclidean distances were calculated. Permutations (9,999) were applied to residuals under the full model for PERMANOVA. Post hoc pair-wise comparisons were then used to explore significant factor effects using 9,999 permutations. We tested for differences in multivariate dispersion between factors using the PERMDISP routine (Anderson et al. 2008).

If the full model revealed significant effects of either factor, response variables were analyzed individually with ANOVA using the same model as above. With a single response variable on an Euclidean distance matrix, the resulting F ratio is the same as in the traditional ANOVA (Anderson et al. 2008). Post hoc pair-wise comparisons were done with significant factor effects.

To determine whether the proportion of male and female individuals differs among the four biogeographic districts and two seasons, a $2 \times 2 \times 4$ three-level contingency table was constructed. Significant differences were analyzed by a chi-square test of independence (Zar 2010).

To examine whether floating time affects floating plants, we compared the proportions of plants in the three temporal categories (short, intermediate, and long floating times) that were reproductive and those that were nonreproductive using a 2×3 contingency table. Significant differences were analyzed with a chi-square test of independence (Zar 2010). A similar test was conducted to examine whether floating time affects plant sizes, i.e., we compared the proportions of plants ≤50 cm in the three temporal categories with the corresponding proportion of plants >50 cm, i.e., sizes at which plants start to become sexually mature.

All statistical analyses were run with the statistical packages Primer v6 (Clarke and Warwick 2001) and GraphPad Prism version 6.00 for Windows (GraphPad Software Inc 2012).

RESULTS

Strandings and morphometric characteristics of plant. Strandings of *D. antarctica* in the study area occurred during all seasonal surveys and on most beaches. On the northernmost beaches in the CCD, no strandings were observed during some surveys. The total stranded biomass varied from 0 to 1,700 kg per km of shoreline, with an overall average of 88 kg per km shoreline and a high variability between beaches. The sizes of stranded plants ranged from 30 to 960 cm with an overall average length of 145 cm. The mean weight of holdfasts was 0.24 kg, while the largest holdfast reached a maximum weight of 5.74 kg. Also, the weight of the fronds fluctuated between 0.005 and 32 kg, with an overall average of 0.96 kg. About half of all collected plants had a holdfast with only one stipe, with an average and maximum of 2 and 16 stipes per holdfast, respectively.

The analysis of the full model for each family of response variables showed that in the case of the stranding 'family', there were significant differences between biogeographic districts ($F_{3,174} = 25.05$; $P < 0.001$). The CCD and MED were different from the SED and MD ($t_{174} = 6.19$; $P < 0.05$), although the latter two did not differ between them (Table 1). There were neither significant differences between years and seasons nor interactions of first and second order (Table 1).

With respect to the morphometric and phenological variables of individuals of *D. antarctica* (plant 'family'), significant differences were found between biogeographic districts ($F_{3,174} = 13.56$; $P < 0.001$). The SED and MD areas were different from each other as well as from the CCD and MED ($t_{174} = 5.09$; $P < 0.05$). However, there were no differences between CCD and MED (Table 1). Also, significant differences between seasons were evident. There were no significant differences between years, or interactions of factors (Table 1).

The individual analysis of the variables showed that for almost all response variables evaluated there were significant differences between biogeographic districts (Table 2). Stranded biomass was low in the CCD, high in the SED, intermediate in

TABLE 1. Results of three-way PERMANOVA for response variables per family of stranded *Durvillaea antarctica* on beaches from the continental coast of Chile (28°S–42°S).

'Family'	Source of variation	df	MS	Pseudo F	P-value	Significant pair-wise comparisons
Stranding	District (D)	3	36.196	25.05	**<0.001**	CCD ≠ SED; CCD ≠ MED; CCD ≠ MD; SED ≠ MED; MED ≠ MD
	Year (Y)	2	0.971	0.67	0.599	
	Season (S)	1	2.199	1.52	0.225	
	D × Y	6	2.386	1.65	0.080	
	D × S	3	1.195	0.82	0.554	
	Y × S	2	2.969	2.05	0.086	
	D × Y × S	6	1.262	0.87	0.565	
	Residuals	174	1.445			
Plant	District (D)	3	74.387	13.56	**<0.001**	CCD ≠ SED; CCD ≠ MD; SED ≠ MED; SED ≠ MD; MED ≠ MD
	Year (Y)	2	7.373	1.34	0.220	
	Season (S)	1	71.107	12.96	**<0.001**	W ≠ S
	D × Y	6	7.187	1.31	0.173	
	D × S	3	4.533	0.83	0.578	
	Y × S	2	8.712	1.59	0.141	
	D × Y × S	6	6.456	1.18	0.259	
	Residuals	174	5.486			

Pair-wise post hoc comparisons were done on significant terms. Significant values ($P < 0.05$) are shown in bold. Pair-wise tests show districts or seasons that differed ($P < 0.05$). Nonsignificant pair-wise tests are not shown.

W, winter, S, summer.

the MED, and high in the MD districts ($t_{174} = 4.09$; $P < 0.05$; Fig. 2A). There was a significant interaction between districts and years, showing that the stranded biomasses in year 2 (2014) were similar between CCD and MED, whereas this was not seen in the other years (2013, 2015; Fig. S1 in the Supporting Information). On the other hand, the proportion of plants with *Lepas* was highest in the northernmost district (CCD), intermediate in the

SED, low in the central MED, and also intermediate in the southernmost district, MD (Fig. 2B). There was a significant interaction for this variable among the factors year and season, showing differences between winter and summer of year 2, while in years 1 and 3 there were no differences between seasons (Table 2).

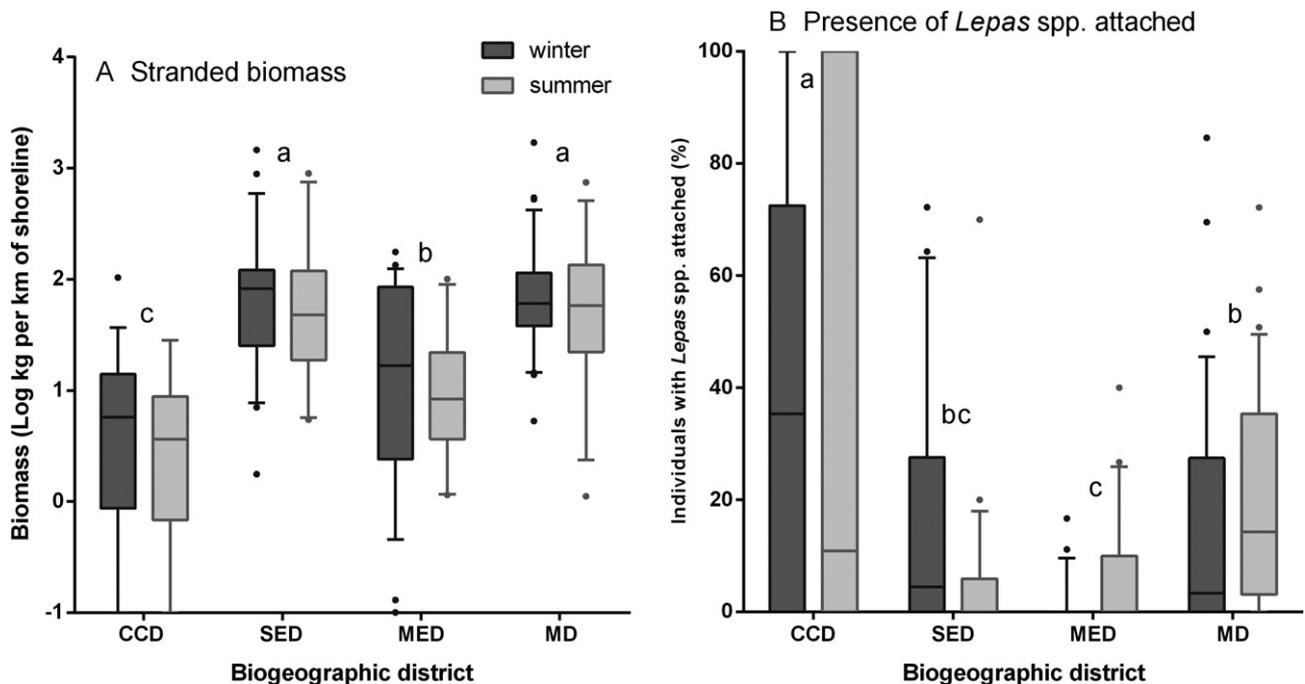In general, the length and weight of the stranded plants tended to be higher in the SED, while in the

FIG. 2. Box plot of response variables of stranded individuals of *Durvillaea antarctica* on beaches from the continental coast of Chile (28°S–42°S), according to marine biogeographic districts during winter and summer (2013–2015). (A) Stranded biomass, and (B) percentage of plants with *Lepas*. Different letters above the box plot indicate differences between biogeographic districts ($P < 0.05$). CCD, Coquimbo-Choros District; SED, Septentrional District; MED, Mediterranean District; MD, Meridional District. Horizontal lines represent the median; boxes, the interquartile range; whiskers, 1.5× of interquartile range; circles, outliers.

TABLE 2. Results of three-way ANOVAs testing the effect of district, year, and season on each response variable of stranded *Durvillaea antarctica* on beaches from the continental coast of Chile (28°S–42°S).

Variable	Source of variation	df	MS	Pseudo F	*P*-value	Significant pair-wise comparisons
Biomass	District (D)	3	65.068	39.32	**<0.001**	CCD < SED; CCD < MED; CCD < MD; SED > MED; MED < MD
	Year (Y)	2	2.017	1.22	0.300	
	Season (S)	1	5.814	3.51	0.060	
	D × Y	6	5.033	3.04	**<0.01**	CCD < MED: Y1, Y3
	D × S	3	0.075	0.04	0.986	
	Y × S	2	0.840	0.51	0.602	
	D × Y × S	6	1.580	0.95	0.455	
	Residuals	174	1.655			
Lepas (%)	District (D)	3	8,370.7	14.59	**<0.001**	CCD < SED; CCD < MED; CCD < MD; MED < MD
	Year (Y)	2	155.84	0.27	0.767	
	Season (S)	1	36.03	0.06	0.808	
	D × Y	6	365.91	0.63	0.702	
	D × S	3	803.38	1.40	0.238	
	Y × S	2	1,829.7	3.19	**<0.05**	S < W: Y2
	D × Y × S	6	466.69	0.81	0.559	
	Residuals	174	573.76			
Length (mean)	District (D)	3	68,880	18.61	**<0.001**	CCD < SED; MED < SED; MD < SED
	Year (Y)	2	3,614.7	0.98	0.368	
	Season (S)	1	877.67	0.24	0.620	
	D × Y	6	3,459.9	0.93	0.467	
	D × S	3	4,774.3	1.29	0.277	
	Y × S	2	8,844	2.39	0.092	
	D × Y × S	6	4,090.6	1.10	0.363	
	Residuals	174	3,702.2			
Length (max)	District (D)	3	0.00007	22.55	**<0.001**	CCD < SED; CCD < MD; MED < SED; MED < MD
	Year (Y)	2	9,391.1	0.29	0.746	
	Season (S)	1	21.946	0.0004	0.980	
	D × Y	6	35,054	1.098	0.365	
	D × S	3	13,719	0.43	0.735	
	Y × S	2	33,742	1.06	0.349	
	D × Y × S	6	20,249	0.63	0.698	
	Residuals	174	31,913			
Weight (mean)	District (D)	3	2.900	13.03	**<0.001**	MED < CCD; MED < SED; MD < SED
	Year (Y)	2	0.235	1.06	0.348	
	Season (S)	1	0.014	0.06	0.801	
	D × Y	6	0.271	1.22	0.306	
	D × S	3	0.092	0.41	0.749	
	Y × S	2	0.097	0.43	0.641	
	D × Y × S	6	0.349	1.56	0.166	
	Residuals	174	0.222			
Weight (max)	District (D)	3	15.921	19.82	**<0.001**	CCD < SED; PP < MD; MED < MD; MED < SED
	Year (Y)	2	0.320	0.39	0.677	
	Season (S)	1	0.336	0.42	0.513	
	D × Y	6	1.036	1.29	0.255	
	D × S	3	0.077	0.09	0.961	
	Y × S	2	0.004	0.005	0.995	
	D × Y × S	6	1.259	1.56	0.165	
	Residuals	174	0.803			
Stipes (mean)	District (D)	3	2.422	13.03	**<0.001**	MED < CCD; MED < SED; MED < MD; SED < CCD; MD < CCD
	Year (Y)	2	1.477	1.06	0.076	
	Season (S)	1	3.850	0.06	**<0.01**	W < S
	D × Y	6	0.556	1.22	0.429	
	D × S	3	0.069	0.41	0.945	
	Y × S	2	0.0002	0.43	0.999	
	D × Y × S	6	0.392	1.56	0.651	
	Residuals	174	0.558			
Stipes (max)	District (D)	3	111.46	10.62	**<0.001**	MED < SED; MED < MD
	Year (Y)	2	5.437	0.52	0.591	
	Season (S)	1	68.677	6.54	**<0.05**	W < S
	D × Y	6	21.524	2.05	0.062	
	D × S	3	15.900	1.51	0.220	
	Y × S	2	2.240	0.21	0.806	
	D × Y × S	6	8.854	0.84	0.533	
	Residuals	174	10.499			

(continued)

Table 2. (continued)

Variable	Source of variation	df	MS	Pseudo F	P-value	Significant pair-wise comparisons
Repro	District (D)	3	636.04	1.74	0.197	
	Year (Y)	2	796.88	2.18	0.093	
	Season (S)	1	39,747	108.73	**<0.001**	S < W
	D × Y	6	635.1	1.74	0.116	
	D × S	3	948.97	2.59	0.055	
	Y × S	2	427.68	1.17	0.089	
	D × Y × S	6	80.418	0.22	0.562	
	Residuals	174	365.54			

Biomass: total stranded biomass; Lepas (%): proportion of plants with *Lepas*; Length (mean): mean length of plants; Length (max): maximum length of plants; Weight (mean): mean wet weight of plants; Weight (max): maximum wet weight of plants; Stipes (mean): mean number of stipes of plants; Stipes (max): maximum number of stipes of plants; Repro: proportion of reproductive individuals. W: winter, S: summer; Y1: year 1; Y2: year 2; Y3: year 3.

Pair-wise post hoc comparisons were done on significant terms. Significant values ($P < 0.05$) are shown in bold. Pair-wise tests show districts or seasons that differed ($P < 0.05$). Nonsignificant pair-wise tests are not shown.

MED plants were smaller and of low weight (Figs. 3, A and B, S2 and S3 in the Supporting Information). Length and weight of stranded plants was not affected by other factors (Table 2). The number of stipes also varied between biogeographic districts, with more stipes per plant in the CCD, while the lowest number was observed in the central MED (Figs. 3C and S4 in the Supporting Information). Likewise, stranded plants in summer had a higher number of stipes than in winter. There were no significant effects of year or interaction between factors (Table 2).

Reproductive stage. The proportion of reproductive individuals did not differ between biogeographic districts, showing only significant differences between seasons (Table 2). The percentage of reproductive individuals was higher in winter than in summer (Fig. 3D). There were differences in the percentages of male and female individuals of *D. antarctica*, according to biogeographic districts and seasons ($\chi^2_{10} = 33.085$; $P < 0.001$). Particularly, during the winters, no difference was observed in the percentages of male and female specimens between biogeographic districts ($\chi^2_7 = 12.010$; $P = 0.213$; Fig. 4, A, C and E). However, the percentage of reproductive females tended to be lower in summer compared to winter, and particularly, no reproductive female individuals were observed in the CCD and MED in summer 2015/2016 (Fig. 4F). For summers 2013/2014 and 2014/2015, there was no difference in the percentage of both sexes between the biogeographic districts ($\chi^2_7 = 7.548$; $P = 0.374$; Fig. 4, B and D).

Floating time. The number of reproductive individuals differed between the three categories of floating times considered ($\chi^2_2 = 101.90$; $P < 0.001$). The proportions of reproductive individuals with intermediate (11.6%) and long floating times (32.5%) were higher than that observed in the reproductive individuals with short floating time (6.7%; Fig. 5A). Also, there were significant differences in the frequencies of large individuals between the different floating times, showing that the proportions of individuals >50 cm with respect to the total were higher in plants with intermediate (92%) and long floating times (91%) than among the plants with short floating times (85%; $\chi^2_2 = 37.36$; $P < 0.001$; Fig. 5B).

DISCUSSION

The current study revealed that there are coastal areas receiving higher supplies of floating seaweeds than others, and throughout this study, the differences between districts remained consistent, regardless of sampling year and season. Also, the morphometric and phenological characteristics of stranded kelps differed between districts, indicating that the dispersal capabilities and reproductive potential of the individuals vary on the regional scale.

Spatial and temporal variations of strandings. There was a high variability in the biomass of stranded kelps along the Chilean coast, being higher on beaches between 30°S–33°S and 38°S–42°S, with high variability between beaches within each district. No annual or seasonal effects were detected in the strandings, which is consistent with observations of the temporal variability of floating kelps in the study area (Hinojosa et al. 2011) and strandings of *D. antarctica* in New Zealand (Marsden 1991). Stranded biomasses observed in this study are within the range of those reported in previous studies (Duarte et al. 2008, 2009) during spring and summer on sandy beaches of southern-central Chile (i.e., Valdivia, ~39°S). The arrival of seaweeds is an extremely dynamic process, both in space and time (Rodríguez 2003, Orr et al. 2005), with frequent events of resuspension and new deposition during different tidal cycles (Colombini et al. 2000, Orr et al. 2005). Monthly samplings in subsequent studies would be useful to detect pulses of arrival of seaweeds, for example, after storm events (Hobday 2000).

We observed low-stranded biomasses on beaches in the CCD (28°S–30°S). The northern distribution limit of *D. antarctica* at the continental coast of Chile reaches to ~30°S (Hoffmann and Santelices 1997, Tala et al. 2013). Given the absence of benthic populations in the CCD, low biomass was
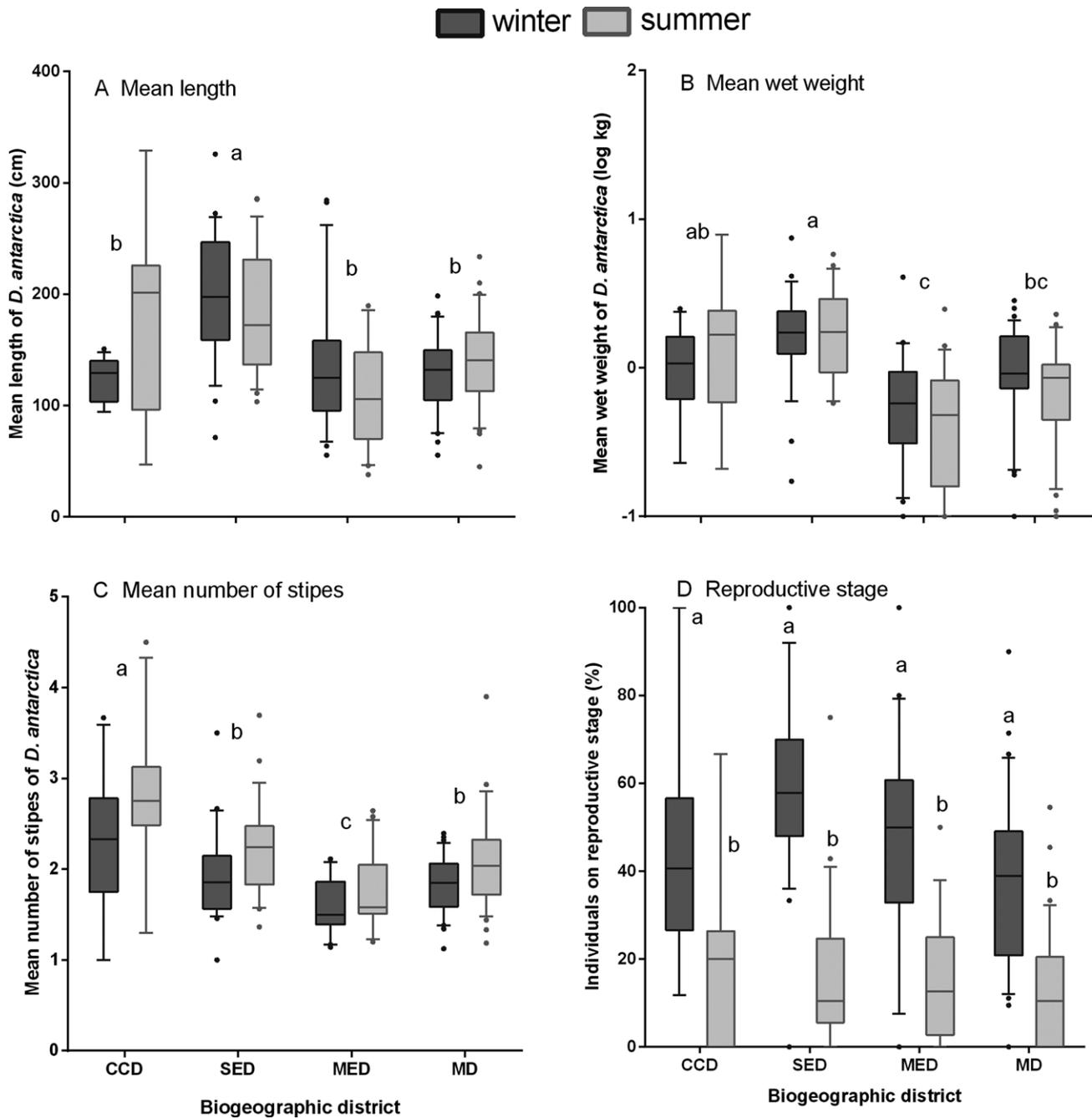
FIG. 3. Box plot of response variables of stranded individuals of *Durvillaea antarctica* on beaches from the continental coast of Chile (28°S–42°S), according to marine biogeographic districts during winter and summer (2013–2015). (A) Mean length of plants, (B) mean wet weight of plants, (C) mean number of stipes of plants, and (D) percentage of plants in reproductive stage. Different letters above the box plot indicate differences between biogeographic districts ($P < 0.05$). CCD, Coquimbo-Choros District; SED, Septentrional District; MED, Mediterranean District; MD, Meridional District. Horizontal lines represent the median; boxes, the interquartile range; whiskers, 1.5× of interquartile range; circles, outliers.

expected, but the regular occurrence of stranded kelp plants on all sampled beaches within this district confirms that they are frequently transported into this area. Previous studies confirmed the presence of floating bull kelps in the CCD (Tala et al. 2013), but many plants had been collected in offshore waters, distant from the coast. Offshore currents that transport coastally upwelled waters to the

open ocean (Marín and Delgado 2003) may keep rafts from returning to the shore, thereby further contributing to the low biomasses of stranded kelps in the CCD.

In the CCD, the percentage of rafts with *Lepas* was higher compared to the other districts. Also, in this district the largest sizes of *Lepas* were observed (see Fig. S5 in the Supporting Information). Hence, this
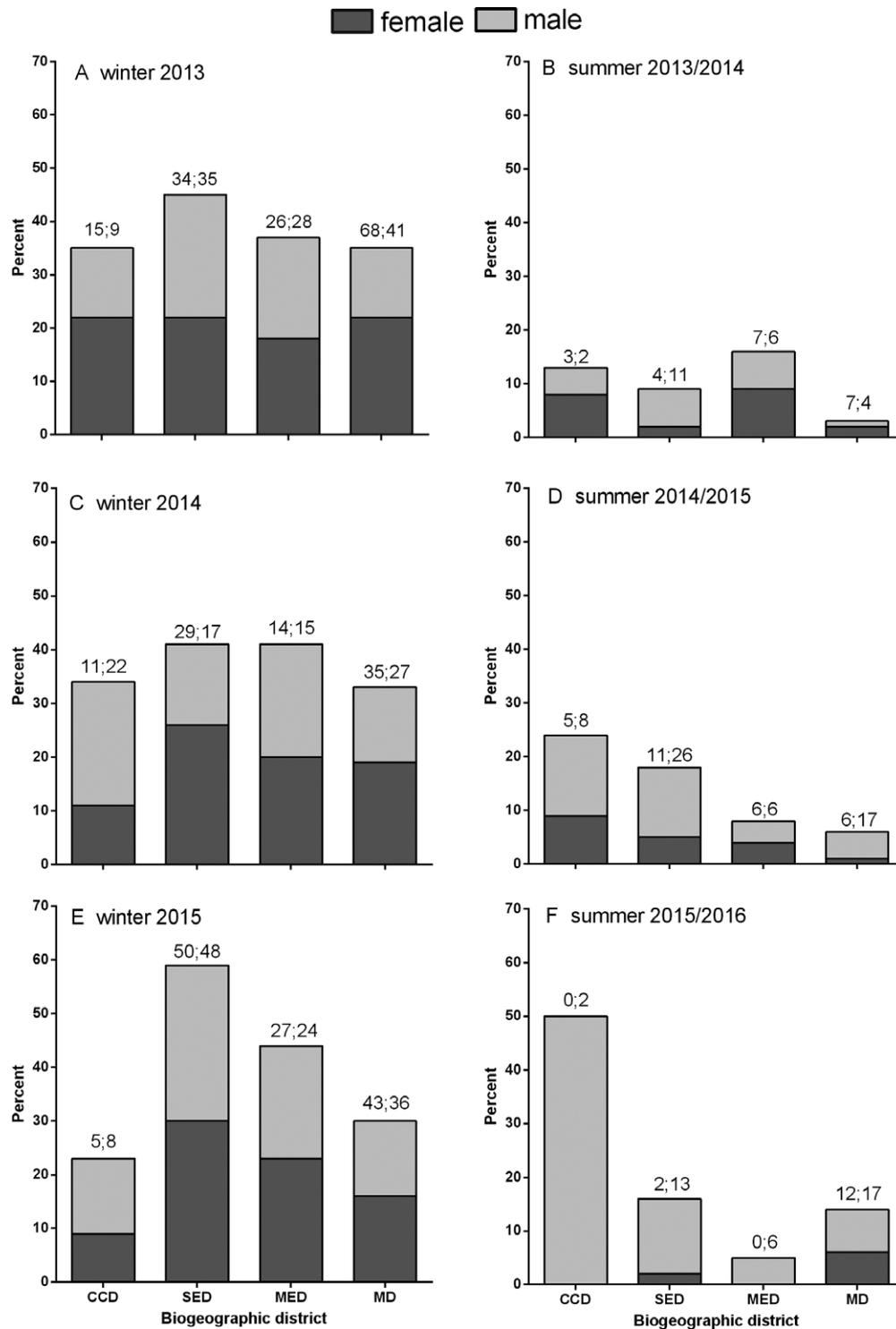
Fig. 4. Percentages of males and females of stranded individuals of *Durvillaea antarctica* on beaches from the continental coast of Chile (28°S–42°S), according to marine biogeographic districts during three consecutive years. (A) Winter 2013, (B) summer 2013/2014, (C) winter 2014, (D) summer 2014/2015, (E) winter 2015, (F) summer 2015/2016. CCD, Coquimbo-Choros District; SED, Septentrional District; MED, Mediterranean District; MD, Meridional District. The numbers on top of each column correspond to frequencies of females and males, respectively.

indicates that rafts of *D. antarctica* can float over relatively long distances (~200–300 km) from their nearest benthic populations (in this case, located in the SED district). Similar dispersal distances had been inferred from genetic and attachment substratum analyses on the coast of southern New Zealand (Collins et al. 2010, Garden et al. 2011, Bussolini and Waters 2015). Studies of floating *D. antarctica* and
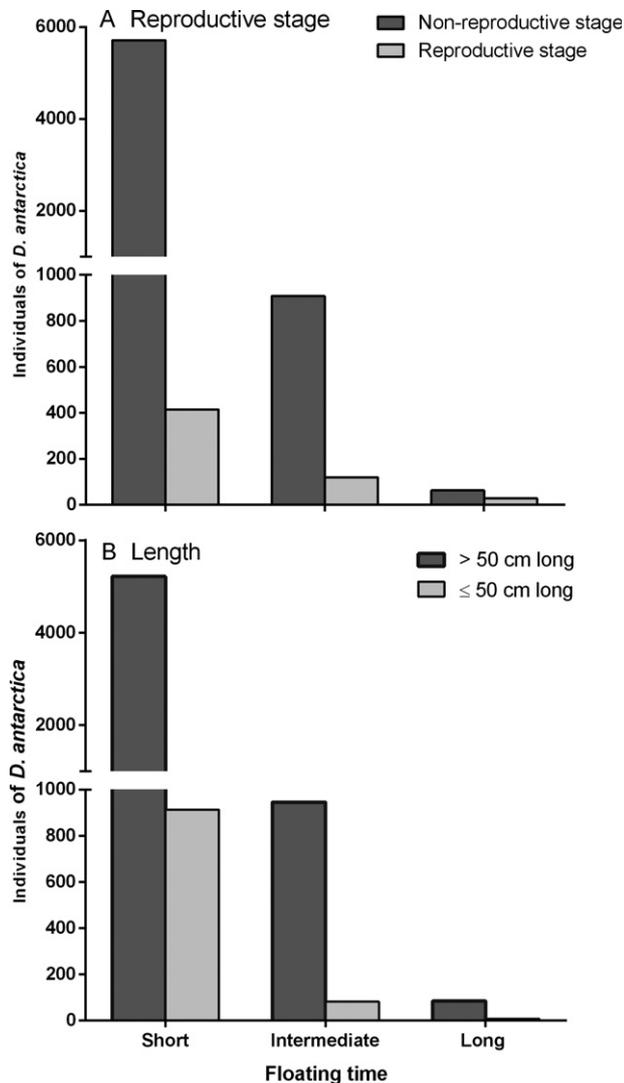
FIG. 5. Frequency of stranded individuals of *Durvillaea antarctica* on beaches from the continental coast of Chile (28°S–42°S), according to three categories of floating times (short, intermediate, long). (A) Number of individuals sampled in non-reproductive and reproductive stage, (B) number of individuals sampled ≤50 cm and >50 cm frond length.

Macrocystis pyrifera (Linnaeus) Agardh 1820 in the Coastal System of Coquimbo (CSC) in Chile (i.e., ~30°S) (Rothäusler et al. 2011, Tala et al. 2013) had shown that physiological performance tends to decline dramatically in kelp rafts with prolonged floating times. This is accentuated in the summer, due to the increase of temperature and solar radiation (Graiff et al. 2013). Furthermore, the annual growth season of benthic kelps modulates the availability of floating plants, particularly in the spring and summer months (Kingsford 1992, Hirata et al. 2001, Hinojosa et al. 2010). However, in our study no seasonal differences were found in the biomass of stranded kelps in the CCD, suggesting low temporal variability in supply from benthic sources.

Biomass of stranded kelps was also low in the MED (33°S–37°S) even though Hinojosa et al. (2011) had reported relatively high densities of floating kelps in offshore waters of this district. Similar as in the CCD, strong upwelling currents in the MED may cause the dense accumulation of kelp rafts in offshore retention zones preventing return to the shore (Sobarzo et al. 2007, Hinojosa et al. 2011). The low proportion of stranded kelps with *Lepas* in the MED further suggests that few kelps from the large floating pool return to the coast. Pelagic retention of floating seaweeds due to the geomorphology of the coastline and local oceanographic processes has also been described from other areas (Komatsu et al. 2007, 2008, 2014). Finally, the low proportion of rocky shores in the MED (see RS/SS index in Fig. 1) indicates that there is comparatively little suitable habitat for benthic populations of *D. antarctica*, further limiting local supplies of floating kelps. This suggests that the low biomass of stranded kelps in the MED is due to local oceanographic dynamics and limited supply from benthic source populations. However, other factors such as harvest of this bull kelp from natural populations, which is highest in the MED (i.e., ~80% of total landings; Subsecretaría de Pesca y Acuicultura 2015), could also affect the amount of source material, although we observed few detached (by knife) plants during surveys on beaches within the MED.

On the other hand, in the SED and MD, high biomasses of stranded bull kelps were observed. In the MD, the supply of floating kelps is high and strong westerly winds may periodically push floating kelps shoreward (Hinojosa et al. 2010), thereby contributing to the observed high stranding biomasses. Furthermore, moderate UV-radiation and lower sea surface temperature in this area may facilitate survival of kelp rafts, as had previously been shown for *M. pyrifera* (Rothäusler et al. 2009), preventing disintegration and sinking at sea, thereby allowing more kelp rafts to return to the shore. For the SED, several oceanographic discontinuities have been described, caused by different wind stress, eddy kinetic energetic, and local upwelling (Hormazábal et al. 2004, Yuras et al. 2005, Thiel et al. 2007, Tapia et al. 2014), which can affect transport of kelp rafts. In this area, the presence of stranded kelps with *Lepas* probably indicates offshore accumulations of floating individuals, which might be transported to the shore during periods of upwelling relaxation. These considerations suggest that a proportion of kelp rafts of *D. antarctica* in these districts, and in particular in the MD, may be transported away from source sites by currents and surface winds and later deposited on distant shores. This has also been described on the southern coast of New Zealand, where short-distance movements of kelp rafts in coastal waters are strongly influenced

by wind and wind-induced surface current (Hawes 2008).

Morphological and reproductive features of stranded individuals. The morphological and phenological characteristics of *D. antarctica* varied between biogeographic districts, which has important implications for rafting dispersal. In general, larger individuals tend to produce more gametes (Collantes et al. 1997), and also larger sizes of floating seaweeds might enhance their floating persistence and consequently their dispersal potential (Thiel and Gutow 2005b, Graiff et al. 2013).

The number of stipes and individual biomass of stranded plants were lowest in the MED compared to the other districts. A plant with more stipes enhances the likelihood that both sexes are present in the same coalesced holdfast. Lizée-Prynne et al. (2016) showed for stranded and benthic holdfasts of *D. antarctica* that between 5% and 17% of all plants contain both sexes in reproductive stage, although only 50% tended to have multiple stipes. Consequently, the probability of successful rafting dispersal is lower in areas with small plants, such as the MED.

The main reproductive season of *D. antarctica* is between autumn and spring (Collantes et al. 2002), which was confirmed herein. Some of the individuals that had been floating for relatively long times (>10 d) were found to be reproductive, potentially contributing to the connectivity within and between districts. This suggests that prolonged floating does not affect their reproductive potential, because they remain viable after long rafting trips. However, Tala et al. (2013), at 30°S, showed for floating specimens of *D. antarctica* that those with large *Lepas* had high frequencies of conceptacles in senescent stage (empty conceptacles) and increased tissue damage, which would compromise the reproductive potential of floating kelps, particularly in summer months. Similar results also have been observed during the disintegration of sporophylls for floating *M. pyrifera* (Macaya et al. 2005, Hernández-Carmona et al. 2006, Rothäusler et al. 2011). This suggests that the release of gametes could also be occurring before the specimens arrive at the shore, and given the restricted movement of zygotes and the absence of primary substrata, this would result in low dispersal success. Viability of gametes from floating individuals might also be different from those in benthic populations, although release of viable zoospores has been reported for floating rafts of *Hormosira banksii* (Turner) Decaisne 1842 (McKenzie and Bellgrove 2008). Previous studies in *D. antarctica* had reported that benthic samples had a higher reproductive potential than stranded samples, although there were no differences between males and females (Lizée-Prynne et al. 2016).

In this study, the percentages of female and male individuals did not vary between biogeographic districts or season, except in summer 2015/2016, where reproductive females were completely absent in the CCD and MED, and their proportion was low in the SED. Unlike previous summers, the summer 2015/2016 was affected by the El Niño phenomenon, with higher sea surface temperatures in northern Chile (between 1.8°C and 2.8°C higher than average), mainly near 30°S (Song et al. 2015). This suggests that female individuals of *D. antarctica* are more susceptible to high temperatures than male individuals, probably due to higher functional costs of producing and protecting female gametes. While in species from the genus *Fucus*, biomass investment in gamete production is less than 0.5% of the total biomass (Vernet and Harper 1980), it cannot be ruled out that the increase in temperature might trigger the release of female (but not of male) gametes during the floating period, which would explain why no female individuals were found on those beaches. As these effects could influence the dispersal potential of floating kelps, this deserves future investigation. In general, though, and especially during the winter, rafted kelps maintained a high reproductive potential after extensive rafting trips, confirming that biological factors do not limit the dispersal potential of *D. antarctica*.

Regional dispersal patterns and population connectivity. Throughout our study most stranded individuals (> 80%) had very short floating times, indicating that most kelp rafts had local sources. However, the presence of rafts with *Lepas* in all biogeographic districts indicates that there can be rafting exchange between these areas. Factors other than local oceanographic conditions and reproductive features of floating specimens have also been suggested as an explanation for the low connectivity among populations. In the case of sessile species like seaweeds, density-dependent factors such as competition for space may be influencing the successful incorporation of immigrants to benthic populations, independent of the dispersal capabilities of the species, and the number of propagules that arrive in an area (i.e., density-blocking, see also Waters et al. 2013). Although, these effects were not measured in this study, these could be even more critical in the case of dioecious species such as *D. antarctica*, particularly in the colonization of new habitats, where the presence of both sexes enhances the possibility of successful dispersal. However, while dispersal potential might be lower in dioecious species, gametes from rafters could also be fertilized by gametes of the opposite sex from the benthic population, thus incorporating these immigrant genes in the resident population.

The relatively low proportion of rafts with large *Lepas* (indicative of prolonged floating, i.e., more than 10 d) suggests that few individuals migrate between populations from different districts (i.e., considering continuous drift in the same direction at conservative current velocities of 10 cm · s^{-1}, ~0.36 km · h^{-1}, see Thiel 2003b), limiting the possibility of successful dispersal (Waters et al. 2013,

Neiva et al. 2014). This could explain the low genetic connectivity evidenced in benthic populations of *D. antarctica* along the continental coast of Chile (Fraser et al. 2010).

As discussed above, local oceanographic factors appear to affect dispersal of kelp rafts of *D. antarctica* on the regional scale. While other studies had shown seasonal variability in the effect of local circulation and surface winds on the abundance and dispersal trajectories of floating seaweeds (Thiel et al. 2011, Rothäusler et al. 2015), herein no strong seasonal signals were detected. In contrast, persistent oceanographic conditions (e.g., upwelling-related offshore transport) appear to affect the geographic dispersal patterns of floating bull kelps, with only minor temporal variability. Nevertheless, successful dispersal, if it occurs, seems to be limited to the winter season, when most *D. antarctica* are reproductive.

CONCLUSIONS AND OUTLOOK

The results of this study, using the strandings of *D. antarctica* on sandy and boulder beaches as proxy for kelp arrival on adjacent rocky shores, allow us to understand how the dynamics of floating kelps could explain the observed patterns of low genetic connectivity between benthic populations of this species along the continental coast of Chile (Fraser et al. 2010). Our results confirm that biological factors (i.e., joint dispersal of the two sexes and seasonal phenological variability) are not as important to explain the low connectivity of coastal populations (Lizée-Prynne et al. 2016) and that oceanographic factors (Rothäusler et al. 2015) are most relevant to explain these patterns. However, ecological processes (i.e., high-density blocking, see Waters et al. 2013, Neiva et al. 2014) could also be important and they should be analyzed in future studies. Additional genetic studies of stranded individuals of this species would allow inference of dispersal distances and trajectories in coastal areas (Collins et al. 2010, Bussolini and Waters 2015).

Examination of stranded specimens of *D. antarctica* had shown that more than 40 species of nonbuoyant seaweeds, especially Rhodophyta, are transported on fronds or holdfast (Macaya et al. 2016). In particular, the recurrence of nonbuoyant species, *Lessonia spicata* (Suhr) Santelices and *Mazzaella laminarioides* (Bory) Fredericq in areas further north of their main geographic range (29°S) had suggested that dispersal occurs via rafting (see also Tellier et al. 2009, Montecinos et al. 2012). Since there is not much information on these secondary rafters (epibiont organisms which are transported by floating seaweeds), future studies should focus on assessing the effects of dispersal by rafting on these organisms at regional scales. If rafting dispersal is effective, it would be expected that species and genetic diversity is greater in areas with more rafting exchange. In the case of our study, this is likely to occur within the SED and MD districts compared with other areas.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's web site:

Figure S1. Box plot of stranded biomass of *Durvillaea antarctica* on beaches along the continental coast of Chile (28°S–42°S), according to marine biogeographic districts during winter and summer (2013–2015).

Figure S2. Box plot of maximum length of stranded individuals of *Durvillaea antarctica* on beaches along the continental coast of Chile (28°S–42°S), according to marine biogeographic districts during winter and summer (2013–2015).

Figure S3. Box plot of maximum wet weight of stranded individuals of *Durvillaea antarctica* on beaches along the continental coast of Chile (28°S–42°S), according to marine biogeographic districts during winter and summer (2013–2015).

Figure S4. Box plot of maximum number of stipes per plant of stranded individuals of *Durvillaea antarctica* on beaches along the continental coast of Chile (28°S–42°S), according to marine biogeographic districts during winter and summer (2013–2015).

Figure S5. Box plot of maximum size of *Lepas* spp. attached in stranded individuals of *Durvillaea antarctica* on beaches to the continental coast of Chile (28°S–42°S), according to marine biogeographic districts during winter and summer (2013–2015).

Table S1. Beaches sampled in the study, according to biogeographic districts (Coquimbo-Choros District and Septentrional District) of continental coast of Chile (28°S–33°S).

Table S2. Beaches sampled in the study, according to biogeographic districts (Mediterranean District and Meridional District) of continental coast of Chile (33°S–42°S).