CONNECTIONS BETWEEN BENTHIC POPULATIONS AND LOCAL STRANDINGS OF THE SOUTHERN BULL KELP *DURVILLAEA ANTARCTICA* ALONG THE CONTINENTAL COAST OF CHILE[1]

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Floating seaweeds are important dispersal vectors in marine ecosystems. However, the relationship between benthic populations and stranded seaweeds has received little attention. After detachment, a fraction of floating specimens returns to the shore, resulting in strandings that fluctuate in space and time. It has been hypothesized that the availability of stranded seaweeds is related to their benthic abundance on adjacent coasts. Using the large fucoid *Durvillaea antarctica*, we tested whether stranded biomasses are higher at sites with dense adjacent benthic populations. Benthic abundance of *D. antarctica* along the continental coast of Chile was estimated using three approximations: (i) availability of potentially suitable habitat (PSH), (ii) categorical visual abundance estimates in the field, and (iii) abundance measurements in the intertidal zone. Higher PSH for *D. antarctica* was observed between 31° S–32° S and 40° S–42° S than between 33° S and 39° S. Lowest benthic biomasses were estimated for the northern latitudes (31° S–32° S). Regression models showed that the association between stranded biomass and PSH was highest when only the extent of rocky shore 10 km to the south of each beach was included, suggesting relatively short-distance dispersal and asymmetrical transport of floating kelps, which is further supported by low proportions of rafts with *Lepas* spp. (indicator of rafting). The results indicate that stranded biomasses are mostly subsidized by nearby benthic populations, which can partly explain the low genetic connectivity among populations in the study region. Future studies should also incorporate other local factors (e.g., winds, currents, wave-exposure) that influence stranding dynamics.

Key index words: benthic populations; connectivity; floating seaweeds; rafting dispersal; strandings

Abbreviations: AIC, Akaike information criterion; C, Carelmapu; CCD, Coquimbo-Choros District; FAD, Fundo Agua Dulce; HD, holdfast diameter; MB, Mar Brava; MD, Meridional District; MED, Mediterranean District; PA, Playa Amarilla; P, Pucatrihue; PSH, potentially suitable habitat; SB, stranded biomass; SD, Santo Domingo; SED, Septentrional District; SP, San Pedro de la Paz; WW, wet weight

Oceanic rafting is a significant dispersal mechanism that facilitates range expansions of marine organisms and contributes to population connectivity (Thiel and Haye 2006, Fraser et al. 2011). Some of the most common rafting substrata are floating seaweeds (mainly large brown algae), which are available in many oceans (Thiel and Gutow 2005a, Thiel and Fraser 2016), and can transport a wide range of organisms (Kingsford 1992, Thiel and Gutow 2005b, Hinojosa et al. 2006, Waters et al.

2018a). However, detailed information about the abundances of floating seaweeds, their trajectories and their sources is still scarce. Previous studies have reported temporal variability in floating seaweed populations, likely caused by seasonal differences in growth and reproduction of benthic populations (Hobday 2000, Komatsu et al. 2008, Rothäusler et al. 2015). Furthermore, storm events contribute to temporal variability in the availability of floating rafts as well as contrasting dispersal patterns (Craw and Waters 2018, Waters and Craw 2018, Waters et al. 2018b).

Oceanographic and climatic factors, such as currents, winds, and solar radiation, determine the distribution of floating seaweeds and affect their buoyancy (Graiff et al. 2013, Tala et al. 2016, Hawes et al. 2017, Tala et al. 2019). Biophysical models may help to understand dispersal routes and population connectivity (Banks et al. 2007, Garden et al. 2011, Rothäusler et al. 2015). While seaweed rafting has been recognized as an important dispersal process in the ocean (Thiel and Fraser 2016), little is known about the links between benthic populations and availability of floating seaweed rafts. Rafting seaweeds may return to shorelines and become stranded (Duarte et al. 2009, Dufour et al. 2012, López et al. 2017a). If floating times are short, the biomass of stranded seaweeds should be closely related to the density and biomass of benthic populations in surrounding areas, whereas at longer floating times, benthic source populations may be distant and current/wind patterns can reveal likely trajectories of rafting seaweeds (Harrold and Lisin 1989, Tapia et al. 2004, Komatsu et al. 2007). Therefore, beach-cast seaweeds may be an indicator of rafting seaweeds and could potentially be used as a proxy for them. Additionally, species composition, attached rocky substrata or genetic analyses can provide information about the origin of floating seaweeds (Collins et al. 2010, Garden et al. 2011, Thiel et al. 2011, Bussolini and Waters 2015). However, no studies have directly assessed the link between the distribution of benthic seaweed populations and rafting algae that became stranded on shorelines.

Detachment of buoyant seaweeds from rocky habitats occurs mainly during storms when strong waves cause the rock substratum to break or part of the specimens get ripped off after being weakened by grazers (e.g., the limpet *Scurria scurra*; Santelices et al. 1980, Garden et al. 2011). For example, López et al. (2019) revealed a positive relationship between stranded biomass of *Durvillaea antarctica* and local storm intensity on sandy beaches along the continental coast of Chile, suggesting that the amounts of beach-cast rafts might be related to the benthic abundances of adjacent rocky shores.

One of the most studied floating seaweed species is the southern bull kelp *Durvillaea antarctica*. This fucoid seaweed species has high buoyancy and long-distance dispersal ability (Fraser et al. 2011, 2018).

This species grows on exposed or semi-exposed rocky areas in the intertidal zone (Santelices et al. 1980, Castilla and Bustamante 1989, Bustamante and Castilla 1990). of the coasts of New Zealand, Chile, and the sub-Antarctic islands (Hay 1977, Hoffmann and Santelices 1997, Batista et al. 2018).

There is evidence of *Durvillaea antarctica* individuals floating over hundreds or thousands of kilometers in the open ocean (Collins et al. 2010, Fraser et al. 2011, 2018), and the interplay of currents and winds ultimately determines the range and direction of the rafts. For instance, unidirectional currents restrict rafting in one direction and thereby create asymmetric dispersal. Collins et al. (2010) showed that in the Canterbury Bight in New Zealand, 92% of stranded *D. antarctica* were genetically linked to populations from the south (direction of the current), whereas only 8% came from the north (counter-current). Using a similar approach on a larger scale, Bussolini and Waters (2015) demonstrated that the majority of stranded *D. antarctica* on the coast of New Zealand was linked to local sources and only a low percentage of rafts originated from remote populations. It has also been suggested that due to its high buoyancy *D. antarctica* is strongly affected by surface winds, and thus long-distance dispersal is likely to occur when offshore winds dominate (Hawes et al. 2017).

Along the Chilean coast several studies have addressed the rafting dynamics and genetic structure of *Durvillaea antarctica* and associated organisms (Fraser et al. 2009, Haye et al. 2012, López et al. 2017a,b, 2018). Interestingly, populations of *D. antarctica* exhibit a strong phylogeographic structure along the central and southern coast of Chile (i.e., 32° S–45° S), which indicates little genetic connectivity between populations (Fraser et al. 2010). Also, there is indication of rafting dispersal through floating bull kelps of the epiphytic seaweed *Gelidium lingulatum* in the same study region (i.e., haplotypes disappear and appear along the geographic range without a clear pattern), which implies that there are areas where dispersal is more effective than in others (López et al. 2017b). Hinojosa et al. (2011) suggested that the majority of floating *Macrocystis pyrifera* and *D. antarctica* along the Chilean coast became stranded relatively close to local source populations. Indeed, López et al. (2017a) reported that most stranded bull kelps have no indication of long-distance dispersal (i.e., presence and size of attached barnacles of the genus *Lepas*, which indicate floating time of buoyant seaweeds; Thiel and Gutow 2005b, Fraser et al. 2011, Rothäusler et al. 2011, Tala et al. 2013), and therefore likely originate from nearby areas.

In this study, we used *Durvillaea antarctica* as a model of rafting seaweeds. We investigated the connection between benthic populations and local strandings of *D. antarctica*, examining the availability of rocky habitat, and their benthic abundances and stranded biomasses on beaches along the continental coast of Chile (31° S–42° S). We tested the

hypothesis that the amount of stranded biomass (hereafter SB) is directly related to the extent and density of adjacent benthic populations. Hence, the specific objectives of our study were: (i) determine the extent of potentially suitable habitat for *D. antarctica*, (ii) determine the degree of association between *D. antarctica* stranded biomasses on beaches and availability of potentially suitable rocky shores for the species, (iii) estimate the benthic biomass of *D. antarctica* along the continental coast of Chile, and (iv) determine the relationship between *D. antarctica* stranded biomasses on beaches and their adjacent benthic biomasses.

MATERIALS AND METHODS

Oceanographic and biogeographic characteristics of the study area. The dominant oceanographic feature of the Intermediate Area is the northward-flowing Humboldt Current, which supplies coastal communities with cold, nutrient-rich waters through upwelling (Thiel et al. 2007). Upwelling is driven by coastal winds that vary seasonally and spatially, creating local upwelling centers (Strub et al. 1998, Narváez et al. 2004). The influence of upwelling can be observed directly in a locally higher abundance of *Lessonia* spp. and *Durvillaea antarctica* cover (Broitman et al. 2001). There is also a latitudinal temperature gradient, with higher water temperatures in the north (Tapia et al. 2014). The availability of suitable rocky substratum for *D. antarctica* and other large seaweeds varies due to the heterogeneous distribution of sandy beaches along the coastline (Thiel et al. 2007). Suitable rocky substratum was defined as coastline stretch composed of rocks of different area extending from coastal rock outcrops to the outermost rocks, excluding sandy beaches or other soft-sediment habitats, such as river deltas (Fenberg and Rivadeneira 2019). From a biogeographic viewpoint, the study area lies within the so-called Intermediate Area (30° S–42° S), where the biogeographic ranges of multiple taxa of the warm-temperate Peruvian province and the cold-temperate Magellan province coexist (Camus 2001). The Intermediate Area comprises three biogeographic districts (Septentrional, 30° S–33° S; Mediterranean 33° S–37° S; and Meridional, 37° S–42° S; Camus 2001).

Availability of primary substratum for Durvillaea antarctica. The Chilean geographical range of the continental clade of *Durvillaea antarctica* is from 30° S to ~44° S (Fraser et al. 2010), but data on stranded rafts are available only from 30° S to ~42° S (López et al. 2017a). The availability of potentially suitable habitat (hereafter PSH) was estimated for the region from 31° S to 42° S using the pathway tool of Google Earth (http://earth.google.com/; Fig. 1). We did not incorporate the area between 30° S and 31° S in the PSH calculation, due to its proximity to the northern limit of the geographic range of *D. antarctica* (~30° S), where the benthic populations usually are small, fragmented and the accessibility to make abundance measurements was more difficult (see below). Potentially suitable habitat included only the length of exposed rocky coastline (Table S1 in the Supporting Information: first step), but we extended the classification of rocky coastline using a finer scale than in previous studies (Thiel et al. 2007, Garavelli et al. 2014). To validate the values for the estimation of PSH, we compared data from the Google Earth (hereafter GE) analysis with benthic abundance estimates of *D. antarctica* (i.e., visually estimated and directly measured) from field trips along the continental coast (31° S–42° S;

see below); for details of our approach with GE, see Supporting Information (Fig. S1, Table S2, and Appendix S1). To present PSH results and subsequent analyses, we examined latitudinal bins of 1° and referred to latitudinal bins according to their northern limit (e.g., the bin 31° S–32° S was referred to as 31° S).

Abundance of benthic populations. To assess the biomass of benthic *Durvillaea antarctica*, visual estimates and direct measurements were done at low tide. Sites where direct measurements were not possible due to wave conditions, high tide, or inaccessibility were visually estimated from the shore (see more details below; Fig. 1, gray points). This information, combined with the availability of suitable habitat, was used to generate a general estimate of the abundance and distribution of *D. antarctica* along the entire continental coast (31° S–42° S). Sampling was carried out during austral spring, between October 2 and November 14, 2017, and corresponded mainly to the non-reproductive period of the species (Collantes et al. 1997, 2002).

Visual abundance estimates: We used seven categories (from 1 to 7 value) to estimate the abundance of *Durvillaea antarctica* (Table S1: second step). The abundance categories were characterized by different, easily distinguishable criteria (Table 1). At each site, we surveyed a linear stretch of coastline (10 s to 100 s of meters) for the abundance estimates. The exact location of the start and end points of the visual abundance estimate were recorded using a handheld Garmin GPS eTrex® 20× with an accuracy of ± 3.3 m. Using the pathway tool of the GPS, we determined the distance between the two points, which is equal to the length of the linear coastline.

Overall abundances were estimated at 83 sites, covering a total distance of 11.1 km across the entire study area. The lengths of classified coastal stretches varied between 14 m and 290 m with an average of 136 m per site. For each 1° bin of latitude, the mean abundance category value was obtained by multiplying each surveyed stretch of category abundance with its length, and dividing by the total extent of all estimated stretches per latitudinal bin. This standardization was done for the total surveyed length to account for different sampling effort within latitudes. Subsequently, these values were used to generate model predictions for benthic biomass of these shores (see below).

Direct abundance measurements: To estimate benthic biomass, direct measurements of *Durvillaea antarctica* were done during low tide at 16 sites (Fig. 1), using 1 m² quadrats placed at regular intervals of 1 m along a 75–100 m horizontal line (parallel to the shore; Table S1: third step). The number of quadrats sampled at each site varied from 6 to 48, depending on general conditions (i.e., accessibility of intertidal platforms and wave conditions that allowed measurements to be made) and the encountered abundance. Sites were selected using two criteria: (i) distance—within a 50 km radius adjacent to beaches (where previous studies had investigated stranded *D. antarctica*; López et al. 2017a), and (ii) accessibility—rocky shore with road-access and proximity to local villages were preferred (inaccessible sites such as steep cliffs or private property were excluded). We counted and measured all individuals of *D. antarctica* >50 cm within the quadrats. For each individual we recorded the maximum holdfast diameter and maximum frond length. The total length of each plant was measured from the base of the holdfast to the tip of the fronds; if individuals had more than one stipe, only the longest stipe was considered. Holdfast diameters and total lengths of small individuals (frond length ≤50 cm) were not measured since they do not contribute significantly to the total biomass of the population (Castilla and Bustamante 1989). The population structure of *D. antarctica* can be highly variable,
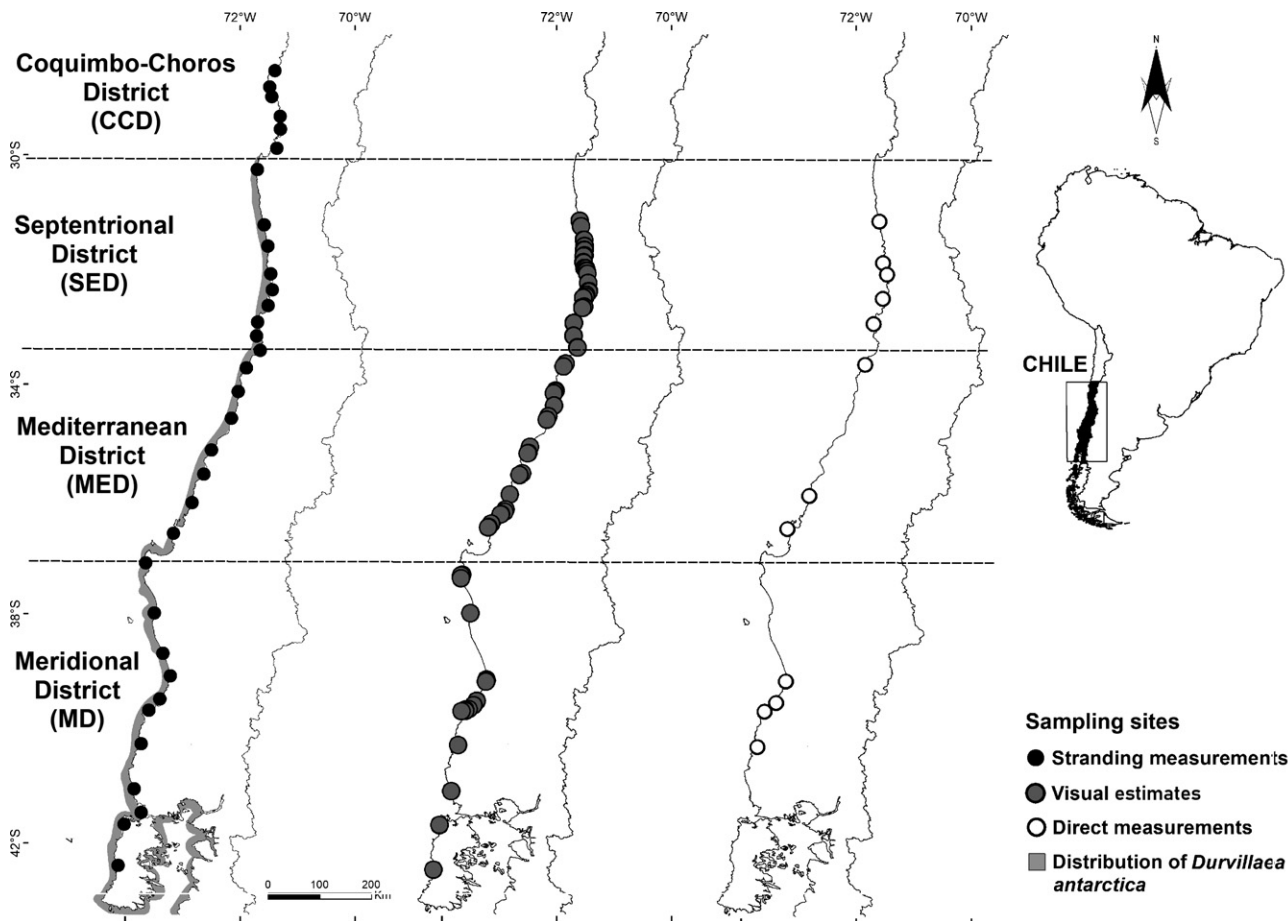
Fig. 1. Geographic distribution of sampling sites. The biogeographic districts described for the coast of Chile by López et al. (2017a; Coquimbo-Choros District: 28° S–30° S, Septentrional District: 30° S–33° S, Mediterranean District: 33° S–37° S, Meridional District: 37° S–42° S) and the geographic distribution of *Durvillaea antarctica* within the study area are also indicated.

TABLE 1. Categories used to visually estimate the abundance of *Durvillaea antarctica* in 10–100 m long stretches along the coast. A small patch is an area with approximately 1 m² extent where the fronds of several individual plants touch each other. A large patch is an area with an extent of more than 1 m² where fronds of many plants touch each other.

Category	Abundance
1	0
2	1–10 plants
3	1–10 plants and at least one small patch
4	Several small patches (<10)
5	Many small patches and at least one large patch
6	Several large patches (<10)
7	Extensive large patches/kelp belt

with some areas containing large numbers of small individuals and only few or no adult plants (Westermeier et al. 1994). Therefore, we aimed to measure at least 50 kelp individuals per site. We sampled a total of 369 quadrats of which 161 quadrats had no *D. antarctica* individuals. The number of plants measured at each sampling site varied between 34 and 137, with an average of 70 ± 21 individuals per site.

Calculation of biomass. Benthic biomass: The wet weight (WW) of each measured individual (frond length >50 cm) was calculated using the holdfast diameter (HD) and the following relationship (Castilla and Bustamante 1989):

$$WW = 0.0021 * HD^{2.5119}; r^2 = 0.95(P < 0.001)$$

This relationship was based on measurements of benthic individuals ($n = 88$; Castilla and Bustamante 1989) and it is similar to other morphometric relationships between holdfast diameter and total weight of benthic individuals described for the Chilean coast (Santelices et al. 1980, Westermeier et al. 1994). After obtaining the wet weight of each measured individual, we calculated the biomass (kg · m⁻²) for each quadrat (Table S1: fourth step).

Using visual abundance estimates to determine benthic biomass: To model predictions of the benthic biomass for sites where only visual abundance estimates were done, we used the data from 16 sites where both (visual abundance estimates and biomass measurements) were available (Table 1). We estimated the mean biomass for each site using a delta distribution to deal with the excess of zeroes (i.e., quadrats without *Durvillaea antarctica*; Pennington 1983). The relationship between estimated mean biomass and visual abundance category was modelled using an exponential regression, with ordinary least squares regression after log-transformation of biomass

(Table S1: fifth step); we used the "dplyr," "fishmethods," and "mgcv" packages in R 3.4 (R Development Core Team 2018). To estimate total benthic biomass across the geographic range of *D. antarctica* (31° S–42° S), we multiplied the distance values of PSH with the estimate values of mean biomass for each 1° bin from the exponential regression model.

Association between the abundances of benthic populations and beach-cast rafts. Previous studies on beach-cast individuals of *Durvillaea antarctica* done in different seasons over three years showed no seasonal or annual patterns (López et al. 2017a). Here, we therefore used the means of the six SB values for further analysis (Table S1: sixth step).

To examine the potential link between stranded biomass and benthic abundances, we used a multiple regression model with the extent of PSH and benthic biomass estimates as predictor variables (because they characterize benthic source populations), and the SB as the dependent variable. In the case of benthic biomass estimates as an abundance measure, we used the mean values of abundance categories for each 1° bin because PSH and total benthic biomass estimates were not independent variables.

Before actually running the multiple linear regression, we computed the correlation between the two predictor variables to explore a possible variable multi-collinearity (Dormann et al. 2013), using the "HH" package in R 3.4 (R Development Core Team 2018). This revealed a moderate degree of dependence between variables (abundance estimates—PSH: 0.50, $P < 0.05$), but the variance inflation factor measured for each variable was very low (1.74 and 1.46, for PSH, and abundance estimates, respectively), which suggest a very low collinearity between variables.

To perform the multiple linear regression to predict SB based on benthic biomass, we calculated several model scenarios, according to different distances to the sampled beaches. As described above, the availability of PSH along the Chilean coast was marked on satellite images using the pathway tool of GE. The distances of each marked stretch were then added for different radii adjacent to the stranded sampling sites (5 km, 10 km, 20 km, 5 km only south, 10 km only south, and 20 km only south), thus representing the total extent of PSH (Table S1: seventh step). Also, to obtain benthic biomass estimates, the mean visual abundance estimates adjacent to stranded sampling sites (using the same radius of PSH) were calculated (Table S1: seventh step). We expected SB to be subsidized by adjacent benthic populations in the specified radii since previous works indicated that the majority of bull kelps along the Chilean coast are washed up on beaches relatively close to local source populations (López et al. 2017a). The latter radii (only south) were chosen according to the northward directed Humboldt Current (Thiel et al. 2007), which we expected to transport kelp northwards after detachment. To confirm the variable selection, we conducted a backward stepwise comparison using AIC-values between models based on different variables to identify the most parsimonious model. For this, each initial model considered both explanatory factors (random factors: PSH and abundance estimates), according to different radii adjacent to the stranded sampling sites (see details above). Model fits were ranked according to their AIC values (relative difference in AIC of more than 2 can be considered to have support). The model with the lowest AIC value was considered the most parsimonious (Burnham et al. 2011). Also, we used r^2 of each model to determine the best fit that explained the SB values (Table S1, eighth step). Additionally, we repeated the analysis using log-transformation of the PSH and SB values to verify if the fit improved. We performed stepwise multiple linear regression using "MASS" package in R 3.4 (R Development Core Team 2018).

To examine if there was a link between SB and percentage of attached *Lepas* a simple linear regression was conducted (Table S1, ninth step), using "lme4" package in R 3.4 (R Development Core Team 2018). This analysis was carried out separately because this predictor variable is more associated with distant benthic populations, since it is associated with floating time of seaweed rafts (i.e., the occurrence and size of attached *Lepas* indicate that stranded individuals spent longer periods floating and kelp individuals with *Lepas* may therefore originate from distant sources; Thiel and Gutow 2005b, Fraser et al. 2011, Rothäusler et al. 2011, Tala et al. 2013). The mean percentage of stranded *Durvillaea antarctica* with *Lepas* attached was taken from López et al. (2017a; Table S1: ninth step).

RESULTS

Availability of primary substratum for Durvillaea antarctica. Potentially suitable habitat was found across all surveyed latitudes between 31° S and 42° S. However, the total amount varied strongly, dependent on the regional topography and extent of sandy beaches (Fig. 2). The largest availability of PSH was at 31° S, 41° S, and 42° S with total values ranging between 136.3 and 171.6 km and low availability between 33° S and 39° S with total values from 16.6 to 57.2 km (Fig. 2, Table S3 in the Supporting Information).

Abundance of benthic populations. Visual abundance estimates: The visual abundance estimates of *Durvillaea antarctica* between 31° S and 42° S (i.e., from the categorical data, Table 1) revealed a trend toward higher abundances (i.e., categories 5, 6, and 7) in the south (Fig. S2 in the Supporting Information), but the number of sampling sites per latitudinal bin and the total surveyed distance were very unevenly distributed (Table 2). Along the coast of latitudes 38° S, 40° S, and 42° S only one visual abundance estimate each was conducted. The absence of *D. antarctica* on exposed rocky shores was frequently noted between 31° S and 34° S, but between 34° S and 42° S bull kelp was encountered at all sampling sites (Fig. S2, Table 2). Also, the distribution of total benthic biomass estimates from abundance categories revealed a trend toward higher abundances in the south ($r^2 = 0.431$, $F_{1,81} = 62.2$, $P < 0.001$).

Direct abundance measurements: At 16 sites, all abundance categories were found except for abundance category 1 (i.e., absence of *Durvillaea antarctica*). Benthic densities varied between 0 and 15 individuals $\cdot$ m^{-2}, with increasing densities at higher latitudes of the study area (>39° S, Fig. S3 in the Supporting Information). The size structure (i.e., length) of the sampled benthic specimens did not vary within the latitudinal gradient of the study area (Fig. S4 in the Supporting Information). Overall, the calculated wet weight varied between 0.01 and 20.84 kg per individual with an average of 1.54 ± 1.21 kg. The resulting biomass values (total wet weight per m^2) ranged from 0 to 42.2 kg $\cdot$ m^{-2}
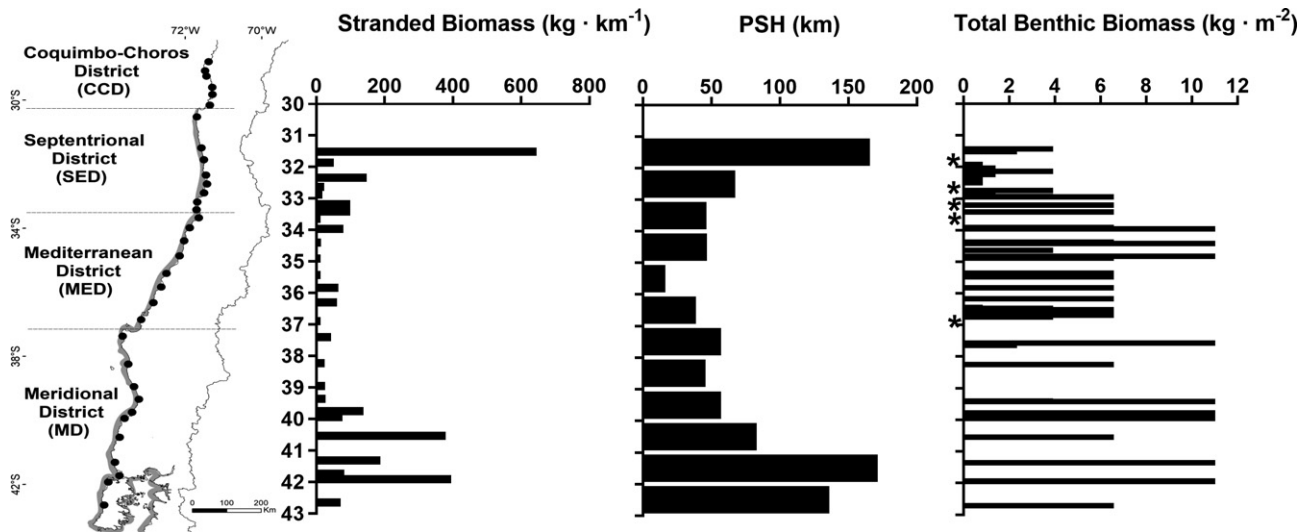
FIG. 2. Stranded biomass, extent of PSH (1° bin of latitude), and total benthic biomass estimates along the continental coast of Chile (31° S–42° S). Mean SB values for 26 beaches were obtained from a previous study (López et al. 2017a). Asterisks on the axis correspond to sampling sites where no benthic individuals of *Durvillaea antarctica* were observed.

TABLE 2. Summary of the results of the visual abundance estimates. The seven abundance categories (see Table 1) were used for the estimation. The mean abundance category values were obtained using the length of the surveyed stretch to account for the differences in the lengths.

Latitude	Sample sites (n)	Distance surveyed (m)	Abundance category							Mean Abundance category
			1	2	3	4	5	6	7	
31	11	875	4	4		1	2			2.0
32	23	3188	4	7	5	1	5	1		2.6
33	8	2541	2			1		4	1	4.1
34	6	874					1	3	2	6.3
35	5	933					1	4		5.8
36	9	1434		1		1	2	5		4.6
37	3	592			1	1			1	5.2
38	1	129						1		6.0
39	10	1185					3	3	4	6.2
40	1	75						1		6.0
41	5	848						1	4	6.7
42	1	155						1		6.0
Total	83	12829								

with an average of 3.34 ± 2.81 kg $\cdot$ m^{-2} (Table S4 in the Supporting Information). Frond length varied between 50 cm (smaller individuals, e.g., 10–40 cm, were only counted) and 895 cm, and the overall average was 126.3 ± 47.8 cm. The holdfast diameter varied between 2 and 39 cm, with an overall average of 12.0 ± 9.4 cm. The direct estimates of mean benthic biomass are strongly related to visual abundance estimates (Fig. S5 in the Supporting Information; $r^2 = 0.86$, $P < 0.001$). The mean biomass per site increased from 0.83 kg $\cdot$ m^{-2} at sites with abundance category 2 to 11.03 kg $\cdot$ m^{-2} at sites with abundance category 7. These predictions are limited to sites with an abundance category 2 or higher.

Association between the abundances of benthic populations and beach-cast rafts. Qualitative comparison: There was a positive correlation between the stranded biomass and the PSH ($r^2 = 0.91$, $F_{1; 10} = 5.62$, $P < 0.001$). The stranding pattern reflects the availability of PSH with high values for the bins 31–32° S, 41–42° S, and 42–43° S, intermediate for bins 32°–33° S and 40°–41° S, and low values between latitudes 32° S and 39° S (Fig. 2). Total benthic biomass estimates (from predictions of exponential regression model between visual abundance estimates and direct abundance measurements) showed some variability between 31° S and 34° S but remained relatively high further south (i.e., >37° S). Sites without *Durvillaea antarctica* were mostly located in the northern part of the study area (Fig. 2).

Quantitative comparison: Multiple linear regression analysis of mean SB on beaches and the surrounding availability of habitat and mean visual abundance estimates as predictor variables revealed significant relationships for all radii, although only PSH was a significant factor presenting low AIC-values in the models that only used PSH as a predictor variable (Tables 3 and S5 in the Supporting Information). The highest mean SB value (646 kg $\cdot$ km^{-1}) was found for a beach at latitude 31° S (Fundo Agua Dulce, marked as an open circle in Fig. 3). This SB value had a disproportionate effect on the strengths of relationships and was thus excluded from further analysis, which led to an improvement of the r^2-values in the majority of fits, in one case from 0.292 to 0.597 (10 km only south). To test for differences between biogeographic districts, the best fit of the previous analysis (10 km) was used and the data were grouped into SED, MED, and MD. The r^2-value of the Meridional

TABLE 3. Summary of the different multiple linear regression models performed between on the PSH, visual abundance estimates, and SB data. The PSH values are the total extent of potentially suitable habitat, and visual abundance estimates according to different radii surrounding the same beaches, where the SB was measured. Mean SB values originate from a previous study ($n = 26$; López et al. 2017a). One outlier (Fundo Agua Dulce) had a disproportionate influence on the trends and was therefore excluded. Significant *P*-values (<0.05) are shown in bold. Details of AIC values and significance for each predictor variables and model are shown in Table S5.

Model	Adjusted r^2	F	df	P
Linear				
5 km radius	0.254	8.31	1, 23	**0.007**
10 km radius	0.572	24.79	1, 23	**<0.001**
20 km radius	0.327	16.34	1, 23	**<0.001**
5 km only south	0.489	22.81	1, 23	**<0.001**
10 km only south	0.597	33.79	1, 23	**<0.001**
20 km only south	0.468	20.06	1, 23	**<0.001**
SED (10 km radius)	0.020	0.06	1, 4	0.816
MED (10 km radius)	0.152	1.03	1, 6	0.320
MD (10 km radius)	0.781	31.35	1, 9	**<0.001**
Linear log-transformed				
5 km radius	0.426	16.53	1, 23	**<0.001**
10 km radius	0.578	19.86	1, 23	**<0.001**
20 km radius	0.293	5.51	1, 23	**0.029**
5 km only south	0.275	9.11	1, 23	**0.006**
10 km only south	0.590	22.80	1, 23	**<0.001**
20 km only south	0.420	15.90	1, 23	**<0.001**
SED (10 km radius)	0.069	0.343	1, 4	0.540
MED (10 km radius)	0.205	1.42	1, 6	0.216
MD (10 km radius)	0.593	12.90	1, 9	**0.007**

MD, Meridional District; MED, Mediterranean District; SED, Septentrional District.

District is 0.781 and notably higher than the value of the Septentrional and Mediterranean Districts (0.02 and 0.152, respectively). Overall, the strongest relationship between SB and predictor variables (particularly PSH) was found for a 10-km radius where only the extent of rocky shore to the south of the beach sampling site was included (Table 3). Prior log-transformation of the SB and PSH data revealed similar results (Fig. 3 and Table 3).

There was no significant relationship between the stranded biomass and mean percentage of attached *Lepas* ($r^2 = 0.04$; $F_{1;23} = 0.075$; $P = 0.786$). Interestingly, percentages of bull kelps with attached *Lepas* were higher in the south (Fig. 4 and Table S6 in the Supporting Information, bottom three sampling sites). For example, stranded kelp on the beach Carelmapu, which is situated just north of the Canal de Chacao (separating Isla Chiloé from continental Chile), reached values of up to 78% of stranded kelps with *Lepas* (Table S6). At other southern sampling sites of our study area with high presence of specimens with attached *Lepas*, mean SB reached values close to 400 kg · km^{-1}, but the corresponding extent of PSH is ~15 km in the first case (Pucatrihue, marked with the letter P in Fig. 3), and ~35 km in the second case (Mar Brava, marked with the letters MB in

Fig. 3). High percentages of attached *Lepas* indicate that stranded individuals spent longer time floating and may therefore originate from distant sources. The highest SB in Pucatrihue was found in summer 2014 (745 kg · km^{-1}) and in this sample, almost 50% of individuals had *Lepas* attached (Table S6). However, in winter 2015 and winter 2016, the SB for this site was also relatively high (>500 kg · km^{-1}) and no *Lepas* were found (Table S6). The percentage of stranded individuals with *Lepas* at Mar Brava, on the other hand, constantly reached values >25% with high variance in SB (Table S6).

DISCUSSION

Along the continental coast of Chile, floating times of *Durvillaea antarctica* are relatively short and thus individuals are expected to strand close to source populations (Hinojosa et al. 2011, López et al. 2017a). Herein, it was shown that the stranding pattern approximately reflects the availability of PSH. Regression models showed that the association of stranded biomass and PSH was highest using a radius of 10 km only south of each beach, suggesting asymmetrical transport of floating bull kelps by the Humboldt Current. Moreover, a general trend of higher benthic abundances toward higher latitudes was observed within the study area, possibly reflecting the influence of more favorable environmental conditions (e.g., lower temperatures and lower solar radiation) for the physiologic machinery of bull kelps (Cruces et al. 2012, 2013) and the northern biogeographical limit of this species.

Availability of primary substratum and benthic biomass. Potentially suitable habitat was found across all surveyed latitudes. Higher availability of rocky shore found at 31° S, 41° S, and 42° S and low availability between 33° S and 39° S coincides with higher extents of sandy beaches between 33° S and 39° S as described by Thiel et al. (2007). The northern biogeographical limit of *Durvillaea antarctica* is approximately 30° S (Hoffmann and Santelices 1997, Graiff et al. 2013), and thus the abundance was expected to be lower close to the limit in the north and higher in the south (Broitman et al. 2001). In our study, low benthic abundances of *D. antarctica* were observed between 31° S and 32° S, which is in agreement with the low occurrence (<20% cover) and densities (<8 adult individuals · m^{-2}) of benthic specimens of *D. antarctica* reported by Aguilera et al. (2015) within the same region. These results are supported by the abundant center hypothesis, which proposes peripheral populations to be smaller and more fragmented than central populations due to higher physiological stress (e.g., Sagarin and Gaines 2002, Sagarin et al. 2006). It is likely that higher water temperatures and higher solar radiation in the north (Tapia et al.
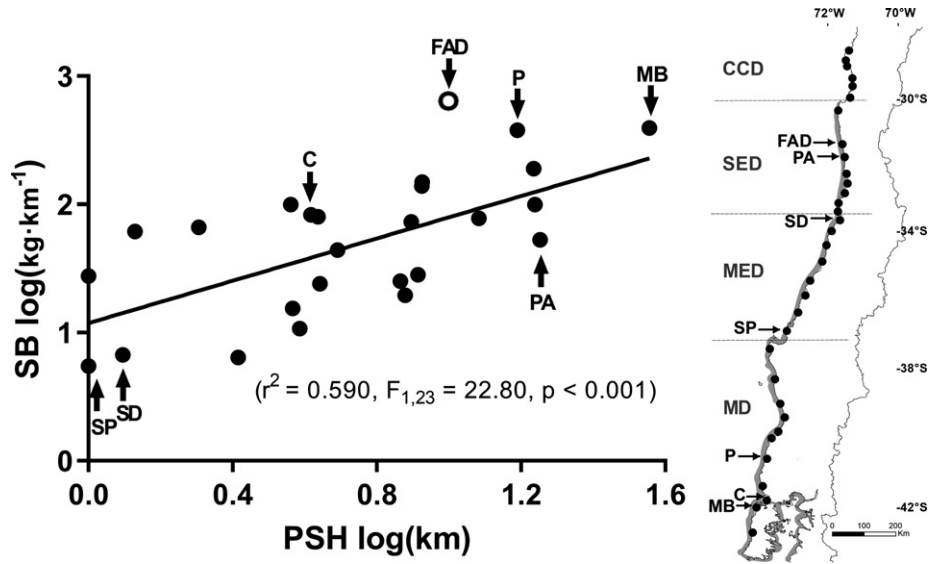
FIG. 3. Correlation between the extent of PSH (potentially suitable habitat) and SB (stranded biomass) of *Durvillaea antarctica*. Mean SB values for 26 beaches originate from a previous study (López et al. 2017a). The PSH values are the total extent of potentially suitable habitat in a 10-km radius south of the beaches, where the SB was measured. The data were analyzed after log-transformation. One outlier (Fundo Agua Dulce, FAD, marked as an open circle) had a disproportionate influence on the trends and was therefore excluded. Sampling sites indicated by acronyms correspond to those interpreted in the Discussion section. Solid black circles, gray abbreviations, and shaded line in map indicate sampling sites, biogeographic districts, and geographic range of *D. antarctica*, respectively. Biogeographic districts (CCD: Coquimbo-Choros District: 28° S–30° S, SED: Septentrional District: 30° S–33° S, MED: Mediterranean District: 33° S–37° S, MD: Meridional District: 37° S–42° S). Sandy beaches (C: Carelmapu, MB: Mar Brava, SD: Santo Domingo, SP: San Pedro de la Paz, P: Pucatrihue, PA: Playa Amarilla).
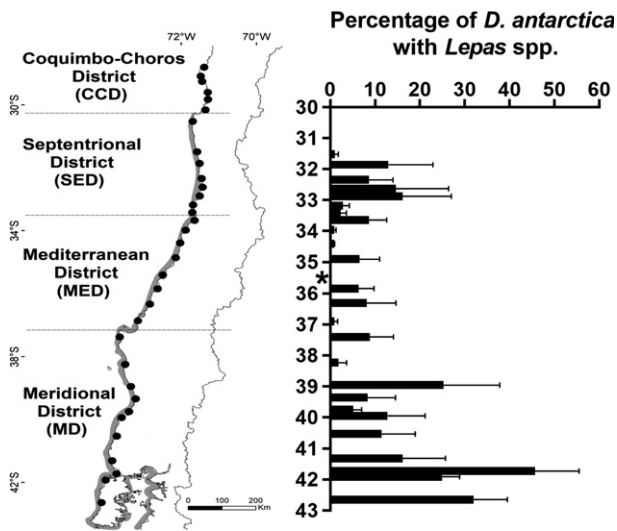

FIG. 4. Mean ± SE percentages of stranded individuals of *Durvillaea antarctica* with attached *Lepas* spp. on beaches along the continental coast of Chile (31° S–42° S). Mean ± SE values for 26 beaches sampled during austral winter and summer in the years 2013 – 2015 are based on data from a previous study (López et al. 2017a). Asterisk on the axis corresponds to a sampling site where no stranded individuals of *D. antarctica* with attached *Lepas* spp. were observed across all seasonal surveys.

2014) negatively affect benthic kelp individuals (e.g., Rothäusler et al. 2012).

Overall, measured biomass and density values lie within the previously reported ranges (Westermeier et al. 1994, Castilla et al. 2007) and a trend of higher biomasses toward higher latitudes was observed within the study area. Biomass and density values differed substantially between quadrats within sampling sites and also between sites of the same latitude. Many biological explanations for the patchy distribution of *Durvillaea antarctica* have been proposed, ranging from competition over dispersal capacity to herbivory (Guiler 1959, Taylor and Schiel 2005). Over a great part of the Chilean coast the two large brown algae *D. antarctica* and *Lessonia spicata* coexist on the intertidal shore and interspecific competition for space may influence population dynamics (Santelices et al. 1980). Fittingly, it has been observed that *D. antarctica* occupies empty substratum when *L. spicata* gets detached (Westermeier et al. 1994). In the northern part of the study area this process should be more important than in the south, where the intertidal shore is almost exclusively dominated by *D. antarctica* (Hoffmann and Santelices 1997). Patchy recruitment of *D. antarctica* may thus be the consequence of limited dispersal capacity (Santelices and Ojeda 1984, Taylor and Schiel 2005). Furthermore, evidence of herbivory (e.g., excavations caused by the limpet *Scurria scurra*) found on detached kelp holdfasts (López et al. 2018) suggests that dislodgement increases with grazing intensity. In this same region (30° S–32° S), the bulldozing chiton *Enoplochiton niger* was found to eliminate small *D. antarctica* recruits

(Aguilera et al. 2015). A comparative study on grazing intensity in different benthic kelp populations along the Chilean coast could improve knowledge about latitudinal differences and its influence on availability of floating kelps.

Association between the abundances of benthic populations and beach-cast rafts. Our results further consolidate the previous estimation that the majority of stranded kelp originate from local sources (Hinojosa et al. 2011, López et al. 2017a). Due to its high buoyancy, *Durvillaea antarctica* is strongly affected by surface winds, and thus individuals may strand relatively close to source populations when onshore winds prevail (Hawes et al. 2017). There may also be convergence areas and local gyres that increase the retention of floating seaweeds in certain coastal zones (e.g., Hinojosa et al. 2011). Moreover, we expected the northward directed Humboldt Current to create an asymmetrical stranding pattern, as seen elsewhere (Collins et al. 2010). This means, that higher amounts of stranded biomass come from sites south of each beach. Indeed, the best fit of the model between the availability of rocky habitat south of sandy beaches and the SB support our assumption of mostly unidirectional transport of floating bull kelp.

The mean SB values used in this study only represent six stranding measurements (i.e., two seasons during 3 years), with low variability among them (López et al. 2017a). However, high inter- and intra-annual fluctuations of *Durvillaea antarctica* strandings have been recently described on beaches on the continental coast of Chile, with marked increases during austral summer and fall, and decreases during spring (López et al. 2019). Elsewhere, several possible factors influencing temporal availability of floating kelp have been described, such as seasonally varying floating persistence (Graiff et al. 2013) and seasonal variation in speed and direction of surface winds (Narváez et al. 2004). Additionally, seasonal fluctuations due to the growth season (Kingsford 1992, Dempster and Kingsford 2004) as well as interannual changes of benthic populations can be observed (Taylor and Schiel 2005, Castilla et al. 2007). Since the field study was carried out in austral spring, when a decrease in the benthic abundances of *D. antarctica* had been reported (Westermeier et al. 1994), this could affect our model fits. Therefore, higher temporal resolution (e.g., monthly) and sampling of benthic kelps and beach-cast rafts in the same season/year on a longer timescale should be implemented in future studies.

When examining the PSH-SB pairs separately, some patterns become visible. Generally, sampling sites with low adjacent PSH were expected to have low SB, such as Pichilemu, Duao and Santo Domingo (Fig. 3). Sampling sites that are located in a convex part of the coastline (i.e., more exposed) also show low SB (e.g., Santo Domingo, San Pedro de la Paz and Queule). To better understand the relationship between benthic populations of *Durvillaea antarctica* and stranded biomasses it is helpful to examine pairs of PSH-SB that do not seem to follow the general trend (Fig. 3). For instance, one conspicuous PSH-SB pair is Playa Amarilla (PA in Fig. 3) with relatively high PSH (16.9 km), but low average SB (51 kg · km^{-1}). In this case, only single specimens were encountered on the rocky substratum in a 10-km radius south of the sampling beach. For all beaches where adjacent benthic abundances are low and no kelp is transported from distant sources, the observed SB should be lower than expected from the overall PSH-SB relationship.

The highest mean SB (646 kg · km^{-1}) was found for a beach at latitude 31° S (Fundo Agua Dulce, FAD). In a 10-km radius south of this site neither high extents of PSH nor high abundances of kelps on the existing rocky shore were encountered. Furthermore, stranded individuals did not show high percentages of attached *Lepas* spp. (Fig. 4), which would have indicated that bull kelps originate from distant sources. There is some indication that surface currents, which favor southward dispersal occur between 31° S and 32° S (Hormazábal 2004), and historical surface wind data taken from earth.nullschool.net for the period before the sampling in winter 2014 (when high SB was recorded) also show events of southward winds. The high abundance of PSH as well as the visual abundance estimates of *Durvillaea antarctica* to the north of FAD reinforce this hypothesis.

Oceanographic and topographic features affect seaweed stranding dynamics. Upwelling centers, river run-offs and wind regimes can transport floating material offshore and block it from returning to the coast (Hinojosa et al. 2011, Hawes et al. 2017). Previous studies on floating seaweeds revealed the existence of oceanic retention zones, where algae are held back and accumulate due to relatively stable wind/current regimes (Komatsu et al. 2008, Rothäusler et al. 2015). Retention zones can also develop close to the coast, when the alongshore current (responsible for the upwelling) is separated from the coastline in areas of convex coastlines, thus creating so-called upwelling shadows (Graham and Largier 1997, Hinojosa et al. 2011). While the majority of the continental Pacific coast of Chile is characterized by a relatively straight North-South orientation (Thiel et al. 2007, Strub et al. 2019), some areas of coastal recess do exist (e.g., north/south of Concepción, Santo Domingo, Queule) and the regional topography on a small scale (tens of km) can be diverse.

Oceanographic conditions (relatively low water temperature) in the SE Pacific, specifically in the southern part of our study area (37° S–42° S), enable prolonged floating (from 59 days in summer to 75 days in winter; Tala et al. 2019), thus further enhancing the potential of offshore accumulation

zones, and eventually contributing to higher amounts of stranded biomasses on beaches in the southern part of the study area. Also, higher percentages of stranded individuals with attached *Lepas* for the southern beaches Hua-Huar, Carelmapu, Mar Brava and Cucao (Fig. 4 and Table S6) and large *Lepas* (indicating long floating times) on *Macrocystis* rafts in that area (Macaya et al. 2005) support this. However, short-term meteorological events (e.g., strong storms) can cause high variability in the proportion of *Lepas*-covered beach-cast *Durvillaea* specimens at a site (Waters and Craw 2018, Waters et al. 2018b). Hence, this reinforces the need for studies of stranding dynamics over shorter timescales.

Another factor that contributes to offshore transport and additionally prevents floating material or propagules from crossing the river plumes are river run-offs (Vargas et al. 2006, Rech et al. 2014). For example, the effect of the Bio-Bio river is directly reflected in the lowest SB for the sampling site San Pedro de la Paz (marked with the letters SP in Fig. 3). When looking at the adjacent availability of PSH and visual abundance estimates, it is conspicuous that benthic populations can be found in the north, but not in the south. However, between the sampling beach and the benthic populations in the north lies the mouth of the Bio-Bio river, essentially blocking most bull kelp that would float southwards. Therefore, our results support the hypothesis that stranded seaweed biomasses are directly related to the extent and density of adjacent benthic populations (particularly the availability of PSH). Future studies should focus on processes after kelp-detachment, such as wind regimes and surface currents because they seem to have a strong influence on stranding dynamics.

CONCLUSIONS

In this study, we demonstrated that the stranding pattern reflects the availability of PSH. Regression models showed that the availability of adjacent PSH to the south is best suited to explain *Durvillaea antarctica* stranding dynamics. This indicates relatively short floating distances and unidirectional transport of floating seaweeds. In cases where PSH–SB pairs do not seem to follow the general pattern, winds/currents, coastal topography, and percentages of attached *Lepas* can be used to infer possible explanations. Moreover, the abundance of benthic populations tended to increase at higher latitudes within the study area. Our results also suggest that patterns in floating seaweed abundances are consistent with the abundant center hypothesis (Sagarin et al. 2006).

The results of this study confirm that the majority of floating *Durvillaea antarctica* strand relatively close to source populations, which helps to explain the low genetic connectivity of benthic populations described along the continental coast of Chile (Fraser et al. 2010). Furthermore, stranded seaweed supplies from nearby areas are important for secondary consumers on the sandy beaches (Duarte et al. 2008, 2009) and rocky shores (Rodríguez 2003, Quintanilla-Ahumada et al. 2018), and they are thus essential to understand the distribution and population dynamics of detritus-feeding shore organisms. Future studies should use combined oceanographic data (winds and currents) and integrate wave-exposure indices to improve stranded biomass predictions (Burrows et al. 2008). *Durvillaea antarctica* is also commercially exploited in Chile (mainly between 34° S–36° S; Gelcich et al. 2006, SERNAPESCA 2017), and although its effect on the supplies of floating individuals and beach-cast rafts remain currently unknown, the influence of harvesting should be investigated and incorporated into future predictive models. Also, evaluating source populations of stranded specimen through genetic studies could improve predictions regarding the dispersal trajectories of floating bull kelps along the Chilean coast.

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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. Example image of Category II measurement in GE. The transition between rock and

water is vague, thus providing a wide area of potentially suitable habitat for *Durvillaea antarctica*. The red line represents the extension of linear coastline showing the specified features of the corresponding category. The blue line represents the width of this zone.

Figure S2. Relative frequency of the abundance categories visually estimated for *Durvillaea antarctica* on surveyed rocky shores of the continental coast of Chile, according to 2° bin of latitude (for details on the visual abundance estimates see Materials and Methods section).

Figure S3. Relative frequency of the benthic densities (individuals · m^2) of *Durvillaea antarctica* on surveyed rocky shores of the continental coast of Chile, according to 2° bin of latitude based on direct measurements (for details on the direct measurements see Materials and Methods section). The latitude intervals 37° S–38° S and 41° S–42° S are not shown because there were no direct measurements in those areas.

Figure S4. Relative frequency of the size (length) of benthic individuals of *Durvillaea antarctica* on surveyed rocky shores of the continental coast of Chile, according to 2° bin of latitude based on direct measurements (for details on the direct measurements see Materials and Methods section). The latitude intervals 37° S–38° S and 41° S–42° S are not shown because there were no direct measurements in those areas.

Figure S5. Relationship between estimated mean benthic biomass and visual abundance category of benthic populations of *Durvillaea antarctica* on surveyed rocky shores of the continental coast of Chile, 31° S–40° S ($n = 16$ sites). Equation of exponential regression, r^2-value, and statistical significance of the model are also shown.

Table S1. Schematic overview of the methodological procedure. Each step is described in more detail in Materials and Methods section.

Table S2 Rocky shore categories. The three categories were used to differentiate rocky shore in GE satellite images dependent on availability of PSH.

Table S3. Results of the GE analysis of potentially suitable habitat (PSH). The sum of the total extension of rocky shore was calculated for each latitudinal bin.

Table S4. Summary of the results of the direct measurements**.** The holdfast diameter was used to estimate the wet weight for each measured individual. With the number of individuals per quadrat and their corresponding wet weight, the biomass (kg · m^{-2}) was obtained. The mean biomass and mean density values were calculated assuming the data to be delta-distributed. A justification for the application of this method and an explanation of the procedure is given in the Materials and Methods section.

Table S5. Results of the stepwise model selection by AIC, using stranded biomass (SB) as dependent variable, and potentially suitable habitat (PSH) and abundance estimates as predictor variables. The PSH values and visual abundance estimates are according to different radii surrounding the same beaches, where the SB was measured. Mean SB values originate from a previous study ($n = 26$; López et al. 2017a). One outlier (Fundo Agua Dulce) was excluded from the analyses. *P*-values, AIC, Δ AIC (differences between AIC for PSH + abundances estimates, and only PSH models) for each model are also shown. Significant values ($P < 0.05$) are shown in bold. MD, Meridional District; MED, Mediterranean District; SED, Septentrional District.

Table S6. Mean stranded biomasses of *Durvillaea antarctica* and percentages of attached *Lepas*. The data originate from a previous study and represent collection of stranded individuals each summer (S)/winter (W) on 26 beaches for three consecutive years (López et al. 2017a). Fundo Agua Dulce is abbreviated as FAD. Conspicuous values are marked in gray and commented in Discussion section.

Appendix S1. Rocky shore categories