Latitudinal and seasonal effects on short-term acclimation of floating kelp species from the South-East Pacific

Fadia Tala [a,b], Marcel Velásquez [a,b], Andrés Mansilla [c,d], Erasmo C. Macaya [e,f,g], Martin Thiel [a,g,h,*]

[a] Facultad de Ciencias del Mar, Universidad Católica del Norte, Larrondo 1281, Coquimbo, Chile
[b] Centro de Investigación y Desarrollo Tecnológico en Algas (CIDTA), Facultad de Ciencias del Mar, Universidad Católica del Norte, Larrondo 1281, Coquimbo, Chile
[c] Laboratorio de Macroalgas Antárticas y Subantárticas (LMAS), Universidad de Magallanes, Punta Arenas, Chile
[d] Instituto de Ecología y Biodiversidad, IEB-Chile, Universidad de Chile, Santiago, Chile
[e] Laboratorio de Estudios Algales (ALGALAB), Departamento de Oceanografía, Facultad de Ciencias Naturales y Oceanográficas, Universidad de Concepción, Casilla 160-C, Concepción, Chile
[f] Centro FONDAP de Investigaciones en Dinámica de Ecosistemas Marinos de Altas Latitudes (IDEAL), Chile
[g] Millennium Nucleus Ecology and Sustainable Management of Oceanic Island (ESMOI), Coquimbo, Chile
[h] Centro de Estudios Avanzados en Zonas Áridas, Coquimbo, Chile

ARTICLE INFO

ABSTRACT

Floating seaweeds are important dispersal vehicles for many organisms in cold-temperate waters between latitudes 30° and 60°. Molecular studies suggested that long-distance rafting of seaweeds is more prevalent at the polar edges of their distribution but knowledge about their physiological status at high latitudes is limited. Seasonal short-term field experiments were conducted along a latitudinal gradient (30°, 37° and 54°S) with floating kelps *Macrocystis pyrifera* and *Durvillaea antarctica*. Kelps were tethered at the sea surface for 14 d during austral winter and summer to examine their acclimation potential in floating conditions. Biomass changes, reproductive status and physiological traits (chlorophyll *a* fluorescence, pigments, phlorotannins and antioxidant capacity) were evaluated after 7 d and 14 d of floating. Biomass changes (positive or negative) depended on species and latitude: at low latitudes (Coquimbo) both species lost biomass during both seasons while at mid latitudes (Concepción) they grew during summer but not in winter. Species-specific responses were observed at high latitudes (Pta. Arenas) with floating *M. pyrifera* growing in summer and *D. antarctica* in winter. Both species were able to maintain reproductive status mainly in winter, but at mid latitudes *M. pyrifera* also showed high reproductive activity during summer. Physiological adjustment was detected for both species at day 7 and upheld until the end of the experiment (14 d). Latitudinal changes in photosynthetic variables (maximum quantum yield and pigments) were more evident in summer conditions, *M. pyrifera* showing decreases in F_v/F_m and pigment levels at low and high latitudes while in *D. antarctica* these variables increased with latitude. Phlorotannin contents varied with latitude but showed an opposing pattern in the two kelp species, with high concentrations at low latitudes for *M. pyrifera* and at high latitudes for *D. antarctica*. The floating kelps maintained high antioxidant capacity during the experiments. The short-term acclimation responses support the hypothesis of long-distance dispersal at high latitudes for both floating kelp species. The acclimation potential differed between the two species depending on the season, especially at mid and high latitudes. Summer conditions were favorable for floating *M. pyrifera* at high latitudes and for both species at mid latitudes in which a combination of increasing radiation and moderate temperature can stimulate growth. The results confirm that kelp rafting is favored at mid/high latitudes but suggest that in polar waters (>60°) low temperatures and light limitations might suppress growth of floating seaweeds.

1. Introduction

Floating patches of various seaweed species occur throughout the world´s oceans, although they are most abundant in temperate and cold waters of both hemispheres (30°–60°) (Kingsford, 1992; Hinojosa et al., 2010, 2011; Thiel et al., 2011; Rothäusler et al., 2012). Long-distance rafting of buoyant, brown seaweeds contributes to the dispersal of marine biota (Edgar, 1987; Thiel and Gutow, 2005; Fraser et al., 2011). Molecular studies confirm the importance of dispersal and recolonization by floating seaweeds especially at high latitudes, where seaweed rafts must cross long distances of open ocean without intermediate stepping stones (e.g. *Ascophyllum* - Olsen et al., 2010; *Durvillaea* -

* Corresponding author at: Facultad de Ciencias del Mar, Universidad Católica del Norte, Larrondo 1281, Coquimbo, Chile.
E-mail address: thiel@ucn.cl (M. Thiel).

Fraser et al., 2009, 2011; *Fucus* - Coyer et al., 2011; *Macrocystis* - Macaya and Zuccarello, 2010a, 2010b). However, the morphological and physiological mechanisms that allow long-distance dispersal of floating seaweeds are not well understood.

Some seaweed species are able to continue floating, growing, and even reproducing for extended time periods after detachment (Macaya et al., 2005; Martinez et al., 2006; Hernández-Carmona et al., 2006; McKenzie and Bellgrove, 2008; Rothäusler et al., 2009, 2011a, 2011b; Tala et al., 2013). However, during their voyage biotic factors, including grazing (by snails, urchins, crustaceans), fouling (by bryozoans, stalked barnacles, epiphytic algae) (Thiel and Gutow, 2005; Rothäusler et al., 2009; Gutow et al., 2012), and abiotic factors such as high water temperatures, intense solar radiation and nutrient depletion negatively affect the floating seaweeds, limiting their persistence at the sea surface (Hobday, 2000; Karsten et al., 2001; Vandendriessche et al., 2007; Rothäusler et al., 2011b; Graiff et al., 2013). Even though initial physiological acclimation can occur, the decline in growth and reproductive capacity are the main changes suppressing the colonization potential of floating kelps (Hobday, 2000; Macaya et al., 2005; Hernández-Carmona et al., 2006; Vandendriessche et al., 2007; Rothäusler et al., 2009, 2011b).

Depending on their geographic origin (latitude) or the time (season) when they are detached, floating seaweeds are confronted with variable environmental conditions during rafting (Wooster and Sievers, 1970; Macaya et al., 2005; Komatsu et al., 2007; Rothäusler et al., 2009; Tapia et al., 2014). In summer, high temperature and solar radiation may affect the photosynthetic efficiency and pigment concentration and cause an increase in tissue degradation, thereby contributing to the sinking of floating kelps (Rothäusler et al., 2009, 2011c; Graiff et al., 2013). In contrast, during winter the conditions at the sea surface are more moderate and floating kelps can persist for longer time periods (Graiff et al., 2013; Tala et al., 2013). Solar radiation shows a general gradient decreasing from the equator towards the poles with greater seasonal changes at higher latitudes than at low latitudes (Kain, 1989). Latitudinal gradients in temperature follow a similar general pattern as radiation (Silva et al., 2009). Consequently, it is expected that floating kelps show efficient acclimation mechanisms that allow them to persist longer at the sea surface during winter and at higher latitudes than during summer and at mid-low latitudes. Current knowledge on the growth and physiology of floating seaweeds and the environmental factors influencing their persistence at the sea surface is mainly limited to mid and low latitudes (<40°S) and experimental conditions (e.g. Vandendriessche et al., 2007; Rothäusler et al., 2009, 2011a, 2011b, 2011c; Graiff et al., 2013). Considering that floating seaweeds are abundant at higher latitudes (>40°S) (Smith, 2002; Hinojosa et al., 2010, 2011; Rothäusler et al., 2012; Wichmann et al., 2012), long-distance rafting appears most relevant at these latitudes (Fraser et al., 2009; Macaya and Zuccarello, 2010a; Fraser et al., 2011; Cumming et al., 2014).

Two important floating kelps *Macrocystis pyrifera* (L.) C. Agardh (Laminariales) and *Durvillaea antarctica* (Chamisso) Hariot (Fucales) are very common along the Chilean coast between 30°S and 55°S (Collantes et al., 2002; Macaya et al., 2005), and their abundances show a clear latitudinal trend in concordance with benthic sources (more abundant in the south) (Macaya et al., 2005; Hinojosa et al., 2010, 2011; Wichmann et al., 2012). In both species, molecular studies support the idea of high dispersal potential with similar genetic structure between distant populations (Fraser et al., 2009, 2010; Macaya and Zuccarello, 2010a, 2010b). In addition to the temperature gradient, there are latitudinal gradients in solar radiation and nutrient supply (upwelling) along the Chilean coast (Cabrera et al., 1995; Thiel et al., 2007; Silva et al., 2009). Consequently, the lifetime of kelp rafts is expected to increase towards higher latitudes. In this sense, the Chilean coast offers an excellent *in situ* laboratory to test the combined latitudinal and seasonal effects on floating kelps using experimental field studies.

Based on the above considerations it was hypothesized that floating kelps *M. pyrifera* and *D. antarctica* are performing better at high latitudes where environmental conditions favor long-term rafting, reproduction and physiological acclimation. In order to test this hypothesis, herein short-term field experiments were conducted to determine the morphological (biomass change), physiological (chlorophyll *a* fluorescents in *PS*II, pigments, phlorotannin contents, and antioxidant capacity) and reproductive status of floating kelps *M. pyrifera* and *D. antarctica* tethered at three sites along the Chilean coast (30°S–54°S, spanning a distance of more than 2500 km) during contrasting seasons (winter vs. summer).

2. Materials and methods

2.1. Experimental zones and sites.

The latitudinal and seasonal effects of floating conditions on adult individuals of *M. pyrifera* and *D. antarctica* were examined in field experiments. The *in situ* experiments were conducted during austral winter 2013 (July–September) and summer 2013/2014 (December–February) for each species separately. Experiments were conducted at low (Coquimbo, Herradura Bay: 29°57′S, 71°20′W), mid (Concepción, Dichato: 36°29′S, 72°54′W) and high latitudes (Punta Arenas, Puerto del Hambre: 53°36′S, 70°55′W) (Fig. 1). These study sites allowed to examine the latitudinal gradient in environmental conditions to which floating rafts are exposed along the coast of the SE Pacific, including extremes of low and high latitudes. Benthic populations of both species occur along this range, with abundances that vary according to factors such as hard substratum availability and wave-exposure (Santelices et al., 1980; Collantes et al., 2002; Buschmann et al., 2004; Mansilla and Avila, 2007). Molecular studies in *D. antarctica* had shown that the populations from central Chile (32°–44°S) are genetically different from the populations of southern Chile (49°–56°S) (Fraser et al., 2009, 2010) whereas *M. pyrifera* showed a homogenous genetic structure along the Chilean coast (Macaya and Zuccarello, 2010b).

2.2. Environmental conditions during the study.

Throughout the experimental period, at each experimental site temperature (°C) and light (Klux) in the upper water layers were monitored every 5 min using a HOBO® Pendant Temperature-Light Datalogger
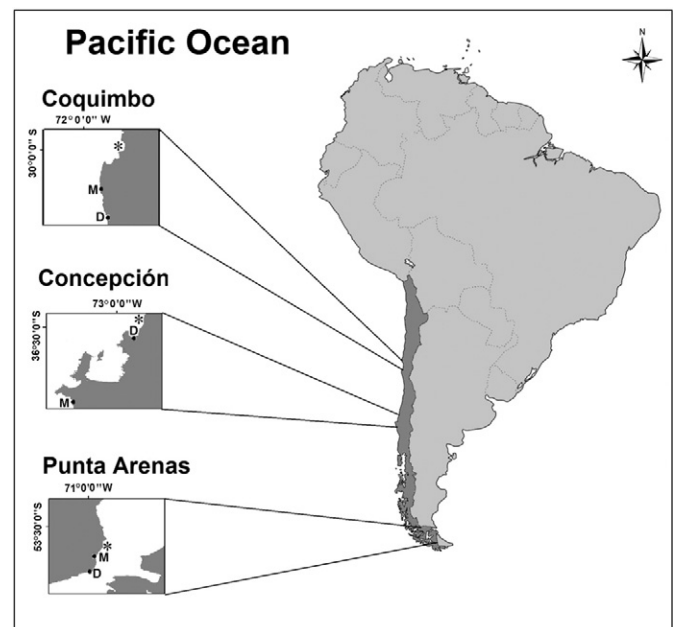

Fig. 1. Map of Chile with the three study sites. Experimental sites (asterisk), and *Macrocystis* (M) and *Durvillaea* (D) source population for Coquimbo, Concepción and Punta Arenas.

(Onset Computer Corporation, Bourne, MA, USA). Each logger was attached 0.5 m below the sea surface in a horizontal position on the experimental line. Using all records from one day, the average daily water temperature was calculated for each day of the experiment.

As day length (daily hours of light) varies with the latitude and season, the logger records between 09:00 and 17:00 were considered every day to calculate the mean daily light intensity per site. Considering latitudinal variations in the hours of light (photoperiod), the daily light length was obtained from the database in www.shoa.cl (Hydrographic and Oceanographic Service of the Chilean Navy). The photoperiod was calculated between the hours of sunrise and sunset for each experimental day.

Additionally, concentrations of seawater nutrients were determined during the field experiments. Specifically, concentrations (mg/L) of nitrites (NO_2^-), nitrates (NO_3^-), ammonium (NH_4^+), and phosphates (PO_4^-) were measured from seawater samples (n = 5) collected around the experimental floating kelps. Samples were taken in 500 mL plastic flasks, fixed with approximately 3 drops of chloroform, and then frozen until analysis by spectrophotometric methods as described in Strickland and Parsons (1972).

2.3. Collection of benthic kelps for floating experiments.

At each experimental site, benthic populations were selected to provide the individuals for the experiments; the same source populations were used in both seasons. Entire individuals (n = 24 for season) of giant kelp *M. pyrifera* and bull kelp *D. antarctica* were detached with their holdfasts at low tide from the benthic populations near the three experimental sites: Coquimbo (*D. antarctica*: Puerto Oscuro 31°25′S, 71°36′W; *M. pyrifera*: Punta de Talca 30°50′S, 71°41′W), Concepción (*D. antarctica*: Burca 36°28′S, 72°54′W; *M. pyrifera*: Desembocadura Río Bio-Bio 36°48′S, 73°10′W), and Punta Arenas (*D. antarctica*: San Isidro Lighthouse 53°47′S, 70°58′W; *M. pyrifera*: Fuerte Bulnes 53°37′S, 70°55′W) (Fig. 1). After collection, kelps were kept in a cooler at ambient temperature and immediately transferred to running seawater tanks in the laboratories where they were prepared for the experiments during the following day.

Considering that both species grow in the low intertidal zone of exposed habitats, kelp collections depended on weather conditions and accessibility at each source population, sometimes limiting the possibility of selecting kelps of similar sizes for experiments at the different sites. Although sizes of the experimental kelps varied seasonally or latitudinally (Table S1), all collected individuals were adult with fully developed floating and reproductive tissues. Benthic *M. pyrifera* differed significantly in total length with site and season and only seasonally in wet weight (Tables S1, S2); large individuals were obtained in Punta Arenas for winter, but in summer the weights were lower and similar between sites (Table S1). The individuals of *D. antarctica* differed significantly in length and weight at both sites and seasons (Table S3); experimental kelps were larger during winter, especially in Concepción (Tables S1, S3), and the bull kelps from Punta Arenas were shorter than those from the other two sites (Table S1). Despite these differences, the size distributions showed extensive overlap among sampling seasons and sites, leading to the assumption that size/age had a negligible effect on the evaluated responses.

2.4. Experimental design for each site.

Identical experimental set-ups were used at the three experimental sites to simulate kelp floating for 14 days. Before being used in the experiments, all individuals were thoroughly rinsed to remove epiphytes and fauna. The 24 kelps for each site and season were randomly assigned to the 3 different treatments (initial, 7-day floating kelps, and 14-day floating kelps). The 16 floating kelps were immediately tethered on a surface long-line system with buoys 1–3 m distance between them. At the same time the eight initial individuals were processed to determine the initial morphological, reproductive and physiological

conditions of the kelps at the moment of detachment (day 0). The tethered individuals were then sampled at days 7 and 14 of the experiment to determine their performance using the same procedures at the three experimental sites.

2.5. Sampling and response variables of benthic and floating kelps.

Morphological, reproductive and physiological responses of initial and floating kelps were measured. At days 7 and 14, the 8 floating, experimental kelps were removed from the long-line systems and transported in a cooler to the respective nearby laboratory for further processing. For the physiological variables, tissue samples were taken with a cork borer from the blades of the main stipe of each replicate individual; all samples were gently cleaned from epibionts with soft paper towels and seawater. Taking into account the differences in morphology and growth patterns between the two kelp species, tissue samples were obtained from photosynthetic active portions in order to evaluate the physiological changes during floating conditions. As previously mentioned (see point 2.3), adults with fully developed floating and reproductive tissues were chosen for the experiments in order to standardize kelp status between species. The tissue samples for *D. antarctica* were obtained from the middle of the largest blade (see e.g. Tala et al., 2013), while in *M. pyrifera* three vegetative blades from the upper part of the sporophyte were used (see e.g. Rothäusler et al., 2011b, 2011c). Although differences in morphology and tissue structure might affect physiological comparisons between different kelp species, previous studies had shown that small pieces of photosynthetically active tissues are suitable to determine physiological responses to environmental change, thus allowing for interspecific comparisons despite morpho-functional differences (e.g. Bischof et al., 1998; Connan et al., 2004; Rothäusler et al., 2011c; Gómez and Huovinen, 2011; Cruces et al., 2012).

Blade samples for *in vivo* chlorophyll *a* fluorescence of photosystem II (*PS*II) were processed immediately in the laboratory. Samples for pigments, soluble phlorotannins and antioxidant capacity were frozen in liquid nitrogen, stored at −80 °C, and then sent on dry ice to the central analysis laboratory at Universidad Católica del Norte in Coquimbo. All analyses were done in similar ways as in previous studies with floating *Macrocystis* (Rothäusler et al., 2011a, 2011c) and *Durvillaea* (Graiff et al., 2013; Tala et al., 2013) and are briefly described below.

2.5.1. Biomass change

Total wet weight of all experimental kelps was measured at day 0 and on the respective days of measurement (7 d and 14 d). Biomass change (BC) was calculated with the equation BC = (FW − IW) / T, where FW and IW are the final and initial wet weight of the individuals at the respective sampling days, and T the time period between each sampling day. Changes in algal biomass were expressed as "percent biomass change per day".

2.5.2. Reproductive stage

The percentage of reproductive individuals was calculated considering the presence of reproductive tissue in accordance with the life history of each species. In *M. pyrifera* reproductive sporophytes were identified by the presence of sporophylls with visible sori (Buschmann et al., 2004). For *Durvillaea antarctica* thin sections of the blade tissue were made and the maturity stages of a total of 30 conceptacles were examined for each individual (following the description in Collantes et al., 2002): individuals that had a majority of conceptacles with fully developed gametes with sex differentiation and open ostioles were classified as mature individual. In both species, the results were expressed as percentage of reproductive/mature individuals with respect to the total number of individuals at each sampling date.

2.5.3. Chlorophyll a fluorescence

Maximal quantum yield of photosystem II (F_v/F_m) was determined via *in vivo* chlorophyll *a* fluorescence with a portable pulse modulation fluorometer. To determine the maximal quantum yield of fluorescence (F_v/F_m), three blade sections from each individual were incubated for 20 min in the dark and measured six times (each section was measured twice). Mean values from the three blade sections value represented the average response for each individual. Due to logistic limitations and simultaneous experiments, different PAM models were used at each site (Coquimbo: PAM 2500; Concepción: MINI-PAM; Punta Arenas: DIVING-PAM; all from Walz, Effeltrich, Germany). Therefore, the F_v/F_m was expressed as relative to the mean of the initial value (day 0) for each experimental situation. Considering the different technical characteristics of the equipments used (Figueroa et al., 2013), this transformation allowed better comparability between experimental localities and seasons.

2.5.4. Pigments

Three blade disks (n = 3) per individual were used for pigment determination and the mean value represented the average response for each individual. The determination of pigments was based on an extraction with *N,N*-dimethylformamide (DMF) for 24 h at 4 °C in darkness. The extinctions of the extract were measured in a scanning UV–visible spectrophotometer (Rayleigh, model UV-1601, China). The chlorophyll *a* (Chl *a*) concentration (mg/g wet weight) was calculated using the dichromatic equations described by Inskeep and Bloom (1985). Chlorophyll *c* and total carotenoid pigments were also determined in the same extract (data not shown), but considering that these showed a similar pattern of variation as those of Chl *a* they were not included in the statistical analyses.

2.5.5. Phlorotannins

The total soluble phlorotannin concentration was determined with the Folin-Ciocalteu assay (Koivikko, 2008). Lyophilized samples (~10 mg) were homogenized with 3 mL of 70% acetone and stirred for 24 h at 4 °C. Subsequently, separation of the supernatant was performed by centrifugation (BOECO, U-320R, Germany) at 4,500 rpm for 15 min. Then, 3 mL of 70% acetone were added to the sample, and again allowed to stir for 24 h at 4 °C, completing three successive extractions. From each supernatant 250 μL was mixed with 1,250 μL of distilled water, 500 μL of 1N Folin-Ciocalteu and 1000 μL of 20% Na_2CO_3. The sample was incubated in the dark for 45 min and centrifuged for 3 min at 4,500 rpm. The absorbance was obtained at 730 nm and purified phloroglucinol (Merck) was used as standard. The concentrations of soluble phlorotannins were obtained from the sum of the three extractions and expressed in mg phlorotannins/g dry weight.

2.5.6. Antioxidant capacity

The antioxidant capacity was tested by the 2,2-diphenyl-1-picrylhydrazyl (DPPH) radical scavenging capacity (Brand-Williams et al., 1995). The frozen samples were ground in a mortar with liquid nitrogen (~240 mg wet weight) and extracted with 1 mL 70% ethanol at 50 °C for 60 min (homogenized every 15 min). Then, 700 μL DPPH (50 mg L^{-1} 70% methanol) were mixed with 300 μL of seaweed extract, and the decay of absorbance was measured at 0 and 30 min at 523 nm. Consumption of DPPH was calculated as a percentage of antioxidant capacity from $[1 - (A_m / A_0)] \times 100$, where A_m represents the absorbance of seaweed extract in solution after reaction with DPPH (at final time), and A_0 is the initial absorbance at time 0 (Molyneux, 2004).

2.6. Statistical analyses.

The initial length and wet weight of both kelp species used in the experiments were analyzed with two-way ANOVAs to compare the size of floating seaweeds between Site (Coquimbo, Concepción, Pta. Arenas) and Season (winter and summer). Length and weight data were log-transformed before being analyzed to comply with requirements of normality and homoscedasticity. A post hoc Tukey's honest significant difference test was applied when significant effects were found.

A three-way ANOVA was used to evaluate the effects of Site (Coquimbo, Concepción, Pta. Arenas), Season (winter and summer), and Floating time (days 7 and 14) on biomass change. The factors were considered as fixed and a post-hoc Tukey HSD was applied when ANOVAs showed significant differences. For the analyses, the constant 10 was added to each value of percent biomass change to make them positive and non-negative to allow the arcsine transformation (McDonald, 2014). Homogeneity of variance was tested using Levene's test. As data transformation did not remove heteroscedasticity, a more conservative $\alpha = 0.01$ was considered (Underwood, 1997).

A Multivariate Analysis of Variance (MANOVA) was applied to determine how site (latitude), season and floating time affected reproductive stage and physiological responses of floating kelps in comparison to the initial status. Site (Coquimbo, Concepción, Pta. Arenas), Season (winter and summer), and Floating time (days 0, 7 and 14) were considered as fixed factors while the outcome were the reproductive and physiological responses of the floating seaweeds. The multinormality of the response variables was significant (Henze–Zirkler test, P = 0.04), indicating some deviation from the MANOVA assumption of multivariate normality. Using the Mahalanobis distance, no outliers were observed. Also, the probability associated with the multivariate test was lower than 0.01, as recommended by Underwood (1997) when assumptions were not fulfilled. In general, the multivariate tests are sufficiently robust to sustain some violation of the assumptions (Quinn and Keough, 2002). In this sense, minor deviations from the assumption for MANOVA should not affect the outcome of the analyses. All analyses were conducted with the free software R (R Development Core Team 2013).

3. Results

3.1. Environmental conditions during the study

Clear latitudinal and seasonal differences in local seawater temperatures were observed during the experiments, with lowest mean values in winter and at high latitudes and then increasing in summer and towards lower latitudes (Table 1A). Light levels were highly variable (Table 1B), sometimes in unexpected directions, which might be caused by continuous movements of sensors in the experimental systems due to wave action. Day length was similar between the three sites in winter, whereas the values increased with latitude during summer (Table 1C).

During the experiments, the essential nutrients (N and P) were present in the experimental area but concentrations were variable and depended on site, season and nutrient types (Table 1D). The most notorious pattern was a higher concentration of nitrate during winter for the three experimental sites with a tendency of higher values for Concepción (Table 1D). In general, lower nutrient concentrations were observed in Punta Arenas for both seasons (Table 1D).

3.2. Performance characteristics

Species-specific responses were observed in biomass change with significant effects of site, season and floating time for *M. pyrifera* and only for site and the interaction site × season in *D. antarctica* (Table 2).

The statistical results showed that reproductive stage and physiological responses of floating kelps during the experimental time (7–14 days) were influenced by different factors (Tables S4–S5). In *M. pyrifera*, significant effects on the response variables were detected for all single factors and the interactions between site (latitude) and season (MANOVA, P < 0.001; Table S4), while in *D. antarctica* significant effects were caused by the single factors site in all variables, and in the other

Table 1
Average (± SD) of daily seawater temperature (A); daily light intensity (B); daily hours of light, and nutrient concentrations (D) (nitrate, nitrite, phosphate and ammonium) for each experimental site during the seasons (winter and summer).

	Coquimbo		Concepción		Punta Arenas	
	Winter	Summer	Winter	Summer	Winter	Summer
	31 Jul–16 Aug	29 Jan–14 Feb	11–27 Jul	07–22 Dec	23 Aug–07 Sept	07–23 Jan
(A) Temperature (°C)						
Mean ± SD	13.6 ± 0.5	19.2 ± 1.1	11.6 ± 0.4	16.9 ± 1.5	6.1 ± 1.2	9.3 ± 1.1
(Min-Max)	(13–15)	(15–20)	(11–14)	(12–19)	(2 − 10)	(8–16)
(B) Light (Klux)	26.7 ± 8.9	16.8 ± 9.1	34.5 ± 13.3	62.3 ± 22.4	29.5 ± 8.6	31.8 ± 21.9
(C) Photoperiod (light h:min)	10:53	13:19	10:00	14:38	10:40	16:19
(D) Nutrients (mg/L)						
NO_3 (Mean ± SD)	8.47 ± 1.27	2.25 ± 0.64	11.13 ± 1.86	5.69 ± 1.06	9.03 ± 0.86	2.89 ± 0.60
NO_2 (Mean ± SD)	0.24 ± 0.02	0.03 ± 0.01	0.13 ± 0.05	0.39 ± 0.22	0.06 ± 0.02	0.07 ± 0.01
PO_4 (mean ± SD)	1.63 ± 0.29	0.44 ± 0.03	1.02 ± 0.83	1.02 ± 0.12	0.80 ± 0.09	0.32 ± 0.06
NH_4 (mean ± SD)	0.62 ± 0.43	0.14 ± 0.13	0.21 ± 0.13	1.38 ± 1.27	0.16 ± 0.10	0.14 ± 0.03

factors and interactions depending on the variable (MANOVA, $P < 0.001$; Table S5).

3.2.1. Biomass change

A loss of biomass was observed in floating sporophytes of *M. pyrifera* during winter at all three experimental sites. During summer, continuous biomass loss was also observed in Coquimbo and during the first seven days in Concepción, but giant kelps grew during the second half of the experiment (7–14 days) in Concepción, and throughout the entire experiment in Punta Arenas (Fig. 2). Biomass change was significantly affected by site, season and floating time and the interaction site × season in *M. pyrifera* (Table 2).

In the case of *D. antarctica*, this species continuously grew in Punta Arenas, but lost biomass in Coquimbo and Concepción in winter. During summer, bull kelps only grew in Concepción, but lost biomass at the other two sites (Fig. 2). Significant effects were caused by site and the interaction site × season (Table 2).

When kelps lost biomass, these losses were usually lower during the second half of the experiment (Fig. 2). In general, both species experienced highest losses of biomass in Coquimbo (northern site) during both experimental seasons, being more evident in summer (Fig. 2).

3.2.2. Reproductive status

High percentages of mature individuals of *M. pyrifera* were found during winter in Coquimbo and in both seasons in Concepción. At these localities, floating kelps maintained their reproductive activity (Fig. 3). Surprisingly, no reproductive *M. pyrifera* were observed in Punta Arenas at the beginning of the experiment, but after floating for 14 d some experimental individuals developed reproductive tissues, mainly in winter. A similar situation occurred in Coquimbo during summer (Fig. 3). The reproductive status was significantly affected by site, season and the interaction site × season (Table 3).

A strong seasonal reproductive pattern was detected for *D. antarctica* with highest reproductive activity during winter for initial and

experimental kelps (Fig. 3). In general, the kelps remained reproductive throughout the entire experiment. In winter, the proportion of reproductive individuals increased during the experiments in Coquimbo and Punta Arenas, whereas a decrease was detected in Concepción (Fig. 3). During summer, reproductive activity was very low (none in Coquimbo), and floating, mature kelps were only observed in Concepción (Fig. 3). The statistical analysis showed significant effects on the reproductive activity of *D. antarctica* for site, season and the interaction season × floating time (Table 4).

3.2.3. Chlorophyll a fluorescence (F_v/F_m)

Maximum quantum yield (F_v/F_m) in *M. pyrifera* and *D. antarctica* was significantly affected by site, season, floating time and most interactions, depending on the species (Tables 3, 4). In general, initial values of F_v/F_m were lower during summer at all localities (see numbers in Fig. 4). During winter, floating individuals of *M. pyrifera* in Coquimbo and Pta. Arenas maintained high F_v/F_m values throughout the experiment, while they decreased in Concepción. In summer, an opposite pattern was observed and only floating *M. pyrifera* from Concepción maintained high F_v/F_m levels during the experiment (Fig. 4).

In *D. antarctica* small changes (~10%) of F_v/F_m values occurred during the experiment at all sites in winter. A clear latitudinal tendency

Table 2
Three way ANOVA for biomass change in experimental floating individuals of *Macrocystis pyrifera* and *Durvillaea antarctica*. Bold p-values are significant (<0.01).

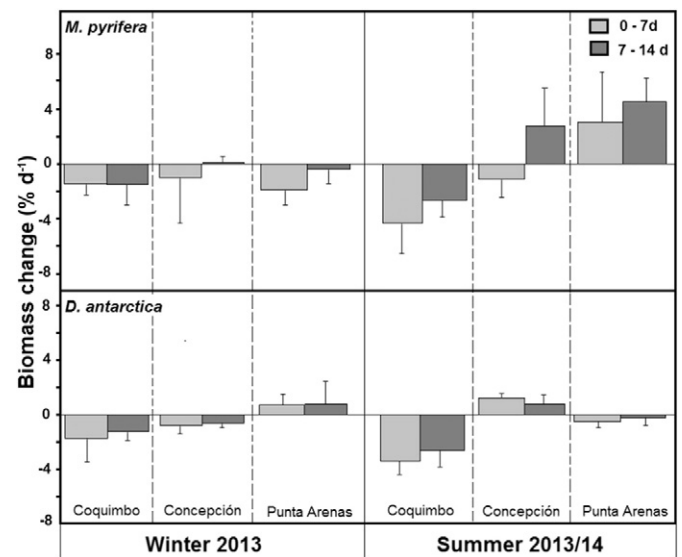|	*M. pyrifera*			*D. antarctica*		
	df	F value	p-Value	df	F value	p-Value
Site A	2	24.959	**<0.001**	2	52.037	**<0.001**
Season B	1	7.199	**0.009**	1	1.9	0.172
Floating day C	1	15.276	**<0.001**	1	1.197	0.277
A × B	2	21.146	**<0.001**	2	18.937	**<0.001**
A × C	2	0.929	0.399	2	1.179	0.313
B × C	1	2.314	0.132	1	0.001	0.970
A × B × C	2	1.05	0.355	2	0.332	0.718
Error	84			84		

Fig. 2. Percent biomass change (d^{-1}) of experimental *Macrocystis pyrifera* and *Durvillaea antarctica* individuals (mean ± SD, n = 8) at each study site for winter 2013 and summer 2013/2014 experiments. The grey bars show the percent biomass change of floating kelps at day 0–7 and dark grey bars at the day 7–14.
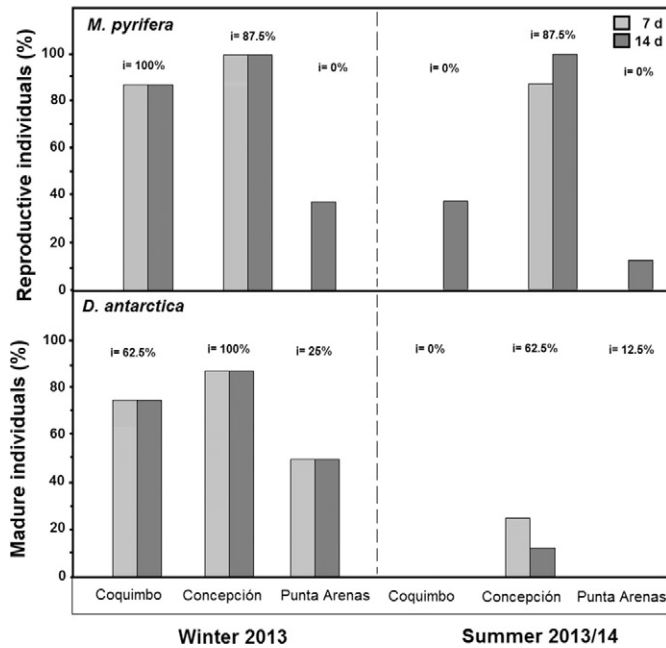
Fig. 3. Percentage of reproductive individuals of *M. pyrifera* (n = 8) and percentage of mature individuals of *D. antarctica* (n = 8) at each study site during winter 2013 and summer 2013/14. Data above bars indicate the mean values at day 0 (initial), the grey bars show the values of floating kelps at day 7 and dark grey bars at the day 14.

was observed during summer, with a notorious decrease of F_v/F_m values at the low latitude site (Coquimbo) followed by Concepción, and minor variation at high latitudes (Pta. Arenas) (Fig. 4).

3.2.4. Chlorophyll a

In both species the variation in the chlorophyll concentration during floating conditions depended on site and season (Fig. 5). The initial concentration of Chl *a* in *M. pyrifera* showed lowest values at the high latitude site (Pta. Arenas) during winter. There was a significant effect of

Table 3
Summary of MANOVA for benthic and experimental floating *Macrocystis pyrifera*. Factors were Site (Coquimbo, Concepción and Punta Arenas), Season (winter and summer) and Floating time (7 and 14 days). Results of the univariate test are given for the response variables in which significant effects of the factors were identified. See text for details. (Full MANOVA is given in the online supplements, Table S4).

Factors	Response variables	P
Site A	Reproductive status	<0.001
	Maximal quantum yield (F_v/F_m)	<0.001
	Chlorophyll *a*	<0.001
	Phlorotannins	<0.001
	Antioxidant capacity	0.006
Season B	Reproductive status	0.005
	Maximal quantum yield (F_v/F_m)	<0.001
	Chlorophyll *a*	<0.001
	Phlorotannins	<0.001
	Antioxidant capacity	<0.001
Floating time C	Maximal quantum yield (F_v/F_m)	<0.001
	Phlorotannins	<0.001
A × B	Reproductive status	<0.001
	Maximal quantum yield (F_v/F_m)	0.003
	Chlorophyll *a*	<0.001
	Phlorotannins	<0.001
A × C	Phlorotannins	<0.001
B × C	Maximal quantum yield (F_v/F_m)	<0.001
	Chlorophyll *a*	<0.001
	Phlorotannins	<0.001
A × B × C	Maximal quantum yield (F_v/F_m)	<0.001
	Chlorophyll *a*	0.005
	Phlorotannins	<0.001

Table 4
Summary of MANOVA for benthic and experimental floating *Durvillaea antarctica*. Factors were Site (Coquimbo, Concepción and Punta Arenas), Season (winter and summer) and Floating time (7 and 14 days). Results of the univariate test are given for the response variables in which significant effects of the factors were identified. See text for details. (Full MANOVA is given in the online supplements, Table S5).

Factors	Response variables	P
Site A	Reproductive status	<0.001
	Maximal quantum yield (F_v/F_m)	<0.001
	Chlorophyll *a*	<0.001
	Phlorotannins	<0.001
	Antioxidant capacity	<0.001
Season B	Reproductive status	<0.001
	Maximal quantum yield (F_v/F_m)	<0.001
	Chlorophyll *a*	<0.001
Floating time C	Maximal quantum yield (F_v/F_m)	<0.001
	Chlorophyll *a*	<0.001
A × B	Maximal quantum yield (F_v/F_m)	<0.001
	Phlorotannins	<0.001
	Antioxidant capacity	<0.001
A × C	Maximal quantum yield (F_v/F_m)	<0.001
	Chlorophyll *a*	<0.001
	Phlorotannins	<0.001
B × C	Reproductive status	<0.001
	Chlorophyll *a*	<0.001
	Phlorotannins	<0.001
A × B × C	Maximal quantum yield (F_v/F_m)	<0.001
	Chlorophyll *a*	0.005
	Phlorotannins	<0.001

site, season and some of the interactions in this species (Table 3). In summer, higher concentrations of chlorophyll *a* were detected at the mid latitude site (Concepción) for both benthic and floating kelps (Fig. 5). During this season, a decrease in concentrations was detected with the floating time mainly at the low latitude site (Coquimbo). Although floating *M. pyrifera* showed minor adjustments in Chl *a* concentrations during the experiment, important changes were observed in Pta. Arenas, with an increase during winter and a decrease during summer (Fig. 5).
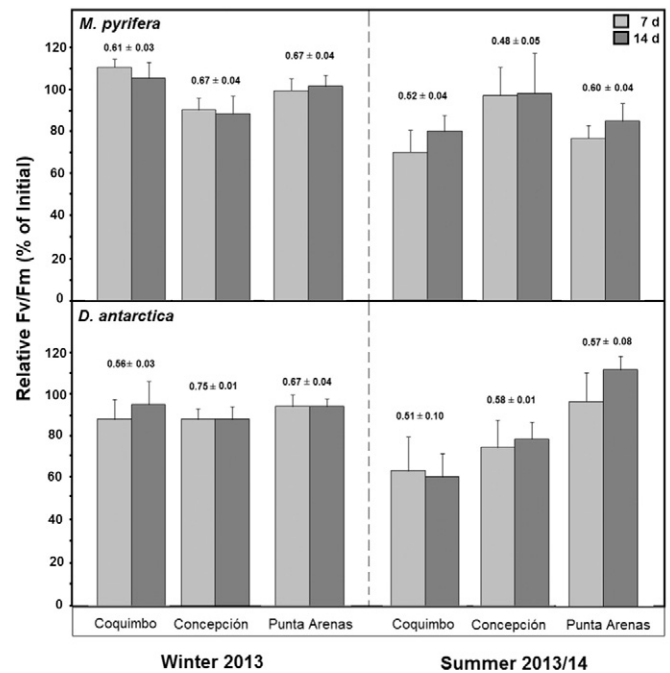

Fig. 4. Maximal quantum yield (F_v/F_m) variation expressed in percentage with respect to the initial value (day 0) from *Macrocystis pyrifera* and *Durvillaea antarctica* at each study site for winter 2013 and summer 2013/2014. Initial values (I) for each locality (mean ± SD) are given above the bars.
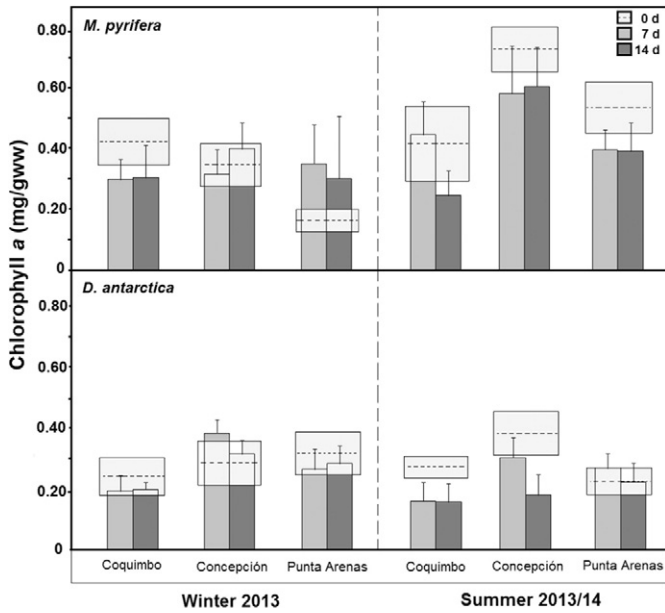
Fig. 5. Pigment concentrations of Chlorophyll *a* in *Macrocystis pyrifera* and *Durvillaea antarctica* at each study site during winter 2013 and summer 2013/2014 for initial (0 d) and floating kelps (7 d, 14 d). Figure shows grand means ± SD; grey bars show the values of floating kelps at day 7 and dark grey bars at day 14. Boxes indicate the values at day 0 (initial) with the broken line showing the mean and the upper and lower edge of the box the SD.

Minor variations in chlorophyll *a* were observed for *D. antarctica* in winter, with a tendency of high values at mid and high latitudes (Fig. 5). The values decreased during floating time especially in summer and at low-mid latitudes (Fig. 5). Minor changes were observed in Pta. Arenas during the experiment in comparison with the initial values (Fig. 5). The factors site, season, floating time and some interactions had a significant effect on the pigment levels of *D. antarctica* (Table 4).

3.2.5. Soluble phlorotannins

Phlorotannin concentrations of *M. pyrifera* were significantly affected by all factors and their interactions (Table 3). Minor changes in winter and an increase during summer was observed for phlorotannin
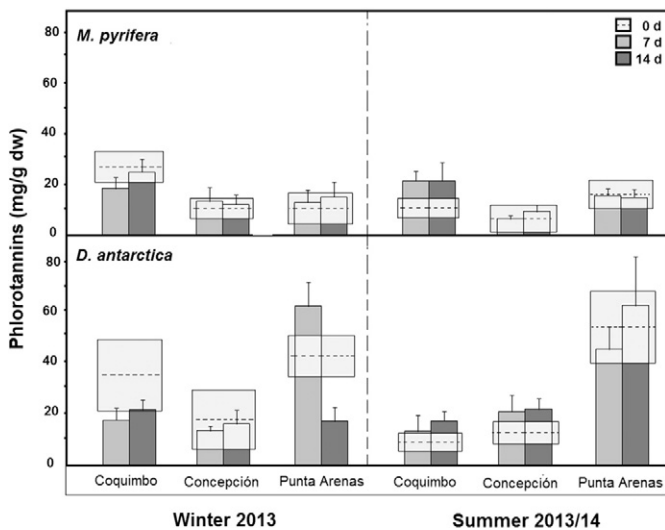

Fig. 6. Soluble phlorotannin concentrations in *Macrocystis pyrifera* and *Durvillaea antarctica* in each site during winter 2013 and summer 2013/2014. Figure shows grand means ± SD; grey bars show the values of floating kelps at day 7 and dark grey bars at day 14. Boxes indicate the values at day 0 (initial) with the broken line showing the mean and the upper and lower edge of the box the SD.
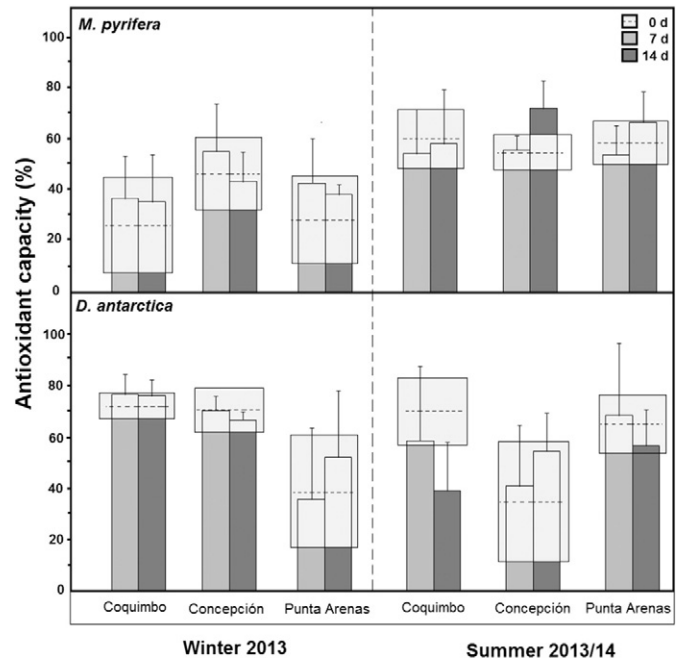
levels at the low latitude site (Coquimbo). Concentrations were consistently low at the mid latitude site in summer (Fig. 6).

In *D. antarctica* the phlorotannin concentrations varied significantly during the experiment at the high latitude site (Pta. Arenas), with only minor variations at the other two sites (Fig. 6). Statistical results showed significant effects on the phlorotannin concentrations caused by site and all the interactions (Table 4). In winter, phlorotannin concentrations decreased during the experiment in Coquimbo and Concepción, with a slight increase at day 14. In summer, initially low concentrations at these two sites increased during the experiment (Fig. 6). In the winter experiment the floating kelps from Pta. Arenas had high phlorotannin concentrations at day 7 but then decreased again, while an opposing pattern was observed during summer (Fig. 6).

3.2.6. Antioxidant capacity

In *M. pyrifera* antioxidant capacity was significantly affected by site and season (Table 3). Lower antioxidant capacity was detected in winter than in summer for all localities (Fig. 7). In winter antioxidant capacity of the floating kelps at all three sites was within the initial ranges, with high values in Concepción (Fig. 7). In summer antioxidant capacity showed an increase with floating time, which was more notorious in Concepción and Pta. Arenas (Fig. 7).

Antioxidant capacity of *D. antarctica* was significantly influenced only by site and the interaction site × season (Table 4), with a decrease during the winter from the northernmost location (Coquimbo) to the south (Punta Arenas) in both initial and floating conditions (Fig. 7). A different pattern of antioxidant capacity was observed in summer for each site (Fig. 7). In Coquimbo, antioxidant capacity of floating bull kelps decreased during the summer experiment. In Concepción initial values were low but increased during the experiment. Antioxidant capacity in Pta. Arenas was comparatively high and showed only minor variations during the summer experiment (Fig. 7).

3.2.7. Overall results

The performance of the floating *M. pyrifera* and *D. antarctica* were significantly affected by the factor site representing latitudinal changes
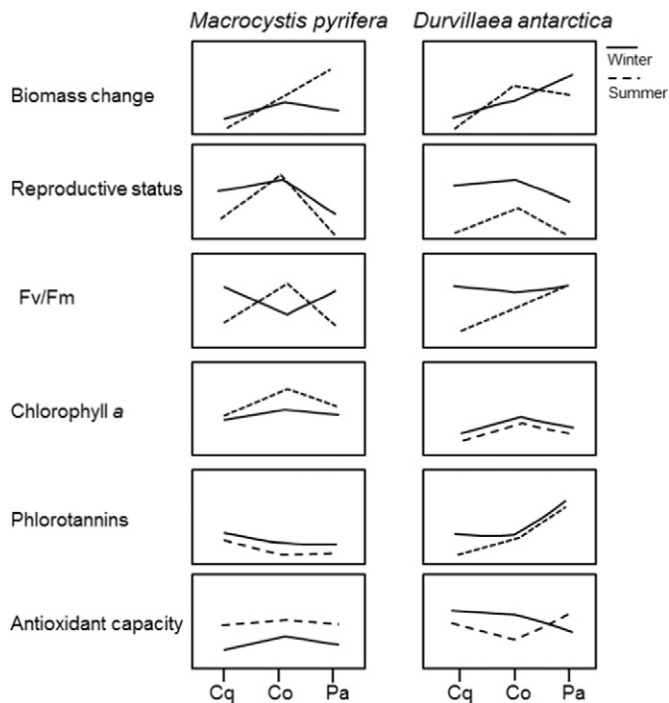

Fig. 7. Antioxidant capacity in *Macrocystis pyrifera* and *Durvillaea antarctica* in each site during winter 2013 and summer 2013/2014. Figure shows grand means ± SD; grey bars show the values of floating kelps at day 7 and dark grey bars at day 14. Boxes indicate the values at day 0 (initial) with the broken line showing the mean and the upper and lower edge of the box the SD.

Fig. 8. Summary of main change tendencies on studied responses of floating *Macrocystis pyrifera* and *Durvillaea antarctica* with the factors Site (Latitude; Cq: Coquimbo; Co: Concepción; Pa: Punta Arenas) and Season.

in all variables studied (Fig. 8). The most notorious effect was the biomass loss observed in both species at low latitudes (Coquimbo), regardless of the season. Species-specific responses according to the season were detected at mid and high latitudes (Concepción and Pta. Arenas) in biomass change, reproduction status and physiological traits. Summer conditions at mid and high latitudes did not negatively affect *M. pyrifera*, with higher values of biomass changes, chlorophyll *a* and antioxidant capacity. In *D. antarctica*, lower reproductive status and photosynthetic characteristics were detected in summer. The significant interaction between site and seasons for almost all variables mirror the importance of latitude on the performance of floating kelps during the experimental time (Tables 2–4).

4. Discussion

The results indicate that *M. pyrifera* and *D. antarctica* have the capacity to acclimate to the floating conditions within a few days, with differences depending on site (latitude) and season. Physiological adjustment at the sea surface was clearly detected at day 7 and it remained until the end of the experimental time (14 days) mainly at mid (Concepción) and high (Punta Arenas) latitudes. The biomass losses at the low latitude site (Coquimbo) in both species and seasons indicate that despite rapid physiological acclimation this response is insufficient to support growth and long-term persistence of floating kelps. At mid and high latitudes, the two species showed different responses depending on the season. Summer conditions can be favorable to floating kelps especially to *M. pyrifera* at high latitudes and for both species at mid latitudes. Characteristics associated with local environmental conditions (site × season) and the biology of these brown seaweeds are likely responsible for these patterns.

4.1. Seasonal effects on floating kelps

Light intensity is the principal factor that promotes seasonal acclimation with changes in growth, photosynthetic efficiency, pigments and other metabolites (Powles, 1984; Falkowski and LaRoche, 1991;

Huovinen et al., 2006; Hurd et al., 2014). Temperature influences metabolic and growth rates, following similar seasonal patterns as light, but local conditions (coastal currents, upwelling zones, cloud cover, and coastal topography) can obscure large-scale patterns (Ramos-Rodríguez et al., 2012; Bearham et al., 2013; Tapia et al., 2014). Deleterious combinations of high light and temperature at the sea surface affect the tissue integrity causing biomass losses at low latitudes (Coquimbo), regardless of the season. Similar results have been described for *in situ* (Graiff et al., 2013) and mesocosm experiments (Rothäusler et al., 2009, 2011c) with *D. antarctica* and *M. pyrifera*, respectively.

Biomass gains during summer in both kelp species at mid latitudes (Concepción) and for *M. pyrifera* at high latitudes (Pta. Arenas) indicate favorable conditions for the persistence of floating kelps. Highest growth rates in the kelp *Ecklonia radiata* have been reported under high light intensities and low temperatures, which contrasted with lowest growth at high temperatures (Bearham et al., 2013). During summer at mid latitudes the combination of high radiation and moderate temperatures could be favoring growth of both floating kelps. At high latitudes the growth capacity (accompanied by high chlorophyll content and antioxidant activity) of *M. pyrifera* is favored by high light levels in summer, but these high growth rates apparently cannot be maintained in low light conditions (limited energy) combined with low temperatures (slow metabolic rates) during winter, similar as reported for benthic giant kelps from 45°S in New Zealand (Hepburn and Hurd, 2005). On the other hand, *D. antarctica* showed a reverse pattern with positive growth in winter despite the low light and temperature conditions at high latitudes. Growing under lower light conditions in winter might be supported by previously accumulated energy reserves, especially in long-lived (perennial) species (Chapman and Craigie, 1978; Lehvo et al., 2001; Wiencke et al., 2007, 2009). The bull kelp *D. antarctica* appears capable to maintain growth by enhancing the rate of photosynthesis. The photobiological characteristics (low saturation irradiance, high efficiency photosynthesis, dynamic photoinhibition) described for *D. antarctica* are considered adaptations for efficient light use (Gómez and Huovinen, 2011; Cruces et al., 2013), which might be associated to the subantarctic origin of this species.

Seasonal changes in growth are the result of metabolic adjustments and energy distribution in response to environmental conditions, which can also affect the reproductive potential. The ability to maintain reproductive activity during floating conditions is an important trait that can determine the colonization potential after extensive rafting journeys, which is especially important considering the short dispersal distances of kelp spores/gametes (Reed et al., 1988; Collins et al., 2010). The reproductive phenology of *M. pyrifera* has been described as both seasonal (winter/spring or summer/autumn) and non-seasonal (all year around), depending on local conditions (temperature, nutrients and wave exposure) (Reed et al., 1996; Buschmann et al., 2004, 2006). At mid latitudes (Concepción), *M. pyrifera* showed high reproductive activity in both seasons indicating their perennial strategies and high potential for rafting dispersal under moderate environmental conditions. In contrast, *Durvillaea antarctica* showed a strong seasonal (fall-winter) reproductive pattern in benthic (Santelices et al., 1980; Collantes et al., 2002) as well as in floating conditions (Tala et al., 2013; Lizée-Prynne et al., 2016) along the SE Pacific. The consistently seasonal reproductive phenology of *D. antarctica* (Santelices et al., 1980; Collantes et al., 2002; Tala et al., 2013), confirmed herein for all three study sites, suggests that successful gamete dispersal is restricted to the cold season throughout its distributional range.

4.2. Latitudinal effect on species-specific responses

The performance of floating kelps showed latitudinal variations in all studied traits, confirming the strong effect of latitudinal environmental gradients on their acclimation and persistence capacities in floating conditions. The giant kelp *M. pyrifera* has an antitropical distribution in cold-temperate zones (Macaya and Zuccarello, 2010a), and the floating

performance varied latitudinally. Negative effects of high radiation, temperature and grazing, as previously described for floating *M. pyrifera* (Rothäusler et al., 2009, 2011a, 2011c), result in deleterious conditions for floating kelps at low latitudes, especially during summer. At mid (southern-central Chile) and high latitudes (Patagonian fjords) high biomasses of floating *M. pyrifera* have been detected in spring-summer (Hinojosa et al., 2011; Wichmann et al., 2012). This may be partly due to the high growth rates of kelp forests during these seasons (Buschmann et al., 2004, 2006), but it may also be due to biomass gains and longer survival of floating kelps, which appear to thrive during the summer at high latitudes.

The floating bull kelp *D. antarctica* is a cold-temperate species, abundant at mid and high latitudes in the South Pacific and subantarctic regions (Santelices et al., 1980; Collantes et al., 2002; Fraser et al., 2009). Limited floating capacity of *D. antarctica* has been previously described from low latitudes (Graiff et al., 2013; Tala et al., 2013) where negative impacts of high temperature and solar radiation on photosynthesis and activation of photoprotective mechanisms (Cruces et al., 2012, 2013) apparently suppress survival and floating capacity of this kelp. At mid/high latitudes, *D. antarctica* appears well adapted to maintain active growth and efficient photoprotection throughout the year. Higher values of phlorotannin and antioxidant capacity of *D. antarctica* in Pta. Arenas compared to other populations (Cruces et al., 2012; Tala et al., 2013) or other brown seaweeds (Van Alstyne et al., 1999; Connan et al., 2004) may be a response to the longer photoperiod (high dose radiation) during summer at high latitudes. The positive relationship between phlorotannin levels and radiation dose has been described for brown seaweeds (Swanson and Druehl, 2002; Arnold, 2003; Abdala-Díaz et al., 2006; Gómez and Huovinen, 2010; Cruces et al., 2013; Gómez and Huovinen, 2015) as key response to environmental stressors. Thus, while *D. antarctica* showed lower growth rates than *M. pyrifera*, physiological acclimatization to seasonal variations in temperature and solar radiation is sufficient to diminish losses or even show minor growth and in this way achieve effective floating persistence at mid/high latitudes.

4.3. Long-distance dispersal potential of floating kelps

Successful dispersal and colonization of new habitats by floating seaweeds will depend mainly on their capacity to sustain reproduction and physiological acclimation during long voyages. Both floating kelps were able to maintain biomass and reproductive activity at the sea surface for more than 14 days, especially at mid and high latitudes. However, species-specific and seasonally varying responses across the latitudinal gradient produced a non-generalized pattern (Fig. 9). During summer, *Macrocystis pyrifera* showed a high potential for dispersal at mid/high latitudes. This pattern is in accordance with its wide geographic distribution and higher biomass production in benthic populations occurring in spring/summer (Hepburn and Hurd, 2005; Graham et al., 2007), but winter conditions appear to limit the potential for rafting dispersal at high latitudes (Fig. 9). In contrast, at low latitudes ($<30°$S), where benthic population of *M. pyrifera* persist throughout the year (Buschmann et al., 2004; Graham et al., 2007), high radiation levels in combination with high water temperatures severely suppress rafting dispersal of this species in summer (Macaya et al., 2005; Rothäusler et al., 2009). Thus, for *M. pyrifera* the window for successful rafting dispersal appears to shift seasonally across its distributional range (Fig. 9). In contrast, in *D. antarctica*, the potential for rafting dispersal appears to be less dependent on seasonal variations in environmental conditions. At mid/high latitudes there is a high potential for rafting dispersal year-round, but conditions prevailing at low latitudes suppress floating survival of *D. antarctica*, regardless of season (Fig. 9); this coincides with the northern limit of its geographic distribution in the SE Pacific (Fraser et al., 2009). Thus, while the results support the hypothesis of high rafting potential at high latitudes, there is also some indication that the conditions in polar waters might temporarily (winter) be unfavorable for some floating seaweeds (e.g. *M. pyrifera*).

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.jembe.2016.06.003.

References

Abdala-Díaz, R.T., Cabello-Pisini, A., Pérez-Rodríguez, E., Conde Alvarez, R.M., Figueroa, F.L., 2006. Daily and seasonal variations of optimum quantum yield and phenolic compounds in *Cystoseira tamariscifolia* (Phaeophyta). Mar. Biol. 148, 459–465.

Arnold, T.M., 2003. To grow and defend: Lack of tradeoffs for brown algal phlorotannins. Oikos 100, 406–408.

Bearham, D., Vanderklift, M.A., Gunson, J.R., 2013. Temperature and light explain spatial variation in growth and productivity of the kelp *Ecklonia radiata*. Mar. Ecol. Prog. Ser. 476, 59–70.

Bischof, K., Hanelt, D., Tüg, H., Karsten, U., Brouwer, P.E.M., Wiencke, C., 1998. Acclimation of brown algal photosynthesis to ultraviolet radiation in Arctic coastal waters (Spitsbergen, Norway). Polar Biol. 20, 388–395.

Brand-Williams, W., Cuvelier, M., Berset, C., 1995. Use of a free radical method to evaluate antioxidant activity. Food Sci. Biotechnol. 28, 25–30.

Buschmann, A.H., Moreno, C., Vásquez, J.A., Hernández-González, M.C., 2006. Reproduction strategies of *Macrocystis pyrifera* (Phaeophyta) in Southern Chile: the importance of population dynamics. J. Appl. Phycol. 18, 575–582.

Buschmann, A.H., Vasquez, J.A., Osorio, P., Reyes, E., Filun, L., Hernandez-Gonzalez, M.C., Vega, A., 2004. The effect of water movement, temperature and salinity on abundance and reproductive patterns of *Macrocystis* spp. (Phaeophyta) at different latitudes in Chile. Mar. Biol. 145, 849–862.

Cabrera, S., Bozzo, S., Fuenzalida, H., 1995. Variations in UV-radiation in Chile. J. Photochem. Photobiol. B. 28, 137–142.

Chapman, A.R.O., Craigie, J.S., 1978. Seasonal growth in *Laminaria longicruris*: relations with reserve carbohydrate storage and production. Mar. Biol. 46, 209–213.

Collantes, G., Merino, A., Lagos, V., 2002. Fenología de la gametogénesis, madurez de conceptáculos, fertilidad y embriogénesis en *Durvillaea antarctica* (Chamizo) Hariot (Phaeophyta, Durvillaeales). Rev. Biol. Mar. Oceanogr. 37, 83–112.

Collins, C.J., Fraser, C., Ashcroft, A., Waters, J.M., 2010. Asymmetric dispersal of southern bull-kelp (*Durvillaea antarctica*) adults in coastal New Zealand: testing an oceanographic hypothesis. Mol. Ecol. 19, 4572–4580.
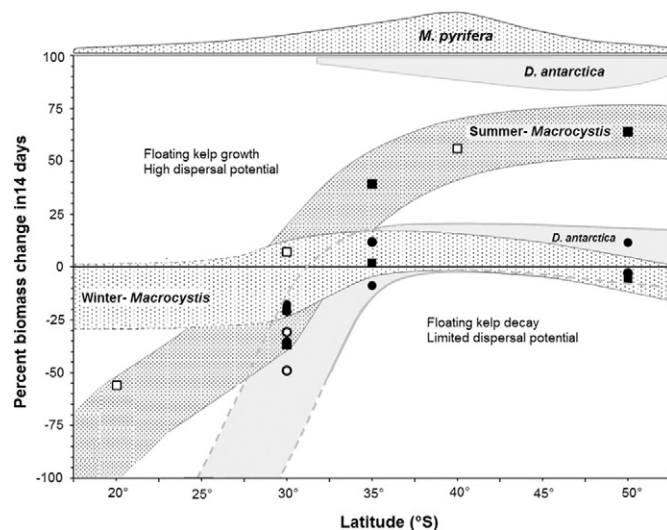

Fig. 9. Influence of the combined effects of latitudinal and seasonal on biomass change of floating kelps during 14 days. Filled symbols were taken from the present study; open symbols from Rothäusler et al. (2009, 2011b) for *M. pyrifera* and from Graiff et al. (2013) for *D. antarctica*. The geographic range of each species in the Chilean Southeast Pacific coast is shown at the top of the graph.

Connan, S., Goulard, F., Stiger, V., Deslandes, E., Ar, G.E., 2004. Interspecific and temporal variation in phlorotannin levels in an assemblage of brown algae. Bot. Mar. 47, 410–416.

Coyer, J.A., Hoarau, G., Costa, J.F., Hogerdijk, B., Serrao, E.A., Billard, E., Valero, M., Pearson, G.A., Olsen, J.L., 2011. Evolution and diversification within the intertidal brown macroalgae *Fucus spiralis/F. vesiculosus* species complex in the North Atlantic. Mol. Phylogenet. Evol. 58, 283–296.

Cruces, E., Huovinen, P., Gómez, I., 2012. Phlorotannin and antioxidant responses upon short-term exposure to UV radiation and elevated temperature in three south pacific kelps. Photochem. Photobiol. 88, 58–66.

Cruces, E., Huovinen, P., Gómez, I., 2013. Interactive effects of UV radiation and enhanced temperature on photosynthesis, phlorotannin induction and antioxidant activities of two sub-Antarctic bronw algae. Mar. Biol. 160, 1–13.

Cumming, R.A., Nikula, R., Spencer, H.G., Waters, J.M., 2014. Transoceanic genetic similarities of kelp-associated sea slug populations: long-distance dispersal via rafting? J. Biogeogr. 41, 2357–2370.

Edgar, G.J., 1987. Dispersal of faunal and floral propagules associated with drifting *Macrocystis pyrifera* plants. Mar. Biol. 95, 599–610.

Falkowski, P.G., LaRoche, J., 1991. Acclimation to spectral irradiance in algae. J Phycol 27, 8–14.

Figueroa, F.L., Jerez, C.G., Korbee, N., 2013. Use of in vivo chlorophyll fluorescence to estimate photosynthetic activity and biomass productivity in microalgae grown in different culture systems. Lat. Am. J. Aquat. Res. 41, 801–819.

Fraser, C.I., Nikula, R., Spencer, H.G., Waters, J.M., 2009. Kelp genes reveal effects of subantarctic sea ice during the last glacial maximum. Proc. Natl. Acad. Sci. 106, 3249–3253.

Fraser, C.I., Nikula, R., Waters, J.M., 2011. Oceanic rafting by a coastal community. Proc. Roy. Soc. Lond. Ser. Biol. Sci. 278, 649–655.

Fraser, C.I., Thiel, M., Spencer, H., Waters, J., 2010. Contemporary habitat discontinuity and historic glacial ice drive genetic divergence in Chilean kelp. BMC Evol. Biol. 10, 203–214.

Gómez, I., Huovinen, P., 2010. Induction of phlorotannins during UV exposure mitigates inhibition of photosynthesis and DNA damage in the kelp *Lessonia nigrescens*. Photochem. Photobiol. 86, 1056–1063.

Gómez, I., Huovinen, P., 2011. Morpho-functional patterns and zonation of South Chilean seaweeds: the importance of photosynthetic and bio-optical traits. Mar. Ecol. Prog. Ser. 422, 77–91.

Gómez, I., Huovinen, P., 2015. Lack of physiological depth patterns in conspecifics of endemic Antarctic brown algae: a trade-off between UV stress tolerance and shade adaptation? Plos One 10 (8), e0134440.

Graham, M.G., Vasquez, J., Buschmann, A.H., 2007. Global ecology of the giant kelp *Macrocystis*: from ecotypes to ecosystems. Oceanogr. Mar. Biol. Annu. Rev. 45, 39–88.

Graiff, A., Karsten, U., Meyer, S., Pfender, D., Tala, F., Thiel, M., 2013. Seasonal variation in floating persistence of detached *Durvillaea antarctica* (Chamisso) Hariot thalli. Botanica Marina 56, 3–14.

Gutow, L., Long, J.D., Cerda, O., Hinojosa, I., Rothäusler, E., Tala, F., Thiel, M., 2012. Herbivosous amphipods inhabit protective microhabitats within thalli of giant kelp *Macrocystis pyrifera*. Mar. Biol. 159, 141–149.

Hepburn, C.D., Hurd, C.L., 2005. Conditional mutualism between the giant kelp *Macrocystis pyrifera* and colonial epifauna. Mar. Ecol. Prog. Ser. 302, 37–48.

Hernández-Carmona, G., Hughes, B., Graham, M., 2006. Reproductive longevity of drifting kelp *Macrocystis pyrifera* (Phaeophyceae) in Monterey Bay, USA. J. Phycol. 42, 1199–1207.

Hinojosa, I.A., Pizarro, M., Ramos, M., Thiel, M., 2010. Spatial and temporal distribution of floating kelp in the channels and fjords of southern Chile. Estuar. Coast. Shelf Sci. 87, 367–377.

Hinojosa, I.A., Rivadeneira, M., Thiel, M., 2011. Temporal and spatial distribution of floating objects in coastal waters of central-southern Chile and Patagonian fjords. Cont. Shelf Res. 31, 172–186.

Hobday, A.J., 2000. Age of drifting *Macrocystis pyrifera* (L.) Agardh rafts in the Southern California Bight. J. Exp. Mar. Biol. Ecol. 253, 97–114.

Huovinen, P., Gómez, I., Lovengreen, C., 2006. A five-year study of solar ultraviolet radiation in southern Chile (39 S): potential impact on physiology of coastal marine algae? Photochem. Photobiol. 82, 515–522.

Hurd, C.L., Harrison, P.J., Bischof, K., Lobban, C.S., 2014. Seaweed Ecology and Physiology. Cambridge University Press, Second ed.

Inskeep, W.P., Bloom, P.R., 1985. Extinction coefficients of chlorophyll *a* and *b* in *N,N*-dimethylformamide and 80% acetone. Plant Physiol. 77, 483–485.

Kain, J.M., 1989. Season in the subtidal. Br. Phycol J. 24, 203–215.

Karsten, U., Bischof, K., Wiencke, C., 2001. Photosynthetic performance of Arctic macroalgae after transplantation from deep to shallow waters. Oecologia 127, 11–20.

Kingsford, M.J., 1992. Drift algae and small fish in coastal waters of northeastern New Zealand. Mar. Ecol. Prog. Ser. 80, 41–55.

Koivikko, R., 2008. Brown algal phlorotannins: improving and applying chemical methods. Ph.D. Thesis. University of Turku, Turku, Finland.

Komatsu, T., Tatsukawa, K., Filippi, J.B., Sagawa, T., Matsunaga, D., Mikami, A., Ishida, K., Ajisaka, T., Tanaka, K., Aoki, M., Wang, W.-D., Liu, H.-F., Zhang, S.-D., Zhou, M.-D., Sugimoto, T., 2007. Distribution of drifting seaweeds in eastern East China Sea. J. Mar. Syst. 67, 245–252.

Lehvo, A., Bäck, S., Kiirikki, M., 2001. Growth of *Fucus vesiculosus* L. (Phaeophyta) in the Northern Baltic proper: energy and nitrogen storage in seasonal environment. Bot. Mar. 44, 345–350.

Lizée-Prynne, D., López, B., Tala, F., Thiel, M., 2016. No sex-related dispersal limitation in a dioecious, oceanic long-distance traveller: the bull kelp *Durvillaea antarctica*. Bot. Mar. (accepted).

Macaya, E.C., Zuccarello, G.C., 2010a. DNA barcoding and genetic divergence in the giant kelp *Macrocystis* (Laminariales). J. Phycol. 46, 736–742.

Macaya, E.C., Zuccarello, G.C., 2010b. Genetic structure of the giant kelp *Macrocystis pyrifera* along the southeastern Pacific. Mar. Ecol. Prog. Ser. 420, 103–112.

Macaya, E., Boltaña, S., Hinojosa, I., Macchiavello, J., Valdivia, N., Vásquez, N., Buschmann, A., Vásquez, J., Vega, A., Thiel, M., 2005. Presence of sporophylls in floating kelp rafts of *Macrocystis* spp. (Phaeophyceae) along the Chilean Pacific coast. J. Phycol. 41, 913–922.

Mansilla, A., Avila, M., 2007. Bases biológicas para el manejo de macroalgas pardas en la XII región. Proyecto Fondo de Investigación Pesquera y Acuicultura FIP N°2005-44. Subsecretaria de Pesca, Ministerio de Economía, Fomento y Turismo, Chile 352pp.

Martinez, E., Maamaatuaiahutapu, K., Payri, C., Ganachaud, A., 2006. *Turbinaria ornata* invasion in the Tuamotu Archipelago, French Polynesia: ocean drift connectivity. Coral Reefs 26, 79–86.

McDonald, J.H., 2014. Handbook of Biological Statistics. third ed. Sparky House Publishing, Baltimore, Maryland.

McKenzie, P.F., Bellgrove, A., 2008. Dispersal of *Hormosira banksii* (Phaeophyceae) via detached fragments: reproductive viability and longevity. J. Phycol. 44, 1108–1115.

Molyneux, P., 2004. The use of the stable free radical diphenylpicrylhydrazyl (DPPH) for estimating antioxidant activity. J. Sci. Technol. 26, 211–219.

Olsen, J.L., Zechman, F.W., Hoarau, G., Coyer, J.A., Stam, W.T., Valero, M., Aberg, P., 2010. The phylogeographic architecture of the fucoid seaweed *Ascophyllum nodosum*: an intertidal 'marine tree' and survivor of more than one glacial-interglacial cycle. J. Biogeogr. 37, 842–856.

Powles, S.B., 1984. Photoinhibition of photosynthesis induced by visible light. Annual Review of Plant Physiology 35, 15–44.

Quinn, G.P., Keough, M.J., 2002. Experimental design and data analysis for biologists. Cambridge University Press, Cambridge.

Ramos-Rodríguez, A., Lluch-Cota, D.-B., Lluch-Cota, S.-E., Trasviña-Castro, A., 2012. Sea surface temperature anomalies, seasonal cycle and trend regimes in the Eastern Pacific coast. Ocean Sci. 8, 81–90.

Reed, D.C., Ebeling, A.W., Anderson, T.W., Anghera, M., 1996. Differential reproductive responses to fluctuating resources in two seaweeds with different reproductive strategies. Ecology 77, 300–316.

Reed, D.C., Laur, D.R., Ebeling, A.W., 1988. Variation in algal dispersal and recruitment: the importance of episodic events. Ecol. Monogr. 58, 321–335.

Rothäusler, E., Gómez, I., Hinojosa, I.A., Karsten, U., Miranda, L., Tala, F., Thiel, M., 2011b. Kelp rafts in the Humboldt Current: Interplay of abiotic and biotic factors limit their floating persistence and dispersal potential. Limnol. Oceanogr. 56, 1751–1763.

Rothäusler, E., Gómez, I., Hinojosa, I.A., Karsten, U., Tala, F., Thiel, M., 2009. Effect of temperature and grazing on growth and reproduction of floating *Macrocystis* spp. (Phaephyceae) along a latitudinal gradient. J. Phycol. 45, 547–559.

Rothäusler, E., Gómez, I., Karsten, U., Tala, F., Thiel, M., 2011a. UV-radiation versus grazing pressure: long-term floating of kelp rafts (*Macrocystis pyrifera*) is facilitated by efficient photoacclimation but undermined by grazing losses. Mar. Biol. 158, 127–141.

Rothäusler, E., Gómez, I., Karsten, U., Tala, F., Thiel, M., 2011b. Physiological acclimation of floating *Macrocystis pyrifera* to temperature and irradiance ensures long-term persistence at the sea surface at mid-latitudes. J. Exp. Mar. Biol. Ecol. 405, 33–41.

Rothäusler, E., Gutow, L., Thiel, M., 2012. Floating seaweeds and their communities. In: Wiencke, C., Bischof, K. (Eds.), Seaweed Biology, Ecological Studies. Springer-Verlag., Berlin, pp. 359–380.

Santelices, B., Castilla, J.C., Cancino, J., Schmiede, P., 1980. Comparative ecology of *Lessonia nigrescens* and *Durvillaea antarctica* (Phaeophyta) in Central Chile. Mar. Biol. 19, 119–132.

Silva, N., Rojas, N., Fedele, A., 2009. Water masses in the Humboldt Current System: properties, distribution, and the nitrate deficit as a chemical water tracer for Equatorial Subsurface Water of Chile. Deep-Sea Res., Pt II 56 (1004–1002).

Smith, S.D.A., 2002. Kelp rafts in the Southern Ocean. Glob. Ecol. Biogeogr. 11, 67–69.

Strickland, J.D.H., Parsons, T.R., 1972. A Practical Handbook of Seawater Analysis. second ed. Bulletin 167. Ottawa, Fisheries Research Board of Canada.

Swanson, A., Druehl, L., 2002. Induction, exudation, and the UV protective role of kelp phlorotannins. Aquat. Bot. 73, 24–253.

Tala, F., Gómez, I., Luna-Jorquera, G., Thiel, M., 2013. Morphological, physiological and reproductive conditions of rafting bull kelp (*Durvillaea antarctica*) in northern-central Chile (30°S). Mar. Biol. 160, 1339–1351.

Tapia, F.J., Largier, J.L., Castillo, M., Wieters, E.A., Navarrete, S.A., 2014. Latitudinal discontinuity in thermal conditions along the nearshore of Central-Northern Chile. PLoS One 9 (10), e110841. http://dx.doi.org/10.1371/journal.pone.0110841.

Thiel, M., Gutow, L., 2005. The ecology of rafting in the marine environment. II. The rafting organisms and community. Oceanogr. Mar. Biol. Annu. Rev. 43, 279–418.

Thiel, M., Hinojosa, I.A., Joschko, T., Gutow, L., 2011. Spatio-temporal distribution of floating objects in the German Bight (North Sea). J. Sea Res. 65, 368–379.

Thiel, M., Macaya, E., Acuña, E., Arntz, W., Bastias, H., Brokordt, K., Camus, P., Castilla, J., Castro, L., Cortés, M., Dumont, C., Escribano, R., Fernández, M., Gajardo, J., Gaymer, C., Gomez, I., González, A., González, H., Haye, P., Illanes, J., Iriarte, J., Lancellotti, D., Luna-Jorquera, G., Luxoro, C., Manríquez, P., Marín, V., Muñoz, P., Navarrete, S., Perez, E., Poulin, E., Sellanes, J., Sepúlveda, H., Stotz, W., Tala, F., Thomas, A., Vargas, C., Vasquez, J., Alonso-Vega, J., 2007. The Humboldt current system of northen and central Chile oceanographic processes, ecological interactions and socioeconomic feedback. Oceanogr. Mar. Biol. Annu. Rev. 45, 195–344.

Underwood, A.J., 1997. Experiments in Ecology. Their Logical Design and Interpretation Using Analysis of Variance. Cambridge University Press, Cambridge, UK.

Van Alstyne, K.L., McCarthy III, J.J., Hustead, C.L., Duggins, D.O., 1999. Geographic variation in polyphenolic levels of Northeastern Pacific kelps and rockweeds. Mar. Biol. 133, 371–379.

Vandendriessche, S., Vincx, M., Degraer, S., 2007. Floating seaweed and the influences of temperature, grazing and clump size on raft longevity a microcosm study. J. Exp. Mar. Biol. Ecol. 343, 64–73.

Wichmann, C.S., Hinojosa, I.A., Thiel, M., 2012. Floating kelps in Patagonian Fjords: an important vehicle for rafting invertebrates and its relevance for biogeography. Mar. Biol. 159, 2035–2049.

Wiencke, C., Clayton, M.N., Gómez, I., Iken, K., Lüder, U.H., Amsler, C.D., Karsten, U., Hanelt, D., Bischof, K., Dunton, K., 2007. Life strategy, ecophysiology and ecology of seaweeds in polar waters. Rev. Environ. Sci. Biotechnol. 6, 95–126.

Wiencke, C., Gómez, I., Dunton, K., 2009. Phenology and seasonal physiological performance of polar seaweeds. Bot. Mar. 52, 585–592.

Wooster, W.S., Sievers, H.A., 1970. Seasonal variations of temperature, drift, and heat exchange in surface waters off the west coast of South America. Limnol. Oceanogr. 15, 595–605.