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Research Article

The chemical composition of *Lessonia berteroana* (ex *L. nigrescens*) in kelp harvest management and open access areas near Coquimbo, Chile

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ABSTRACT. *Lessonia berteroana* (ex *L. nigrescens*) is kelp freely harvested from Open Access Areas (OAA), and to some extent controlled, from Management and Exploitation Areas for Benthic Resources (MEABR). Harvesting pressures can change population dynamics, mainly in OAAs. In particular, harvesting may alter the chemical components of plants. Therefore, the aim of this study was to determine the harvesting effects on the chemical composition of *L. berteroana* from MEABR and OAA sampled during different seasons (spring and fall) and at two sites (Talquilla and Lagunillas) near Coquimbo (30°S), Chile. The crude protein (13.5 ± 1.0%), total lipids (0.9 ± 0.2%), crude fiber (16.3 ± 1.6%), ash (30.1 ± 1.5%), and nitrogen-free extract (39.2 ± 2.0%) contents of *L. berteroana* were within reference values for Laminariales species. Population descriptors and chemical analyses showed that harvesting had local effects, rather than being affected by a resource management strategy (OAA *vs* MEABR). The seasonal anticipator nature of *L. berteroana* may explain the detected seasonality of it's chemical composition. Regarding functional morphological structures, chemical composition in the fronds was more variable than in the stipes and perennial holdfast, probably since leaves are ephemeral structures susceptible to environmental changes and that play a functional, rather than structural, role in kelp. In the context of Chilean kelp resource management, monitoring chemical composition is useful for determining optimal harvesting periods to local scale and for deciding when commercially valuable compounds, such as alginate, should be extracted. These data also complement harvesting pressure indicators based on *L. berteroana* demographic parameters.

Keywords: *Lessonia*, kelp, protein, harvest, management, ecological indicator, northern Chile.

INTRODUCTION

The kelps are commercially relevant as they contain alginate, a complex structural carbohydrate, and energy reserve (Percival *et al.*, 1983). This natural polymer is a gel with medical potential and industrial applications, such as in the food, agricultural, and cosmetic industries (Mišurcová *et al.*, 2012). Among the Chilean kelps of economic interest, *Lessonia nigrescens* complex represents near 70% of the national annual brown algae harvest (Vásquez *et al.*, 2012).

In the context of Chilean regulations, two strategies are in place to manage the exploitation of algal resources, Open Access Areas (OAA) and Management and Exploitation Areas for Benthic Resources (MEABR) (Vásquez *et al.*, 2012). Currently, 95% of harvested kelp originates from natural populations located in OAAs, where any registered fisherman can harvest this resource (Vega *et al.*, 2014). In turn, only 5% of harvested kelp originates from MEABR, areas in which fishery associations exploit resources under co-management plans (Vásquez *et al.*, 2012). Since 2013, OAA kelps have been included within regional management plans that emphasize ecosystem preservation and precautionary exploitation (Vega *et al.*, 2014). Distinct ecological indicators show that management plans tend to support the sustainability of exploited *Lessonia* populations (Vásquez *et al.*, 2012; Vega 2016).

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Recent phylogenetic, demographic, and morphological studies indicate that *L. nigrescens* is a complex constituted by two cryptic species, *Lessonia berteroana*, distributed north of 30°S, and *Lessonia spicata*, distributed south of this latitude (González *et al*., 2012). The crossover point for the distribution of both species occurs in geopolitical regions that harvest the largest volumes of *L. nigrescens* complex (*ca*. 30°S, Coquimbo, and Atacama Regions; Tellier *et al.*, 2011). Thus, in northern Chile, *L. berteroana* is a conspicuous species of the rocky intertidal zone, a wave-exposed area in which this commercial kelp dominates in terms of coverage and biomass (Vásquez & Vega, 2004). In addition, it is in the intertidal zone where the harvest takes place on the *Lessonia* populations.

The bio-ecological foundations for the management of *Lessonia* populations only consider the production of gels and not the total chemical composition (Santelices, 1982; Edding *et al.*, 1994; Vásquez, 1995). Studying the chemical composition of kelp and other seaweeds is important for determining potential applications, such as a nutritional supplement for animals and humans and/or as bioproducts (Fleurence, 1999; Mišurcová *et al.*, 2012). Furthermore, concentrations of chemical components in algae are species-specific (MacArtain *et al.*, 2007), and the chemical constituents of *Lessonia* also vary between the functional morphological structures of this brown algae, with greater temporal variability in the laminae than in the stipes or holdfasts (Westermeier & Gómez, 1996).

Harvesting pressure appears to be another factor that modifies the chemical composition of kelp, such as *Macrocystis pyrifera* (Borras-Chavez *et al.*, 2016). Related to this, OAA populations of *L. berteroana* are submitted to greater harvesting pressure than MEABR populations, thus modifying the dynamics of the exploited populations (Vega *et al.*, 2014). Differentiated harvesting pressures could specifically affect the chemical composition of *L. berteroana* populations by modifying the proportion of nutrients available to algae.

The objective of this study was to determine the effect of harvesting pressure on the chemical composition of *L. berteroana* (ex *L. nigrescens*). For this, the chemical compositions of *L. berteroana* specimens collected from either OAAs or MEABRs were compared. Moreover, these resource management areas were compared during the Austral spring and fall. The collected data suggest a possibility of using *L. berteroana* chemical composition as an indicator for quantifying the effects of exploitation on Chilean kelps.

MATERIALS AND METHODS

Samples of *L. berteroana* were collected from both OAA and MEABR, close to Talquilla (30º50’S, 71º41’W) and Lagunillas (30º01’’S, 71º23’’W). Sampling was performed during low tide in November (Austral spring) and May (Austral fall).

For each *Lessonia* kelp bed present at the OAA and MEABR sites, plant abundance was estimated along three permanent, 50 m long transects. Each transect was parallel to the coast and covered a 5 m width of the intertidal habitat of *L. berteroana*. To determine the sizing structure of populations, three 1 m^2 quadrants were selected at random (Vásquez *et al.*, 2012). In each quadrant, the maximum diameter of the holdfast was measured and used to estimate the size and weight of the plant. Plants with basal diameters up to 5 cm were considered recruits. In turn, plants with a holdfast diameter $\geq$20 cm were considered adults (Vásquez *et al.*, 2012), which is also the minimum legal harvest size within management plans (Vega *et al.*, 2014).

At each sampling site, six adult plants were detached from the substrate. The plants were washed with distilled water and dried. Three complete plants were ground, and the fronds, stipes, and holdfast from another three plants were separately ground. The ground samples were stored until chemical analyses.

The humidity content of each plant was determined by drying the samples in a furnace at 95°C until reaching a constant weight (Method 934.01; AOAC, 1990). Crude protein contents were determined using Kjeldahl digestion (Method 976.05) (AOAC, 1990; Di Dio, 2010). Total lipids content was determined using the Soxhlet method (Method 920.39) (AOAC, 1990; Di Dio, 2010). Crude fiber contents were assessed via acid and alkaline digestion (Method 962.09) (AOAC, 1990; Di Dio, 2010). The ashes were quantified through sample combustion at 500°C in a muffle furnace (Method 942.05) (AOAC, 1990; Di Dio, 2010). The Nitrogen Free Extract (NFE) was calculated by subtracting the sum of all fractions over 100 (Tacon, 1989). All samples were assessed in triplicate and expressed as a percentage of dry weight.

Analysis of variance (ANOVA) was used to detect significant differences in chemical components between management strategies (MEABR *vs* OAA), seasons (spring *vs* fall), and localities (Talquilla *vs* Lagunillas). Prior to analyses, percentage values were arcsine square root transformed, data normality and homoscedasticity of variance were confirmed (Quinn & Keough, 2002). Tukey’s *a posteriori* test was used to identify significant differences between levels of each factor ($P < 0.05$) (Quinn & Keough, 2002). Data are presented as the average ± standard deviation.

RESULTS

L. berteroana density was significantly higher in Talquilla than in Lagunillas ($F_{(1.64)} = 10.616$, $P < 0.01$), but both localities evidenced a significant increase in population density in spring as compared to fall ($F_{(1.64)} = 25.832$, $P < 0.01$) (Figs. 1a-1b). Kelp biomass at Lagunillas was significantly greater than at Talquilla ($F_{(1.64)}=10.616$, $P < 0.01$), although both localities showed significant increases in biomass during the fall ($F_{(1.64)} = 18.172$, $P < 0.01$) (Figs. 1c-1d). Plant density and population productivity were uninfluenced by management strategy at either locality.

Local differences were detected in the sizing structures of *L. berteroana* populations (Fig. 2). In Lagunillas during the fall, recruits represented 7 and 19% of the MEABR and OAA, respectively, with only a fraction (≈30%) of harvestable adult plants (Figs. 2a-2b). In Talquilla during the fall, recruits represented 22 and 37% of the MEABR and OAA, respectively, whereas only 13 and 18% of adult plants were harvestable (Figs. 2c-2d). In spring for both localities and management strategies, recruit representation increased while the fraction of adult plants decreased (Fig. 2). However, changes in the population structure of *Lessonia* were more notable in Talquilla than in Lagunillas.

The crude protein content in *L. berteroana* samples was 13.5 ± 1.0%. The levels of crude protein content in the different functional morphological structures and in the whole plants were significantly higher in fall (Table 1). Although protein levels in the functional morphological structures significantly differed between Lagunillas and Talquilla, when comparing between the OAA and MEABR at the same locality, no differences were found (Table 1). Maximum average crude protein levels were found in fronds from Talquilla, independent of season or management strategy (Table 1).

The fraction of total lipids in *L. berteroana* was 0.9 ± 0.2%. The fronds contained more lipids than the stipes, holdfast, or the whole plant, particularly in fall (Table 1). The total lipid levels in the functional morphological structures differed between localities, but no between management strategies at either locality (Table 1).

The crude fiber in *L. berteroana* was 16.3 ± 1.6%. The fiber content of whole plants and fronds was significantly higher in the spring (Table 1). Furthermore, crude fiber levels in whole plants, stipes, and holdfast were greater in Talquilla, whereas levels were higher in fronds from Lagunillas. No differences were detected between OAA and MEABR strategies at either locality (Table 1).

The NFE contents in *L. berteroana*, which included alginate, were recorded as 39.2 ± 2.0%. The NFE contents in functional morphological structures and whole plants were significantly greater in the fall than in the spring (Table 1). These contents were significantly higher in the whole plants and stipes of Lagunillas, while the fronds and holdfast showed no variations between management strategies or seasons (Table 1).

Finally, the ash content of *L. berteroana* was 30.1 ± 1.5%. There was a significantly higher amount of ash content in whole plants and functional morphological structures in the primavera than in fall (Table 1). The ash content in fronds and holdfast was higher in Lagunillas, whereas the ash content in whole plants and stipes did not vary in regard to management strategy or locality (Table 1).

DISCUSSION

Abundance, biomass, and sizing structure data were used as indicators for the status of kelps exploitation (Vásquez *et al.*, 2012; Vega *et al.*, 2014); with findings suggesting that *L. berteroana* populations from the OAA and MEABR at Talquilla are subjected to greater harvesting pressures than populations at Lagunillas. At Talquilla, harvesting occurs all year, whereas harvesting at Lagunillas is limited only to the spring or summer. Harvesting is a factor that can modify the chemical composition of Laminariales seaweeds, such as observed in *Costaria costata* and *M. pyrifera* (Wu *et al.*, 2014; Borras-Chavez *et al.*, 2016); however, the effects on *L. berteroana* occurred independently of the management strategy (*i.e.*, OAA, MEABR). Due to this, good management practices (Vásquez *et al.*, 2012) could be an adequate strategy for maintaining the nutritional properties of plants in naturally exploited populations of this kelp, which will ultimately provide higher quality compounds on harvest (*e.g.*, proteins, lipids, natural polymers).

In addition to harvesting pressures, bromatological analyses demonstrated that the chemical composition of *L. berteroana* differed between localities (Lagunillas and Talquilla), rather than being affected by a resource management strategy (*i.e.*, OAA, MEABR). Table 2 shows the variability in chemical composition presented by Chilean and foreign algae species. This variety could be due in part to different methodologies (Patarra *et al.*, 2011). However, these differences are primarily a reflection of the climate, season, and geographical

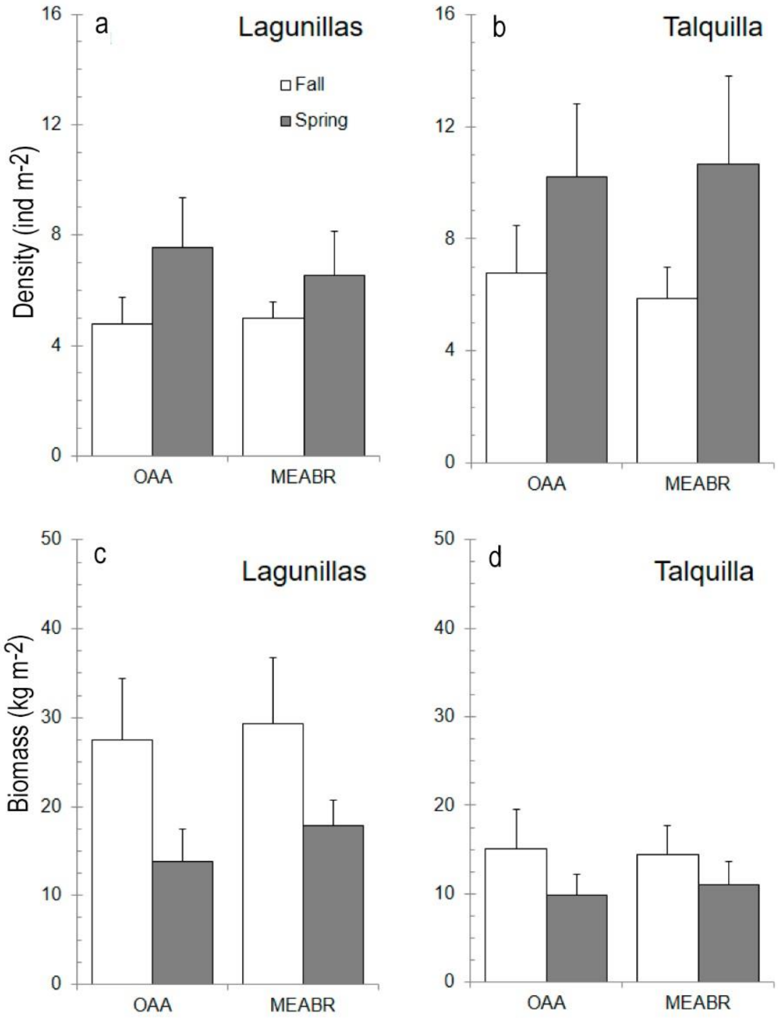

Figure 1. (a-b) Density and (c-d) biomass of *Lessonia berteroana* plants by site, management strategy, and season. OAA: open access area, MEABR: management and exploitation areas for benthic resources.

origin of the plants (Rodríguez-Montesinos & Hernández-Carmona, 1991; Fleurence, 1999; Tala, 2013; Borras-Chavez *et al.*, 2016). In cryptic species, such as the *L. nigrescens* complex, chemical composition can reflect species-specific and local traits (Koch *et al.*, 2015). As such, to characterize and adequately monitor the chemical composition of *L. berteroana*, it is important to design a system able to trace samples to corresponding collection sites (Tellier *et al.*, 2011; Fleurence *et al.*, 2012).

The protein content was less in brown algae than in red or green algae (Table 2). While some Laminariales present slightly increased protein contents, such as *C. costata*, the results obtained for *L. berteroana* were within reference levels (Table 2). Lipid content in algae is generally low (Table 2; Nelson *et al.*, 2002), as corroborated in *L. berteroana* samples, although lipid content can increase by culturing selected algae strains (Westermeier *et al.*, 2012). Crude content fiber is low in red and green algae, and, as compared to other Laminariales species, *L. berteroana* presented crude fiber values nearly double that of most brown algae (Table 2), reaching levels close to those reported in tropical algae (Patarra *et al.*, 2011). It is worth mentioning that there is an inverse relationship between fiber and the nutritional quality of the algae (Wu *et al.*, 2014). NFE values were grouped with soluble carbohydrates, the most common chemical component in algae (MacArtain *et al.*, 2007). The carbohydrate contents in *L. berteroana* were principally accounted for by alginate (Percival *et al.*, 1983), which has adaptive functions in a coastal environment (*e.g.*, with waves and water movement; Venegas *et al.*, 1993), and by reserve components such as starch, mannitol and laminarin (Etcheverry, 1958). The levels of carbohydrates in *L. berteroana* were within the reference values

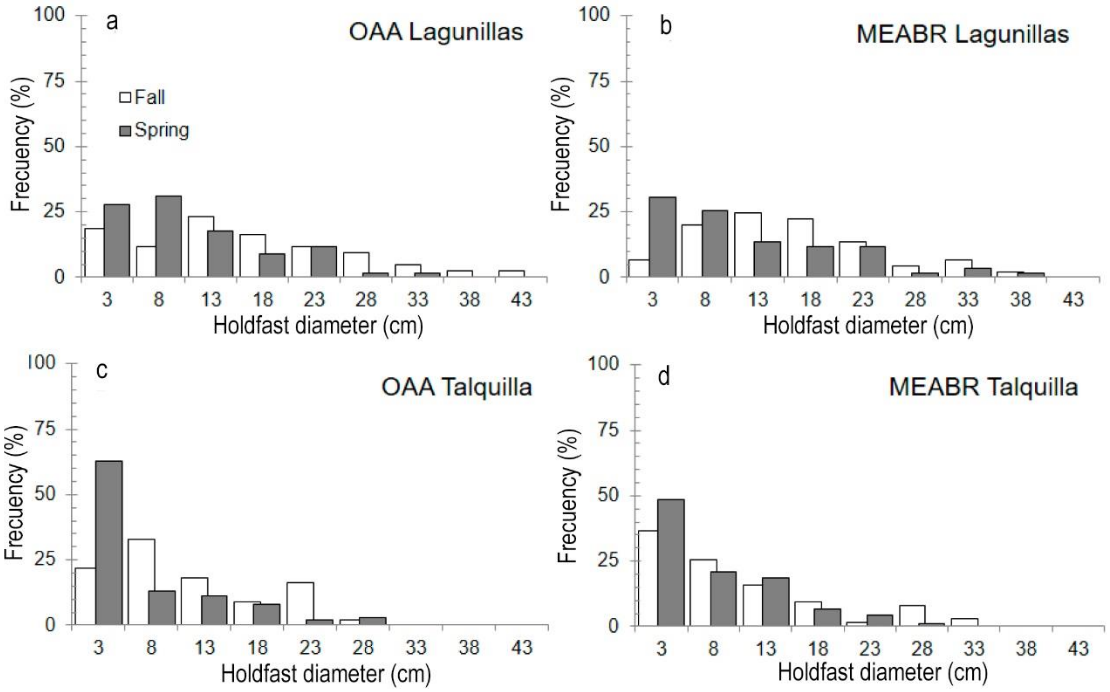

Figure 2. Sizing structure of *Lessonia berteroana* plants by locality, management strategy, and season. OAA: Open Access Area, MEABR: Management and Exploitation Areas for Benthic Resources.

cited for other Laminariales species (Table 2). These compounds are commercially important, a fact that has resulted in the exploitation and subsequent public regulation of wild populations of kelps in Chile. Finally, the ash content in brown and red algae is greater than in green algae, and levels found in *L. berteroana* were comparable to those in other Laminariales (Table 2), with a high concentration of minerals (Toledo *et al.*, 2009; Schiener *et al.*, 2015).

The seasonal patterns of chemical composition in seaweeds, including *L. berteroana*, are historically related to environmental and oceanographic parameters (Etcheverry, 1958; Kain, 1989; Westermeier *et al.*, 2012; Borras-Chavez *et al.*, 2016). The primary environmental factors that regulate physiology and that impact algal chemical composition are temperatures and nutrient availability in seawater (Lüning, 1989), both factors that inversely vary at temperate latitudes (Tala & Edding, 2005; Tala, 2013). Considering adaptive responses to an oceanographic climate, *L. berteroana* is classified as a seasonally anticipatory species (Kain, 1989; Lüning, 1989). In cold periods, plants increase nitrogen fixation rates, grow, and reproduce (Gómez & Huovinen, 2012; Tala, 2013). In contrast, in warm seasons, plants must use energy to maintain physiological processes, resulting in the inherent loss of nitrogen reserves (Tala & Edding, 2005; Gómez & Huovinen, 2011).

Considering this, protein content seasonally varies in *L. berteroana* (Toledo *et al.*, 2009), just as in other Laminariales species (Rosell & Srivastava, 1985; Hernandez-Carmona *et al.*, 2009; Toledo *et al.*, 2009; Westermeier *et al.*, 2012; Schiener *et al.*, 2015).

In the case of lipids, the heterogeneous metabolic origin of distinct fractions is modified by external factors, such as harvesting (Nelson *et al.*, 2002; Borras-Chávez *et al.*, 2016), and by internal factors that make it difficult to explain seasonality (Westermeier & Gómez, 1996). Carbon content in algae reflects the magnitude and intensity of photosynthetic metabolism in the stems (Gómez & Huovinen, 2012; Tala, 2013). In Laminariales, carbohydrates can evidence an inverse seasonal pattern to that described for nitrogenous compounds (Rosell & Srivastava, 1985; Schiener *et al.*, 2015). However, the chemical composition of an unexploited population of *L. spicata* in the south of Chile presents minimal seasonality (Westermeier & Gómez, 1996). Likewise, harvesting can affect the chemical composition of other Laminariales, such as *Macrocystis pyrifera* (Rodríguez-Montesinos & Hernández-Carmona, 1991; Borras-Chavez *et al.*, 2016), *Costaria costata* (Wu *et al.*, 2014), among others kelp (Schiener *et al.*, 2015).

The physical characteristics of the habitat can also affect the chemical content of plants. For example, the content and composition of alginate in *L. trabeculata*

Table 1. Chemical composition of *Lessonia berteroana* in whole plants and functional morphological structures by season and management strategy at each site (OAA: Open Access Area, MEABR: Management Area). In each raw the superscript letters indicates homogeneous groups (significant differences Tukey test; $P < 0.05$). Values are represented as the average dry weight ± standard deviation.

Parameter	Site	Strategy	Season	Average dry weight (%)			
				Whole plant	Frond	Stipe	Holdfast
Crude protein			Fall	14.15 ± 0.59^{b}	15.52 ± 1.72^{b}	13.69 ± 0.59^{b}	12.94 ± 0.67^{a}
			Spring	12.83 ± 0.84^{a}	14.19 ± 3.10^{a}	12.87 ± 1.17^{a}	12.12 ± 1.64^{b}
	Talquilla	OAA		13.45 ± 1.37^{c}	17.96 ± 0.59^{b}	12.43 ± 0.85^{b}	11.31 ± 0.93^{b}
	Talquilla	MEABR		13.33 ± 1.43^{b}	15.81 ± 0.91^{b}	12.61 ± 0.85^{b}	11.96 ± 1.36^{b}
	Lagunillas	OAA		13.49 ± 0.47^{a}	12.74 ± 1.96^{a}	13.92 ± 0.33^{a}	13.45 ± 0.50^{a}
	Lagunillas	MEABR		13.67 ± 0.43^{b}	12.90 ± 1.50^{a}	14.16 ± 0.45^{a}	13.39 ± 0.78^{a}
Total lipids			Fall	1.03 ± 0.12^{b}	1.18 ± 0.09^{b}	0.93 ± 0.12^{b}	0.78 ± 0.19^{b}
			Spring	0.70 ± 0.16^{a}	1.06 ± 0.27^{a}	0.71 ± 0.14^{a}	0.76 ± 0.29^{a}
	Talquilla	OAA		0.72 ± 0.22^{a}	1.27 ± 0.10^{b}	0.70 ± 0.14^{b}	0.52 ± 0.09^{b}
	Talquilla	MEABR		0.76 ± 0.21^{a}	1.20 ± 0.13^{b}	0.70 ± 0.13^{b}	0.56 ± 0.04^{b}
	Lagunillas	OAA		0.98 ± 0.14^{b}	1.02 ± 0.19^{a}	0.91 ± 0.09^{a}	0.98 ± 0.06^{a}
	Lagunillas	MEABR		0.99 ± 0.19^{b}	0.97 ± 0.25^{a}	0.98 ± 0.13^{a}	1.02 ± 0.05^{c}
Crude fiber			Fall	15.47 ± 1.23^{b}	11.09 ± 2.22^{b}	15.30 ± 1.01^{b}	15.47 ± 1.86^{b}
			Spring	17.16 ± 1.44^{a}	15.98 ± 1.46^{a}	15.15 ± 2.56^{ab}	16.06 ± 1.66^{a}
	Talquilla	OAA		17.52 ± 0.91^{a}	11.90 ± 3.28^{a}	16.86 ± 0.91^{b}	18.02 ± 0.62^{c}
	Talquilla	MEABR		17.19 ± 1.66^{a}	11.95 ± 3.20^{a}	16.78 ± 1.03^{b}	16.44 ± 0.62^{b}
	Lagunillas	OAA		14.95 ± 1.30^{b}	14.95 ± 2.06^{b}	13.81 ± 0.95^{a}	13.97 ± 0.84^{a}
	Lagunillas	MEABR		15.61 ± 0.76^{b}	15.34 ± 2.55^{b}	13.45 ± 1.29^{a}	14.63 ± 0.78^{a}
NFE			Fall	40.27 ± 2.18^{a}	46.27 ± 1.29^{a}	40.35 ± 1.86^{a}	41.95 ± 1.07^{a}
			Spring	38.18 ± 0.99^{b}	40.97 ± 1.21^{b}	38.73 ± 1.18^{b}	39.21 ± 1.38^{b}
	Talquilla	OAA		38.63 ± 0.90^{a}	43.28 ± 3.63^{c}	38.27 ± 0.68^{c}	41.35 ± 1.64^{c}
	Talquilla	MEABR		38.76 ± 0.67^{a}	44.14 ± 4.16^{c}	39.67 ± 0.54^{b}	40.30 ± 1.16^{b}
	Lagunillas	OAA		40.15 ± 3.42^{b}	43.10 ± 1.68^{c}	40.90 ± 2.08^{b}	39.97 ± 2.36^{b}
	Lagunillas	MEABR		39.35 ± 1.79^{ab}	43.98 ± 2.50^{c}	39.32 ± 2.13^{b}	40.69 ± 2.21^{b}
Ash			Fall	29.08 ± 0.84^{b}	25.95 ± 1.06^{b}	29.57 ± 0.67^{b}	29.04 ± 0.58^{b}
			Spring	31.14 ± 1.40^{a}	27.80 ± 1.60^{a}	31.62 ± 1.00^{a}	32.76 ± 1.52^{a}
	Talquilla	OAA		29.68 ± 0.56^{c}	25.59 ± 0.96^{c}	30.59 ± 0.98^{c}	29.96 ± 1.73^{c}
	Talquilla	MEABR		29.96 ± 0.70^{b}	26.90 ± 0.68^{b}	30.58 ± 0.77^{b}	30.40 ± 1.03^{b}
	Lagunillas	OAA		30.43 ± 2.61^{a}	28.19 ± 1.90^{a}	30.30 ± 1.41^{a}	31.79 ± 2.94^{a}
	Lagunillas	MEABR		30.38 ± 1.69^{b}	26.81 ± 1.78^{b}	30.91 ± 2.13^{b}	31.46 ± 2.67^{b}

varies in relation to the hydrodynamic gradient produced by waves (Venegas *et al.*, 1993). In addition to this, chemical content reserves are accumulated and used by Laminariales algae depending on storm cycles and local and regional oceanographic conditions (Rosell & Srivastava, 1985; Rodríguez-Montesinos & Hernández-Carmona, 1991; Tala & Edding, 2005; Tala, 2013; Schiener *et al.*, 2015). Related to this, the "El Niño" y "La Niña" events, together with coastal upwelling events within the ecosystem of the Humboldt Current, generate productivity gradients on the mesoscale that profoundly affect the distribution patterns and population dynamics of kelps (Edding *et al.*, 1994; Thiel *et al.*, 2007), as well as the physiology and metabolism of *Lessonia* plants (Gómez & Huovinen, 2012; Tala, 2013). The interconnected impact between harvesting pressure and the oceanographic phenomena that act on distinct temporal and spatial scales could explain the differences in chemical composition found in *L. berteroana* between Talquilla and Lagunilla, as well as from referential studies (Westermeier & Gómez, 1996; Toledo *et al.*, 2009). A more detailed characterization of the chemical composition of the *Lessonia* species along a geographical gradient would facilitate fully understanding the latitudinal effects that harvesting has on kelps, in addition to determining species-specific traits of *Lessonia*.

The Laminariales algae as *L. berteroana* are composed of three morphologically and functionally differentiated structures (Gómez & Huovinen, 2011, 2012). Regarding functional morphological structures, chemical composition in the fronds was more variable than in the stipes and perennial holdfast of *L. berteroana* plants. In *L. spicata*, the sensitivity of sea-

Table 2. Referential chemical composition (in dry weight) of Chilean brown, green, and red algae, and of national and foreign Laminariales species. [a]Fronds, [b]Stipe, [1]California, [2]New Zealand; nd: no data.

Species	Crude protein	Total lipids	Crude fiber	NFE	Ash	Reference
Lessonia berteroana	13.5 ± 1.0	0.9 ± 0.2	16.3 ± 1.6	39.2 ± 1.2	30.1 ± 1.5	This study
L. berteroana (Lagunillas)	13.6 ± 0.5	1.0 ± 0.2	15.3 ± 1.1	39.8 ± 2.6	30.4 ± 2.1	This study
L. berteroana (Talquilla)	13.4 ± 1.3	0.8 ± 0.2	17.4 ± 1.3	38.7 ± 0.8	29.8 ± 0.7	This study
Lessonia nigrescens	13.3 ± 1.1	0.6 ± 0.4	22.7 ± 3.6	nd	28.7 ± 1.9	Toledo *et al.* (2009)
Lessonia trabeculata	12.9 ± 1.2	1.7 ± 0.3	7.0 ± 1.0	48.3 ± 2.4	37.0 ± 2.3	Di Dio (2010)
Durvillaea antarctica[a]	10.4 ± 0.3	0.8 ± 0.1	nd	71.4 ± 0.5	17.9 ± 1.2	Ortiz *et al.* (2006)
Durvillaea antarctica[b]	11.6 ± 0.9	4.3 ± 0.6	nd	56.4 ± 0.4	25.7 ± 2.5	Ortiz *et al.* (2006)
Macrocystis pyrifera	10.6 ± 0.0	0.6 ± 0.1	5.6 ± 0.1	46.6 ± 0.1	36.6 ± 0.1	Borras *et al.* (2016)
Macrocystis pyrifera	13.2 ± 0.0	0.7 ± 0.1	nd.	75.3 ± 0.2	10.8 ± 0.3	Ortiz *et al.* (2009)
Macrocystis pyrifera	12.0 ± 3.7	0.6 ± 0.2	18.5 ± 2.7	nd	33.6 ± 3.3	Mansilla & Ávila (2011)
Macrocystis pyrifera[1]	14.4 ± 0.3	0.3 ± 0.0	5.0 ± 0.1	42.6 ± 0.8	37.9 ± 0.3	Borras *et al.* (2016)
Eisenia arborea	9.4 ± 2.0	0.6 ± 0.1	5.2 ± 0.8	49.4 ± 3.0	24.8 ± 2.7	Hernández *et al.* (2009)
Costaria costata	18.2 ± 0.9	2.2 ± 0.0	5.7 ± 0.0	nd	29.3 ± 0.0	Wu *et al.* (2014)
Eklonia radiata	9.6 ± 0.2	1.8 ± 0.6	nd	66.9 ± 1.7	22.1 ± 0.9	Smith *et al.* (2010)
Undaria pinnatifida	19.7 ± 2.3	3.3 ± 0.1	nd	50.4 ± 2.4	26.6 ± 4.2	Smith *et al.* (2010)
Laminaria digitata	6.9 ± 1.1	nd	nd	nd	31.6 ± 7.1	Schiener *et al.* (2015)
Laminaria hiperborea	6.8 ± 1.3	nd	nd	nd	32.0 ± 9.6	Schiener *et al.* (2015)
Sacharina latissima	7.1 ± 1.7	nd	nd	nd	31.7 ± 7.6	Schiener *et al.* (2015)
Alaria esculenta	11.0 ± 1.4	nd	nd	nd	25.3 ± 5.8	Schiener *et al.* (2015)
Durvillaea antarctica[2]	7.3 ± 0.3	2.0 ± 0.8	nd	58.8 ± 11.6	22.1 ± 0.5	Smith *et al.* (2010)
Dictyota kunthii	16.8 ± 0.8	6.6 ± 2.0	9.2 ± 1.7	46.2 ± 2.2	29.6 ± 1.1	Di Dio (2010)
Codium fragile	10.8 ± 0.0	1.5 ± 0.0	nd	66.8 ± 0.4	20.9 ± 0.2	Ortiz *et al.* (2009)
Ulva lactuca	20.2 ± 1.8	2.6 ± 1.1	6.3 ± 0.6	57.2 ± 1.4	19.9 ± 2.1	Di Dio (2010)
Ulva lactuca	27.2 ± 1.1	0.3 ± 0.0	nd	60.5 ± 1.5	10.8 ± 0.3	Ortiz *et al.* (2006)
Chondracanthus chamissoi	15.0 ± 2.8	1.4 ± 1.0	0.7 ± 1.2	44.9 ± 5.1	38.7 ± 3.8	Di Dio (2010)
Asparagopsis armata	24.6 ± 3.1	3.0 ± 1.7	5.0 ± 0.1	36.0 ± 3.0	36.5 ± 5.5	Di Dio (2010)
Gracilaria chilensis	13.7 ± 0.2	1.3 ± 0.0	nd	66.1 ± 1.2	18.9 ± 0.1	Ortiz *et al.* (2009)
Gracilaria chilensis	17.5 ± 3.7	2.1 ± 0.7	4.8 ± 0.5	49.3 ± 2.8	31.0 ± 5.8	Di Dio (2010)

sonal chemical composition in the fronds as compared to the stipes and holdfast appears related to the regeneration of tissue, the functional role of the organism, and to susceptibility to local environmental changes (Gómez *et al.*, 2007; Tala, 2013). More studies on these aspects are required in *L. berteroana*.

Selective harvesting pressure in OAA and MEABR at Talquilla maintains young *L. berteroana* populations principally comprised by annual plants, which would also explain the differences in chemical composition as compared to Lagunilla plants; a site where management plans are correctly implemented in both OAA and MEABR (Vega *et al.*, 2014). These differences in chemical composition between sites can be explained because in adult plant of *Lessonia* for harvesting (≥20 cm Ø holdfast), the energy assigned to the morphological structures it varies little as compared to recruits and juveniles (Westermeier & Gómez, 1996). The processes of translocating reserve compounds between ephemeral laminae, stipes, and holdfast contribute to the accumulation of biomass on the perennial parts of *Lessonia* (Gómez *et al.* 2005, 2007; Tala, 2013). When coupled with coalescence between individuals, algae are able to rapidly renovate post-harvest of a population (*i.e.*, OAA and MEABR Lagunillas; Oróstica *et al.*, 2014; Rodríguez *et al.*, 2014). However, under strong harvesting pressures, the renewed population is constituted by fused infertile plants (*i.e.*, OAA and MEABR Talquilla; Vega *et al.*, 2014; Vega, 2016) characterized by a chemical composition representative of juveniles (Westermeier & Gómez, 1996).

Chemical composition can be used to complement demographic parameters, when establishing the degree of exploitation in *L. berteroana* populations to a local scale (Vega *et al.*, 2014). In the context of *Lessonia* management, monitoring chemical composition is a useful tool for determining the optimum moment or location for harvesting (*i.e.*, site, OAA, AMERB) and for the extraction of commercially valuable compounds (*i.e.*, bioproducts; MacArtain *et al.*, 2007). The seasonal monitoring of chemical composition in *L. berteroana* and others Chilean kelp could also help to establish seasonal patterns of lipid content, a key component for refining biofuels, obtaining agricultural biostimulants, and/or improving the nutritional content of this fresh product (Fluerence, 1999; Fluerence *et al.*, 2012; Mišurcová *et al.*, 2012; Westermeier *et al.*, 2012). On the other hand, the proportion between carbon and nitrogen (Rosell & Srivastava, 1985), alginate quality (Venegas *et al.*, 1993), distinct type of carbohydrate and other compounds (*i.e.*, amino acids, lipid classes, polyphenols, carotenoids) (Hernandez-Carmona *et al.*, 2009; Schiener *et al.*, 2015) are potential indicators of the entire chemical composition, which can be used to improve the management strategy implemented for kelp, as *L. berteroana*. These aspects should be explored in the immediate future to provide added value to the biomass harvest of wild populations of Chilean kelp.

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