

A new record of kelp *Lessonia spicata* (Suhr) Santelices in the Sub-Antarctic Channels: implications for the conservation of the “huero negro” in the Chilean coast

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ABSTRACT

The Katalalixar National Reserve (KNR) lies in an isolated marine protected area of Magellan Sub-Antarctic channels, which represent an important area for marine biodiversity and macroalgal conservation. The present study is the first report of the species *Lessonia spicata*, “huero negro”, in the Magellan Sub-Antarctic channels. This finding has implications for macroalgal biogeography and conservation concerns in the Chilean coast. In the ecological assessments of the KNR in 2018 we found populations of *L. spicata*, specifically on rocky shores of Torpedo Island and Castillo Channel. The morphological identification and molecular phylogeny based on nuclear (ITS1) sequences revealed that these populations of *Lessonia* are within the lineage of *L. spicata* of central Chile. This report increases the species richness of kelps for the Magellan Sub-Antarctic Channels from two to three confirmed species (*L. flavicans*, *L. searlesiana* and *L. spicata*), and it also extends the southern distribution range of *L. spicata*. This species has high harvest demand and is moving towards southern Chile; thus, these populations should be considered as essential for macroalgal conservation in high latitudes of South America.

Subjects Biodiversity, Marine Biology, Taxonomy

Keywords Conservation, Extension, Biogeography, Kelp, Sub-Antarctic, Magellan

INTRODUCTION

Lessonia Bory (Laminariales, Phaeophyceae) is one of the most conspicuous brown macroalgal genera that inhabit the littoral to sublittoral zone of rocky coasts (~20 m depth) in temperate-cool waters of the South Pacific Ocean (*Cho et al., 2006; Martin & Zuccarello,*

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2012). There are currently records of 11 species of the genus *Lessonia* that are taxonomically accepted, distributed along the coasts of South America, New Zealand, Tasmania and Sub-Antarctic islands (Cho et al., 2006). These species have major ecological roles in the structure of benthic marine communities (Villouta & Santelices, 1984; Vásquez & Santelices, 1984), and are commercially exploited for the extraction of alginic acid (Steneck et al., 2002). *Lessonia* species are one of the most characteristic and abundant macroalgae (12–56°S) that inhabit the rocky shores of the Chilean coast (17–56°S) (Searles, 1978; Ávila, Hoffmann & Santelices, 1985; Villouta & Santelices, 1986; Vásquez, Camus & Ojeda, 1998; Tellier et al., 2011; Martin & Zuccarello, 2012; Mansilla et al., 2014). Currently, six species have been recorded in Chile: *Lessonia nigrescens* Bory, *L. berteroana* Montagne, *L. spicata* Suhr, *L. trabeculata* Villouta & Santelices, *L. searlesiana* Asensi & De Reviere and *L. flavicans* Bory (Guiry & Guiry, 2019). A recent morphological and molecular analysis showed that the species distributed from Peru (17°) to Puerto Montt (41°), commonly known as *L. nigrescens*, is actually two cryptic species; the populations distributed from Peru (17°S) to central Chile (30°S) correspond to *L. berteroana* Montagne, and those occurring from central Chile (29°S) to Puerto Montt (41°S) correspond to *L. spicata* (Suhr) Santelices (González et al., 2012; Vega, 2016). However, *L. nigrescens* is still a valid species, because no material of the referred species has been found near its type locality, Cape Horn.

The huiro negro kelps, which include *L. berteroana* and *L. spicata*, are heavily exploited and represent almost 70% of the kelp biomass landed annually (Vega, Broitman & Vásquez, 2014). This economic activity is mainly practiced in northern Chile (18–32°S), through a complex productive chain with high social impact and low added value (Vásquez, 2008). *L. berteroana* and *L. spicata* are exported as a natural commodity to more than 20 countries mainly due to their alginate, which has high economic value (Westermeier et al., 2019). Thus populations of huiro negro have economic interest along Chilean coasts, being essential to generate a stewardship from a local and large scale.

The Katalalixar National Reserve (KNR) is a national reserve area created in 1983. KNR comprises 674,500 ha and is located in a remote zone next to the village of Tortel. This area includes a wilderness temperate rainforest with a complex ecosystem of islands and fjords (Bell, Pedersen & Newton, 2007). The offshore area (western side) of the Magellan Sub-Antarctic Channels is one of the few places of the Magellan Biogeographic Province (MBP) (43–56°S; Camus, 2001) that has not been explored systematically by scientific expeditions (Gorny & Zapata-Hernández, 2018) (Figs. 1A and 1B). KNR is located at the southern limit of the Humboldt Current System (HCS). The HCS is a key component of the general oceanic circulation in the eastern South Pacific, being one of the most productive marine ecosystems on the earth (Thiel et al., 2007). The Humboldt Current System originated in southern Chile between 42 and 48°S and is characterized by a northward flow in front of South American coasts with a strong upwelling of cool nutrient-rich waters (Silva, Rojas & Fedele, 2009). The origin of the HCS induced a large-scale redistribution of biota, and nowadays plays a key role in the biogeography of the South Pacific (Camus, 2001). Thus KNR provides an enormous opportunity to

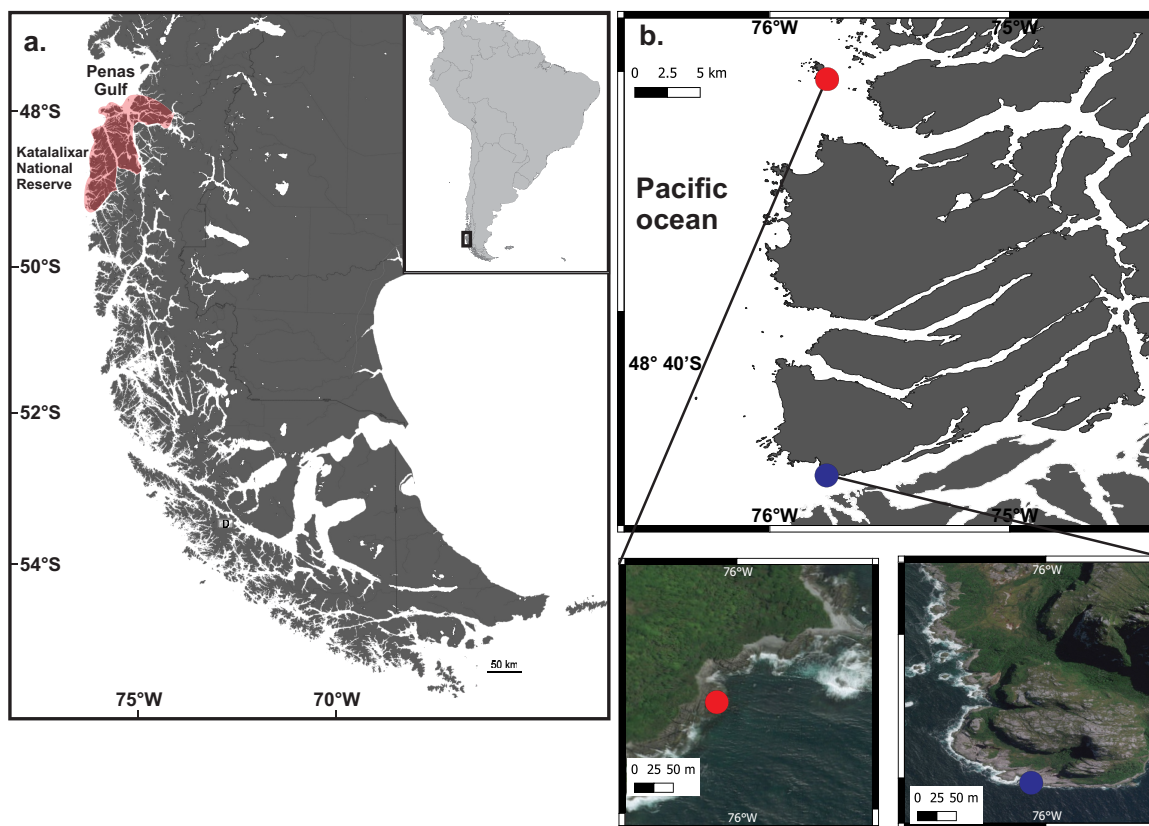


Figure 1 Collection points of *Lessonia spicata*. (A) Map showing the location of Katalalixar National Reserve (KNR) in central Patagonia, (B) Collection sites of *Lessonia spicata*, Torpedo Island (red circle) and Castillo Channel (blue circle) in the oceanic margin of the Campana Archipelago (KNR). [Full-size !\[\]\(ba1b80118482ccef74a5d718ca4d7242_img.jpg\) DOI: 10.7717/peerj.7610/fig-1](https://doi.org/10.7717/peerj.7610/fig-1)

understand the taxonomic composition and biogeography of macroalgae that inhabit the southern boundary of the Humboldt Current (*Camus, 2001; Thiel et al., 2007*).

The present study contributes the first report of the species *L. spicata* in the Magellan Sub-Antarctic Channels. The distribution of this was thought to be limited to 41°S, but appears to be extended south of the Golfo de Penas (46° 59'–47° 40'S). Continuing survey studies will be necessary to understand the occurrence patterns of populations of *L. spicata* in the MBP.

MATERIALS AND METHODS

Three individuals of *Lessonia spicata* were collected in the intertidal zone of Torpedo Island and Castillo Channel (Figs. 1A and 1B) in July, 2018. The specimens were air-dried and then pressed on herbarium sheets for morphological observation and molecular analysis. The Chilean Hydrographic and Oceanographic Service of the Navy (N° 13270/24/337) approved field sampling.

External and internal morphological observations were made. The anatomical observations were performed by sectioning with a razor and staining with 1% aqueous aniline blue acidified with 1% diluted HCl, and mounted in 70% glycerin.

Photomicrographs were taken with a Canon Powershot S5 IS camera attached to a BX 51

Olympus microscope (Canon USA, Melville, NY, USA; Olympus Corp., Tokyo, Japan, respectively). A total of 15 replicates from the three individuals were selected for measurement of cortical cell diameter following [González et al. \(2012\)](#); means and standard deviations were calculated. Samples of other species occurring in the Sub-Antarctic region (*L. flavicans* and *L. searlesiana*) were also analyzed for comparative purposes. Voucher specimens were deposited in the herbarium of University of Magallanes, Punta Arenas, Chile.

Molecular analyses

Genomic DNA was extracted from ~5 mg of dried thallus ground in liquid nitrogen using a NucleoSpin Plant II Kit (Macherey-Nagel, Düren, Germany) according to the manufacturer's protocol. The PCR primers for the ITS were ITSP1-ITSr1 ([Tai, Lindstrom & Saunders, 2001](#); [Martin & Zuccarello, 2012](#)) and KP5- KG4 ([Lane et al., 2006](#)). Polymerase chain reaction products were purified using a NucleoSpin Gel and PCR Clean-up (Macherey-Nagel, Düren, Germany) and commercially sequenced (Macrogen, Seoul, South Korea). The electropherograms were edited using the Chromas v1.45 software ([McCarthy, 1998](#)) and the new generated sequences were deposited in GenBank (www.ncbi.nlm.nih.gov/genbank/).

A total of 34 ITS sequences (731 bp) were included in the construction of the phylogeny: 31 sequences belonging to the genus *Lessonia* and three outgroups, *Cymathaere triplicata* (Postels & Ruprecht) J. Agardh, *Ecklonia cava* Kjellman and *Macrocystis pyrifera* (Linnaeus) C. Agardh ([Table 1](#)). Sequences were aligned using the MUSCLE algorithm in MEGA5 v.6.06 software using the default settings ([Tamura et al., 2013](#)).

The phylogenetic analysis was constructed using maximum likelihood (ML) and Bayesian inference (BI) analyses. The program PartitionFinder ([Lanfear et al., 2012](#)) were used to choose the best-fitting nucleotide substitution model under the Bayesian Information Criterion. The general time-reversible nucleotide substitution model with a gamma distribution and a proportion of invariable sites (GTR + Γ + I) was selected as the best substitution model. Maximum likelihood analysis was performed with the RAxML HPC-AVX program ([Stamatakis, 2014](#)) implemented in the raxmlGUI 1.3.1 interface ([Silvestro & Michalak, 2012](#)) with the statistical support obtained by 1,000 bootstrap replications. Bayesian inference was performed with the MrBayes v. 3.2.5 software ([Ronquist et al., 2012](#)) using Metropolis-coupled Markov Chain Monte Carlo (MC³). The inference of Bayesian posterior probability (BPP) was inferred following [Calderon & Boo \(2017\)](#).

The neighbor-joining analysis was performed in MEGA5 v.6.06 with the default settings software, using 1,000 bootstrap replicates.

RESULTS

This is the first confirmed report of *L. spicata* in the Sub-Antarctic region, extending its distribution to the south by seven degrees of latitude ([Fig. 2A](#)). The sporophytes collected in the two localities have cylindrical stipes, flattened toward the beginning of the blades, with a regular, almost dichotomous long lanceolate blade with a spike ([Figs. 2B–2E](#)).

Table 1 List of species used in DNA analyses, information on collections and accession numbers in GenBank (sequences generated in the present study are shown in bold).

Species	Collection site	Voucher code	ITS
LesA	Torpedo island, Aysen, Chile		MN061669
LesB	Channel Castillo, Aysen Chile		MN061670
LesC	Channel Castillo, Aysen, Chile		MN061671
<i>Lessonia adamsiae</i>	South Promontory, The Snares, New Zealand	A626	GU593802 ¹
<i>Lessonia adamsiae</i>	Tahi, The Snares, New Zealand	A614	GU593799 ¹
<i>Lessonia berteroa</i> (as <i>L. nigrescens</i> northern lineage)	San Marcos, Tarapaca, Chile	B858	GU593781 ¹
<i>Lessonia berteroa</i> (as <i>L. nigrescens</i> northern lineage)	San Marcos, Tarapaca, Chile	B859	GU593782 ¹
<i>Lessonia brevifolia</i>	Smoothwater Bay, Campbell Is., New Zealand	A548	GU593803 ¹
<i>Lessonia brevifolia</i>	Antipodes, New Zealand	A973	GU593804 ¹
<i>Lessonia brevifolia</i>	Perseverance Harbour, Campbell Is., New Zealand	B296	GU593805 ¹
<i>Lessonia corrugata</i>	Gov. Is. Reserve, Tasmania, Australia		AY857902 ²
<i>Lessonia corrugata</i>	Bicheno, Tasmania, Australia	A985	GU593794 ¹
<i>Lessonia corrugata</i>	Skeleton Pt., Tasmania, Australia	C057	GU593795 ¹
<i>Lessonia flavicans</i>	Rookery Bay, East Falkland, Falkland Islands	A634	GU593786 ¹
<i>Lessonia flavicans</i> (as <i>Lessonia vadosa</i>)	Punta Arenas, Patagonia, Chile	B985	GU593789 ¹
<i>Lessonia spicata</i> (as <i>L. nigrescens</i> IA lineage)	La Pampilla, Coquimbo, Chile	A581	GU593775 ¹
<i>Lessonia spicata</i> (as <i>L. nigrescens</i> IA lineage)	Bahia Mansa, Osorno, Chile	B719	GU593780 ¹
<i>Lessonia tholiformis</i>	Wharf reef, Owenga, Chatham Is, New Zealand	A518	GU593797 ¹
<i>Lessonia tholiformis</i>	Wharekauri, Chatham Is, New Zealand	A532	GU593798 ¹
<i>Lessonia trabeculata</i>	Punihuil, Chiloe Is, Chile	B715	GU593783 ¹
<i>Lessonia trabeculata</i>	Punihuil, Chiloe Is, Chile	B716	GU593784 ¹
<i>Lessonia variegata</i> (as <i>L. variegata</i> lineage N)	North Cape, Northland, New Zealand	A557	GU593808 ¹
<i>Lessonia variegata</i> (as <i>L. variegata</i> lineage N)	Maitai Bay, Northland, New Zealand	B129	GU593809 ¹
<i>Lessonia variegata</i> (as <i>L. variegata</i> lineage N)	The Sailors Grave, Coromandel, New Zealand	B312	GU593810 ¹
<i>Lessonia variegata</i> (as <i>L. variegata</i> lineage K)	South Bay, Kaikoura, New Zealand	A138	GU593817 ¹
<i>Lessonia variegata</i> (as <i>L. variegata</i> lineage K)	New Wharf, Kaikoura, New Zealand	A606	GU593818 ¹
<i>Lessonia variegata</i> (as <i>L. variegata</i> lineage S)	Curio Bay, Catlins, New Zealand	A434	GU593820 ¹
<i>Lessonia variegata</i> (as <i>L. variegata</i> lineage S)	Causet Cove, Doubtful Sound, New Zealand	C154	GU593821 ¹
<i>Lessonia variegata</i> (as <i>L. variegata</i> lineage W)	Princess Bay, Wellington, New Zealand	A001	GU593811 ¹
<i>Lessonia variegata</i> (as <i>L. variegata</i> lineage W)	Cape Palliser, Wairarapa, New Zealand	A613	GU593815 ¹
<i>Lessonia variegata</i> (as <i>L. variegata</i> lineage W)	Riversdale Beach, Wairarapa, New Zealand	A025	GU593816 ¹
<i>Cymathaere triplicata</i>	Whiffen Spit, Sooke, BC, Canada		AY857884 ²
<i>Macrocystis pyrifera</i>	California, USA		AF319037 ³
<i>Ecklonia cava</i>			GU593773 ¹

Notes:¹ Martin & Zuccarello (2012).² Lane et al. (2006).³ Yoon et al. (2001).**Internal anatomy**

Our specimens showed several layers of cortical tissue with cells of smaller diameter compared to *L. searlesiana* (Figs. 3B, 3E, and 3H) and *L. flavicans* (Figs. 3C, 3F, and 3I), moreover no lacunas were observed in our samples, unlike *L. flavicans* (Figs. 3C and 3H).

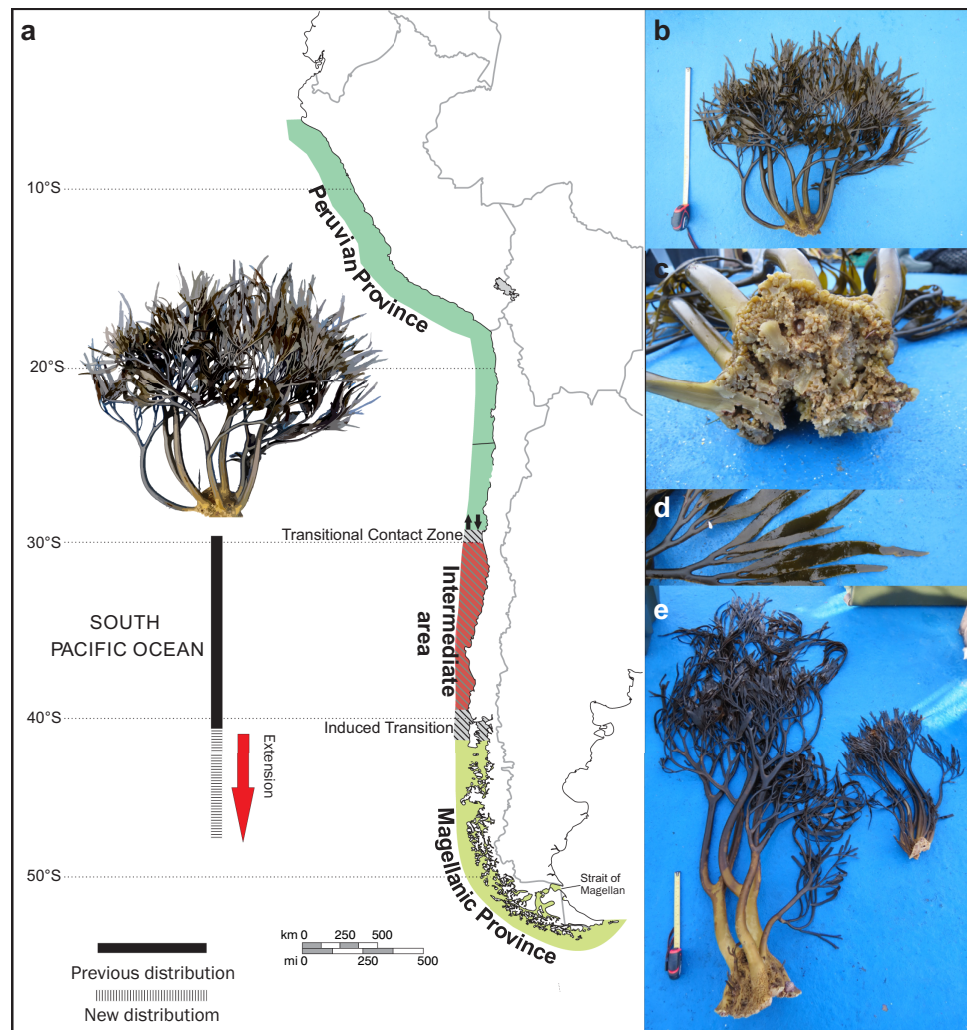


Figure 2 Distribution of *Lessonia spicata* (interspersed bars), showing its previously known distribution (solid bars). (A) Habitat of specimen collected in both sites (Torpedo Island and Castillo Channel). We included the Chilean biogeographical classification of Camus (2001). (B) Habitat of specimen collected in Torpedo Island (LMS000001). (C) Discoid holdfasts of specimen collected in Torpedo Island (LMS000001), (D) Blades of specimen collected in Torpedo Island (LMS000001), (E) Habitat of specimen collected in Castillo Channel (LMS000002, LMS000003).

Full-size DOI: 10.7717/peerj.7610/fig-2

The medulla was composed of elongated medullary cells with filamentous elements (Fig. 3G). The internal anatomy was composed of a narrow cortex (Fig. 3A), with cortical cell diameter of 25.91 ± 2.90 for the individual 1, 28.22 ± 2.10 for individual 2 and 27.02 ± 2.27 for the individual 3 (Table 2).

Phylogenetic analysis

The ITS phylogeny placed our specimens within the lineage of *L. spicata* of central Chile (Fig. 4A). The phylogenetic trees constructed by ML and BI had the same topology except for the phylogenetic position of *L. corrugata* and *L. variegata* from northeastern South Is. The three specimens analyzed consistently formed a strongly supported clade with

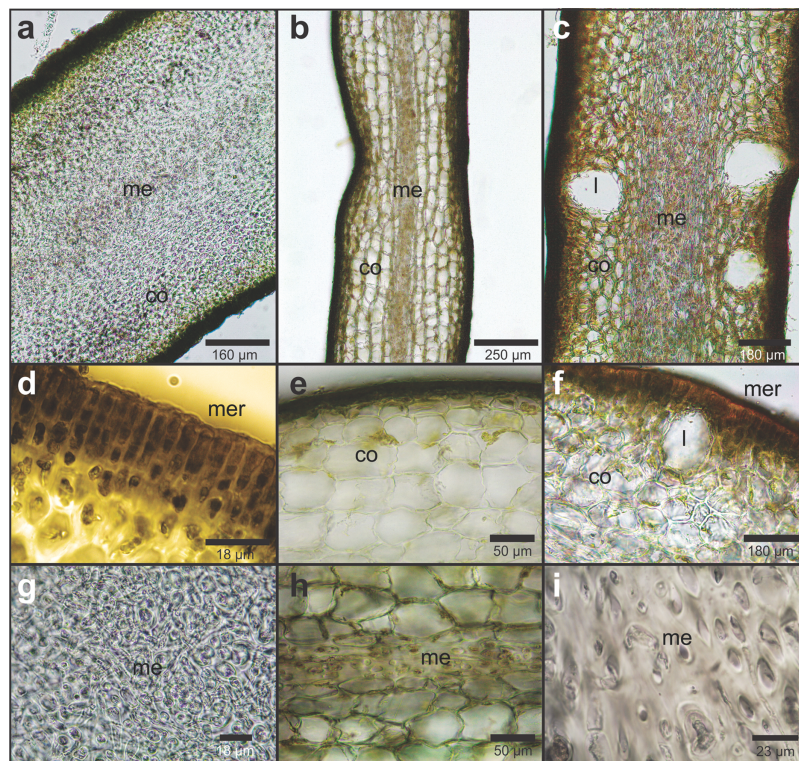


Figure 3 Cross section of the medial part of mature fronds of *Lessonia* species who inhabit the Sub-Antarctic channels. Cross section of the medial part of mature fronds of *Lessonia spicata* collected in the Katalalixar Reserve (A, D and G), of *L. searlesiana* from Fuerte Bulnes (B, E and H) and *L. flavicans* from Horn Island (C, F and I); mer = meristoderm, co = cortex and me = medulla, l = lacuna.

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Table 2 Morphological measurements (mean \pm SE) of individuals collected in Torpedo Island and Castillo Channel.

Individual	Site	External measurements			Internal measurements	
		TL	DD	NS	DC	
1	Torpedo Island	68	10	9	25.91 \pm 2.90	This study
2	Castillo Channel	166	21	6	28.22 \pm 2.10	This study
3	Castillo Channel	55	5	13	27.02 \pm 2.27	This study
Average		96.33 \pm 60.68	12 \pm 8.19	9.33 \pm 3.51	27.05 \pm 1.15	This study
<i>L. spicata</i>						
	Maintencillo	150 \pm 13.3	–	–	25.7 \pm 1.4	(González et al., 2012)
	Matanzas	160 \pm 5.0	–	–	27 \pm 1.6	(González et al., 2012)
	Calfuco	120 \pm 7.2	–	–	30 \pm 1.8	(González et al., 2012)

Note: External morphological data: TL, thallus length (cm); DD, disc diameter; NS, number of stipes. Internal morphological data: DC, diameter of cortical cells.

sequences of *L. spicata* (97% for ML and 0.96 for BPP) collected in Chile; having to *L. berteroa* and *L. trabeculata* as sister taxa. The cladogram was consistent with the phylogenetic tree (Fig. 4B). Variable sites occurred at 201 positions (27.5%), and 123

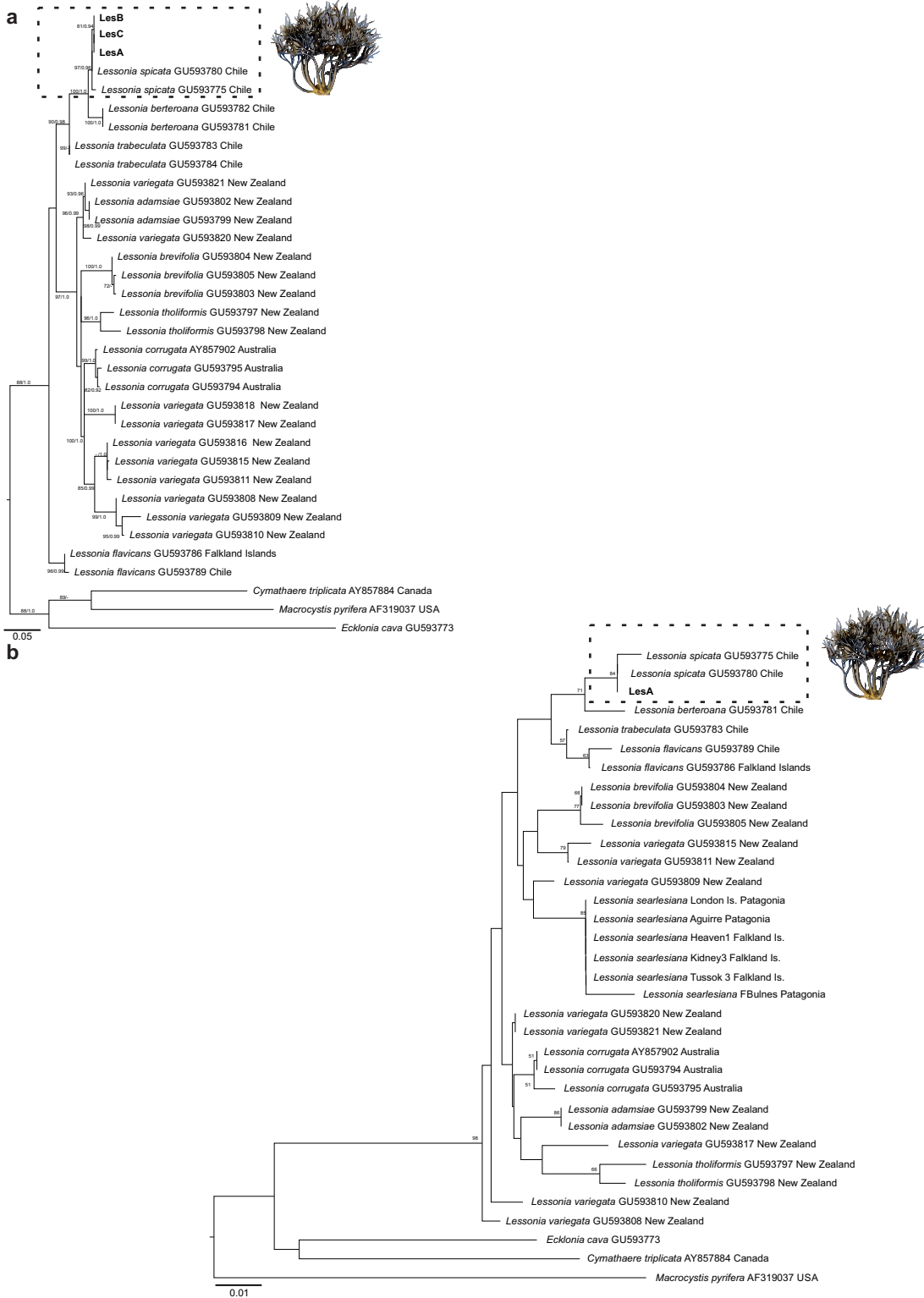


Figure 4 Phylogenetic tree of ITS sequences obtained by maximum likelihood (ML) inference. (A) Phylogenetic tree of ITS sequences obtained by maximum likelihood (ML) inference. ML bootstrap values ($\geq 50\%$) and Bayesian posterior probabilities (≥ 0.90) are indicated next to branches. (B) Cladograms of ITS sequences obtained by the neighbor joining (NJ) method. Bootstrap values ($\geq 50\%$) are indicated next to branches. The sequence for taxa in bold was generated in this study. [Full-size !\[\]\(5fd6ef84f97f42d7f8b34275f1b65312_img.jpg\) DOI: 10.7717/peerj.7610/fig-4](https://doi.org/10.7717/peerj.7610/fig-4)

positions (16.8%) were parsimoniously informative. Intraspecific divergence of *L. spicata* from three different populations ranged between 0.0% and 0.2% (0–3 bp). *L. spicata* differed by 0.8–1.0% from *L. berteroana* and by 1.1–1.3% from *L. trabeculata*. *L. variegata* is a non-monophyletic species complex of four different species.

DISCUSSION

We confirm here the presence of *L. spicata* both morphologically and genetically, whose individuals correspond to the central Chile lineage described by [González et al. \(2012\)](#). Morphologically these features correspond to those described for *L. spicata* by [von Suhr \(1839\)](#) and [González et al. \(2012\)](#). These values also agree with those mentioned by [González et al. \(2012\)](#) for *L. spicata*. Genetically our phylogeny is consistent with those of previous studies that show *Lessonia* as a monophyletic lineage ([Lane et al., 2006](#), [Martin & Zuccarello, 2012](#)).

Lessonia species are a characteristic component of benthic ecosystems in this region ([Searles, 1978](#); [Martin & Zuccarello, 2012](#)). We highlight two aspects about the importance of this report of *L. spicata* for this area: (a) we increase the knowledge of the species richness of kelps for the Sub-Antarctic Channels, and (b) this species has a strong extraction activity which we hypothesize that will move southward in the near future, therefore these populations should be properly preserved in order to prevent high risk of human impact.

The name *L. spicata* was proposed because it was the oldest name available to assign the lineage of central Chile, populations between 29° and 43°S. However, *L. spicata* would be a provisional name mainly because no representative specimens of *L. nigrescens* have been found near the type locality Cape Horn. Therefore, if the true *L. nigrescens* belongs to one of the lineages already described or to a new one, this name would have priority ([González et al., 2012](#)). In the MBP *L. nigrescens* has been recorded not only for Cape Horn; [Searles \(1978\)](#) reported a population in the Trinidad Channel (Puerto Alert 49° 53.6 'S), and two others in the Aysén region ([Searles, 1978](#)). Puerto Alert is 126 km south of Castillo Channel where we found the population of *L. spicata*. Therefore, it is likely that Searles' records (1978) correspond to populations of *L. spicata*. Finally, it is important to mention that, like [González et al. \(2012\)](#), in recent expeditions to the Diego Ramirez and Cape Horn archipelago—which are related to the characterization of the Diego Ramírez-Drake Passage Marine Park ([Rozzi et al., 2017](#))—we have not found populations of *L. nigrescens*, only individuals of *L. flavicans* ([Rozzi et al., 2017](#)). Therefore, in the absence of biological material from the type locality the status of *L. nigrescens* is still in doubt, and the lineage of central Chile that now extends south of 43°S should continue to be named as *L. spicata*.

Several bio-geographical breaks have been described along the coast of Chile ([Santelices & Meneses, 2000](#); [Tellier et al., 2009](#); [Fraser et al., 2010](#)); one of the most relevant for many taxa is at 42°S ([Brattström & Johanssen, 1983](#); [Lancellotti & Vásquez, 1999](#); [Valdovinos, Navarrete & Marquet, 2003](#)). For macroalgae and particularly for kelp species such as *Durvillaea antarctica*, a marked divergence is present south of 43°S, where populations between 49 and 55°S are genetically different from the rest of the populations

occurring in the Chilean coast (32 and 43°S) (Fraser et al., 2010). These authors suggested that although *D. antarctica* has a high dispersion capacity due to its buoyancy (rafting), it could only colonize free coasts, since it would have limited potential to increase gene flow between established populations. Therefore, it is interesting that although *L. spicata* has a low-dispersal capacity in comparison to *D. antarctica* (Oppliger et al., 2012), since it does not have the buoyancy capacity, there is a single genetic unit in the individuals collected in this study and individuals from the central zone of Chile. *L. spicata* must have some physiological adaptations which allowed it to colonize and inhabit areas of high latitudes. In this sense, this species has been described as a perennial seaweed and has not been found in the “bank of microscopic forms” in the Chilean central coast (boulders and water from tidal pools) (Santelices et al., 1995; Santelices, Aedo & Hoffmann, 2002). However, it has been observed that microscopic form of *L. spicata* can survive up to 90 days in total darkness and propagules can germinate in total absence of light (Santelices, Aedo & Hoffmann, 2002). This high capacity for tolerance to darkness could be a key strategy to colonize new areas with a significant seasonal changes in daylight hours and luminosity (Photosynthetically Active Radiation) during the winter period (Ojeda et al., 2019). Nevertheless, future studies and a greater number of samples along the Chilean coast (mainly the area between 41 and 48°S) will help to elucidate its biogeographic history and how much structure and connectivity the populations of *L. spicata* present throughout their distribution (29–48°S).

The harvesting pressure on the genus *Lessonia* has increased alarmingly along the Chilean coast, so we should take a precautionary approach to potential harvesting of *L. spicata* in its austral distribution range. *L. berteroa* (sister species of *L. spicata*) is currently the most exploited seaweed in South America; the main landings are in northern Chile (Westermeier et al., 2019). *Lessonia* is socially important in this region because many artisanal fishers depend directly or indirectly on its harvest (Vega, Broitman & Vásquez, 2014). However, high demand, lack of oversight and harvest methods have created a concerning scenario for kelp forests (Vega, Broitman & Vásquez, 2014; Westermeier et al., 2019). The extraction of *L. spicata* in southern Chile began in 2012, and its extractive pressure has been moving southward, mainly between 33 and 41°S (SERNAPESCA, 2019). In the Chilean Los Lagos Region (41°S), between 2014 and 2017 landing increased from 494 to 747 dry tons of *L. spicata* (SERNAPESCA, 2019). This gradual increase should draw attention to kelp forest conservation, since there is evidence on sustainability problems that *Lessonia* populations have experimented and their biodiversity in northern Chile (Vega, Asorey & Piaget, 2016). This concern acquires significant relevance if we consider that the Magellan Sub-Antarctic Channels are the austral distribution range of *L. spicata*, where kelp forest populations are important for sustainability of small-scale fisheries (e.g., king crab; Cárdenas, Cañete & Mansilla, 2007), indigenous traditions (Ojeda et al., 2018) and terrestrial and marine biodiversity (Darwin, 1839; Rosenfeld et al., 2014).

CONCLUSION

Despite the geographical distance and the presence of important biogeographic breaks (41 and 46°S), our results confirm that the individuals collected in the coastal zone of the

Katalalixar Reserve are the species *L. spicata*. The strong morphological and genetic evidence are indicating that the individuals analyzed are associated with the lineage of central Chile, and the populations of *L. spicata* would inhabit the area exposed to the Pacific.

With diverse industrial uses, including providing phycocolloids in the form of alginate *L. spicata* is a potentially important economic resource in the Chilean coast. However, with extractive pressure moving to the south, caution is needed given that this kelp serves not only as a habitat for many animals but also as a spawning ground for some benthic (e.g., gastropods) species.

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ADDITIONAL INFORMATION AND DECLARATIONS

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Competing Interests

The authors declare that they have no competing interests.

Author Contributions

- Sebastián Rosenfeld conceived and designed the experiments, performed the experiments, analyzed the data, contributed reagents/materials/analysis tools, prepared figures and/or tables, authored or reviewed drafts of the paper, approved the final draft, identify the species in the field, and collect it.

- Fabio Mendez conceived and designed the experiments, contributed reagents/materials/analysis tools, approved the final draft, help in the expedition.
- Martha S. Calderon conceived and designed the experiments, performed the experiments, analyzed the data, contributed reagents/materials/analysis tools, authored or reviewed drafts of the paper, approved the final draft.
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- Juan Pablo Rodríguez conceived and designed the experiments, contributed reagents/materials/analysis tools, prepared figures and/or tables, approved the final draft.
- Jaime Ojeda conceived and designed the experiments, contributed reagents/materials/analysis tools, prepared figures and/or tables, authored or reviewed drafts of the paper, approved the final draft.
- Johanna Marambio conceived and designed the experiments, contributed reagents/materials/analysis tools, prepared figures and/or tables, authored or reviewed drafts of the paper, approved the final draft.
- Matthias Gorny conceived and designed the experiments, contributed reagents/materials/analysis tools, approved the final draft, help in the expedition.
- Andrés Mansilla conceived and designed the experiments, contributed reagents/materials/analysis tools, approved the final draft, he contributed with the funding.

Field Study Permissions

The following information was supplied relating to field study approvals (i.e., approving body and any reference numbers):

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DNA Deposition

The following information was supplied regarding the deposition of DNA sequences:

The *Lessonia spicata* ITS sequences are accessible via GenBank: LesA [MN061669](#), LesB [MN061670](#), LesC [MN061671](#).

Data Availability

The following information was supplied regarding data availability:

The detailed information on the new records of *Lessonia spicata* are available in [File S1](#).

Supplemental Information

Supplemental information for this article can be found online at <http://dx.doi.org/10.7717/peerj.7610#supplemental-information>.

REFERENCES

- Ávila M, Hoffmann A, Santelices B. 1985. Interacciones de temperatura, densidad de flujo fotónico y fotoperíodo sobre el desarrollo de etapas microscópicas de *Lessonia nigrescens* (Phaeophyta, Laminariales). *Revista Chilena de Historia Natural* **58**:71–82.
- Bell NE, Pedersen N, Newton AE. 2007. *Ombronesus stuvensis*, a new genus and species of the Ptychomniaceae (Bryophyta) from south west Chile. *TAXON* **56**(3):887–896 DOI 10.2307/25065870.
- Brattström H, Johanssen A. 1983. Ecological and regional zoogeography of the marine benthic fauna of Chile: Report no. 49 of the Lund University Chile Expedition 1948–49. *Sarsia* **68**(4):289–339 DOI 10.1080/00364827.1983.10420583.
- Calderon MS, Boo SM. 2017. The Phyllophoraceae (Gigartinales, Rhodophyta) from Peru with descriptions of *Acletoa tarazonae* gen. & sp. nov. and *Gymnogongrus caespitosus* sp. nov. *Phycologia* **56**(6):686–696 DOI 10.2216/16-126.1.
- Camus PA. 2001. Biogeografía marina de Chile continental. *Revista Chilena de Historia Natural* **74**(3):587–617 DOI 10.4067/S0716-078X2001000300008.
- Cárdenas CA, Cañete JI, Mansilla A. 2007. Podding of juvenile king crabs *Lithodes santolla* (Molina, 1982) (Crustacea) in association with holdfasts of *Macrocystis pyrifera* (Linnaeus) C. Agardh, 1980. *Investigaciones Marinas* **35**:105–110 DOI 10.4067/s0717-71782007000100010.
- Cho GY, Klochkova NG, Krupnova TN, Boo SM. 2006. The reclassification of *Lessonia laminarioides* (Laminariales, Phaeophyceae): *Pseudolessonia* gen. nov. *Journal of Phycology* **42**(6):1289–1299 DOI 10.1111/j.1529-8817.2006.00280.x.
- Darwin C. 1839. *Voyages of the Adventure and Beagle. Vol. III. Journals and Remarks. 1832–1836.* London: Henry Colburn.
- Fraser CI, Thiel M, Spencer HG, Waters JM. 2010. Contemporary habitat discontinuity and historic glacial ice drive genetic divergence in Chilean kelp. *BMC Evolutionary Biology* **10**(1):203 DOI 10.1186/1471-2148-10-203.
- González A, Beltrán J, Hiriart-Bertrand L, Flores V, de Reviers B, Correa JA, Santelices B. 2012. Identification of cryptic species in the *Lessonia nigrescens* complex (Phaeophyceae, Laminariales). *Journal of Phycology* **48**(5):1153–1165 DOI 10.1111/j.1529-8817.2012.01200.x.
- Gorny M, Zapata-Hernández G. 2018. On the bathymetric and latitudinal distributions of *Coelrorinchus* cf. *cookianus* (Gadiformes: Macrouridae): first record documented with a remotely operated vehicle (ROV) in interior waters of the Campana Archipelago in central Patagonia, Chile (48°S). *Anales del Instituto de la Patagonia* **46**(2):29–36 DOI 10.4067/S0718-686X2018000200029.
- Guiry MD, Guiry GM. 2019. AlgaeBase. Available at <http://www.algaebase.org> (accessed 7 April 2019).
- Lancellotti DA, Vásquez JA. 1999. Biogeographical patterns of benthic macroinvertebrates in the Southeastern Pacific littoral. *Journal of Biogeography* **26**(5):1001–1006 DOI 10.1046/j.1365-2699.1999.00344.x.
- Lane CE, Mayes C, Druehl LD, Saunders GW. 2006. A multi-gene molecular investigation of the kelp (Laminariales, Phaeophyceae) supports substantial taxonomic re-organization. *Journal of Phycology* **42**(2):493–512 DOI 10.1111/j.1529-8817.2006.00204.x.
- Lanfear R, Calcott B, Ho SYW, Guindon S. 2012. PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution* **29**(6):1695–1701 DOI 10.1093/molbev/mss020.

- Mansilla A, Ávila M, Ramírez ME, Rodríguez JP, Rosenfeld S, Ojeda J, Marambio J. 2014. Macroalgas marinas bentónicas del submareal somero de la ecorregión Subantártica de Magallanes. *Chile Anales del Instituto de la Patagonia* 41(2):49–62 DOI 10.4067/S0718-686X2013000200004.
- Martin P, Zuccarello GC. 2012. Molecular phylogeny and timing of radiation in *Lessonia* (Phaeophyceae, Laminariales). *Phycological Research* 60(4):276–287 DOI 10.1111/j.1440-1835.2012.00658.x.
- McCarthy C. 1998. Chromas version 1.45. School of Health Science, Griffith University, Southport, Queensland Australia. Available at <http://www.technelysium.com.au/chromas.html>.
- Ojeda J, Marambio J, Rosenfeld S, Contador T, Rozzi R, Mansilla A. 2019. Seasonal changes of macroalgae assemblages on the rocky shores of the Cape Horn Biosphere Reserve, Sub-Antarctic Channels, Chile. *Aquatic Botany* 157:33–41 DOI 10.1016/j.aquabot.2019.06.001.
- Ojeda J, Rozzi R, Rosenfeld S, Contadora T, Massardo F, Malebrán J, González-Calderón J, Mansilla A. 2018. Interacciones bioculturales del pueblo yagán con las macroalgas y moluscos: una aproximación desde la filosofía ambiental de campo. *Magallania* 46(1):155–181 DOI 10.4067/S0718-22442018000100155.
- Oppliger VL, Correa JA, Engelen AH, Tellier F, Vieira V, Faugeton S, Valero M, Gomez G, Destombe C. 2012. Temperature effects on gametophyte life-history traits and geographic distribution of two cryptic kelp species. *PLOS ONE* 7(6):e39289 DOI 10.1371/journal.pone.0039289.
- Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP. 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61(3):539–542 DOI 10.1093/sysbio/sys029.
- Rosenfeld S, Ojeda J, Hüne M, Mansilla A, Contador T. 2014. Egg masses of the Patagonian squid *Doryteuthis* (Amerigo) *gahi* attached to giant kelp (*Macrocystis pyrifera*) in the sub-Antarctic ecoregion. *Polar Research* 33(1):1–5 DOI 10.3402/polar.v33.21636.
- Rozzi R, Massardo F, Mansilla A, Squeo FA, Barros E, Contador T, Frangopulos M, Poulin E, Rosenfeld S, Goffinet B, González-Weaver C, MacKenzie R, Crego RD, Viddi F, Naretto J, Gallardo MR, Jiménez JE, Marambio J, Pérez C, Rodríguez JP, Méndez F, Barroso O, Rendoll J, Schüttler E, Kennedy J, Convey P, Russell S, Berchez F, Sumida PYG, Rundell P, Rozzi A, Armesto J, Kalin-Arroyo M, Martinic M. 2017. Parque Marino Cabo de Hornos—Diego Ramírez. Technical report to the proposal for creation of the Cape Horn—Diego Ramírez Marin Park. Punta Arenas: Ediciones Universidad de Magallanes. Available at https://issuu.com/umag9/docs/ebook_low_parque_marino_umag_fin_di.
- Santelices B, Aedo D, Hoffmann A. 2002. Banks of microscopic forms and survival to darkness of propagules and microscopic stages of macroalgae. *Revista Chilena de Historia Natural* 75(3):547–555 DOI 10.4067/S0716-078X2002000300006.
- Santelices B, Hoffmann AJ, Aedo D, Bobadilla M, Otaíza M. 1995. The bank of microscopic forms on disturbed boulders and stones in tide pools. *Marine Ecology Progress Series* 129:215–228 DOI 10.3354/meps129215.
- Santelices B, Meneses I. 2000. A reassessment of the phytogeographic characterization of Temperate Pacific South America. *Revista Chilena de Historia Natural* 73(4):605–614 DOI 10.4067/S0716-078X2000000400005.
- Searles RB. 1978. The genus *Lessonia* Bory (Phaeophyta, Laminariales) in Southern Chile and Argentina. *British Phycological Journal* 13(4):361–381 DOI 10.1080/00071617800650421.

- SERNAPESCA. 2019.** Informe Final Control Cuota Algas Pardas I, III, IV y VII año 2018; Huiro Negro (*Lessonia berteroana/spicata*), Huiro Palo (*Lessonia trabeculata*), Huiro Macro (*Macrocystis pyrifera*) y Cochayuyo (*Durvillaea antarctica*). Unidad de Control de Cuotas, Subdirección De Pesquería, Chile. Available at http://www.sernapesca.cl/sites/default/files/informe_final_2018_bentonicos_algas_iii_y_iv.pdf.
- Silva N, Rojas N, Fedele A. 2009.** Water masses in the Humboldt current system: properties, distribution, and the nitrate deficit as a chemical water mass tracer for equatorial subsurface water off Chile. *Deep Sea Research Part II: Topical Studies in Oceanography* **56(16)**:1004–1020 DOI [10.1016/j.dsr2.2008.12.013](https://doi.org/10.1016/j.dsr2.2008.12.013).
- Silvestro D, Michalak I. 2012.** RaxmlGUI: a graphical front-end for RAxML. *Organisms Diversity & Evolution* **12(4)**:335–337 DOI [10.1007/s13127-011-0056-0](https://doi.org/10.1007/s13127-011-0056-0).
- Stamatakis A. 2014.** RAxML version 8: a tool for phylogenetic analysis and postanalysis of large phylogenies. *Bioinformatics* **30(9)**:1312–1313 DOI [10.1093/bioinformatics/btu033](https://doi.org/10.1093/bioinformatics/btu033).
- Steneck RS, Graham MH, Bourque BJ, Corbett D, Erlandson JM, Estes JA, Tegner MJ. 2002.** Kelp forest ecosystems: biodiversity, stability, resilience and future. *Environmental Conservation* **29(4)**:436–459 DOI [10.1017/S0376892902000322](https://doi.org/10.1017/S0376892902000322).
- Tai V, Lindstrom SC, Saunders GW. 2001.** Phylogeny of the Dumontiaceae (Gigartinales, Rhodophyta) and associated families based on SSU rDNA and internal transcribed spacer sequence data. *Journal of Phycology* **37(1)**:184–196 DOI [10.1046/j.1529-8817.2001.037001184.x](https://doi.org/10.1046/j.1529-8817.2001.037001184.x).
- Tamura K, Stecher G, Peterson D, Filipowski A, Kumar S. 2013.** MEGA6: molecular evolutionary genetics analysis version 6.0. *Molecular Biology and Evolution* **30(12)**:2725–2729 DOI [10.1093/molbev/mst197](https://doi.org/10.1093/molbev/mst197).
- Tellier F, Meynard AP, Correa JA, Faugeron S, Valero M. 2009.** Phylogeographic analyses of the 30°S south-east Pacific biogeographic transition zone establish the occurrence of a sharp genetic discontinuity in the kelp *Lessonia nigrescens*: vicariance or parapatry? *Molecular Phylogenetics and Evolution* **53(3)**:679–693 DOI [10.1016/j.ympev.2009.07.030](https://doi.org/10.1016/j.ympev.2009.07.030).
- Tellier F, Vega JMA, Broitman BR, Vasquez JA, Valero M, Faugeron S. 2011.** The importance of having two species instead of one in kelp management: the *Lessonia nigrescens* species complex. *Cahiers de Biologie Marine* **52(4)**:455–465.
- Thiel M, Macaya EC, Acuña E, Arntz WE, Bastias H, Brokordt K, Camus PA, Castilla JC, Castro LR, Cortés M, Dumont CP, Escribano R, Fernández M, Gajardo JA, Gaymer CF, Gomez I, González AE, González HE, Haye PA, Illanes JE, Iriarte JL, Lancellotti DA, Luna-Jorquera G, Luxoro C, Manriquez PH, Marín V, Muñoz P, Navarrete SA, Perez E, Poulin E, Sellanes J, Sepúlveda HH, Stotz W, Tala F, Thomas A, Vargas CA, Vasquez JA, Vega JMA. 2007.** The Humboldt current system of northern and central Chile: oceanographic processes, ecological interactions and socioeconomic feedback. *Oceanography and Marine Biology* **45**:195–344.
- Valdovinos C, Navarrete SA, Marquet PA. 2003.** Mollusk species diversity in the Southeastern Pacific: why are there more species towards the pole? *Ecography* **26(2)**:139–144 DOI [10.1034/j.1600-0587.2003.03349.x](https://doi.org/10.1034/j.1600-0587.2003.03349.x).
- Vásquez JA. 2008.** Production, use and fate of Chilean brown seaweeds: re-resources for a sustainable fishery. *Journal of Applied Phycology* **20(5)**:457–467 DOI [10.1007/s10811-007-9308-y](https://doi.org/10.1007/s10811-007-9308-y).
- Vásquez JA, Camus PA, Ojeda FP. 1998.** Diversidad, estructura y funcionamiento de ecosistemas rocosos del norte de Chile. *Revista Chilena de Historia Natural* **71**:479–499.
- Vásquez JA, Santelices B. 1984.** Comunidades de macroinvertebrados en discos adhesivos de *Lessonia nigrescens* Bory (Phaeophyta) en Chile central. *Revista Chilena de Historia Natural* **57**:131–154.

- Vega JMA. 2016.** Fauna asociada a discos de adhesión del complejo *Lessonia nigrescens*: Es un indicador de integridad ecológica en praderas explotadas de huiro negro, en el norte de Chile? *Latin American Journal of Aquatic Research* **44**(3):623–637
DOI [10.3856/vol44-issue3-fulltext-21](https://doi.org/10.3856/vol44-issue3-fulltext-21).
- Vega JMA, Asorey CM, Piaget N. 2016.** Asociación *Scurria-Lessonia*, indicador de integridad ecológica en praderas explotadas de huiro negro *Lessonia berteroa* (ex *L. nigrescens*) en el norte de Chile. *Revista de Biología Marina y Oceanografía* **51**(2):337–345
DOI [10.4067/S0718-19572016000200011](https://doi.org/10.4067/S0718-19572016000200011).
- Vega JMA, Broitman BR, Vásquez JA. 2014.** Monitoring the sustainability of *Lessonia nigrescens* (Laminariales, Phaeophyceae) in northern Chile under strong harvest pressure. *Journal of Applied Phycology* **26**(2):791–801 DOI [10.1007/s10811-013-0167-4](https://doi.org/10.1007/s10811-013-0167-4).
- Villouta E, Santelices B. 1984.** Estructura de la comunidad submareal de *Lessonia* (Phaeophyta, Laminariales) en Chile norte y central. *Revista Chilena de Historia Natural* **57**:111–122.
- Villouta E, Santelices B. 1986.** *Lessonia trabeculata* sp. nov. (Laminariales, Phaeophyta), a new kelp from Chile. *Phycologia* **25**(1):81–86 DOI [10.2216/i0031-8884-25-1-81.1](https://doi.org/10.2216/i0031-8884-25-1-81.1).
- von Suhr JN. 1839.** Beiträge zur Algenkunde. [N°3]. *Flora* **22**:65–75.
- Westermeier R, Murúa P, Patiño DJ, Manoli G, Müller DG. 2019.** Evaluation of kelp harvest strategies: recovery of *Lessonia berteroa* (Phaeophyceae, Laminariales) in Pan de Azucar, Atacama. *Chile Journal of Applied Phycology* **31**(1):575–585 DOI [10.1007/s10811-018-1500-8](https://doi.org/10.1007/s10811-018-1500-8).
- Yoon HS, Lee JY, Boo SM, Bhattacharya D. 2001.** Phylogeny of Alariaceae, Laminariaceae, and Lessoniaceae (Phaeophyceae) based on plastid-encoded RuBisCo spacer and nuclear-encoded ITS sequence comparisons. *Molecular Phylogenetics and Evolution* **21**(2):231–243
DOI [10.1006/mpev.2001.1009](https://doi.org/10.1006/mpev.2001.1009).