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Population biology and long-term mariculture studies in the brown alga *Lessonia trabeculata* in Atacama, Chile

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Abstract *Lessonia trabeculata* is one of the most valuable seaweeds in Chile, especially in the northern zone where its harvest has been going on for decades. We carried out population dynamics studies in the Atacama Desert coast (Bahia Chasco), in order to assess its productivity under natural and harvesting scenarios. We found very slow but consistent growth (1.98 cm month^{-1}) and density (3–4 individuals m^{-2} with no monthly variation) during 18 months of observations in an undisturbed subpopulation. However, after total harvesting, *L. trabeculata* exhibited different responses. Its recruitment was season-specific, with exceedingly high values in autumn (ca. 80 individuals m^{-2} in 5 months) and a dramatic reduction of recruits in summer (1–5 individuals m^{-2} in 7 months, with many areas with no recruitment). Gradually, density values tended to stabilize to growth rates under unaltered conditions. In parallel, pruning systems at three different thallus levels (frond meristem base cuts, removal of half and total canopy) were all inefficient and harmful: (i) Biomass takes longer to be harvested; (ii) pruned individuals die off; and (iii) do not detach easily from the substrata, delaying the recovery by potentially emerging *L. trabeculata* juveniles. Some of these results agreed with our culture experiments, where 26 months were needed to obtain up to 100 cm long thalli with shrub-like morphology. We conclude that management of *L. trabeculata* beds must be improved in order to guarantee survival of the industry, and we propose some practices that at some stage should involve the complete removal of older/senescent individuals.

Keywords *Lessonia trabeculata* · Huiro palo · Population dynamic · Kelp aquaculture · Wild harvest · Pruning · Sustainable management

Introduction

Kelps are key components in coastal communities worldwide (Schiel and Foster 2015). Since its taxonomical characterization by Villouta and Santelices (1986), *Lessonia trabeculata* (a.k.a. huiro palo) has been one of the most preferred target species for kelp ecology and fishery studies in Chile. Its unique characteristics (2 m plants forming perennial populations in the subtidal, slow growth and long life span) have made it one of the most exploited kelps in the country for alginate production. Morphological and phylogenetic studies confirmed its presence from Peru along the entire Chilean coast, forming non-continuous populations down to 20-m depth (Villouta and Santelices 1984; Hoffmann and Santelices 1997; Cho et al. 2006; Martin and Zuccarello 2012), and occasionally in intertidal areas when substratum is available (Villouta and Santelices 1986). This stability makes it one of the most important biomass resources in the Southeastern Pacific, sustaining a significant number of understory marine organisms within its forests (Villegas et al. 2008; Uribe et al. 2015; Stotz et al. 2016). It also has been

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suggested as a pollution bioindicator and putatively as a candidate to clean mining wastewaters, due to its capacity to retain heavy metals for long periods as living or dehydrated material (Sáez et al. 2012; Escudero et al. 2015; Manoli et al. 2015).

Lessonia trabeculata is also one of the most economically important kelps in Chile, being intensely harvested for alginate extraction and abalone feed (Westermeier et al. 2011). By the beginning of 2000, only ca. 18,000 t FW were annually produced, almost all collected from naturally drifted biomass (Sernap 1990; Vásquez and Santelices 1990). In only 15 years, this amount has been increased by more than three times with an important input from direct subtidal harvesting (Westermeier et al. 2006), especially fresh fronds collected for abalone feed. Clandestine fisheries have become increasingly more common since then, affecting the local beds with direct consequences on the associated flora and fauna (Ortiz 2010). So far, several alternatives for management plans and culture have been developed in order to stop the cumulative deforestation on this species (Edding and Tala 2003; Westermeier et al. 2006; Vásquez 2008; Ortiz 2010). In spite of having significant knowledge about kelp biology and ecology, there is no total agreement among local fishermen, governmental entities and the academia about how this resource should be managed. However, new Chilean seaweed policies that are currently developed include proposals such as (i) transformation of significant coastline sections from free access areas to fisher-managed areas that require detailed management plans and (ii) encouraging kelp aquaculture and restoration. This new scenario gives optimism about the fate of *L. trabeculata* and other macroalgae in Chile.

In Bahia Chasco, 40 t of kelps (mainly *M. pyrifera*) are harvested every day from the subtidal (Westermeier et al. 2014). In this locality, *L. trabeculata* is subjected to harvest by local fishermen usually when the sympatric *M. pyrifera* population decreases, since abalone facilities demand fresh kelp biomass on a regular basis. In contrast to *M. pyrifera*, where usually the whole thallus of older/senescent plants is collected, in *L. trabeculata*, only fronds are selectively harvested, and the remaining stipes and holdfasts are left attached to the sea bottom. It is doubtful whether this is the best way to harvest *L. trabeculata*, since the meristems in the stipes are unable to regenerate the fronds because of the slow growth of the species. As a final outcome, plants remained strongly attached to the substrata but with a reduced capacity to growth, which finalize in the premature death of the individuals. Our present work aimed to study *L. trabeculata* population dynamics in order to look for appropriate ways to manage the resource and to establish guidelines for its long-term sustainability.

Materials and methods

Species main features

Lessonia trabeculata is a laminarean species (Lessoniaceae) with a haplo-diplont life cycle, with the sporophyte as the visible thallus in nature. It usually can be found not only in the subtidal growing on rocky platforms or strongly attached on boulders, but also may overlap with the intertidal species *L. nigrescens* (Villouta and Santelices 1986). Meristematic zones of *L. trabeculata* may be grouped as apical (apical region of the fronds, meristoderm) and intercalary (e.g. basal blade and main stipe) (Hoffmann and Santelices 1997 and references therein). In spite of having similar anatomical characteristics with other *Lessonia* species, *L. trabeculata* is the kelp with the slowest growth rate in northern Chile, making a challenge to implement effective aquaculture and restoration programs for its populations nowadays (Westermeier et al. 2006).

Study area

A population biology study was conducted between December 2013 and May 2015 at Bahia Chasco in the Atacama coast (27°41′ S; 71°00′ W), within a *L. trabeculata* kelp bed estimated to cover 221–246 ha and 31,000 t FW (Zavala et al. 2010). Three years before (December 2010), an experimental mariculture facility was installed 62 km north, in a Hidrocultivos S.A. aquaculture facility in Bahia Inglesa (27°05′ S; 70°52′ W). According to Westermeier et al. (2014), around Bahia Chasco nutrients (ammonium $\leq 10\ \mu g\ L^{-1}$, nitrate $= 212\ \mu g\ L^{-1}$ and orthophosphate $= 84\ \mu g\ L^{-1}$) were abundant in winter, whereas the temperature (19 °C) and primary productivity (3 m water transparency with Secchi disc) reached their peaks in summer seasons between 2011 and 2013.

Population dynamics in intact areas

Our population biology studies followed the details given by Westermeier et al. (2014). An area of 45 m^2 at 8 m within the Bahia Chasco *L. trabeculata* bed was marked and, in cooperation with local fishermen, excluded from human interference during the sampling period. With a monthly frequency, the recruitment, total length, holdfast diameter, density and individual's reproductive were counted and measured from twelve 1-m^2 quadrats randomly placed on this area. The recruitment (recruits m^{-2}, detectable >0.5 cm thallus length) was quantified by identifying and counting new and older recruits, in each 1 m^2 replicate. Average frond length (cm), holdfast diameter (cm) and density were determined by counting and measuring all specimens in each 1 out 12 m^2 replicate. Prevalence of reproductive individuals was expressed as the average percentage of individuals within each quadrat bearing vegetative fronds (with visible sori).

Recovery after complete harvesting

In two 30-m^2 areas, all the biomass from visible *L. trabeculata* and other prominent algae was completely harvested (sensu Westermeier et al. 2014), one per season: autumn (May 2014) and summer (December 2015). Within these areas, twelve 1-m^2 quadrats were also randomly distributed and new recruits as well as additional indicators (see above) were sampled monthly in each quadrat after these interventions.

Recovery after pruning treatments

Adult and juvenile specimens of *L. trabeculata* (sensu Villouta and Santelices 1986) were randomly selected and individually labelled within the bed at Bahia Chasco. Pruning treatments were applied at three different thallus levels: (i) cuts above the basal meristem in the blades (frond meristem base cuts), (ii) removal of half and (iii) all of the canopy (Fig. 1a–c). The thallus recovery after pruning was assessed monthly in 15 replicates, measuring the total length and holdfast growth.

Long-term mariculture studies

Unialgal gametophyte cultures were started following the cultivation method detailed in Westermeier et al. (2005) and Murúa et al. (2013) from sori collected during 2009 in Bahia Inglesa. Culture conditions for gametogenesis, fertilization and sporophyte growth followed Westermeier et al. (2006), upscaling from 400 mL bags with Provasoli enriched seawater to 1–5 L bottles, 20–50 L cylinders and 1000-L greenhouse tanks with constant seawater supply. Once seedlings reached 6 cm, they were outplanted to Bahía Salado on 10 m polypropylene long-lines at a density of 6 individuals m^{-1}. These lines were installed horizontally at 8 m depth. Total length, holdfast diameter and weight were measured regularly in random thalli.

Growth rate under different growth conditions

In every experiment, 10–15 individuals were labelled and their growth (thallus length and holdfast diameter) was tracked during the entire sampling period. Relative growth rates (RGR) were calculated after Evans (1992), using the ratio between (i) the difference of the natural logarithm of final and the initial size, and (ii) the time they were sampled. Rates were adjusted to percentage per month (% month^{-1}) for graphics. Box plot graphs were generated using the R package ggplot2 (Wickham 2009).

Statistical analyses

Statistical analyses were carried out using R (R Core Team 2013). In order to demonstrate monthly differences in size (thallus and holdfast diameter), density, weight and prevalence of reproductive individuals, Kruskal-Wallis tests were performed for every treatment (intact zone, total harvests in autumn and summer, pruning systems and mariculture). Additionally, a Kruskal-Wallis test was carried out to compare different treatments in terms of their RGR (total thallus length and holdfast diameter). Post hoc Wilcoxon rank-sum pairwise tests with Bonferroni corrections were run to determine different RGR groups. A p value less than 0.05 was considered statistically significant.

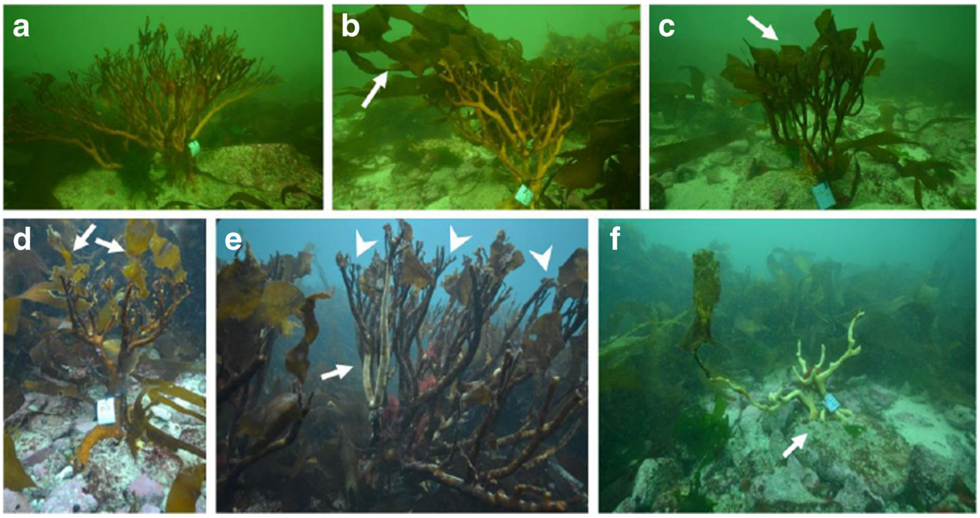

Fig. 1 Pruning consequences in *L. trabeculata*. **a** Total canopy removal. **b** Half canopy removal, leaving the other half untouched (*arrow*). **c** Cuts at the frond base, leaving part of the frond basal meristems (*arrow*). **d** Apical erosion of fronds (*arrows*). **e** Erosion and bleaching of stipes (*arrow*) and loss of frond leftovers (*arrowhead*). **f** Frond destruction and stipe bleaching but holdfast still strongly attached to substrata (*arrow*)

Results

Population dynamics in intact areas

Fully grown individuals of *L. trabeculata* (above 120-cm length) at Bahia Chasco formed a stable population if human intervention was excluded. In 17 months, they increased ca. 50 cm in total length and almost kept constant their holdfast diameter at 30 cm (Figs 2a, b). These growths were mild but significant ($p < 0.05$, Table 1). This stagnancy was also reflected by the mild increases of the main stipe diameter (median around 3.5 cm) and number of stipes (median = 3 stipes) (not shown), as well as population density and reproductive individuals, which statistically did not change ($p > 0.05$; Table 1). Density was unchanged after the second month (median = 4 individuals m^{-2}) as well as the prevalence of the reproductive individuals of the populations (above 90% individuals reproductive; Figs 2c, d). The population consisted mainly of adult individuals, with no evidence of recruitment in the entire period.

Recovery after complete harvesting

Recruitment of *L. trabeculata* in harvested areas was highly seasonal, and both thallus size and holdfast increase over the sampling time ($p < 0.05$, Table 1). It was highest after autumn removal, started within 3 months and showed exceedingly high numbers in the fourth and fifth month around 60 and 85 individuals m^{-2}, respectively, with sizes no more than 20 cm (Figs 3a, c). Once young individuals started to grow, their density declined dramatically, dropping to ca. 12 individuals m^{-2} when plants reached between 40 and 50 cm, 8 cm holdfast and several stipes 1 year after the intervention.

Summer removal was unfavourable. First very scattered recruits appeared only after 5 months. Maximum densities were found with 5 individuals m^{-2} after 7 months (Fig. 3d). Only 5 out of 12 quadrants were actually repopulated by *L. trabeculata*, while the others were occupied by *Ulva* and similar ubiquists. Some *Lessonia* thalli reached up to 50 cm, but most did not exceed 25 cm in length (Fig. 3b), 2 cm holdfast and 2 stipes. None of the recruitment cohorts from autumn or summer harvests developed reproductive fronds within 1 year.

Recovery after pruning systems

Within the first months after pruning, a decrease of the total length in almost all our treatments occurred by apical erosion (Fig. 1d). Even though an increase in total length and holdfast size was recorded for many treatments in most labelled specimens, thallus destruction was observed afterwards. This deterioration was more evident in the holdfast, which usually decreased in size. In spite of the growth stagnation, thallus discolorations by meristem and cortex erosions in stipes were often associated with dead individuals after the fourth month, especially in completely pruned plants (Fig. 1e). From the sixth month onward, these moribund thalli were dramatically bleached and remained strongly attached to the substrate during the whole sampling period (Fig. 1f). There was no significant variation in thallus size for any of these pruning treatments ($p > 0.05$, Table 1).

Long-term mariculture studies At least 30 weeks was needed to produce seedlings larger than 6 cm in the laboratory (Figs 4a, b). These specimens developed holdfasts

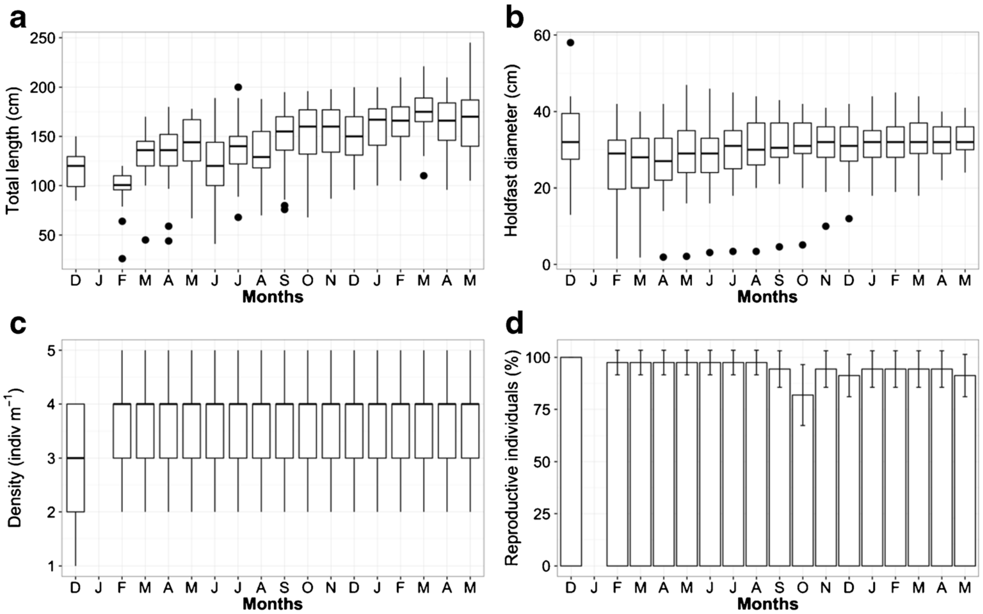

Fig. 2 Growth and development of *L. trabeculata* in a natural population at Bahia Chasco between December 2013 and May 2015. **a** Total length (cm). **b** Holdfast diameter (cm). **c** Density (individuals m^{-2}). **d** Reproductive individuals (%). *Boxes* show median (*horizontal line*) ± 1.5 times the interquartile range (*whiskers*). *Black dots* represent deemed outliers

Table 1 Statistical results (Kruskal-Wallis) of seasonality on *L. trabeculata* anatomical parameter variations and growth rates after different harvest methods

	Monthly variation			
Treatment	Parameter	Chi-squared	*df*	*p* value
Intact area (control)	**Thallus length**	**153.77**	**16**	**
	Holdfast diameter	**26.317**	**16**	*
	Density	14.337	16	#
	Reproductive individuals	18.409	16	#
Total harvest in autumn	**Thallus length**	**758.32**	**12**	**
	Density	**781.83**	**12**	**
Total harvest in summer	**Thallus length**	**48.401**	**7**	**
	Density	**49.366**	**7**	**
Pruning of the complete canopy	Thallus length	19.606	13	#
Half-canopy pruning	Thallus length	4.3613	13	#
Pruning keeping frond basal meristems	Thallus length	20.745	13	#
Long-line culture	**Thallus length**	**186.81**	**10**	**
	Holdfast diameter	**173.13**	**10**	**
	Weight	**213.09**	**10**	**
	Reproductive individuals	10.000	10	#
	Harvest treatment			
	Parameter	Chi-squared	*df*	*p* value
Relative growth rate (RGR)	**Thallus length**	**71.558**	**6**	**
	Holdfast diameter	**70.877**	**6**	**

Factors were considered fixed for all the analyses. Statistical differences are highlighted in bold

$^{**}p < 0.001$; $^{*}p < 0.05$; $\#p \geq 0.05$

with strong unfused haptera of 4 mm thickness. After explantation to the long lines, growth was also slow but constant and statistically significant in terms of size and weight ($p < 0.05$; Table 1). During the first 3 months, total length was tripled (Figs. 4c, d and 5a). Subsequently, growth was restricted to length increase. Maximum length

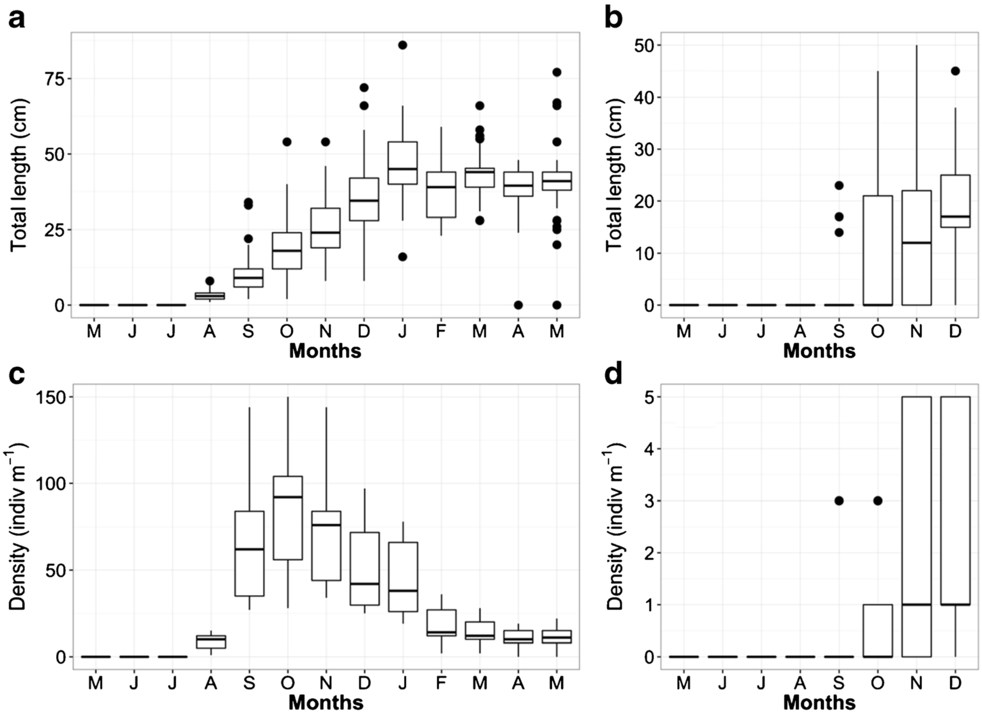

Fig. 3 Growth and density of *L. trabeculata* recruits in areas after a total harvest regime in autumn (**a**, **c**) and summer (**b**, **d**), between May 2014 and July 2015. *Boxes* show median (*horizontal line*) ± 1.5 times the interquartile range (*whiskers*). *Black dots* represent deemed outliers

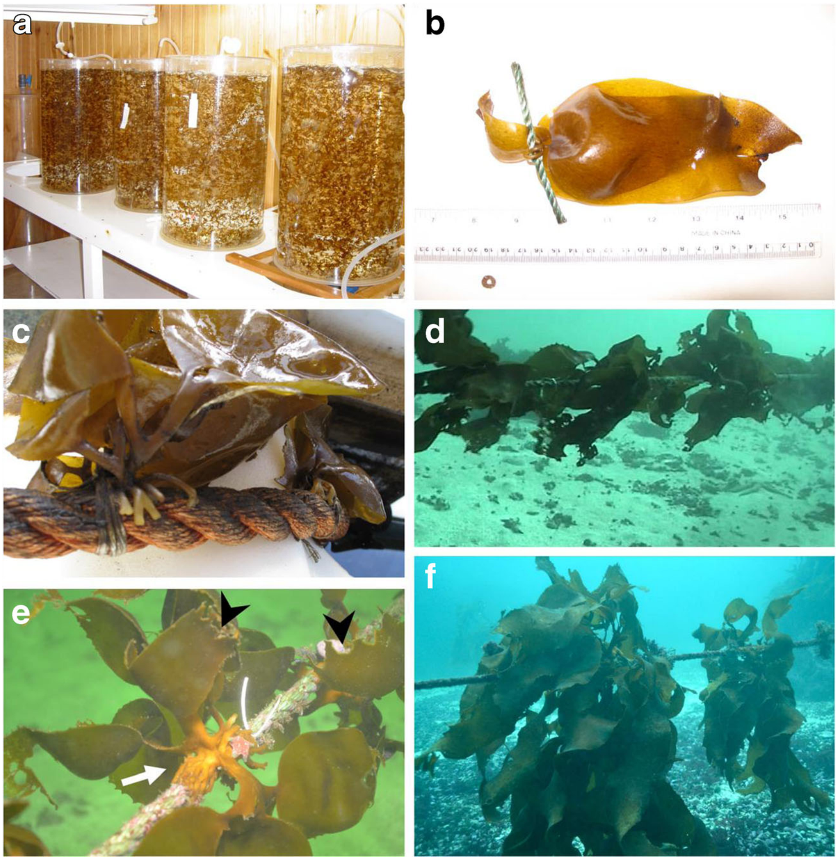

Fig. 4 *L. trabeculata* farming at Bahia Inglesa, between December 2010 and January 2013. **a** Sporophytes up to 1 cm are produced under laboratory conditions in cylinders of 50 L. **b**, **c** Seedlings usually reach over 6 cm in the laboratory. Then, they are manually attached to a small cord and fastened to a long line. **d** During the first months, sporophytes can triple their initial size in few months. **e** Holdfasts strongly spread on the long line (*arrow*), with a sporophyte increasing in diameter and stipe and frond number more than in total length. At this point, they are also affected by grazers (*arrowhead*). **f** Ninety-centimetre sporophytes are characterized by shrub-like morphology, wide fronds and short stipes

was observed after 14 months in the sea (median = 60 cm, up to 90 cm individuals), when erosion started. Erosion by grazing was commonly observed all year-round (Fig. 4e). The holdfast on the other hand was always increasing, achieving up to 18 cm (median = 14 cm) in 25 months (Fig. 5b). Weight was also highest towards the last months of sampling, with some thalli reaching 1250 g FW, with a median of 950 g FW per individual (Fig. 5c). Morphology in these cultivated specimens was different. Instead of tree-like shape typically observed in juvenile and adult subtidal individuals, we obtained shrub-like morphotypes with reduced stipes and strong blade development (Fig. 4f). About 60% of these individuals reached reproductive maturity in our mariculture facility (Fig. 5d).

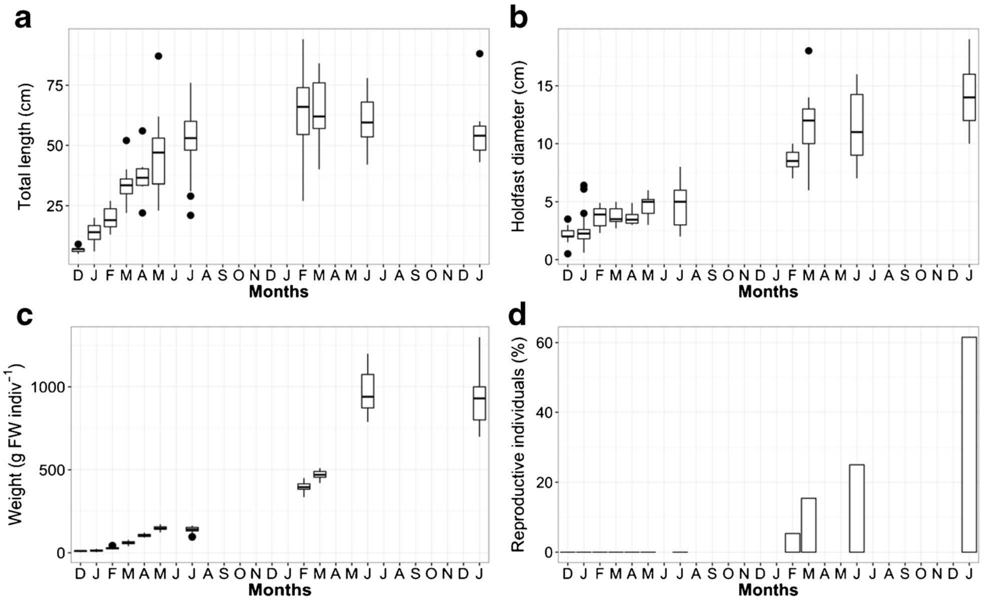

Fig. 5 Growth and productivity of outplants of *L. trabeculata* in long-line culture between December 2010 and January 2013. **a** Total length (cm). **b** Holdfast diameter (cm). **c** Weight (g FW individual^{-1}). **d** Reproductive individuals (%). *Boxes* show median (*horizontal line*) ± 1.5 times the interquartile range (*whiskers*). *Black dots* represent deemed outliers

Growth rates under different growth conditions

Our study revealed different growth rates in *L. trabeculata* (Table 1, Fig. 6). Individual recruits developing after autumn and summer harvests were most productive, with rates over 70 and 20% month^{-1} ($p < 0.05$; Fig. 6). Rates obtained from culture explants were statistically similar to recruits appearing in April/May 2015 (summer harvest) and wild adult individuals from the Bahia Chasco populations. Growth rates after pruning experiments were lowest, and sometimes negative. Holdfasts showed similar growth trends.

Discussion

Growth rate, prevalence of reproductive individuals and recruitment varied slightly over the sampling period of our study, suggesting that *L. trabeculata* is part of a mature subtidal community. Our results agree with observations reported by Villouta and Santelices (1984), Vásquez et al. (2006), Uribe et al. (2015) and Stotz et al. (2016). The slow growth may be underestimated by natural blade erosion, which in *L. trabeculata* from northern Chile may reach up to 0.39 cm day^{-1}, leading to a loss of about 50% biomass within 1 year (Tala and Edding 2005). Usually, growth is positive, but sometimes erosion may be higher. In our study, *L. trabeculata* net elongation was slightly negative in two seasons of the year. In summer, nutrient depletion could be limiting *L. trabeculata* growth as is reported for several subtidal macroalgae (Hurd et al. 2014). In winter, light and temperature are not high enough to promote growth. Specifically in these two seasons, sporulation, which occurs all year round in *L. trabeculata*, may contribute significantly to biomass losses.

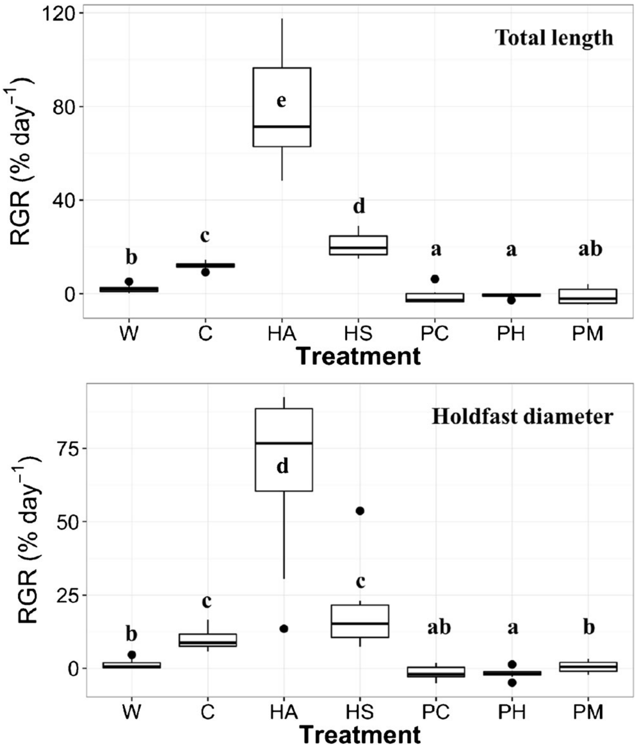

Fig. 6 Relative growth rate of *L. trabeculata* (% month^{-1}). *W* wild (intact) adult population, *C* long-line culture, *HA* total harvest in autumn, *HS* total harvest in summer, *PC* pruning of the complete canopy, *PH* half-canopy pruning, *PM* pruning keeping frond basal meristems. *Boxes* show median (*horizontal line*) ± 1.5 times the interquartile range (*whiskers*). *Black dots* represent deemed outliers. *Letter on bars* were used to designate statistical differences (Wilcoxon rank-sum test), where $a < b < c < d < e$

In order to avoid these underestimations, it is appropriate to measure more than one variable. For *L. trabeculata* holdfast length, stipe number, diameter and weight measurements have shown that positive growth occurred under certain experimental or natural conditions, indicating that these parameters are less susceptible to erosion (Vásquez 1991; Camus and Ojeda 1992; Westermeier et al. 2016). After Camus and Ojeda (1992), morphometric relationships in natural populations are quite variable at different spatial scales and probably mirror water motion and temperature regimes, making it difficult to foresee growth and development patterns. Our mariculture study may suggest that substratum quality also affects *L. trabeculata* plasticity. Our outplants were able to attach and grow on the long-lines, but their blade shape was significantly different from local stocks. Morphological plasticity has been reported for several kelps as a response to environmental conditions or inherited traits (Demes et al. 2009; Westermeier et al. 2011). According to this, some characteristics of our mariculture system (e.g. long-lines) could cause the unusual shrub-like morphotype, as they were growing in similar environments. Alternatively, this morph could be an early developmental stage of *L. trabeculata*, before reaching the adult shape after several years of growth.

According to Tala et al. (2004), major blade formation occurs in spring and summer, but major reproductive activity (such as spore release, germination and gametophyte formation) takes place in autumn. In contrast, Murúa et al. (2013) found that autumn spores were completely unviable in both northern and southern Chile *L. trabeculata.* Most successful cohorts were produced by sporulations in winter and spring. Edding et al. (1993) reported that *L. trabeculata* individuals in areas of strong water movement have better reproductive vitality than specimens in quieter waters. It appears that several factors act as drivers for *L. trabeculata* recruitment: inter-annual variation in spore viability, in addition to the presence of latent gametophytes from previous sporulation events, and environmental variables. According to our observations, recruitment was significantly encouraged by substratum availability provided by human activity, a situation also reported for *Durvillaea antarctica* and *Macrocystis pyrifera* (Castilla et al. 2007; Westermeier et al. 2014). When seasonal conditions are optimum, *L. trabeculata* can be highly competitive and reach up to 80 recruits m^{-2} after 3 months. In contrast, total harvesting in summer may cause very low recruitment followed by overgrowth with undesired understory algae.

Our study shows that an event of total harvest will require 1 year or more to fully restore recruitment and growth of a *L. trabecula*ta kelp bed. Similar, but still worse effects are caused by pruning. Besides of damaging both juveniles and adults, moribund pruned specimens remained attached to the substratum and blocked the recruitment of new individuals for more than 14 months. Kelp harvest by pruning is not detrimental for natural *M. pyrifera* stocks (Borras-Chavez et al. 2012), but current practises are efficient enough for natural repopulation (Westermeier et al. 2014). In contrast, similar to *L. trabeculata*, *L. spicata* (formerly *L. nigrescens*) and *D. antarctica* cannot regenerate after pruning, and Westermeier et al. (1994) discouraged this practice. Pruning is therefore one of the least productive strategies that local fishermen can follow to manage these populations. However, full removal is especially laborious in subtidal *L. trabeculata*. Therefore, for future management plans, we suggest to explore intermediate options that include the seasonal variation of recruitment and the total removal of individuals. From a commercial point of view, *L. trabecula*ta has markets for all parts of the thallus, especially stipes and fronds, which should be considered after harvesting. Even more promising strategies are selective harvest techniques that leave reproductive adults from collecting. This would support a constant gametophyte supply and recruitment and lead to faster recovery than with other management methods. As a compromise, we propose to evaluate pruning of individuals, and some months later to manually remove the thallus leftovers in order to promote recruitment recovery. The impact of these practises must however be analysed in a community context, including consequences on the associated assemblages, which have demonstrated to be highly susceptible to the disruption of this foundational species (Vásquez and Santelices 1990; Uribe et al. 2015).

In comparison to wild stocks, *L. trabeculata* productivity was higher in culture but still slow. Slow growth rates were first reported by Westermeier et al. (2006), who obtained 29.2 cm in 4 months. Our present study extended the culture period to 18 months, which resulted in up to 90-cm long sporophytes. This slow growth was aggravated by grazing, which occurred in our experiments (see Fig. 4e). Grazing also affects natural stock recruitment and development (Vásquez and Buschmann 1997; Villegas et al. 2008). Under current market conditions, the very slow growth rates of *L. trabeculata* make commercial aquaculture unprofitable. However, our results show the feasibility to cultivate this species for repopulation projects, since it is able to survive, grow and develop reproductive fronds on artificial substrata. Its high recruitment rate in winter plus its stability in culture conditions should favour its proliferation in kelp-free areas in the subtidal, making the long-line system a potential tool for restoration projects of this species. From preliminary unpublished results from the authors, it also appears possible that holdfast fragmentation may be used in this context as in the case of *L. berteroana* and *M. pyrifera* (Westermeier et al. 2016), which might help to improve the restoration of *L. trabeculata* populations.

Our results show that the population dynamics of *L. trabeculata* are rather different from other commercial kelps in Chile like *Macrocystis pyrifera* and *Lessonia berteroana*. Its slow growth, lacking recovery after pruning and highly seasonal recruitment make it necessary to design individualized management plans for this species. We emphasize that special attention must be paid to the recovery times, in order to have fully productive stocks and to avoid genetic or ecological bottlenecks at local or regional levels. These measures should be included in future policies for seaweed production in the country, taking into account social, environmental and economic dimensions of *L. trabeculata* fishery.

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