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Holdfast fragmentation of *Macrocystis pyrifera* (*integrifolia* morph) and *Lessonia berteroana* in Atacama (Chile): a novel approach for kelp bed restoration

Renato Westermeier[1] · **Pedro Murúa**[1,2] · **David J. Patiño**[1] · **Liliana Muñoz**[1,2] · **Dieter G. Müller**[3]

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Abstract The kelps *Macrocystis pyrifera* (*integrifolia* morph) and *Lessonia berteroana* (northern lineage of *Lessonia nigrescens*) are intensely harvested in Atacama, northern Chile, for abalone forage and alginate production. Local situations call for simple restoration techniques for over-exploited kelp beds. We excised holdfast portions from parental specimens, including parts of stipes and phylloids. Untreated adult thalli and unmanipulated specimens served as controls. Fragments of both species were attached to boulders or rock platforms with elastic bands or cyanoacrylate glue. Transplanted fragments quickly formed new haptera, colonized new substrata, and reached reproductive maturity. *Macrocystis* regenerates increased in total length and holdfast diameter in one or both directions of the rhizome, forming a pair of stipes, followed by rhizome and haptera development. In *Lessonia*, tissue of non-injured zones took over new holdfast growth. Success of this propagation method varied with season and substrata. Both species proceeded to complete regeneration of holdfasts. However, holdfasts of older *Macrocystis* thalli partly decomposed, resulting in two apparently identical individuals. Advantages of these propagation methods are discussed in ecological and restoration contexts.

Keywords Kelp bed repopulation · Holdfast fragments · *Macrocystis* · *Integrifolia* morph · *Lessonia berteroana* · Phaeophyta · Chile

Introduction

The ecological significance of *Macrocystis* and *Lessonia* beds along the coast of Chile has been discussed repeatedly by various authors, stressing their role as natural microhabitats, nurseries, protection structures, substrata, and food (Santelices et al. 1980; Santelices & Ojeda 1984a; Ojeda & Santelices 1984; Westermeier & Möller 1990; Westermeier et al. 1994; Graham et al. 2007). Various studies not only evaluated the effects of harvesting techniques, including their immediate impact, but also tried to forecast long-time consequences. In addition, they expressed concern about high extraction levels, harvesting procedures, and unprofessional management techniques practiced by local fishermen (Santelices & Ojeda 1984b; Vasquez et al. 2012; Westermeier et al. 2013a).

The Chilean kelp fishery is an industry that produced more than 300,000 t yearly, and it is carried out mainly by local fishermen (Westermeier 2014a). The incapacity to reproduce high-energy tolerant culture systems for *Lessonia nigrescens* and economically feasible installations for *Macrocystis pyrifera* led to 100 % of kelp biomass collected just from natural beds in Chile, despite of already having developed several aquaculture alternatives for them. Although significant volumes of *Macrocystis* and *Lessonia* originate from stranded specimens, direct extraction is practiced especially in open access areas. In Bahia Chasco, commercial *Macrocystis integrifolia* harvesting is based on the thinning of weak adult specimens and the pruning of younger individuals (Westermeier et al. 2014a). In contrast, *Lessonia berteroana* (northern lineage of *L. nigrescens*; sensu Gonzalez et al. 2012)

✉ Renato Westermeier
rwesterm@uach.cl

[1] Instituto de Acuicultura, Universidad Austral de Chile, Sede Puerto Montt, PO Box 1327, Puerto Montt, Chile

[2] Present address: Oceanlab, School of Biological Sciences, University of Aberdeen, Newburgh, Scotland AB41 6AA, UK

[3] Fachbereich Biologie der Universität Konstanz, 78457 Konstanz, Germany

biomass is totally removed from high-energy rocky intertidal areas in the Atacama coast, since pruning schemes have not been successful (Westermeier et al. 1994). The age of kelp individuals is frequently ignored, and juvenile specimens are harvested before sexual maturity, with negative consequences.

Even though *Macrocystis* and *Lessonia* are present along almost the entire coastline of Chile (Hoffmann & Santelices 1997), main extraction activity occurs in northern Chile, since legal and environmental factors reduce costs. *Macrocystis*, for instance, is used in abalone feeding, where the most important producers are located in Atacama and Coquimbo regions (26° 04′–32° 10 S; ProChile 2013: Sernapesca 2013). Similarly, *L. berteroana* harvest is concentrated between Antofagasta and Huasco (23° 40′–28° 30′ S; Sernapesca 2013), where high air temperatures allow faster biomass drying and reduce costs.

Increasing harvest pressure has caused growing concern about the consequences of over-exploitation in the Atacama region. Facing this situation, we have initiated since 2010 various studies for restoration of the *M. integrifolia* morph in Bahia Chasco, using sporophylls, recruits, and seedlings on different substrata (Westermeier et al. 2012a; 2013a; 2014b). In addition, growth of holdfast fragments on ropes was found to be of considerable value for aquaculture and restoration (Westermeier et al. 2013a).

Concepts of vegetative reproduction in kelps (Lobban 1978), combined with our field observations over 3 years in Atacama, offered the possibility to explore new restoration techniques. For both kelps, *Macrocystis* and *Lessonia*, we saw the chance that holdfast fragmentation and exposure on new substrata—through different attachment methods—may constitute simple fishermen-feasible techniques with a good cost-benefit ratio. Here, we report the productivity of these approaches in terms of growth and detachment, in order to propose them like suitable alternatives to restore major extensions of these economically important kelp forests along Chilean coasts.

Materials and methods

Study areas

The restoration experiments reported here were performed in the years 2012 and 2013 at the following locations of the Atacama coast (Table 1): sandy and rocky subtidal habitats of Bahía Chasco for *Macrocystis* and rocky intertidal habitats at Chañaral and Pan de Azúcar for *Lessonia*. Bahía Chasco fishermen are among the most important suppliers of *Macrocystis* biomass for abalone forage in Chile, and currently, there is no evidence of over-exploitation at this location (Westermeier et al. 2014a). Bahia Chañaral, on the other hand, was severely affected for more than 35 years by mining dump deposition into Salado River (Castilla 1983). In 1975, the river

Table 1 Repopulation schedule carried out with *M. pyrifera* and *L. berteroana* fragments in Atacama

Specie	Locality	Latitude	Habitat	Depth (m)	Substrata	Seeding Dates
M. pyrifera (*integrifolia* morph)	Bahia Chasco	27° 40′ 41″ S	Sandy	8 ± 1	Boulder–elastic band	Mar, Jul, Sep, Dec 2012
					Boulder–acrylate glue	
			Rocky	8 ± 1	Rocky platform	Jul 2012
					Rocky platform (parental and unmanipulated controls)	Jul 2012
L. berteroana (formerly *L. nigrescens*)	Bahia Chañaral	26° 18′ 23″ S	Rocky	Intertidal	Boulder–elastic band	Jun 2012
					Boulder–acrylate glue	Jul 2012
					Rocky platform	Jul, Oct 2012; Jan, Apr 2013
L. berteroana (formerly *L. nigrescens*)	Pan de Azúcar National Park	26° 09′ 39″ S	Rocky	Intertidal	Rocky platform	Oct 2012
					Rocky platform (parental and unmanipulated controls)	Jul 2012

flow and mouth were redirected to Caleta Palito (26° 16′ S). Presently, the impacts of these heavy metal tailings declined substantially due to new practices by mining industries (Codelco–Salvador Department, 2013, personal communication). However, except for individuals transplanted by Correa et al. (2006), there are no further records of *Lessonia berteroana* on more than 35-km shoreline between Pan de Azúcar National Park (26° 09′ S) and Villa Alegre (26° 30′ S). In addition, there is no evidence for gene flow in *L. berteroana* between these two locations (Faugeron et al. 2005). In fact, Pan de Azúcar is the first zone North of Chañaral where *L. berteroana* appears naturally.

Restoration experiments

1. *Holdfast fragment source.* Holdfast fragments of *Macrocystis* were obtained according to Westermeier et al. (2012a; 2013b; 2013c) by excision of one or two fragments from adult individuals (Fig. 1a). In the case of *L. berteroana*, we generated triangular fragments in order to leave one intact holdfast side (Fig. 2a). Care was taken that these fragments contained some fronds, in order to conserve their photosynthetic activity. Donor individuals were sampled in order to check their viability—in terms of growth and survivorship—after excision. Unmanipulated adult specimens from subtidal *Macrocystis pyrifera* (Bahia Chasco) and intertidal *L. berteroana* (Pan de Azúcar) populations (Figs. 1a and 2a) were also selected as controls.
2. *Types of substrata.* In a first approach, excised kelp fragments ($n = 20$–30) were exposed on boulders and rocky platforms in Bahia Chasco (*M. pyrifera*) and in Chañaral and Pan de Azúcar (*L. berteroana*), following the methods described by Westermeier et al. (2014b). Fragments were attached with elastic bands to boulders and with cyanoacrylate glue to boulders and rocky platforms (Figs. 1b, c and 2b–d). On large flat areas, only glues were acceptable (Figs. 1e and 2e).
3. *Seasonal assessment*. Since, presently, no over-exploitation problems are known for Bahia Chasco (Westermeier et al. 2014a), we selected sandy areas in this location for a series of pilot repopulation experiments. At different seasons, we exposed four holdfast fragments m^{-2}, fixed to boulders with elastic bands and cyanoacrylate glue. In this way we created an artificial *Macrocystis* bed within a 1500-m^2 area (Fig. 1e, f). Similarly, in view of the absence of *L. berteroana* in Bahia Chañaral, we restored 30 m^2 of rocky intertidal with excised fragments (initial density six individuals m^{-2}; Fig. 2f, g). Twenty to thirty individuals were randomly selected for sampling every month.
4. *Sampling and statistical analysis.* Kelp growth parameters (total length, holdfast diameter, and stipe number), reproductive phenology (percentage of reproductive individuals), and mortality/detachment were quantified monthly, and thallus regeneration were recorded. Net growth was determined at 4 months for *M. pyrifera* experiments and at 8 months for *L. berteroana*. Following homoscedasticity tests, net growth was compared using a one-way ANOVA (5 % confidence level) for substrata types and seasonality (Zar 1999). Tukey tests were also performed in order to detect specific statistical groups (Zar 1999).

Results

Type of substrata

The development of *M. pyrifera* and *L. berteroana* fragments on different substrata is illustrated in Fig. 3. In *M. pyrifera*, net growth was particularly pronounced in total length and holdfast diameter (Fig. 3a, c), followed by a moderate but non-significant increase in stipe number in relation to the parental (Fig. 3e). At 4 months, maximum growth was seen on the rocky platform ($p < 0.05$), with fronds reaching over 200 cm and holdfasts over 30 cm in size. Fragments attached to boulders also showed good growth irrespective of fixation methods (elastic bands or acrylate glue), but significantly lower than on rocky platform (only 100 cm in length and less than 20 cm in holdfast diameter). Parent and unmanipulated control individuals showed a less growth during the study time (≤80-cm length and less than 10-cm holdfast diameter). Moreover, we detected no statistical differences in stipe formation, and only up to six new stipes appeared in 4 months ($p > 0.05$; Fig. 3e). While all individuals reached reproductive maturity within this time (Fig. 3g), considerable detachment occurred only in the boulder–acrylate treatment, where close to 50 % of specimens became detached and were lost (Fig. 3i).

Growth of *L. berteroana* fragments resulted basically in transplated fragments that did increase in size, but at the same rate as the parentals and controls. There were no statistical differences in total growth on different substrata ($p > 0.05$), and thalli grew up to 25–80 cm in 8 months (Fig. 3b). Statistically significant differences were seen in holdfast growth ($p < 0.05$), particularly with the higher ones in rocky platform plants and the lowest at boulders (cyanoacrylate) and the unmanipulated controls (Fig. 3d). Overall, *L. berteroana* showed a very high stipe formation (up to 40 new stipes; Fig. 3f). Moreover, we also detect statistical differences in stipe production ($p < 0.05$) with major capacity of stipe propagation on boulder specimens and minimum in controls. Between 40 and 100 % of individuals became reproductive under all treatments (Fig. 3h), with the least degree in controls. Transplanted fragments developing on

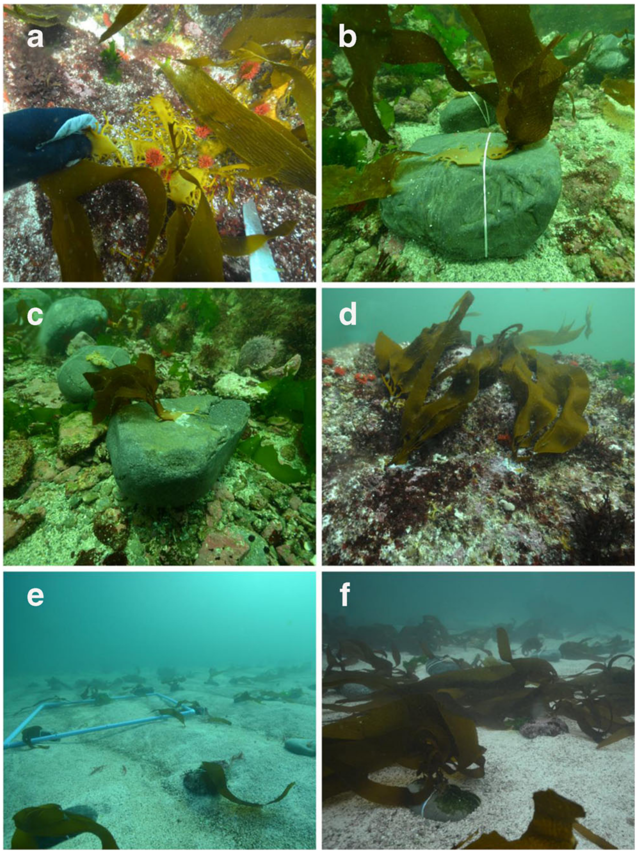


Fig. 1 *Macrocystis pyrifera* (*integrifolia* morph) restoration, using holdfast fragments. **a** Parental and excised holdfast fragment. **b**–**d** Fragment attachment methods and substrata: **b** boulder–elastic band, **c** boulder–acrylate glue, and **d** rocky platform–acrylate glue. **e**, **f** Initial and final panoramic views of *M. pyrifera* pilot repopulation in Bahia Chasco sandy bottom

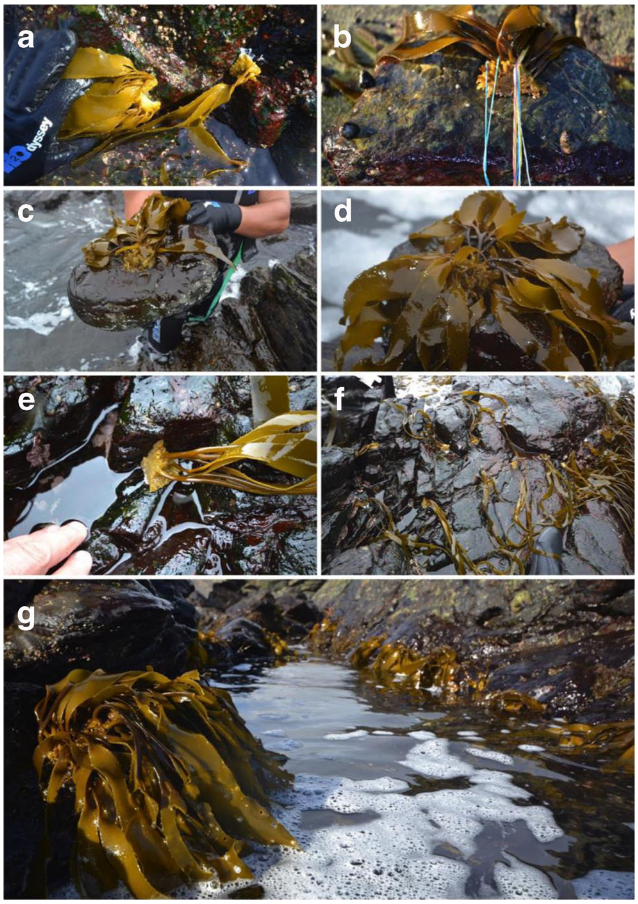


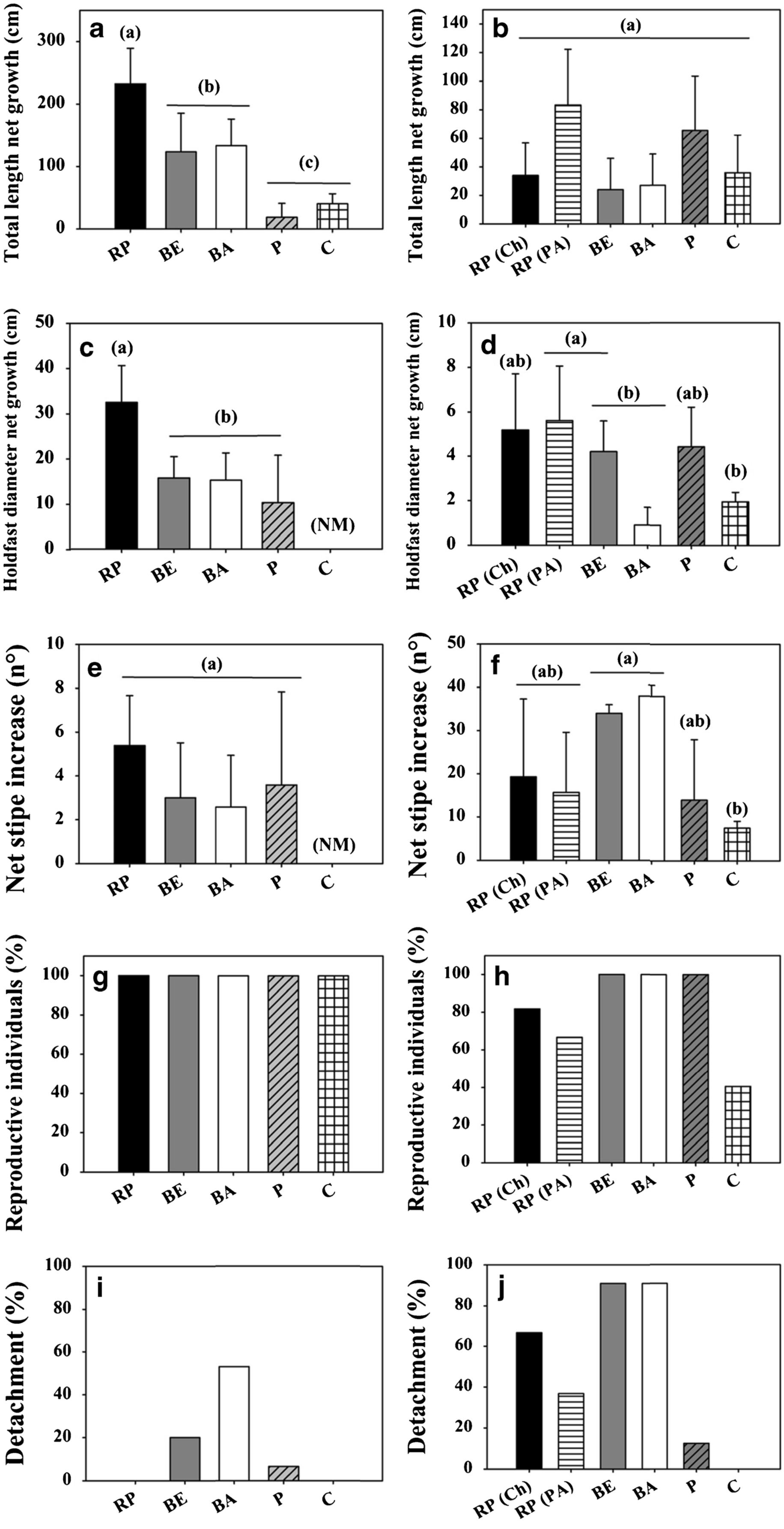
Fig. 2 *Lessonia berteroana* restoration, using triangular holdfast fragments. **a** Parental and excised holdfast fragment. **b**–**e** Fragment attachment methods and substrata: **b** boulder–elastic band, **c**, **d** boulder–acrylate glue, and **e** rocky platform–acrylate glue. **f**, **g** Initial and final panoramic views of *L. berteroana* pre-pilot repopulation in Chañaral rocky intertidal

boulders were most unstable, with detachments up to 90 % (Fig. 3j).

Seasonal variation

Figure 4 shows net growth, reproductive phenology, and seasonal variation of detachment in pilot planting experiments with *M. integrifolia* morph on boulders in Bahia Chasco and *L. berteroana* fragments on rocky platforms in Chañaral. *Macrocystis* showed a marked seasonal pattern, with higher growth in spring (200–300 cm; $p < 0.05$), irrespective of fixation method (Fig. 4a, b). Summer inoculants were unsuccessful, with massive detachment after the second month. In contrast, *L. berteroana* growth was lower without significant seasonal variation (Fig. 4c; $p > 0.05$). We detected seasonal variation in holdfast development of *Macrocystis* fragments, with higher values in spring ≥ winter ≥ autumn (13–17-cm net holdfast growth, $p < 0.05$), irrespective of attachment method (Fig. 4d, e). Seasonal differences were also seen in *L. berteroana*, where summer plantation produced maximum increase of holdfast diameter ($p < 0.05$; Fig. 4f). Reproductive individuals of both species were found in all seasons, except for a summer minimum in *M. pyrifera* due to premature detachment. In *Macrocystis*, regenerates fixed to boulders with elastic bands more than 80 % were found reproductive without clear seasonal differences. In contrast, individuals fixed to boulders with acrylate glue were found reproductive exclusively in spring (Fig. 4g, h). Reproductive phenology of *L. berteroana* showed clear seasonality, with highest indexes in winter (≈100 %) and lowest values in autumn (approx. 40 %; Fig. 4i). Seasonality was also detected in the detachment of fragment regenerates in both species. In *M. pyrifera*, detachment was lowest in spring and increased sharply to 100 % in summer (Fig. 4j, k). The pronounced effect of fixation method mentioned above resulted in 25 % higher survival with elastic band fixation compared to acrylate glue technique (Fig. 4j, k). In *L. berteroana*, detachment paralleled

Fig. 3 Net growth, reproductive phenology, and mortality of *M. pyrifera* (**a**, **c**, **e**, **g**, **i**) and *L. berteroana* (**b**, **d**, **f**, **h**, **j**) fragments under different attachment methods and substrata. *RP* rocky platform, *BE* boulder–elastic band, *BA* boulder–acrylate glue, *P* parental, *C* unmanipulated adults (controls), *Ch* Chañaral, *PA* Pan de Azucar, *NM* not measured. *Letter on bars* were used to designate statistical differences (Tukey test), where *a* > *b* > *c*



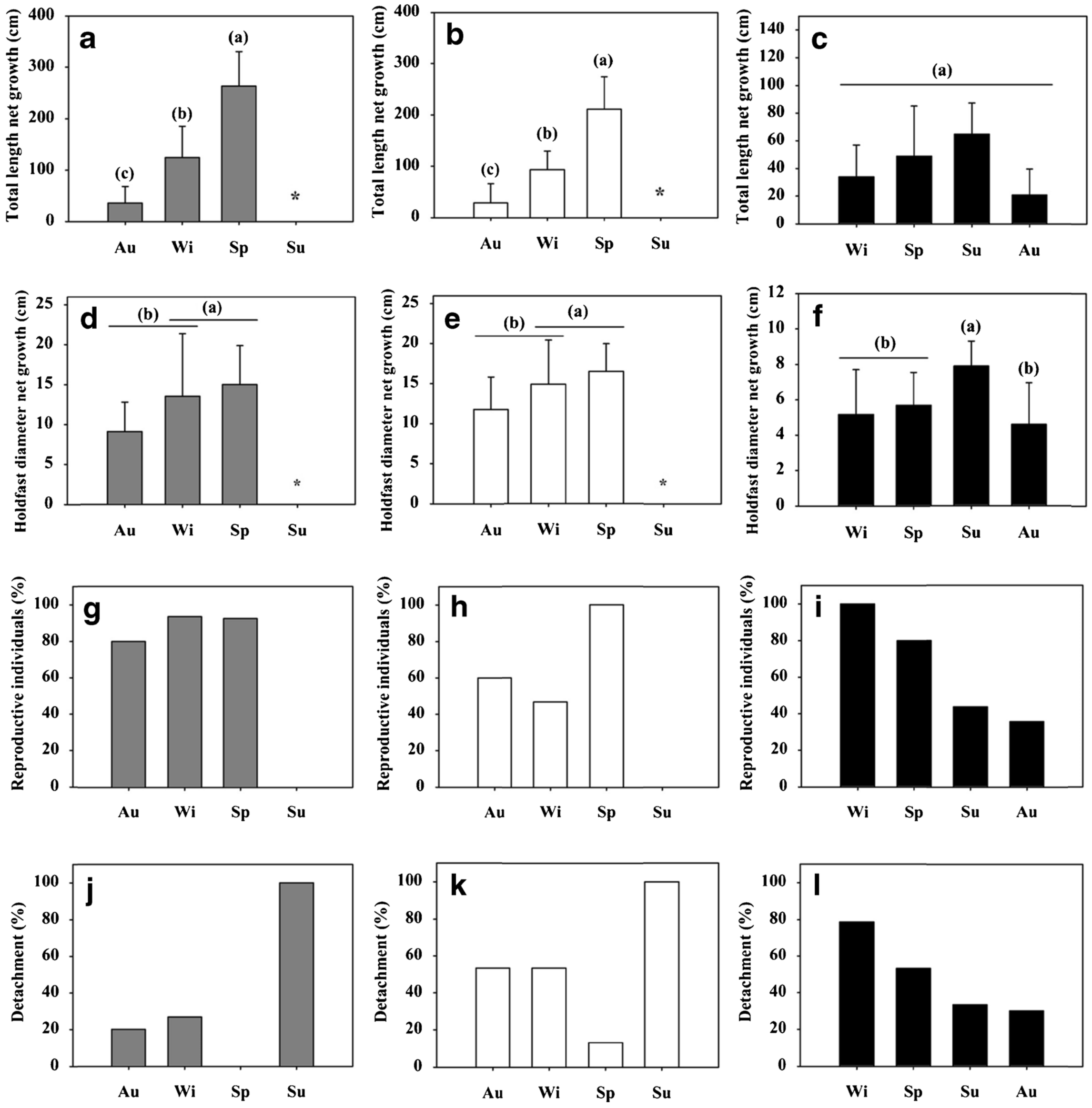


Fig. 4 Seasonal variation of pilot repopulation attempts of *M. pyrifera* and *L. berteroana* in Atacama. Net growth, reproductive phenology, and mortality of *M. pyrifera* seeded on boulders by elastic bands (**a**, **d**, **g**, **j**) and acrylate glue (**b**, **e**, **h**, **k**) and *L. berteroana* seeded on rocky platforms with acrylate glue (**c**, **f**, **i**, **l**). *Letter on bars* were used to designate statistical differences (Tukey test), where $a > b > c$. *Au* autumn, *Wi* winter, *Sp* spring, *Su* summer

reproductive phenology, with highest values in winter, decreasing toward autumn (Fig. 4l).

Discussion

Thallus fragmentation has been described in many macroalgae as a strategy enhancing either survivorship or habitat spreading. In many cases (e.g., filamentous algae), any thallus section has the potential to regenerate the entire individual. In other examples, only specific organs or tissue sections are capable to regenerate the whole specimen (e.g., *Caulerpa* species).

The Chilean kelps *Macrocystis* and *L. berteroana* are characterized by pronounced holdfast structures which have the potential to colonize adjacent areas through haptera formation (Lobban 1978). Our kelp restoration experiments make use of this function, although the two kelp species involved exhibit different regeneration patterns. In *Macrocystis*, new haptera tended to grow up on both sides of the rhizome (Fig. 5a–c), in contrast to their reaction on long-line cultures (Westermeier et al. 2013a). Successively, they formed a stipe pair, swelling the definitive holdfast complex later (Fig. 5c). In *L. berteroana*, on the other hand, tissue from intact holdfast zones covered the damaged areas. After 1 month, there were no scars left (Fig. 5f–h), and concentric growth continued. In

Fig. 5 Differential growth/regeneration patterns in kelp holdfasts. **a** Morphology of adult *Macrocystis integrifolia* holdfast with a fragment recently excised (*right*). **b**, **c** First- and fourth-month *Macrocystis* fragments, respectively, growing on a boulder. *White arrow*: senescent zone; *black arrow*: renewed zone. **d**, **e** Propagation of parental individuals after 4 months showing **d** starting of holdfast separation (*black arrow*) and **e** holdfast coalescence. **f** Morphology of adult *L. berteroana* holdfast with a fragment recently excised. **g**, **h** Development of *L. berteroana* fragments after one and six months respectively. **i**, **j** Recovery of *L. berteroana* parental specimen after 1 and 2 months after excision

our study, donor individuals showed a good regeneration potential. Both *Macrocystis* and *Lessonia* adults repaired their scars to initial holdfast size within 1–2 months (Fig. 5d, i, j). Furthermore, growth and reproductive potential were not negatively affected compared to parental and non-altered individuals (Westermeier et al. 2013b; c; this study). This shows clearly that our propagation technique would not be disturbing the dynamics of natural populations. Parental individuals and regenerating fragments were capable not only of repair, but also of normal growth as single or chimeric holdfasts. Specifically in *Macrocystis*, senescent holdfast sections resulted in the formation of two separated clonal individuals (Fig. 5c, d, e).

Our fieldwork at Atacama coast revealed advantages and limits of the novel fragment transplant technique in comparison to conventional reforestation trials: Holdfast fragments can be easily attached to diverse hard substrata using elastic bands or glue. These are better acclimated to environmental conditions than kelp seedlings and recruits, have an appropriate size, and reach sexual maturity earlier (Westermeier et al. 2013a; 2014b). Some inherent physical/oceanographic aspects of our fragmentation technique, however, cause problems that cannot be overlooked. For instance, fixation of kelp fragments to boulders may be critical, because this type of substratum can be easily displaced by mechanical forces and cause wounding or even crushing of plants. Furthermore, the abrasive effect of sand particles may be critical, damaging stipes, and detaching complete individuals.

Seasonality has been repeatedly reported for Chilean kelps (Murúa et al. 2013 and references therein) and was also encountered in our reforestation study. *Macrocystis* showed best development in spring, followed by growth reduction and death/detachment in summer (Westermeier et al. 2014a). In contrast, seasonal variations in *L. berteroana* were not statistically significant, although highest growth values were also recorded in spring (e.g., Westermeier et al. 1994; Tala & Edding 2005). Consequently, we strongly recommend the spring season for pilot experiments, since kelp growth is stimulated and mortality/detachment at minimum.

Herbivores play an important role in kelp communities, modulating important processes such as recruitment, spore dispersal, and growth (Graham et al. 2007). They may also be important factors in kelp restoration efforts (Carney et al. 2005).

In Bahia Chasco, conic snails *Turritella* sp. and Chilean kelp crabs *Taliepus dentatus* were the most important grazers on *Macrocystis*. Their pressure was mainly concentrated on recruits rather than adult fronds (Westermeier et al. 2012a; 2013b). Chañaral is a habitat rich in intertidal grazers (genera *Calyptraea*, *Fisurella*, *Enoplochiton*, *Taliepus*, *Tegula*, and *Prisogaster* among others), causing high mortality for *L. berteroana* fragments. For the same reason, earlier repopulation experiments with *Macrocystis* fragments in this zone ended in a failure (Westermeier et al. 2013c). The most common measures against herbivory are the installation of grazer exclusion devices like cages, nets or fences, and/or cleaning areas from herbivores prior to restoration experiments (Carney et al. 2005). Higher seeding densities or “artificial plants” could also help to remove potential grazers by a “whip effect” (Vasquez & McPeak 1998). Such techniques, however, are likely to increase costs. In order to avoid this problem, Westermeier et al. (2013c) seeded *L. berteroana* within patches of *Dictyota*, which increased survival over fivefold. Dictyotalean algae are known to produce and accumulate secondary metabolites such as terpenes and diterpenes as a defense strategy by reducing their palatability (Cronin & Hay 1996). We suggest to use this protective mechanism in order to reduce herbivory in kelp transplantation projects.

The ecological benefits of kelp reforestation are evident and were emphasized repeatedly (North 1976; Deysher et al. 2002; Carney et al. 2005; Westermeier et al. 2014b). The fragment technique described here has additional benefits: It is much easier to apply than the handling of young recruits or hatchery seedlings and attractive by low cost. Up to eight fragments can be obtained from one *Macrocystis* creeping “stolon” and more than 14 clones from one elliptical *Lessonia* holdfast (Westermeier et al. 2013c).

On global scale, repopulation experiments have been described with several kelp species. Contrasting results ranged from high mortality to non-predictability, especially if based on direct use of spores (Vasquez & Tala 1995; Westermeier et al. 2012a). Successful repopulation projects were both very expensive and unaffordable for low-budget economies like local fisherman communities and governments (Westermeier et al. 2014a) or required high amounts of natural biomass (Correa et al. 2006). Contrary, within the framework of the same project where some of these results were originated, Westermeier et al. (2012a) used long-line cultivars from Bahia Chasco in order to evaluate the restoration degree after reaching sexual maturity. This seemly was a simpler and easier way to restore huge extension with minor initial biomass and cost, although the healthy and reproductive active kelp bed nearby the study area made difficult to interpret the final results. Hence, more complex techniques are needed for obtaining unbiased specific recruitment data and its subsequent yield.

Kelp repopulation projects are also strongly subject to environmental factors. *Macrocystis* in Bahia Chasco is a healthy population, producing vital sporophytes and recruits from either natural or restored origin (Westermeier et al. 2014a; b). Chañaral, in contrast, was one of the most heavy-metal-polluted habitats in Chile. Although recently, mining discharges have been reduced, we have not observed any new recruits in this locality during more than 2 years. This is in agreement with restoration efforts by Correa et al. (2006), who were unable to detect new sporophytes at Chañaral. Surprisingly, we obtained in the laboratory healthy crops of sporophytes up to 4 cm in size starting from Chañaral *Lessonia* spores (Westermeier et al. unpublished). Moreover, our studies did not reveal high heavy metal levels in the water column, but instead strong metal document heavy metal effects in kelp ultrastructure, physiology, and development (Leonardi & Vasquez 1999; Andrade et al. 2006; Contreras et al. 2007). For the moment, it remains open how heavy metal prevalence in higher trophic levels might affect the microscopic reproductive stages of kelps and, in consequence, prevent passive *Lessonia* repopulation in Chañaral.

In addition to these considerations, from our experiments we conclude that *M. integrifolia* and *L. berteroana* are especially suitable for restoration projects in large intertidal or subtidal rocky platforms. In the pilot experiments described here, we exclusively used single parental fronds. For future projects, however, we recommend incorporation of fragments from multiple parent individuals and even from different populations. This will enlarge the genetic diversity of a desired artificial/restored population, avoid consanguinity problems, and promote a sustainable natural recruitment.

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