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Aspects of the reproductive phenology of *Lessonia trabeculata* (Laminariales: Phaeophyceae) from three populations in northern Chile

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Abstract *Lessonia trabeculata* is a brown seaweed inhabiting the rocky subtidal zone along the coast of central and northern Chile, where it is the dominant kelp, and an important species in community structure. Morphological and reproductive aspects of this alga are dependent on environmental conditions and geographic distribution, and the present study gives data on its reproductive periodicity. The reproductive phenology for three populations from northern Chile (29–30°S) was evaluated by means of seasonal examination of morphological and reproductive characteristics of both macroscopic sporophytes and microscopic gametophytes. Comparative laboratory cultures of spores were made to determine seasonal differences in their capacity to produce viable plants. This species is perennial, and demonstrates year-round presence of reproductive tissues, although showing variation in reproductive phenology over time and among populations. The size of blades increases in spring and summer, whereas its reproductive potential (e.g., area and proportion of the reproductive tissue and the release of spores) increases in autumn. Culture experiments showed that spring and summer reproductive tissue released zoospores which had low germination rates compared to those of autumn and winter, and which produced female gametophytes of low fertility. The population differences depended on the character analysed and the season of the year. The development of both phases of the life cycle of *L. trabeculata* may be influenced by the local environmental conditions and their seasonal changes, and were expressed as morphological and/or reproductive changes in the plants. A better understanding of the seasonal adaptations may be obtained if future comparisons are made between widely separated populations or between individuals from the extremes of geographic distribution of the species.

Keywords Phaeophyceae; *Lessonia trabeculata*; kelp; reproductive phenology; spore culture; Chile

INTRODUCTION

Lessonia trabeculata Villouta *et* Santelices is a species endemic to Chile, distributed between 20°S and 40°S in rocky subtidal habitats of varying exposure to waves and currents. This species forms dense populations, dominant in biomass, with individual adult plants which may exceed 2 m in length and 3 kg in fresh biomass (Edding et al. 1994). The typical morphology of the alga includes an adhesive holdfast from which 1–5 stipes arise, each of which is dichotomously branched, and supports at least two blades. The blades form c. 50% of the plant biomass, whereas the remaining biomass occurs in the holdfast and stipes (Tala 1999). There are few data available on this species with regard to its population and reproductive dynamics, even though it is ecologically important in the structure of subtidal communities; and is of economic importance as a commercial source of alginic acid (Camus & Ojeda 1992; Vásquez 1992; Edding et al. 1994; Tala 1994; Tala 1999). In recent years, natural beds of this species have been harvested as a source of fresh food for land-based tank cultures of *Haliotis* spp. (abalone) being developed in Chile (Edding & Tala 2003).

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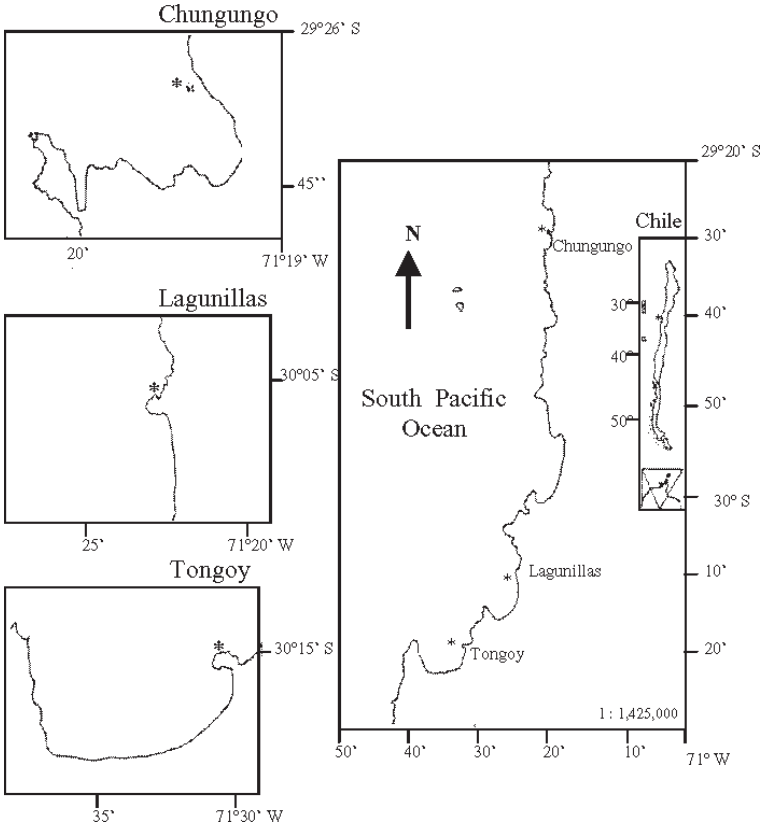

Fig. 1 Area map to show locations of *Lessonia trabeculata* populations sampled in this study.

Camus & Ojeda (1992) described patterns of morphology and abundance based on a geographic distributional scale for populations of *L. trabeculata* in northern and central Chile. Edding et al. (1993) suggested that populations of *L. trabeculata* in areas of strong water movement had greater reproductive vitality than plants in quiet waters. Available information does not, however, detail seasonal variations in morphological and reproductive characteristics. In temperate and cold regions, growth and reproduction of algae may occur all the year round and fluctuate in intensity during the year, or they may be restricted to specific seasons (Kain 1989; Santelices 1990). In general, in algae which are in reproductive condition throughout the year, only the spores released at a given time of the year are successful in generating new individuals, suggesting a seasonally adapted reproductive strategy (De Wreede & Klinger 1988; Santelices 1990). The environmental conditions of each locality exercise important influences on the fecundity of species that reproduce throughout the year, with variation related to both locality and season (De Wreede & Klinger 1988; Reed et al. 1996). Also, morphological changes associated with individual growth may produce differences in quantity of structural tissue and/or differences in the surface/volume ratio of algal tissue. This in turn may influence reproductive potential and development based on differential assignment of resources for ecophysiological processes within the species (De Wreede & Klinger 1988; Gerard 1990).

The life cycle of the Laminariales includes alternation of phases between the macroscopic sporophyte and microscopic gametophytes, each of which must successfully survive, grow, and reproduce to maintain the population. Seasonal and interpopulational differences may be expected to occur in both phases of the life cycle because of local environmental conditions, particularly in perennial species that live long enough to experience successive environmental variations (De Wreede &

Klinger 1988; Reed et al. 1996). The present study describes aspects of the reproductive phenology of *L. trabeculata* in the microscopic (spores, gametophytes) and macroscopic (blade) phases, considering seasonal and spatial (population) variability.

MATERIALS AND METHODS

Study areas and collections

The sites selected in northern Chile were at Caleta Chungungo (29°26′S–71°16′W), Punta Lagunillas (30°06′S–71°16′W), and the Tongoy Peninsula (30°15′S–71°15′W). These sites were selected because they were inhabited by extensive populations of *L. trabeculata* at 1.5–20 m depths on stable rocky substrates. The localities were of comparative interest because of their marked differences in exposure to wave and current energy. The first site was a cove protected from the prevailing south-west and other winds, the second a rocky point fully exposed to winds and waves, and the third was a site protected from south-west winds, but exposed on the north (Fig. 1). North winds are more frequent in winter, and cause large wrack beds in the supralittoral often observed on Chile's northern coast (Edding 1998). The sites are under the influence of a strong upwelling center in northern Chile near Point Lengua de Vaca (Vasquez et al. 1998).

Mature reproductive blades were harvested haphazardly from numerous adult *L. trabeculata* plants at each site by SCUBA diving at intervals of c. 1 month over a 1-year period (October 1991–September 1992). The *Lessonia* reproductive blades are considered to be mature when the distal sorus tissues become colourless and/or part the sorus tissue is lost. Collections were made near the centre of each population at 8–10 m depth, where they occurred uniformly distributed over the substrate. The samples were returned wet to the laboratory in coolers at temperatures similar to those at the collection sites.

Morphological and reproductive characteristics of the macroscopic phase

Blades were utilised to describe the macroscopic phase (sporophyte) of *L. trabeculata* as this portion of the plant bears the reproductive tissue (sori). Morphological characteristics measured were the length, width, and fresh biomass of reproductive blades (n = 10–15 per sampling time and per site). The reproductive characteristics measured in the same blades included the area and biomass of reproductive tissue per blade. The surrounding halo of each sorus was drawn using tracing paper, and this area (cm^2 $blade^{-1}$) was measured using a polar planimeter (±0.01 cm^2). The percentage of reproductive tissue to total tissue of each blade was determined in terms of dry biomass. Both tissues were separately dried to constant biomass in an oven at 60°C. The reproductive's measurements were used to evaluate reproductive assignation in algae, and their relation to the size of the blades.

Reproductive characteristics of the microscopic phase

The number of spores released and their development under controlled laboratory conditions were used to describe the characteristics of the microscopic phase of *L. trabeculata*. Spore release was determined on 9 mm diam. discs of sorus obtained from the blades using a cork borer. Samples were taken from 10 different blades, from 10 different plants for each sampling site and time. Tissue samples were induced to sporulate by desiccation for 3 h, followed by immersion for 90 min in 4 ml of 0.45 µm filter-sterilised sea water. Previous observations had shown that the maximum sporulation from induction occurred within 70 min, with no further sporulation after 100 min (M. Edding unpubl. data). Spore numbers were determined separately for each tissue sampled using a hemacytometer chamber (Thoma®, Kayagiki Corp., 1/10 mm depth and 1/400 mm^2 area) and expressed as spores released per cm^{-2} of sorus.

Cultures of the microscopic phase were carried out using pooled spores released from 10–20 reproductive blades from each site for each sampling time. The cultures were carried out using pooled spores from different plants, assuming that in nature each reproductive event that led to recruitment of new individuals was produced by a mixture of spores of different parental origins. Here, no consideration was made of variations among blades and plants, and also, only mature blades were used to supply spores for the cultures. Release of spores was carried out using the method described by Edding et al. (1990) following the additional recommendations of Fonck et al. (1998) for this species. Spore numbers were determined using the hemacytometer chamber, and the number per chamber (between 5 and 100 spores) depended on sampling time. When the spores were released as aggregates, these were separated into individual spores using mild agitation on a shaker table. Each remaining aggregate was counted as one spore in the hemacytometer counts. The final

concentration of spores was adjusted to c. 5×10^4 spores ml^{-1}; and this suspension provided a settlement density of c. 100 spores mm^{-2} in 5.6 cm diam. plastic Petri dishes. Each time that a culture was made for a population, 16 reticulated Petri dishes were seeded with 6 ml of spore suspension and maintained for 24 h at 15° ± 1°C and 25 µmol photons m^{-2} s^{-1}, during which time spore settlement proceeded. After 24 h the water with non-settled spores was discarded, and replaced with 10 ml of sea water enriched with Provasoli medium (Starr & Zeikus 1993).

Desiccation of the Petri dishes was avoided by sealing them with parafilm®. The enriched sea water was renewed weekly with cultures maintained in an environmentally controlled culture chamber at 15° ± 1°C, 12L:12D h photoperiod, and 75 µmol photons m^{-2} s^{-1}. Previous experiments showed that these culture conditions were optimal for the observation of the complete life cycle of *Lessonia* species (Avila et al. 1985; Orrego 1992; Edding et al. 1993; Fonck et al. 1998). These methods did not, however, allow for determination of whether the physiology and development of the spores were adapted to the different seasons of the year as has been observed in other Laminariales (Lee & Brinkhuis 1988), and it was assumed that differences in the development of the spores were a result of their intrinsic characteristics.

To examine the relationships between aeration and the development of the microscopic phase, eight of the 16 Petri dishes were maintained in small individual aquariums with constant aeration under the same environmental conditions as above. The mixing of the culture water could increase absorption of nutrients, thus improving gametogenesis and production of sporophytes (Yoneshigue 1990; Reed et al. 1991).

The reproductive variables were recorded in permanently marked 0.6793 mm^2 optical fields using a Nikon inverted phase contrast microscope. Germination of the spores was recorded as a percentage after 7 days in culture in contrast with the original settled density (Fonck et al. 1998). The fertility of the female gametophytes was determined at 30 days of culture and expressed as the percentage of female gametophytes bearing oogonia compared with the total number of female gametophytes observed (Lee & Brinkhuis 1986). Reproductive success was expressed as the percentage of sporophytes with more than three cells, of the total individuals (female gametophytes + sporophytes) found after 40 days of culture (Lee & Brinkhuis 1986). The control times for reproductive variables were chosen following data in the literature for the same species (Edding et al. 1990, 1993; Fonck et al. 1998) permitting comparison among all the cultures, where different development times reflected the maturity of the spores.

Data analysis

Since climatic and oceanic conditions sometimes prevented simultaneous collection of samples from the three populations, the statistical analyses were carried out by grouping the monthly values by season, to avoid any impact on the interpretation of the patterns by missing or non-existent data. Culture data were grouped by season, with October–December representing spring, January–March summer, April–June autumn, and July–September winter. This grouping was designed to determine seasonal variations in development rather than month to month variation, as monthly variations could change between years because of climatic and oceanographic interannual changes.

Morphological and reproductive variables from the blades, and release of spores were analysed using 2-way ANOVA, with seasons and population as fixed factors. The variables obtained from the cultures of the microscopic phase were analysed using 3-way ANOVA with seasons, population, and aeration as a constant factor. In both instances statistical analyses were carried out at the 95% level of confidence. The statistical analyses were selected to observe the interaction between the factors evaluated (Sokal & Rohlf 1981). A *post hoc* Tukey test was applied when significant differences for main factors were encountered and not for the interactions. The Pearson correlation was carried out for the morphological and reproductive variables measured on the blades. Since all the cultures were maintained under the same environmental conditions during the year-long study, changes observed in the development of the microscopic phase were attributed to differential internal characteristics of the zoospores which developed in different months, and not to the culture conditions. The normality (Kolmorov-Smirnov test) and homoscedasticity (Levene test) of the data were obtained using logarithmic transformations (base 10) for the morphological measurements, and square-root arcsine transformations for percentage values. Spore counts and reproductive areas were square-root transformed (Sokal & Rohlf 1981).

RESULTS

Morphological and reproductive characteristics of the macroscopic phase

The morphological and reproductive characteristics of the blades showed significant seasonal variations ($P < 0.05$) among the three populations studied (Table 1). Similarly, the magnitude and the patterns of change were a property of each population, among which significant differences were observed with regard to seasons, population, and season/population interactions (Table 1). Despite the variability, the size and biomass of blades was highest toward the middle of spring and in summer (November–March), with a later decline to autumn (Fig. 2). During the study, the blade sizes varied from 40 to 100 cm in length and from 4 to 10 cm in width (Fig. 2). The differences of blades sizes between localities would depend on seasons, since the interaction was significant ($P < 0.05$). Tongoy blades were larger and wider than those from Chungungo and Lagunillas (Table 1), mainly in autumn and winter (Fig. 2A,B). The wet biomass was between 10 and 45 g per blade (Fig. 2C), and there were significant ($P < 0.05$) differences only between seasons (Table 1).

Lessonia trabeculata blades with bifacial reproductive tissue were found throughout the year of the study, although the reproductive areas and proportions of reproductive biomass increased significantly ($P < 0.05$) toward autumn months (April–June) in the three populations (Fig. 3A,B). The reproductive biomass per blade varied between 5% and 25%, with areas on the blade of less than 200 cm^2. Although the largest reproductive areas were found on blades at Tongoy, the Chungungo and Lagunillas blades showed significantly higher

Table 1 Two-way analyses of variance for morphological and reproductive characteristics of *Lessonia trabeculata* blades used to evaluate differences between seasons, locations, and interaction between them.

Source	d.f.	Mean square	*F* ratio	*P*
Length of blade (cm)				
Seasons	3	0.358	43.627	<0.0001
Locality	2	0.119	24.275	<0.0001
Seasons×locality	6	3.197×10^{-2}	3.897	0.001
Error	849	8.204×10^{-3}		
Width of blade (cm)				
Seasons	3	0.314	23.273	<0.0001
Locality	2	0.123	9.019	<0.0001
Seasons×locality	3	6.11×10^{-2}	4.536	<0.0001
Error	849	1.347×10^{-2}		
Blade wet biomass (g)				
Seasons	3	0.641	20.641	<0.0001
Locality	2	8.693×10^{-2}	2.800	0.063
Seasons×locality	6	3.951×10^{-2}	1.272	0.270
Error	251	3.951×10^{-2}		
Area of sorus per blade (cm^2)				
Seasons	3	300.248	44.131	<0.0001
Locality	2	35.274	5.185	0.006
Seasons×locality	6	33.700	4.953	<0.0001
Error	829	6.804		
Blade reproductive biomass (%)				
Seasons	3	689.076	27.623	<0.0001
Locality	2	80.320	3.220	0.042
Seasons×locality	6	88.230	3.537	0.002
Error	252	24.945		
Spores released cm^{-2} sorus (*n*)				
Seasons	3	7251418	40.515	<0.0001
Locality	2	11700942	65.375	<0.0001
Seasons×locality	6	3962393	22.138	<0.0001
Error	698	178983		

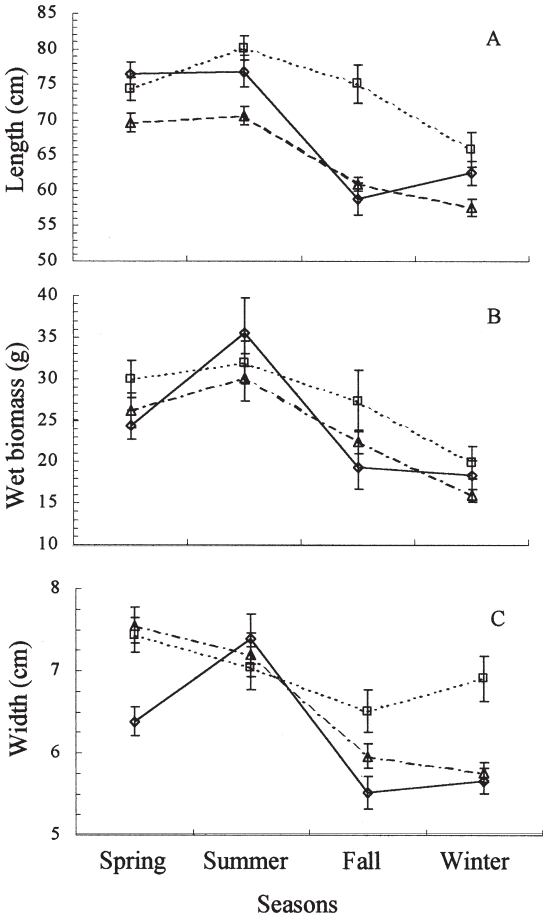

Fig. 2 *Lessonia trabeculata*. Seasonal variation of: **A**, length; **B**, wet biomass; and **C**, width of blades from Lagunillas (◇), Tongoy (□), and Chungungo (△) populations studied from northern Chile. Values are means ± SE.

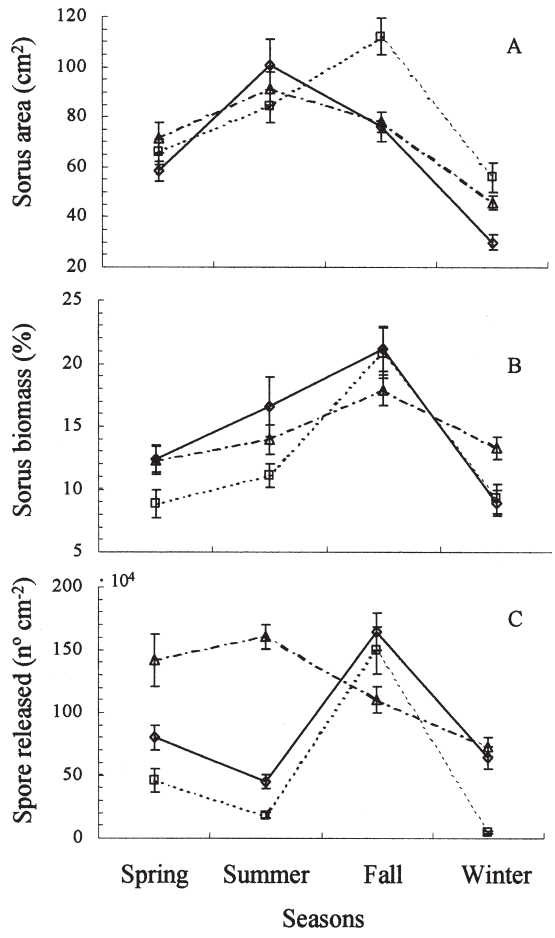

Fig. 3 *Lessonia trabeculata*. Seasonal variation of: **A**, absolute reproductive tissue area per blade; **B**, reproductive biomass per blade; and **C**, spores released per unit area of reproductive tissue from the Lagunillas (◇), Tongoy (□), and Chungungo (△) populations studied from northern Chile. Values are means ± SE.

proportions of reproductive tissue in terms of relative biomass (Table 1). These differences did not, however, correspond in all seasons and showed a significant interaction ($P < 0.05$) between seasons and localities (Table 1; Fig. 3A,B).

The correlation analysis of the morphological and reproductive characteristics of *L. trabeculata* showed that blades of greater biomass were longer and wider and had larger reproductive areas (Table 2). However, the reproductive biomass per blade only showed positive and significant correlation with the reproductive area per blade, and not with the size of the blades (Table 2).

Reproductive characteristics of the microscopic phase

The release of spores per area of sorus showed significant seasonal differences with a population-specific pattern, because of the significant interaction ($P < 0.05$) between the main factors (Table 1; Fig. 3C). The blades from Lagunillas and Tongoy showed a marked maximum release of spores only in autumn, whereas the blades from Chungungo showed a maximum release in summer, and a decrease only in winter (Fig. 3C).

The development of the microscopic phase under controlled culture conditions showed both seasonal

and population differences. Germination of the spores fluctuated significantly ($P < 0.001$) with low values toward spring and summer, later becoming stabilised at up to 80%, between autumn and winter (Table 3; Fig. 4A,B). Despite the lack of differences between localities (Table 3), the season/locality interaction was significant ($P = 0.004$), indicating that the differences between the seasons were dependent on the locality evaluated. The high germination shown by the Tongoy culture was only observed during spring and winter, both in aerated and non-aerated cultures (Fig. 4A,B). The aeration in the culture significantly ($P < 0.001$) decreased germination of spores from all three populations and for all seasons (Table 3; Fig. 4B).

The gametophytes fertility showed a significant seasonal pattern ($P < 0.001$) similar to that observed for germination, with low values in spring and summer, reaching averages of lower than 40% in summer (Table 3; Fig. 4C,D). In autumn and winter the fertility of the female gametophytes was similar, with average values above 60% (Fig. 4C,D). Here, the season/locality interaction was not significant ($P = 0.293$), indicating that the differences between the seasons were similar based on the locality evaluated (Table 3). Although the female gametophytes were capable of producing oogonia in all the seasons, fertilised eggs and/or microscopic sporophytes were not always observed. In these instances the gametophytes grew vegetatively, reaching several cells in length and were observed to form more than one oogonium. In the seasons of highest fertility, the gametophytes formed one or two cells, and fertilised eggs were detected at an early stage (20 days of culture). The main factors of locality and aeration did not show significant effect on the gametophyte fertility differences, but their interactions were significant (Table 3).

Reproductive success showed significant differences among seasons, among populations, and between aeration conditions (Table 3). Also, it was the only variable that showed that all interactions between the factors were significant ($P < 0.01$), indicating that the differences between populations were not the same in all combinations of the season and aeration factors (Table 3). Aeration of the cultures strongly influenced the development of the sporophytes (Fig. 4F). Thus the formation of sporophytes without aeration occurred only in spring and a very low percentage during summer for Tongoy and winter for Lagunillas (Fig. 4E). Whereas in the cultures with aeration, sporophytes were formed all year long, with greatest success in summer–autumn for Chungungo, autumn for Lagunillas, and winter–spring for Tongoy (Fig. 4F).

DISCUSSION

The present study describes the seasonal pattern of key morphological and reproductive characteristics of *L. trabeculata* populations for the first time. Although there were some differences among populations, blades of *L. trabeculata* were greater in size, but with smaller relative reproductive areas and reproductive biomass in spring and summer months. This pattern coincides with the maximum rates of elongation and productivity found in blades of

Table 2 Pearson correlation coefficient for morphological and reproductive characteristics of *Lessonia trabeculata* blades. Analyses included all paired measurements obtain during study time. They are the coefficient (r), significant probability (P), and n.

		Length	Width	Wet biomass	Area of sorus
Width	*r*	0.265			
	P	>0.001			
	n	861			
Wet biomass	*r*	0.775	0.767		
	P	>0.001	>0.001		
	n	263	263		
Area of sorus	*r*	0.309	0.388	0.643	
	P	>0.001	>0.001	>0.001	
	n	841	841	263	
Reproductive biomass	*r*	–0.077	0.014	0.029	0.690
	P	0.212	0.825	0.641	>0.001
	n	264	264	256	246

L. trabeculata toward the end of winter and beginning of spring (Tala 1999; Edding & Tala 2003). The autumn blades, which had greater reproductive areas and biomass, released spores that produced gametophytes having higher fertility and reproductive success than spores released in other seasons of the year. Occurrence of seasonal variation in spore development has been recognised in *L. saccharina* (Lee & Brinkhuis 1986), *Ecklonia maxima* (Osbeck) Papenfuss (Joska & Bolton 1987), and *Macrocystis pyrifera* (L.) C. Agardh (Reed et al. 1996).

Because all the cultures during the study were kept in a stable regime known to be optimal for *Lessonia* (Avila et al. 1985; Edding et al. 1990; Orrego 1992; Fonck et al. 1998), the seasonal variations observed in the development of the microscopic phase were assumed to be dependent on the intrinsic characteristics of the spores. Intrinsic properties such as energy reserves, photosynthetic capacity, and respiratory demand, as well as extrinsic environmental conditions, strongly influence the viability of the spores, and pre-determine their subsequent development (Santelices 1990; Amsler & Neushul 1991; Reed et al. 1996). Periods of low temperature and light, presumably correlated with the presence of high environmental levels of nutrients, have been related to maximum production of spores in kelps (Novaczek 1984; Lee & Brinkhuis 1986; Kain 1989; Reed et al. 1996). Growth of spores, gametophytes, and sporophytes obtained in different seasons of the year may have different requirements for light and temperature for their growth and development resulting more from a seasonal effect than from variability among plants (Lee & Brinkhuis 1988). The present study was not sufficient in scope to evaluate possible seasonal variations, which would have required special manipulation of the culture conditions to simulate seasonal environmental variation.

The reproductive tissue area, reproductive biomass, and release of spores observed for *L. trabeculata*, lie within ranges reported for other Laminariales (Anderson & North 1966; Joska &

Table 3 Three-way analyses of variance for reproductive characteristics of *Lessonia trabeculata* in culture to evaluate differences between seasons, locations, aeration, and the interaction between them.

Source	d.f.	Mean square	*F* ratio	*P*
Viability (%)				
Seasons	3	4834.689	37.438	>0.0001
Locality	2	321.317	2.488	0.084
Aeration	1	4372.875	33.862	>0.0001
Seasons×locality	6	423.913	3.283	0.004
Seasons×aeration	3	394.577	3.055	0.028
Locality×aeration	2	26.784	0.207	0.813
Seasons×locality×aeration	6	106.832	0.827	0.549
Error	431	129.138		
Fertility (%)				
Seasons	3	13273.266	54.027	>0.0001
Locality	2	735.788	2.995	0.051
Aeration	1	238.346	0.970	0.325
Seasons×locality	6	300.758	1.224	0.293
Seasons×aeration	3	99.460	0.405	0.750
Locality×aeration	2	1923.182	7.828	>0.0001
Seasons×locality×aeration	6	100.764	0.410	0.872
Error	410	245.679		
Reproductive success (%)				
Seasons	3	3045.777	8.918	>0.0001
Locality	2	3230.886	9.460	>0.0001
Aeration	1	83787.320	245.330	>0.0001
Seasons×locality	6	1923.236	5.631	>0.0001
Seasons×aeration	3	4685.119	13.718	>0.0001
Locality×aeration	2	1850.226	5.417	0.005
Seasons×locality×aeration	6	1532.065	4.486	>0.0001
Error	386	341.529		

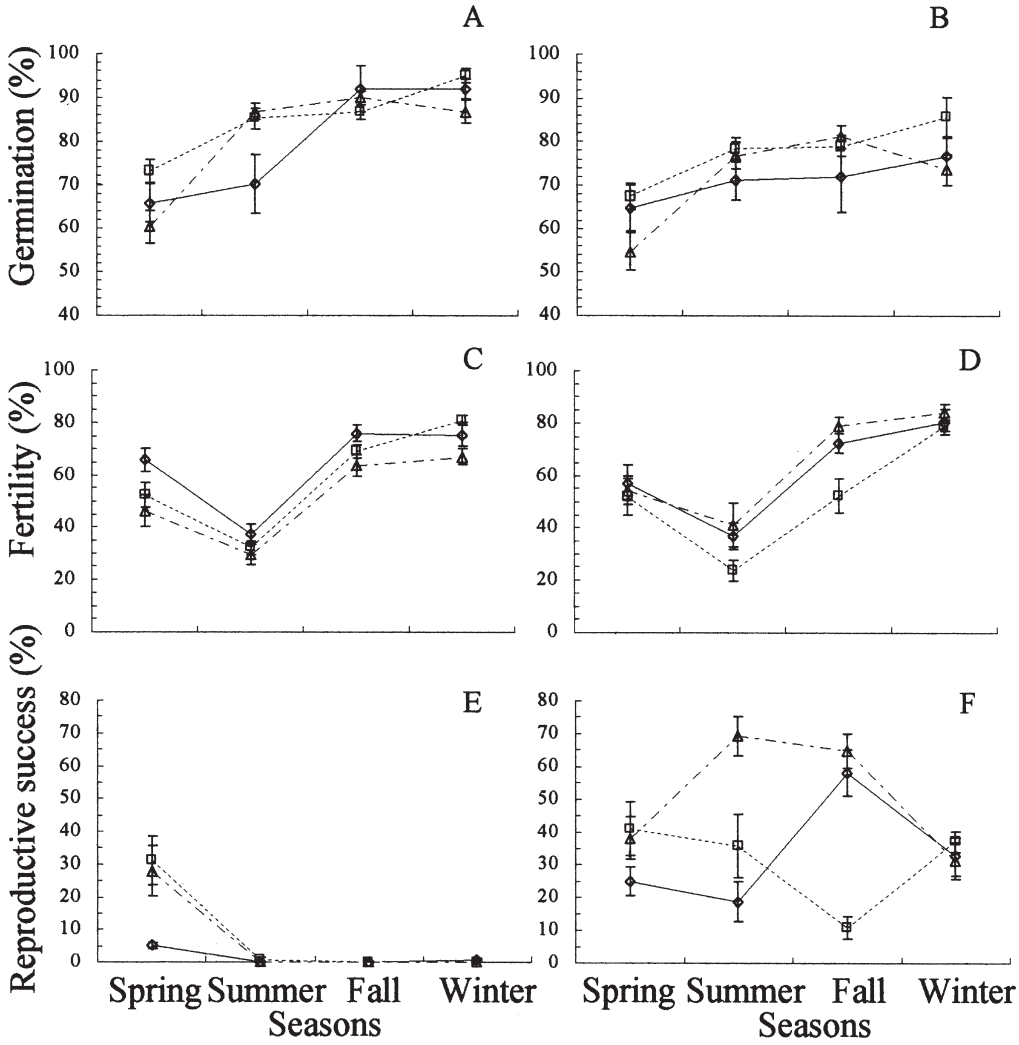

Fig. 4 *Lessonia trabeculata*. Seasonal variation in: **A**, **B**, the germination of spores; **C**, **D**, fertility of the female gametophytes; and **E**, **F**, reproductive success of the microscopic phases as formation of sporophytes from the Lagunillas (◇), Tongoy (□), and Chungungo (△) populations studied from northern Chile. One group of cultures was maintained without aeration (left) and another with aeration (right). Values are means ± SE.

Bolton 1987; Santelices 1990; Van Patten & Yarish 1993). Although the populations showed similar individual blade biomass, those from Tongoy had greater reproductive areas but less reproductive biomass and spore release. This pattern was found despite the correlation analysis, which showed that the reproductive biomass was positively correlated with the reproductive area. It is possible that sporangial density of the tissue influences the reproductive potential and seasonally of *L. trabeculata* as described for *Laminaria longicruris* de la Pylaie (Van Patten & Yarish 1993). Seasonal formation and total biomass of reproductive tissue may be related to changes in growth, energetic requirements, or directly by differentiation of reproductive tissue which occurs during the year (Santelices 1990).

At the population level, the morphological and reproductive characteristics studied did not show a clear interpopulational difference. One reason may be that in the present study, the populations were not geographically far apart, and occurred near the centre of distribution of the species (Edding et al. 1994).

The magnitude of interpopulation difference may increase when populations are compared which occupy opposite extremes of the geographic distribution of the species (Kain 1989; Camus & Ojeda 1992), or between localities that show more clearly differing environmental conditions such as temperature, nutrients, and others. On the other hand, the study was made only during 1 year, and the differences between localities may not occur in other study time, because of environmental heterogeneity. Nevertheless, the seasonal tendency of the development of blades as much as of the microscopic phases have been observed in later studies for *L. trabeculata* (Edding 1998; Tala 1999).

The populations studied were selected principally on the basis of water movement differences, factors associated with algae morphological, physiological, and productivity changes (Hurd 2000). Edding et al. (1993) suggested that *L. trabeculata* inhabiting zones of greater water movement showed better reproductive development. This was not observed in this study, since the authors did not consider the possible seasonal variation shown by the reproductive characteristics. The seasonal pattern observed in one population is not necessarily the same as observed in another one. Whereas the population at Tongoy (exposed to north winds) had greater reproductive areas and liberation of spores in autumn months (April–June), the population at Chungungo (semi-protected) did so in summer (January–March). Also, these localities showed no differences in relation to the production of sporophytes in culture, but did show differences in seasonal pattern of sporophyte formation. Lagunillas (exposed) occupied an intermediate position for some morphological and reproductive characteristics among the populations. Interpopulational differences in reproductive characteristics have been associated with localised environmental conditions in *M. pyrifera* (Anderson & North 1966; Reed et al. 1996), *Pterygophora californica* Ruprecht (Reed et al. 1996), *Ascophyllum nodosum* (L.) Le Jolis (Cousens 1986), and *E. maxima* (Joska & Bolton 1987). The interaction between season and locality was, however, significant for most of the variables studied, except for the biomass of the blades and the fertility of the gametophytes, indicating that the seasonal differences were dependent on the population analysed. Morphological and reproductive differences may also exist within a population related to the size structure and age of the population.

Although the simulation of water movement by aeration of the cultures does not completely simulate water movement in nature, it does give an indication of how certain processes are affected when this factor is varied. The germination of *L. trabeculata* spores in the cultures decreased with aeration, but did stimulate the formation of new sporophytes from all the populations. Under natural conditions the settlement and subsequent germination of spores may be strongly influenced by water movement (Hurd 2000). A higher degree of formation of sporophytes under aerated conditions has been observed in *Laminaria abyssalis* Joly et Oliveira (Yoneshigue 1990), *M. pyrifera* and *P. californica* (Reed et al. 1991). Increase in water movement could increase absorption of nutrients, thus improving gametogenesis and production of sporophytes. Formation of sporophytes under these conditions suggests that there may be potential recruitment throughout the year in nature. There are, however, other physico-chemical or biological environmental factors, which may influence the success of development and recruitment of sporophytes (Deysher & Dean 1986; Reed et al. 1988, 1991; Santelices 1990). Studies of *L. trabeculata* report recruitment events in the summer months (Tala 1994; Mendieta 1997). Given the time required by the microscopic phase to produce macroscopic sporophytes in *L. trabeculata* (Edding et al. 1990; Edding & Tala 2003), it is probable that the recruits observed in summer arose from spores released in autumn or winter. Data for *M. pyrifera* suggested that at least 3 months passed between spore settlement and detection of the first macroscopic sporophyte plants (Deysher & Dean 1986).

Considering the mean values for blade density per plant as determined for the Tongoy population (Tala 1999), and results obtained in the present study, it is estimated that a single adult *L. trabeculata* plant having c. 100 blades may liberate c. 4×10^9 spores (c. 1.6×10^{10} spores m^{-2}) in a major reproductive event. These values differ little from values obtained for other Laminariales, and reflect the high mortality that occurs in the microscopic stages of the life cycle of these species (Anderson & North 1966; Joska & Bolton 1987; Martinez & Santelices 1998). Also, it is important to mention that *Lessonia* living in exposed-to-the-wave areas have a high mortality rate, then the plant needs to occupy the available free space to avoid predation by herbivores and competition of other algae. The formation of reproductive tissue throughout the year in perennial species had been related to the low energetic cost of reproduction compared with other Laminariales (De Wreede & Klinger 1988; Santelices 1990). The

success of the microscopic phase appears to depend on the local environmental conditions, and their seasonal variations. The pattern observed in morphological and reproductive characteristics of *L. trabeculata* is similar to a seasonal pattern of cold temperate zone algae (Kain 1989; Lüning 1990), with maximum growth to spring-summer and maximum reproduction in autumn.

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