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Growth and loss of distal tissue in blades of *Lessonia nigrescens* and *Lessonia trabeculata* (Laminariales)

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Abstract

Meristematic growth and loss of distal tissue from blades of two ecologically important species in the south-east Pacific, *Lessonia nigrescens* and *Lessonia trabeculata*, was evaluated during 1 year. Comparative growth was determined by a hole-punch method, loss of distal tissue from the blades was determined by subtracting final blade length (with loss) from expected blade lengths (without loss); growth and tissue loss were transformed to fresh biomass units for calculation of inter-algae differences. The results showed that blade elongation rate increased at the beginning of spring, and declined towards the end of summer, with mean values between 0.40 and 0.08 cm day^{-1} for *L. nigrescens*, and 0.65–0.17 cm day^{-1} for *L. trabeculata*. Loss of distal tissue varied seasonally when examined as length units for both species; with mean values between 0.24 and 0.10 cm day^{-1} for *L. nigrescens*, and 0.51–0.25 cm day^{-1} for *L. trabeculata*. Variations in fresh biomass units were only observed in *Lessonia trabeculata*, increasing in spring, with mean values to 0.13 g (fresh weight) day^{-1}. Annual growth and loss of distal tissue were higher in *L. trabeculata* (0.41 and 0.39 cm day^{-1}, respectively) than in *L nigrescens* (0.19 and 0.15 cm day^{-1}). When growth and tissue loss were considered as fresh biomass, monthly gains significantly outweighed loss of distal tissue in both species, but parallel results based on length data followed a different trend. *L. trabeculata* released about 50% of its growth biomass as particulate organic matter, while the comparative value for *L. nigrescens* was about 20%.

Keywords: Chile; Growth; Erosion; Lessonia; Macroalgae; Particulate organic matter; Tissue loss

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1. Introduction

Among marine algae, Laminariales form one of the orders with the greatest dominance in biomass; they are highly productive in temperate and sub-Antarctic zones. These algae are important within ecosystems as producers of structural habitat allowing the settlement and development of a great variety of invertebrates and fishes, offering refuge for them from environmental disturbances (Novaczek, 1984; Mann, 1988; Vásquez, 1992; Edding et al., 1994; Lobban and Harrison, 1994). They are of economic importance, given the presence in their cell walls of alginic acid, a commercially valuable polysaccharide in the pharmaceutical and food industries (Guiry and Blunden, 1991; Lobban and Harrison, 1994).

Organic matter produced by algal growth may enter the food web by several pathways. Waves and currents may cause portions of biomass to be dislodged from the substrate and cast a shore forming wrack beds (Guiry and Blunden, 1991; Kirkman and Kendrick, 1997). Wrack bed zones are sources of particulate and dissolved nutrients utilized by small organisms including crustaceans (isopods, amphipods) and insects; they also serve as feeding and breeding areas for a variety of coastal birds (Kirkman and Kendrick, 1997). Another portion of the algal biomass is consumed by herbivores, including invertebrates and fish that consume drift algae as well as algae fixed to the substrate (Lobban and Harrison, 1994). Finally, a large portion of the algae passes to the detritivorous route (Mann, 1988). Most species of Laminariales release particulate and dissolved organic matter due to fragmentation of distal end portions of blades, providing a food source for both benthic and pelagic filter feeders and detritivores (Mann, 1988; Duggins et al., 1989; Bustamante and Branch, 1996).

Growth in simple morphologies *Laminaria* could be estimated by determining the change in length of the blade over time (Chapman and Craigie, 1978; Gagné and Mann, 1981). In contrast, morphologically complex species such as *Macrocystis*, *Ecklonia*, and *Lessonia*, the characteristics utilized have included the length of the stipe, nodes number, and total length of the alga or its main blade (Kirkman, 1989; van Tussenbroek, 1989; Brown et al., 1997). Repeated measurements of length may, however, lead to underestimation of growth, given the continuous loss of tissue that occurs at the blades distal ends. Growth measurements have been useful in evaluating the contribution of particulate matter to natural environments (Chapman and Craigie, 1978; Novaczek, 1984; Brown et al., 1997). The loss of tissue provides suspended particulate organic matter, which serves as a continuous food source to organisms in the trophic system that do not depend strictly on seasonal phytoplankton blooms (Mann, 1988; Duggins et al., 1989; Bustamante and Branch, 1996). The importance of algal detritus has been supported by analyses with a stable carbon isotope ($\delta^{13}C$), showing a 20–50% contribution on the assimilation of carbon derived from the algae on secondary consumers both in the subtidal and intertidal zones of sub-antarctic islands (Duggins et al., 1989; Simenstad et al., 1993).

Among Laminariales distributed on the rocky coast of the South east Pacific (Peru-Chile) *Lessonia trabeculata* Villouta and Santelices forms extensive beds in subtidal areas, while *Lessonia nigrescens* Bory de Saint-Vincent is distributed in the low intertidal (Edding et al., 1994). Some studies have provided basic information on the biology and ecology of *L. trabeculata* (Camus and Ojeda, 1992; Vásquez, 1992; Edding et al., 1994;

Tala et al., 2004). Due to logistical reasons and ease of access, the greatest study efforts have been developed on intertidal areas dominated by *L. nigrescens* (e.g. Edding et al., 1994; Camus, 1994; Martínez, 1996; Westermeier and Gómez, 1996; Martínez and Santelices, 1998). Growth measurements on *Lessonia* spp. are scarce, and there are no estimates of productivity and tissue loss from its blades. The present study is a contribution to the knowledge of growth dynamics of the two *Lessonia* species, with particular emphasis on the fraction of distal biomass lost during their growth cycles. This loss represents particulate organic matter import to the local ecosystem rich in invertebrate and fish species, many of which are commercially harvested by artesanal fishing activity.

2. Materials and methods

Growth measurements and loss of distal tissue estimates from blades of *L. trabeculata* and *L. nigrescens* were carried out between November 1996 and October 1997. At the site selected for *L. trabeculata* (Tongoy, 30°15′S–71°15′W), it forms an extensive perennial bed between 2 and 20 m depth, with an homogeneous distribution over the rocky substrate and a mean density of 5 ± 2 algae m^{-2} (Tala, 1999). For *L. nigrescens* (La Pampilla Sur, 29°57′S–71°22′W), the site was selected having a continuous belt on the rocky substrate in the infra-mesolittoral fringe with algae growing on horizontal and vertical rock surfaces, at a mean density of 6 ± 1 algae m^{-2} (Tala, 1999). Both sites are wave exposed and are typical habitats for the distribution of these species in Chile.

At the beginning of the study 20 adult algae of each species were haphazardly selected and marked at the base of the stipes for identification. Since selection was not made at random, the values depend on the sizes of the algae selected and do not reflect influence of the population structure in growth and loss of distal tissue. Two blades per month were marked in each alga at different distances distally from the first dichotomy of the stipe. The growth of the blades was quantified after using the method of Parke (1948) in which a 5-mm diameter hole is made in the blade centrally and above the meristem with a cork borer, and the displacement of the hole is measured over time as the alga grows. Based on the differences in sizes of blades between the two species and on previous punching trials to determine meristematic zone, holes in *L. trabeculata* were made at 10 cm above the base, while in *L. nigrescens*, they were made at 5 cm. above the meristematic zone.

The sampling design (Fig. 1), consisted of marking, punching, and measuring the total length of the blades at time zero, and then after 25–35 days, depending on the sampling month and species, punched blades were harvested for individual re-measurement in the laboratory. In each sampling month, two new blades haphazardly selected from each alga were marked, punched, and measured on each alga and left until the end of the next evaluation period (Fig. 1). When, for uncontrollable reasons, test blades could not be recovered at any given monthly sampling, this data set was discarded, and new blades were marked for growth determination in the subsequent growth period. This was done in order to avoid making growth measurements which were over 2 months long, and which could interfere with the observations of month-to-month differences.

Care had to be taken to initially select adult algae having many blades in order to obtain sufficient sample material during the harvesting period. Since both species occurred in

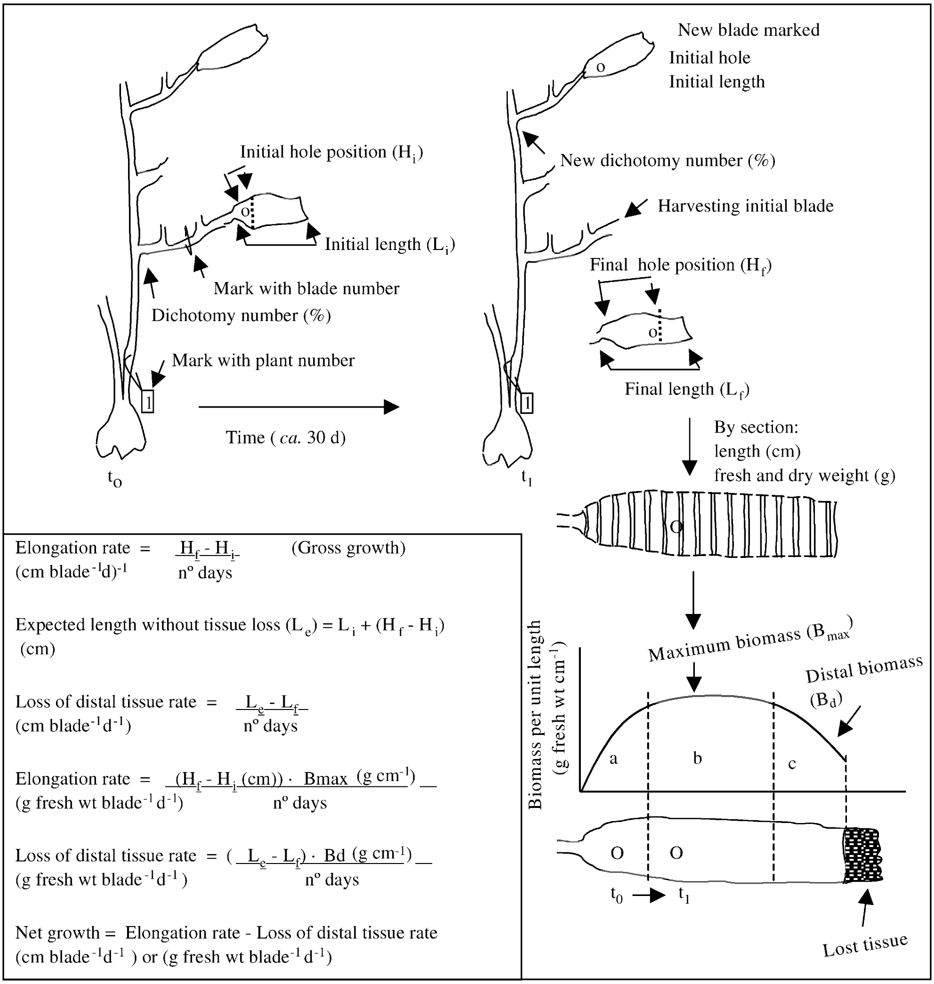

Fig. 1. Sampling design used for the determination of growth and loss of distal tissue from blades of *Lessonia nigrescens* and *Lessonia trabeculata*. In the upper side is showed the sampling design of mark and harvest blades over the time. Left down are showed the formulae for expression of the variables measured. Right down is showed the sampling design to obtain biomass distribution in each blade.

wave-exposed habitats it was not possible to enumerate the number of blades on marked algae in situ. It was assumed that the amount of blades was within the range of blade density and biomass found in standing stock estimates that were carried out in the same populations (*L. nigrescens*: 350 ± 245 blades alga^{-1} to 584 ± 170 g fresh weight alga^{-1}, $n = 50$; *L. trabeculata*: 117 ± 67 blades alga^{-1} to 1700 ± 500 g fresh weight alga^{-1}, $n = 139$; Tala, 1999). *Lessonia* spp. typically consist of a basal disc (holdfast) from which arise various stipes, each one of which becomes dichotomously branched at various heights above the holdfast with each branch having at least two blades (Edding et al., 1994).

Meristematic growth in *Lessonia* was expressed as daily elongation rates (cm day^{-1}) and represented the gross growth of the blade (Fig. 1). Summing the initial length (L_i, cm) and distance of displacement of holes ($H_f - H_i$) on each blade, the expected length measure (L_e) without loss of distal tissue was obtained (Fig. 1). The difference between the expected length and the observed final length (L_f) allowed estimation the loss of distal tissue from the blade in cm day^{-1}, during the test period (Fig. 1).

The gross growth in length units was transformed to a biomass units (g fresh weight day^{-1}) based on the method of maximum blade biomass developed for estimation of productivity in *Ecklonia radiata* (C.Ag) J.Agardh (Mann and Kirkman, 1981). Distribution of biomass was determined individually for each blade harvested, for each sampling month. Blades were cut into small pieces, 3 cm apart for *L. nigrescens* and 5 cm for *L. trabeculata*, each of which was weighed fresh. Fresh weight distribution of a blade was visualized by plotting the weights of each section (g fresh weight cm^{-1}) along the length of the blade (cm). An estimate of fresh biomass growth was obtained by multiplying the growth in cm by the biomass in g cm^{-1} present in the maximum biomass zone (B_{max}) of each individual blade (Fig. 1).

In order to estimate the loss of distal tissue as fresh biomass, the same principle was employed but taking into account the distal biomass (B_d) found in the last third portion of each blade. It was assumed that this would be the fresh weight attained in the distal end of the blade, prior to the loss as particulate matter. Since tissue ‘‘broken’’, by erosion was observed only on the distal end of the blade, and not in the blade edges, it was assumed that there is not lateral tissue loss. Distal tissue biomass lost (g fresh weight day^{-1}) was calculated by multiplying centimetres lost ($L_e - L_f$) by the distal biomass (g fresh weight cm^{-1}) for each blade (Fig. 1).

The experimental design corresponded to repeated-measures, where monthly data were not independent since observations were always made on the same 20 marked algae, with the month factor repeated on all algae. Since the assumption of sphericity (Mauchly test), needed in ANOVA repeated-measures was not met, potentially exceeding Type I error, multivariate analysis of variance (MANOVA) with $\alpha = 0.05$, was considered (SPSS 10.0). The Wilks' lambda statistic was used, which has been suggested in analysis of experimental designs with repetitive measurements without depending on an assumption of sphericity (Zar, 1999, p. 259). The independent variable was species of *Lessonia* (with two levels), and the dependent variables were daily rates (cm day^{-1} or g day^{-1}) of elongation and loss of distal tissue; and maximum and distal biomass per blade in successive time intervals. All variables analysed were transformed to ln (x + 10), to comply with requirements for homogeneity of the variances and normality. Although normality was obtained only in some cases, the test applied is robust enough to support violation of this requisite, and has a weak effect on the rate of Type I error (Zar, 1999, p. 320). In order to generate a balanced design, the analyses included only the months in which there occurred simultaneous measurements on both species and for all the marked algae (November, December, January, February, April, July, and October). Lengths and fresh weights of the blades were also analysed with a MANOVA, and the weight variable was log-transformed to comply with normality and homocedasticity requirements (Zar, 1999).

A paired sample *t*-test was used to compare individual growth and loss of distal tissue values to evaluate whether the growth attained by individual blade overcame the loss of distal tissue. The comparison was made separately for each species, both in length and in fresh biomass units. Although the monthly measurements were not independent, the analysis considers individual data obtained during the entire study period without separation due to the monthly repetition factor. Growth and loss of distal tissue were plotted graphically in relation to the position of the dichotomy of each marked blade. Because of the difference between the species in the number of dichotomy and length per stipe in the marked algae (1–11 for *L. nigrescens* and 3–18 for *L. trabeculata*), the position of the blade was expressed as a percentage of its distance from the holdfast, where 100% represented the greatest relative distance of the blade from the base in each marked alga, distal portion. A Spearman rank correlation was used to determine if any correlation existed among the variables studied and the position of the dichotomy (Zar, 1999).

3. Results

Both species showed a marked seasonal growth pattern (Wilks' $\Lambda = 0.053$; $F_{(6,33)} = 98.359$; $P < 0.001$) with a maximum in the austral spring and minimum values in fall and winter (Fig. 2). However, while in *L. nigrescens* the minimum growth rates extended toward the winter, in *L. trabeculata* blades showed a progressive increase in growth from the end of fall (Fig. 2). Loss of distal tissue from the blades was also greater during spring, and summer for both species (Fig. 2), but only *L. trabeculata* showed a significant seasonal change in tissue loss (Wilks' $\Lambda = 0.276$; $F_{(6,14)} = 6.129$; $P = 0.003$). Although loss of distal tissue from blades of *L. nigrescens* showed variation between months (Fig. 2), differences were not significant (Wilks' $\Lambda = 0.551$; $F_{(6,14)} = 1.899$; $P = 0.151$). The growth and loss of distal tissue of *L. trabeculata* was significantly higher (growth: Wilks' $\Lambda = 0.190$; $F_{(7,33)} = 19.482$; $P < 0.001$; loss: Wilks' $\Lambda = 0.277$; $F_{(7,33)} = 11.953$; $P < 0.001$) than *L. nigrescens* (Fig. 2).

Upon analyzing the sizes reached after growth, the final values did not reflect the total elongation that occurred in the blades. In both species lengths and weights of blades decreased approaching fall and winter months (Fig. 3), follow the same pattern as the elongation rate. The blades of *Lessonia* species showed different sizes (length: Wilks' $\Lambda = 0.096$; $F_{(7,33)} = 42.887$; $P < 0.001$; fresh weight: Wilks' $\Lambda = 0.046$; $F_{(7,33)} = 94.475$; $P < 0.001$), thus when the elongation rate was expressed as a percentage (% day^{-1}) with respect to the initial length of their blades, there were not significant differences between species (Wilks' $\Lambda = 0.728$; $F_{(7,33)} = 2.050$; $P = 0.087$). *L. nigrescens* grows an annual average of $0.44 \pm 0.05\%\ \text{day}^{-1}$, and *L. trabeculata* to $0.45 \pm 0.06\%\ \text{day}^{-1}$. Growth expressed in relative units showed a significant seasonal pattern (Wilks' $\Lambda = 0.170$; $F_{(6,33)} = 26.871$; $P < 0.001$) in both species which was similar to the growth in absolute units. Widths of the blades were also different, with *L. trabeculata* having a mean width of 5 ± 1 cm and *L. nigrescens* 2 ± 1 cm.

It was observed that the biomass was not distributed uniformly over the length of the blade in the *Lessonia* spp. In plotting the biomass (g fresh weight cm^{-1}) against the distance from the base of the blade, three zones were detected: (a) a basal growth zone, where the g fresh weight cm^{-1} was increasing, (b) an intermediate zone with maximum accumulation of fresh biomass cm^{-1}, and (c) a zone where the g fresh weight cm^{-1}

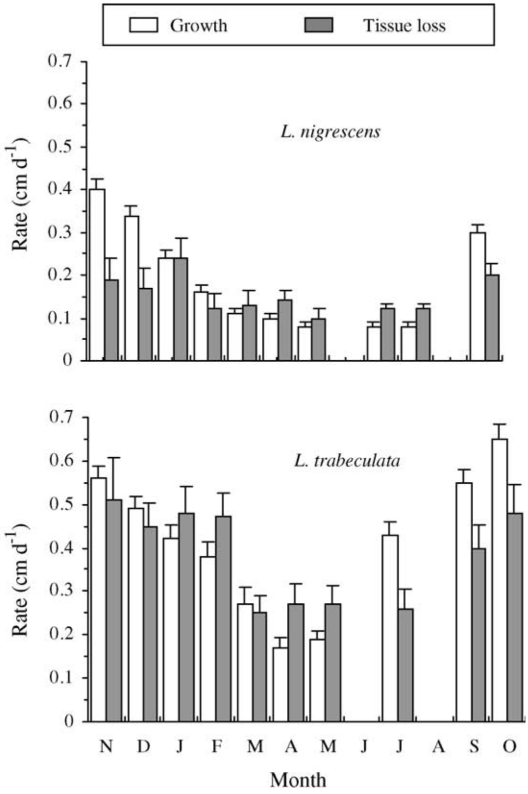

Fig. 2. Seasonal variation (mean ± standard error) in growth and loss of distal tissue from blades of *Lessonia nigrescens* (upper) and *Lessonia trabeculata* (lower) in units of length (cm day^{-1}). Annual mean growth: *L. trabeculata* 0.41 ± 0.05 cm day^{-1}, *L. nigrescens* 0.19 ± 0.04 cm day^{-1}; annual mean distal loss: *L. trabeculata* 0.39 ± 0.03 cm day^{-1}, *L. nigrescens* 0.15 ± 0.001 cm day^{-1}.

decreased towards the distal part of the blade (Fig. 4). The zone of maximum biomass in the blades coincided with the location of the largest number of the holes following growth. However, when the zones were superposed, only a few blades demonstrated significant differences between zones, while others showed differences between the intermediate zone and the distal zone. The tendency of this non-homogeneous biomass distribution pattern was observed in all the blades evaluated over the entire study period in both species, and the extension of these zones, varied depending on the total length of the blades. In some cases, the biomass decrease towards the distal zone is accompanied by a narrowing of the blades, whereas in other cases this does not happen with a defined pattern (Fig. 4).

L. trabeculata blades showed an annual mean accumulation of biomass of 0.44 ± 0.08 g fresh weight cm^{-1} and distal biomass of 0.25 ± 0.01 g fresh weight cm^{-1}, significantly greater than *L. nigrescens* with values of 0.26 ± 0.14 g fresh weight cm^{-1} and 0.07 ± 0.01 g fresh weight cm^{-1}, respectively (maximum biomass: Wilks' $\Lambda = 0.08$; $F_{(7,33)} = 52.32$; $P < 0.001$; distal biomass: Wilks' $\Lambda = 0.036$; $F_{(7,33)} = 121.82$; $P < 0.001$).

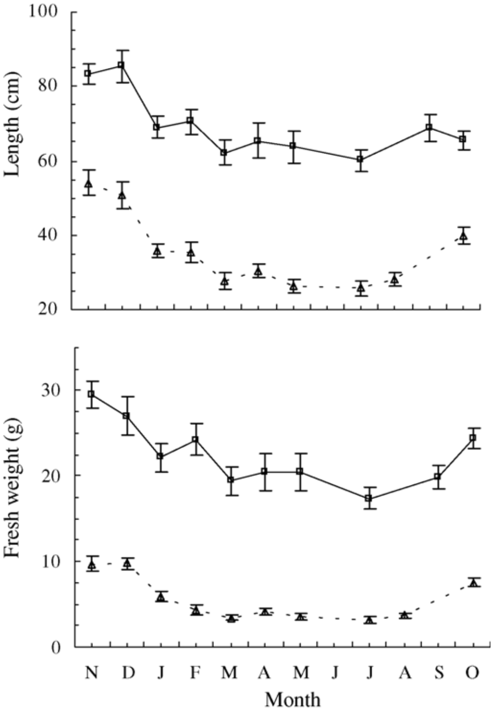

Fig. 3. Seasonal variation (mean ± standard error) in length (cm) and fresh weight (g) of *Lessonia nigrescens* (△) and *Lessonia trabeculata* (□) blades.

The maximum biomass and the distal biomass of the blades showed a significant seasonal pattern of variability (maximum biomass: Wilks' $\Lambda = 0.186$; $F_{(6,33)} = 24.114$; $P < 0.001$; distal biomass: Wilks' $\Lambda = 0.467$; $F_{(6,33)} = 6.266$; $P < 0.001$) with a increase during spring months, October to December (Fig. 5). For *L. nigrescens* blades, the biomass tended to remain constant particularly in fall and winter months, while *L. trabeculata* showed a greater fluctuation in monthly values (Fig. 5).

The growth and loss of distal tissue showed the same temporal pattern in fresh biomass units as in length units, with a significant decrease over the fall-winter months for both species (growth: Wilks' $\Lambda = 0.082$; $F_{(6,33)} = 61.268$; $P < 0.001$; loss of distal tissue: Wilks' $\Lambda = 0.302$; $F_{(6,33)} = 12.691$; $P < 0.001$) (Fig. 6). Although the variation in biomass growth was significant for the two species ($P < 0.001$), only the blades of *L. trabeculata* showed a significant difference (Wilks' $\Lambda = 0.179$; $F_{(6,14)} = 10.668$; $P < 0.001$) in loss of distal tissue over time (Fig. 6). For both variables, the values found for *L. trabeculata* were significantly higher (growth: Wilks' $\Lambda = 0.140$; $F_{(7,33)} = 28.194$; $P < 0.001$; distal loss: Wilks' $\Lambda = 0.277$; $F_{(7,33)} = 11.953$; $P < 0.001$), than for *L. nigrescens* (Fig. 6).

The difference between elongation and loss of tissue per blade was species-specific. In *L. nigrescens* blades, the growth and loss of distal tissue were significantly different both in terms of length ($t_{(179)} = 0.383$, $P < 0.001$) and biomass ($t_{(179)} = 8.279$, $P < 0.001$), and the

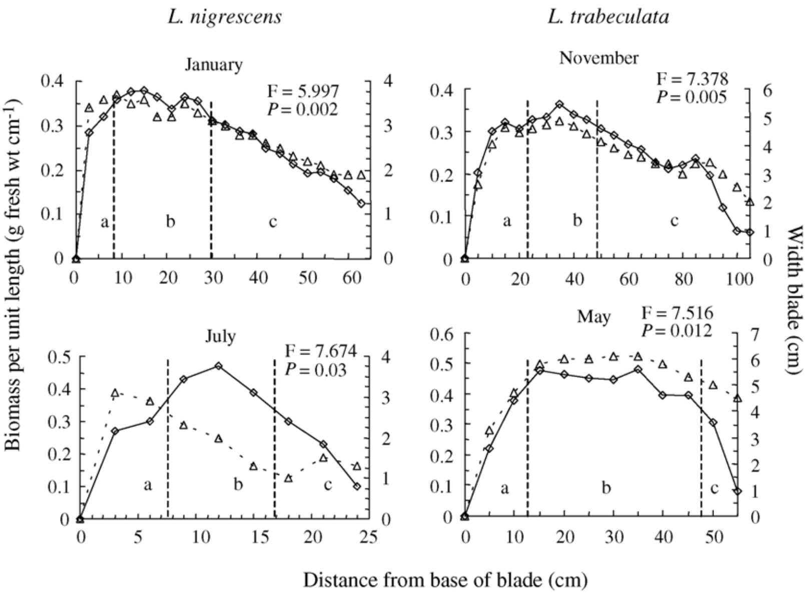

Fig. 4. Biomass per unit length (g fresh weight cm^{-1}) plotted against the distance from the base of the blade, for four representative blades of *Lessonia nigrescens* (△) and *Lessonia trabeculata* (□). From all blades sampled, blades were selected as example which had been measured at different times throughout the sampling period (January and July for *L. nigrescens*, November and May for *L. trabeculata*), as well as from different algae. Note the different scales on the horizontal axes due to differences in blade lengths. Also the blade width (△) is included.

tissue gain by growth was greater than loss of distal tissue (Figs. 2 and 6). In *L. trabeculata*, the relation was dependent upon the measurement units. When expressed as length units, the loss of distal tissue did not differ significantly from growth ($t_{(139)} = 1.782$, $P = 0.077$), in some cases the growth was greater, and in others, loss of tissue was greater (Fig. 2). However, in biomass units, tissue gains were significantly greater ($t_{(139)} = 110.892$, $P < 0.001$) than the loss of distal tissue from the blades (Fig. 6). The elongation rate and loss of distal tissue expressed in these two units (cm and g fresh weight) showed a significant linear relation for each species, although an exponential fit produces a better coefficient of determination (r^2) and lower standard error in the model (Fig. 7).

Influence of position of the dichotomy of the blade on growth and loss of distal tissue also was species-specific. *L. nigrescens*, showed no significant correlation for the elongation rate ($r = -0.05$, $n = 222$, $P = 0.421$) and loss of distal tissue ($r = -0.08$, $n = 222$, $P = 0.224$) with the height of the dichotomy on which the blade was located (Fig. 8). Blades located at a 50% dichotomy level showed the same growth range as those at the most distal portions of the stipe representing 100% dichotomy distance (Fig. 8). In the case of *L. trabeculata*, a significant tendency was observed toward greater elongation ($r = 0.37$, $n = 135$, $P < 0.001$) and losses of tissue ($r = 0.21$, $n = 135$, $P = 0.014$) from blades located nearer the more distal dichotomy (Fig. 8). In both species, a similar pattern was observed when the variables were expressed as fresh biomass.

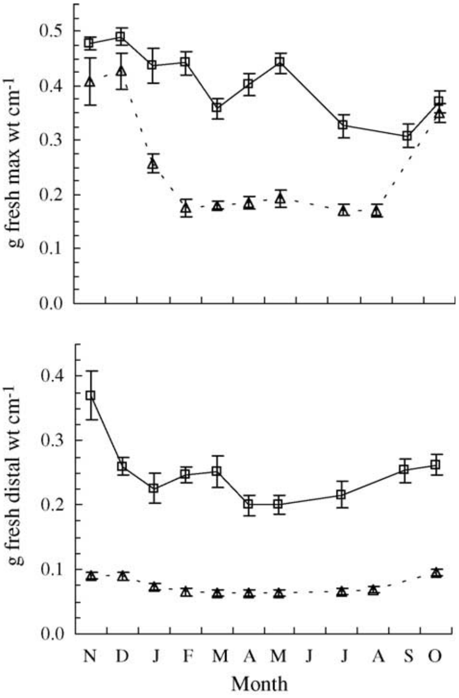

Fig. 5. Seasonal variations (mean ± standard error) in the maximum (upper) and minimum (lower) fresh biomass values per cm of blade for *Lessonia nigrescens* (△) and *Lessonia trabeculata* (□).

4. Discussion

Similar to many Laminariales, the seasonal growth pattern of *L. nigrescens* and *L. trabeculata* showed maximum rates in mid-spring and minimum towards late summer to early winter. Seasonal availability of nutrients has been one of the environmental factors most related to the annual growth patterns in the subtidal Laminariales (Chapman and Craigie, 1978; Gagné and Mann, 1981; Gerard, 1982; van Tussenbroek, 1989; Lobban and Harrison, 1994; Brown et al., 1997). The locations selected for this study occur within one of the four major Chilean upwelling areas (Coquimbo - Lengua de Vaca Pt, 30°S) with higher frequency of upwelling events between winter and spring months (Vásquez et al., 1998). Both *Lessonia* species may be classified as ‘‘season anticipators’’ by the criterion of Kain (1989) or ‘‘Type 2’’ of Lüning and tom Dieck (1989), where the growth cycle would not be directly related to light, as they show weak growth based on photosynthesis when irradiance is maximal at the summer solstice. The pool reserve produced in summer would be utilized in the initial growth in winter, when light is reduced and seawater nutrient availability rises. This pattern was most notable in *L. trabeculata* (subtidal), with an increase growth beginning in winter, while the intertidal species, *L. nigrescens*, showed an increase in growth rate beginning in the spring, suggesting a differential response of the

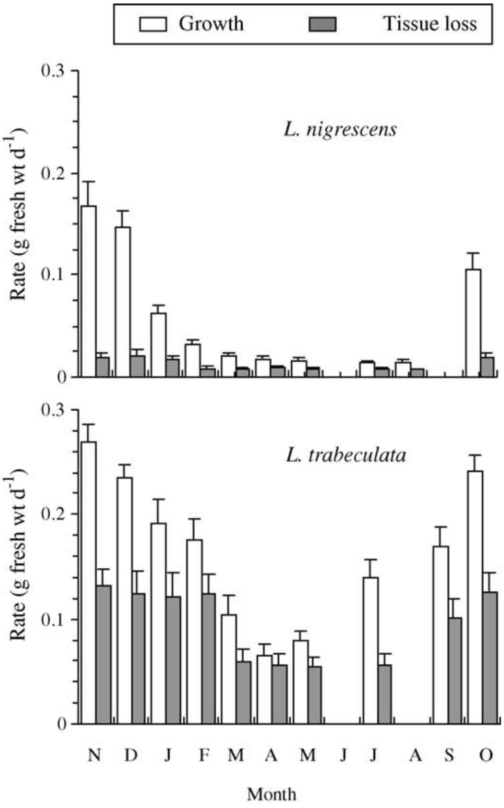

Fig. 6. Seasonal variation (mean ± standard error) in growth and loss of distal tissue from blades of *Lessonia nigrescens* (upper) and *Lessonia trabeculata* (lower) in units of fresh biomass (g day^{-1}). Annual mean growth: *L. trabeculata* 0.17 ± 0.02 g day^{-1}, *L. nigrescens* 0.06 ± 0.02 g day^{-1}; annual mean distal loss: *L. trabeculata* 0.10 ± 0.01 g day^{-1}, *L. nigrescens* 0.01 ± 0.001 g day^{-1}.

growth pattern to the habitat of these species. Since this study was carried out on a single population of each species, general conclusions cannot be made due to local environmental variations. Morphological and abundance patterns based on large geographic distributional scale (Camus and Ojeda, 1992), and reproductive patterns (Tala et al., 2004) have been described for *L. trabeculata*.

Annual elongation rates found in *L. nigrescens* and *L. trabeculata* are similar to those obtained for other Laminariales (Chapman and Craigie, 1978; Gagné and Mann, 1981; Novaczek, 1984; Kirkman, 1989; Brown et al., 1997). Also, the growth observed was similar to those obtained in the same species that were not subjected to harvesting (Edding et al., 1994; Edding and Tala, 2003). Over the entire study period, up to 20% of the blades of the algae were removed in *L. trabeculata*, and only 6% in *L. nigrescens*, with average of 100 blades alga^{-1} and 350 blades alga^{-1}, respectively. Removal of the blades may have permitted the entry of greater quantities of light energy into the bed, thus influencing local photosynthetic rates and growth. However, it should be considered that the removal of

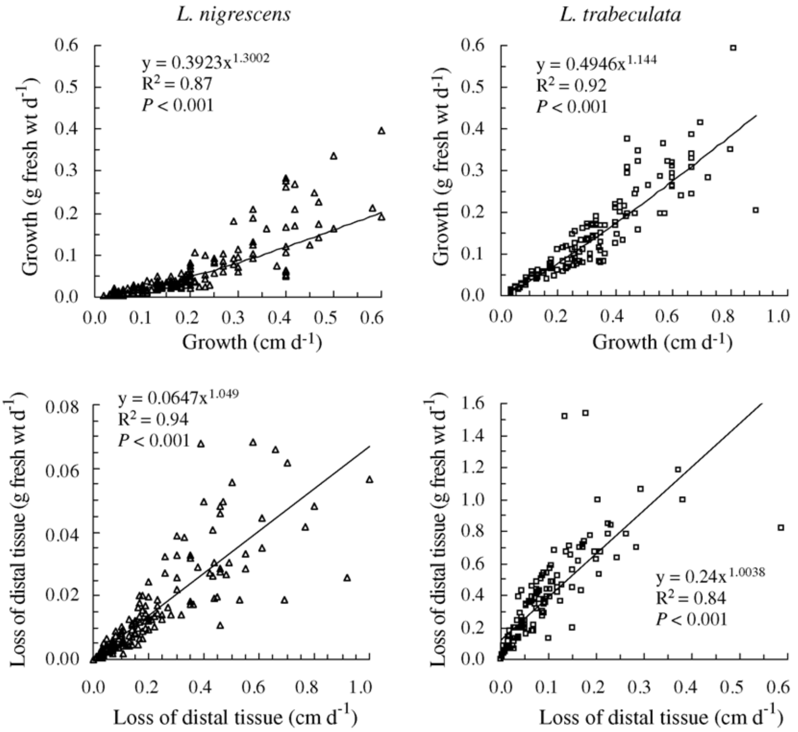

Fig. 7. Relation between growth (upper) and loss of distal tissue (lower) in units of length and fresh biomass for blades of *Lessonia nigrescens* (△) and *Lessonia trabeculata* (□). The exponential regression model generated between these variables is included, as is the significance of the model obtained with ANOVA.

blades was not carried out in one operation, but rather at approximate monthly intervals where 2% or less were taken. There is evidence that translocation of inorganic nutrients/photosynthetic can occur within Laminariales (Lobban and Harrison, 1994; Mizuta et al., 1994, 1996), thus affecting growth, although there are no data on translocation of nutrients within *Lessonia*. During the study period, new dichotomies were indeed recorded in stipes of marked algae, which indirectly indicated that the algae had continued to grow and they produced new blades. Thus, it was assumed that harvesting of sample blades over the study year had little or no effect neither on the growth of the alga nor on the other blades, although algae may sporadically lose some blades due to herbivory and/or wave action. Future studies should make more observations on the comparative growth of harvested and non-harvested algae to determine if there are any important effects of the harvesting on the growth of individual algae and of the population.

Similar to most Laminariales, the blades of *Lessonia* spp. lose senescent tissue from distal portion, and the net increase in blade length was less than the gross increase. The continuous loss of tissue may lead to a decrease in the available photosynthetic surface, and probably of reserve substances, producing a decrease in growth (Chapman and Craigie, 1978; Mizuta et al., 1994, 1996). The *Lessonia* blades may be characterized as having a

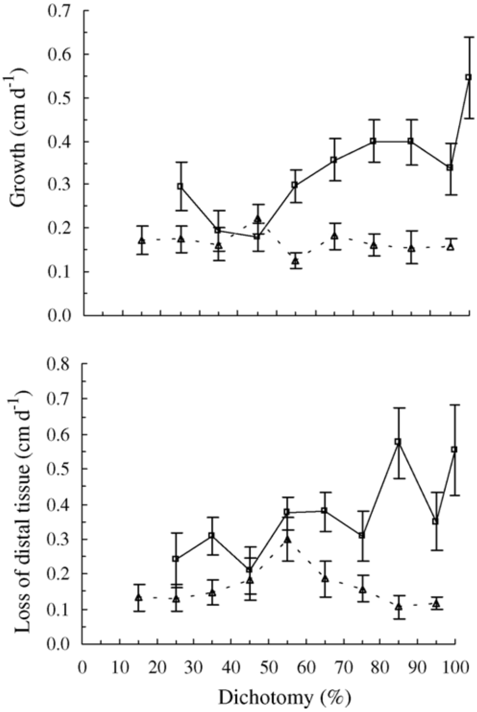

Fig. 8. Variation (mean ± standard error) in growth and loss of distal tissue in units of length (cm day^{-1}) in relation to position of dichotomy of the blades (%) between *Lessonia nigrescens* (△) and *Lessonia trabeculata* (□).

biomass gradient along their central axis similar to blades of *E. radiata* (Mann and Kirkman, 1981) and *L. longicruris* (Gagné and Mann, 1987). The decrease of biomass towards the distal zone of the blade would be related to the aging of the distal tissue, translocation of cellular nutrients, loss of dissolved matter through mechanisms of nitrogen recycling that would generate decomposition of insoluble organic compounds (e.g. protein, nucleic acids, pigment) and in some cases high ammonium concentrations with cellular death and lost of particulate matter (Mizuta et al., 1994, 1996). With this pattern, the biomass generated by meristematic growth is not the same that the biomass loss in the distal end of the blade, being able to obtain a maximum biomass and a distal biomass. If the beds and the algae are in a dynamic equilibrium, annual loss of distal tissue must not exceed growth. The elongation rate of the blade in biomass may better reflect the net rate of production of new tissue, as it is less variable than the size of the blade. Mann and Kirkman (1981) methods would be more conservative in estimating the production, since in *L. longicruris* this method overestimated production by 20%, less than the 80–100% overestimated when using exponential relations between length and weight (Gagné and Mann, 1987).

For the species studied, only *L. trabeculata* showed marked seasonal changes in loss of tissue, with increases in spring and summer months. It was observed that loss of tissue from blades of *M. pyrifera* was highly variable when comparing senescent blades with mature blades, with a slight tendency towards increase in spring–summer (Brown et al., 1997). The increase in loss of tissue could be a consequence of deleterious effects of high irradiance, sedimentary deposition, and dense encrustation of bryozoans, or by a lower density of blades during summer, which makes them more susceptible to erosion (Brown et al., 1997). The reproductive processes may also be of importance in the loss of distal tissue, either through action of the environment, or as a reproductive strategy for dispersion. The genus *Lessonia* is characterised by forming reproductive tissue on unspecialised blades all year around, but with maximum in fall (Edding et al., 1994; Tala et al., 2004). Towards spring, the increase in irradiance and senescence of the post-mature tissues of the blade could contribute to the loss of tissue. In the present study, considering annual averages of growth and loss per blade in biomass units, *L. trabeculata* may lose approximately 50% of its gross production while *L. nigrescens* may be losing about 20%. Although loss of distal tissue is a widely recognised process within the Laminariales, there are few estimations of its significance in natural beds and this may represent between 40 and 70% of the total yearly gross biomass produced (Chapman and Craigie, 1978; Kirkman, 1984; Novaczek, 1984; van Tussenbroek, 1989; Brown et al., 1997; Yoshikawa et al., 2001).

Lessonia species are often dominant in wave-exposed environments. Its was found in *L. nigrescens* that growth and loss of tissue were not influenced by the positions of dichotomy in the blades. The flexibility of the blades and the stipes allow resistance to wave impact and would permit horizontal orientation of the blades at low tide, thus providing equal probabilities of growth and erosion. In the subtidal zone, *L. trabeculata* algae are oriented vertically whereby the blades in higher dichotomies are better exposed to light, showing better growth than blades in lower dichotomies. Their distal portions, however, are less protected against the erosive action of currents, mutual abrasion, and herbivorous fishes, all of which might increase tissue losses. The gain and loss of tissue found in *Lessonia* species may be related to the algae size, the blades number in each individual alga and population densities (number algae m^{-2}), as was observed in *Ecklonia* (Novaczek, 1984; Kirkman, 1989) and *Laminaria longicruris* (Creed et al., 1998).

A gross estimation of the contribution of organic matter as detritus from the blades of *Lessonia* may be obtained by considering the annual mean growth and distal biomass lost, a mean of 100 blades alga^{-1} and on the population densities. Thus, 1 m^2 with five *L. trabeculata* algae could produce 31 kg fresh weight of blade year^{-1}, of which 18 kg fresh weight may be lost during the year. Six *L. nigrescens* per square meter would produce about 13 kg fresh weight of blade year^{-1} and lose about 2.2 kg fresh weight of blade year^{-1}. For reference, in the geographic zone in which most of this algal biomass is exploited on a national level (Atacama Region, c.a. 26°05′S–29°05′S), populations of *L. trabeculata* occupy an area of 22,323 ha, while those of *L. nigrescens* occupy 975 ha (Edding, 1998). Greater standing stocks of *L. trabeculata*, suggest that subtidal algal populations constitute a larger relative contribution of particulate matter than intertidal populations of *L. nigrescens* do, and reflects the important energy source both in inshore systems, and deeper systems which may receive imports of algal matter. The use of algal detritus as a food source has been described for molluscs, polychaetes, amphipod crustaceans and fishes (Mann, 1988; Simenstad et al., 1993). The food subsidy contributed by the Laminariales in subtidal and intertidal habitats has been reported for the South African coast (Bustamante and Branch, 1996) and the Northeast Pacific (Duggins et al., 1989). It is of interest that the great majority of the faunas within and among algal holdfasts of these algal species (Edding et al., 1994) are typically filter feeders or detritivores. In addition to their role in providing spatial habitat, *Lessonia* detritus forms an important source of nutrients for grazers, suspension and deposit feeding organisms, particularly in areas where the production of phytoplankton has a marked seasonal pattern. The present results reflect the important levels of *Lessonia* primary production within coastal communities of the Southern Hemisphere, which are poorly studied in comparison with analogous communities dominated by Laminariales in the Northern Hemisphere.

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References

Brown, M.T., Nyman, M.A., Keogh, J.A., Chin, N.K., 1997. Seasonal growth of the giant kelp *Macrocystis pyrifera* in New Zealand. Mar. Biol. 129, 417–424.

Bustamante, R., Branch, G., 1996. The dependence of intertidal consumers on kelp-derived organic matter on the west coast of South Africa. J. Exp. Mar. Biol. Ecol. 196, 1–28.

Camus, P., 1994. Recruitment of the intertidal kelp *Lessonia nigrescens* Bory in Northern Chile – succeccional constraints and opportunities. J. Exp. Mar. Biol. Ecol. 184, 171–181.

Camus, P., Ojeda, F., 1992. Scale-dependence variability of density estimates and morphometric relationships in subtidal stands of the kelp *Lessonia trabeculata* in northern and central Chile. Mar. Ecol. Prog. Ser. 90, 193–200.

Chapman, A.R.O., Craigie, J.S., 1978. Seasonal growth in *Laminaria longicruris*: relations with reserve carbohydrate storage and production. Mar. Biol. 46, 209–213.

Creed, J., Kain, J., Norton, T., 1998. An experimental evaluation of density and plant size in two large brown seaweeds. J. Phycol. 34, 39–52.

Duggins, D., Simenstad, C., Estes, J., 1989. Magnification of secondary production by kelp detritus in coastal marine ecosystems. Science 245, 170–173.

Edding, M., 1998. Investigación y manejo para la extracción de huiros, III Región. Final Project Report BIP 20109880. Atacama Regional Government, Chile, p. 197.

Edding, M., Fonck, E., Macchiavello, J., 1994. Lessonia. In: Akatsuka, I. (Ed.), Biology of Economic Algae. Academic Publishing bv, The Hague, The Netherlands, pp. 407–446.

Edding, M., Tala, F., 2003. Development of techniques for the cultivation of *Lessonia trabeculata* Villouta et Santelices (Phaeophyceae: Laminariales) in Chile. Aquat. Res. 34, 507–515.

Gagné, J., Mann, K., 1981. Comparison of growth strategy in Laminaria populations living under differing seasonal patterns of nutrient availability. In: International Seaweeds Symposium Proceeding 10. pp. 297–302.

Gagné, J., Mann, K., 1987. Evaluation of four models used to estimate kelp productivity from growth measurements. Mar. Ecol. Prog. Ser. 37, 35–44.

Gerard, V., 1982. In situ rates of nitrate uptake by giant kelp *Macrocystis pyrifera* (L.) C. Ag: tissue differences environmental effects, and predictions of nitrogen-limited growth. J. Exp. Mar. Biol. Ecol. 62, 211–224.

Guiry, M.D., Blunden, G., 1991. Seaweed Resources in Europe: Uses and Potential. John Wiley & Sons, England, 432.

Kain, J., 1989. The seasons in the subtidal. Br. Phycol. J. 24, 203–215.

Kirkman, H., 1984. Standing stock and production of *Ecklonia radiata* (C.Ag.) J.Agardh J. Exp. Mar. Biol. Ecol. 76, 119–130.

Kirkman, H., 1989. Growth, density, and biomass of *Ecklonia radiata* at different depths and growth under artificial shading of Perth, Western Australia. Aust. J. Mar. Freshwater Res. 40, 169–177.

Kirkman, H., Kendrick, G., 1997. Ecological significance and commercial harvesting of drifting and beach-coast macro-algae and seagrasses in Australia: a review. J. Appl. Phycol. 9, 311–326.

Lobban, C., Harrison, P., 1994. Seaweeds Ecology and Physiology. Cambridge University Press, New York, USA, p. 366.

Lüning, K., tom Dieck, I., 1989. Environmental triggers in algal seasonality. Bot. Mar. 32, 389–397.

Mann, K.H., 1988. Production and use of detritus in various freshwater, estuarine, and coastal marine ecosystems. Limnol. Oceanogr. 33, 910–930.

Mann, K., Kirkman, H., 1981. Biomass method for measuring productivity of *Ecklonia radiata*, with the potential for adaptation to other large brown algae. Aust. J. Mar. Freshwater Res. 32, 297–304.

Martínez, E., 1996. Micropopulation differentiation in phenol content and suceptibility to herbivory in the chilean kelp *Lessonia nigrescens* (Phaeophyta, Laminariales). Hydrobiologia 326–327, 205–211.

Martínez, E., Santelices, B., 1998. Selective mortality on haploid and diploid microscopic stages of *Lessonia nigrescens* Bory (Phaeophyta, Laminariales). J. Exp. Mar. Biol. Ecol. 229, 219–239.

Mizuta, H., Maita, Y., Kuwada, K., 1994. Nitrogen recycling mechanism within the thallus of *Laminaria japonica* (Phaeophyceae) under the nitrogen limitation. Fish Sci. 60, 763–767.

Mizuta, H., Maita, Y., Yanada, M., Hashimoto, S., 1996. Functional transport of nitrogen compounds in the sporophytes of *Laminaria japonica*. Fish Sci. 60, 763–767.

Novaczek, I., 1984. Development and phenology of *Ecklonia radiata* at two depths in Goat Island Bay. N.Z. Mar. Biol. 81, 189–197.

Parke, M., 1948. Studies of British Laminariaceae. I. Growth in *Laminaria saccharina* (L.) Lamour. J. Mar. Biol. Ass. U.K. 27, 651–709.

Simenstad, C., Duggins, D., Quay, P., 1993. High turnover of inorganic carbon in kelp habitats as a cause of $\delta^{13}C$ variability in marine food webs. Mar. Biol. 116, 147–160.

Tala, F., 1999. Crecimiento, productividad y aprote de material particulado en frondas de *Lessonia trabeculata* y *Lessonia nigrescens* (Laminariales, Phaeophyta). M.Sc. thesis. Universidad Católica del Norte, Coquimbo, Chile.

Tala, F., Edding, M., Vásquez, J., 2004. Aspects of the reproductive phenology of *Lessonia trabeculata* (Laminariales: Phaeophyceae) from three populations in northern Chile. N.Z. J. Mar. Fresh. Res. 38, 255–266.

van Tussenbroek, B.I., 1989. Seasonal growth and composition of fronds of *Macrocystis pyrifera* in the Falkland Islands. Mar. Biol. 100, 419–430.

Vásquez, J., 1992. *Lessonia trabeculata*, a subtidal bottom kelp in northern Chile: a case of study for structural and geographical comparison. In: Seeliger, U. (Ed.), Coastal Plant Communities of Latin America. Academic Press Inc., NY, USA, pp. 77–89.

Vásquez, J., Camus, P., Ojeda, P., 1998. Diversidad, estructura y funcionamiento de ecosistemas costeros rocosos del norte de Chile. Rev. Chile Hist. Nat. 71, 479–499.

Westermeier, R., Gómez, I., 1996. Biomass, energy contents and major organic compounds in the brown alga *Lessonia nigrescens* (Laminariales, Phaeophyceae) from Mehuín. South Chile Bot. Mar. 39, 553–559.

Yoshikawa, T., Takeuchi, I., Furuya, K., 2001. Active erosion of *Undaria pinnatifida* Suringar (Laminariales, Phaeophyceae) mass-cultured in Otsuchi Bay in northeastern Japan. J. Exp. Mar. Biol. Ecol. 266, 51–65.

Zar, J., 1999. Biostatistical Analysis. Prentice-Hall, Inc., NJ, USA, 929.