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First estimates of productivity in *Lessonia trabeculata* and *Lessonia nigrescens* (Phaeophyceae, Laminariales) from the southeast Pacific

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SUMMARY

Lessonia is the main Laminariales found along the southeast Pacific coast. *Lessonia nigrescens* Bory de Saint-Vincent in the intertidal and *Lessonia trabeculata* Villouta et Santelices in the subtidal, are the most important habitat constructors in rocky coastal communities in northern and central Chile. In both species, the seasonal production and erosion of distal tissue were estimated in biomass units using the Area of Constant Biomass Model that combined the individual blade elongation, obtained with the traditional hole-punching method, with the blade length and biomass distribution along the blade. In austral late spring (December 96) and autumn (May 97), blade production and erosion were transformed to the level of population from standing stock measurements (number and biomass of blades and plants per substrate area), considering that previous blade weight analysis showed the highest and lowest values at these times, as well as the population parameter extremes that were expected to occur. Both species displayed a seasonal pattern, with a production increase in later winter and spring and decrease towards the end of summer that coincided with higher distal tissue erosion. At the level of individual blades, *Lessonia trabeculata* showed higher mean production (0.026 g dw d^{-1}) and erosion (0.01 g dw d^{-1}) than *L. nigrescens* (production 0.01 g dw d^{-1} and loss 0.002 g dw d^{-1}). The standing stocks, with respect to density and biomass, were similar in spring and autumn for both populations. Nevertheless, the net productivity (production minus erosion) of the intertidal *L. nigrescens* showed greater values due to the greater density of blades (2112 ± 1360 (SE) blades m^{-2}) compared with the subtidal *L. trabeculata* (527 ± 151 (SE) blades m^{-2}). Spring net productivities of 42 g dw $m^{-2}d^{-1}$ (254 g ww $m^{-2}d^{-1}$; 11.46 gC $m^{-2}d^{-1}$) for *L. nigrescens* and 11 g dw m^{-2} d^{-1} (64 g ww m^{-2} d^{-1}; 2.46 gC $m^{-2}d^{-1}$) for *L. trabeculata* were estimated. A preliminary model of production and biomass fate for *Lessonia* populations is proposed.

Key words: Chile, erosion, kelp, *Lessonia*, macroalgae, productivity, standing stock.

INTRODUCTION

Among the marine algae, Laminariales are often the largest biomass component, and are one of the major contributors to coastal primary production in temperate and subpolar zones, from the lower intertidal to depths of 30 m (Mann & Chapman 1975; Lobban & Harrison 1994). As well as serving as an important food source for herbivores, detritivores and filter feeders, these algae produce spatial structure within the habitat, offering sites for settlement, early development, and refuge for a large number of invertebrate and fish species (Mann & Chapman 1975; Edding *et al*. 1994; Lobban & Harrison 1994; Vega *et al*. 2005). The detachment of plants and their subsequent accumulation on beaches provides an important feeding zone for crustaceans and birds, as well as sites for nutrient regeneration by bacteria and fungi (Kirkman & Kendrick 1997). Furthermore, Laminariales are economically important mainly for the alginate industry and derivates, as human food and as feed for cultured herbivores (Kirkman & Kendrick 1997; Edding & Tala 2003; McHugh 2003).

Macroalgal productivity has been estimated mainly by growth measurements of marked thallus (Mann 1972; Gerard & Mann 1979; Gagné & Mann 1987; Creed *et al*. 1998). Mann (1972) carried out one of the first studies of kelp productivity off the coast of Nova Scotia (Canada). The productivity was estimated on morphologically simple species including *Laminaria longicruris* Pyl., *Laminaria digitata* (Huds.) Lamour. and

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Agarum clathratum Dumortier, where length increases were converted to biomass increments by means of an exponential length-weight relationship (Exponential Model). In this study an annual production of 1.75 kg C m^{-2} was estimated in an area occupied by the macroalgae (Mann 1972). An alternative biomass method (Area of Constant Biomass Model) was developed for the morphologically complex *Ecklonia radiata* (C. Ag.) J. Agardh, where measurements of elongation are combined with biomass distribution in the blades (Mann & Kirkman 1981). In this model, the production can be calculated by multiplying the biomass in the zone of maximum accumulation with the elongation for each individual blade (Mann & Kirkman 1981; Gagné & Mann 1987). Annual productivity has also been estimated by observation of seasonal variations in standing stock biomass (Littler & Murray 1974; Murthy *et al*. 1986). However, this later method is useful mainly for annual species at the end of their maximal growth period.

Among Laminariales distributed on the rocky coast of the southeast Pacific, *Lessonia trabeculata* Villouta *et* Santelices forms extensive beds in subtidal areas with strong to medium water movement, between depths of 0.5 and 20.0 m, from Peru (12°S) to southern Chile (40°S) (Edding *et al*. 1994). *Lessonia nigrescens* Bory de Saint-Vincent dominates the lower intertidal zone of coasts exposed and semiexposed to wave action, from Peru (12°S) to Cape Horn (55°S) in Chile (Edding *et al*. 1994). Information on the population dynamics of *L. trabeculata* is limited to a few studies (Villouta & Santelices 1984; Camus & Ojeda 1992; Vásquez 1992; Edding *et al*. 1993; Tala *et al*. 2004; Vega *et al*. 2005). Due to its easy access, research has been directed towards intertidal areas dominated by *L. nigrescens* (e.g. Santelices *et al*. 1980; Santelices & Ojeda 1984; Venegas *et al*. 1992; Camus 1994; Vásquez & Tala 1995; Westermeier & Gómez 1996; Martínez & Santelices 1998; Martínez *et al*. 2003; Ortiz 2003; Faugeron *et al*. 2005). The reproductive phenology of *L. trabeculata* describes an increase in blade size (length, width, and thickness) towards spring, whereas the optimal microscopic development was observed in autumn, although reproductive tissues are present throughout the entire year (Tala *et al*. 2004). For *L. nigrescens*, maximum reproductive plant frequency has been mentioned for the autumn months in central Chile, with massive recruitment observed in late winter (Edding *et al*. 1994). In spite of the ecologic and economic importance of these species, similar to that described for other Laminariales from the Northern Hemisphere, growth measurements on *Lessonia* spp. are scarce, and there are no estimates of productivity.

In the present study, the blade production of the two *Lessonia* species was estimated over one year based on direct measurements of elongation rate. Relating individual blade production to population standing stock allowed us to estimate the productivity at the population level. This study represents the first record of productivity for two *Lessonia* species of importance in the subtidal and intertidal rocky inshore coastal communities, and it provides a possible method for the evaluation of alterations in population dynamics in the presence of environmental disturbances, such as the El Niño phenomena, as well as for the management of protected areas.

MATERIALS AND METHODS

Sampling sites

The selected *Lessonia trabeculata* bed is located on the Tongoy Peninsula (30°15′S–71°15′W) about 50 km southwest of Coquimbo (30°S) (Fig. 1). An extensive perennial bed is present on the exposed northeast margin of the peninsula, between the depths of 0.5 and 20 m. It is considered to be one of the densest beds in Chile, containing over four plants per square meter (Villouta & Santelices 1984). The selected area for tagging plants was in the middle of a homogeneous population, at a depth of about 8 m. For *L. nigrescens*, a perennial bed was selected on the south of Tinajas Point on the Pampilla Peninsula of Coquimbo (29°57′S–71°22′W) in a wave-exposed area which is influenced by predominating southwesterly winds (Fig. 1). The population forms a continuous belt over the rocky substratum from the low intertidal to the upper subtidal zone (<1 m depth), in vertical and horizontal platforms, as well as in channels. No data for the population density exist for this area. Both selected populations are in the central part of the latitudinal distribution of these species along the southeast Pacific coast (Edding *et al*. 1994), and the habitats are typical of their distribution in Chile.

The irradiance patterns found in a latitudinal population study (30°S) showed highest levels in the austral summer (c.a. midday 1500–2500 μmol photons m^{-2}s^{-1}), and lowest in winter (c.a. midday 500–800 μmol photons m^{-2}s^{-1}) (Edding *et al*. 1990). In concordance with the irradiance, the surface seawater temperature showed a similar seasonal pattern, with a maximum mean of 18.5°C in the middle of summer and minimum mean of 13.5°C in the middle of winter during a normal year (Edding *et al*. 1990). Although the north of Chile is characterized by the recurrent El Niño-Southern Oscillation (ENSO) phenomena (Vásquez *et al*. 1998), the studied populations are in latitudes where its effect is diminished because of their proximity to an area of permanent coastal upwelling (Pta. Lengua de Vaca, Tongoy, 30°S–71°W). During El Niño, the spatial-temporal patterns of abundance of the kelp assemblage

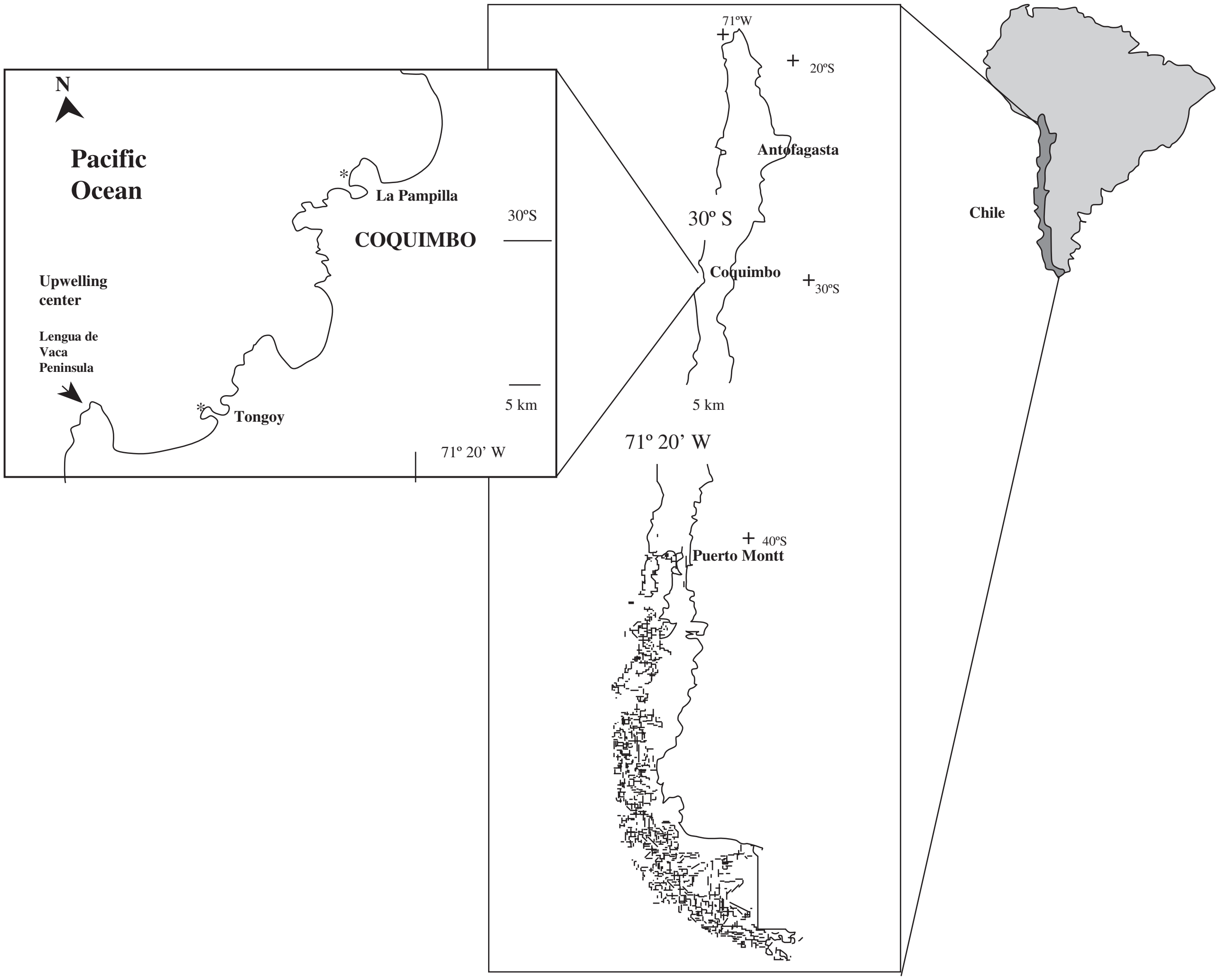


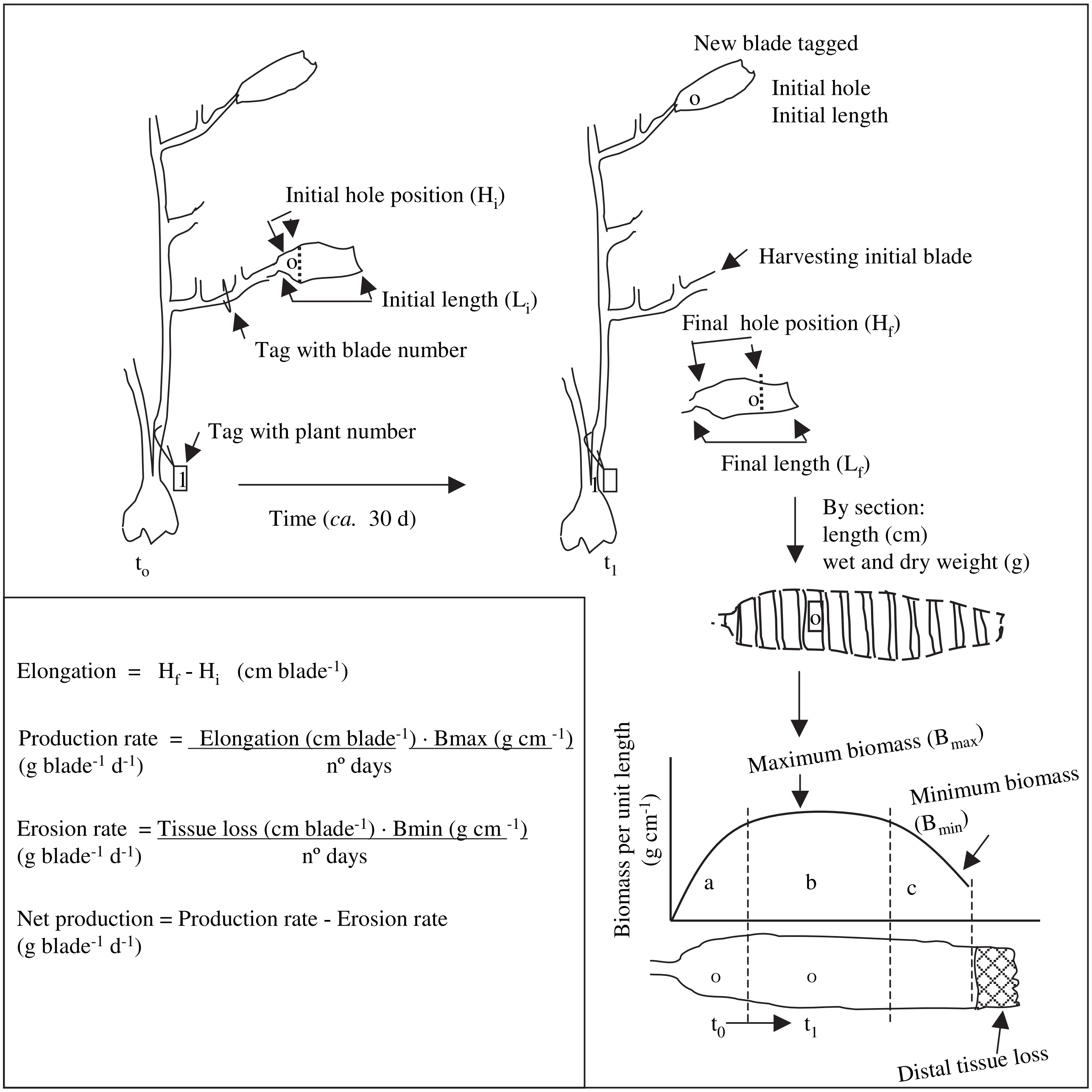
Fig. 1. Geographic location of the studied *Lessonia* populations.

(*Macrocystis integrifolia* Bory de Saint-Vicent and *L. trabeculata*) were maintained by the continuity of coastal upwelling, which buffered and moderated superficial warming of the ocean and prevents the depletion of nutrients (Vásquez *et al*. 1998; Vega *et al*. 2005). The negative effects of El Niño are considered to be more important in the northern border of Chile (<25°S) and Peru, affecting the populations of Laminariales (Camus 1994; Martínez *et al*. 2003) in those latitudes. Therefore, it was considered that El Niño from 1997–1998 did not influence the production pattern observed in *Lessonia* populations during the study time.

Production by blades

The annual variation in blade biomass production was determined between November 1996 and October 1997 for both *Lessonia* species. Twenty adult plants in each population were selected randomly at the beginning of the study, and the stipes were tagged with plastic bands and numbered. The total length, maximum diameter of the holdfast, number of stipes per plant and number of dichotomies per main stipe were recorded for each plant at the beginning and end of the study.

The blade growth of 20 tagged plants was determined using the hole-punching method, which has been widely employed in Laminariales (Mann 1972; Chapman & Craigie 1978; Gagné & Mann 1981, 1987; Mann & Kirkman 1981; Creed *et al*. 1998; Fairhead & Cheshire 2004), including *Lessonia* (Edding *et al*. 1990; Escobar 1994; Edding & Tala 2003; Tala & Edding 2005). The sampling design was destructive, and comprised at time zero, the tagging, punching, and measuring of the initial length of two blades per plant, *in situ*, as described in Fig. 2. At the next sampling time, punched blades were harvested for individual remeasurement in the laboratory, and two new blades were randomly selected from each plant, tagged,



$$\text{Elongation} = H_f - H_i \quad (\text{cm blade}^{-1})$$

$$\underset{(\text{g blade}^{-1}\ \text{d}^{-1})}{\text{Production rate}} = \frac{\text{Elongation (cm blade}^{-1}) \cdot \text{Bmax (g cm}^{-1})}{\text{n}^{\text{o}}\ \text{days}}$$

$$\underset{(\text{g blade}^{-1}\ \text{d}^{-1})}{\text{Erosion rate}} = \frac{\text{Tissue loss (cm blade}^{-1}) \cdot \text{Bmin (g cm}^{-1})}{\text{n}^{\text{o}}\ \text{days}}$$

$$\underset{(\text{g blade}^{-1}\ \text{d}^{-1})}{\text{Net production}} = \text{Production rate} - \text{Erosion rate}$$

Fig. 2. Sampling design used for determination of production and erosion from blades of *Lessonia nigrescens* and *Lessonia trabeculata*. The upper side shows the sampling design of tag and harvest blades over the time. From the left down are shown the formulae used for expression of the variables measured. From the right down is shown the blade biomass distribution.

punched and used for the next measurement period (Fig. 2).

Based on the differences in the size of the blades between the two species and on previous hole-punching trials to determine the meristematic zone, a 5 mm diameter hole was punched, with a cork borer, at 10 cm from the stipes/blade junction in *L. trabeculata*, and at 5 cm in *L. nigrescens*. The measurements were carried out over different time periods between 25 and 35 days, based on suitability of environmental conditions for working and making measurements in wave-exposed areas. The net change in blade length was also obtained between the final and initial length of each blade measured.

The production was considered to be the rate at which new tissue (biomass) was formed on the blades by meristematic activity (Kirkman 1984), and it was estimated separately for each individually harvested blade using the Area of Constant Biomass Model (Mann & Kirkman 1981). The model assumes that the biomass production is equal to the product of elongation and the mean weight per centimeter of blade tissue in the 'area of maximum biomass accumulation', according to the equation:

$$P = g \cdot (w/L)$$

where: P = production (dry weight); g = elongation of the blade (cm); w = dry weight of a blade section cut at the area of maximum biomass accumulation; L = length of the section of maximum biomass (cm). The three zones on the blade (growth, maximum biomass accumulation and erosion) previously described for *Ecklonia radiata* (Mann & Kirkman 1981) were also observed in *Lessonia* spp. (Tala & Edding 2005). Biomass distribution was determined individually for each blade harvested in each sampling month, by cutting them into small pieces (2–5 cm) and recording the wet (ww) and dry (dw) weight (Fig. 2). Dry weight was obtained by drying algal tissue for 48 h at 60°C.

The growth activity in the most Laminariales includes the formation of a new tissue from meristematic tissue in blade base accompanied by tissue loss in blade tip, defined as a 'conveyor-belt' growth (Mann 1972). When relating the measurements of growth (hole-punching method) with the initial length of the blade it is possible to obtain a measurement of the amount of distal tissue loss, herein referred to as erosion. In order to estimate the erosion in biomass units, the same procedure of the Biomass Model was employed but taking into account the weight found in the erosion zone of each blade, prior to loss as particulate matters (Fig. 2). Since eroded 'damaged' tissue was observed only on the distal end of the blade and not along blade margins, it was assumed that there is no lateral tissue loss. Therefore the erosion rate (g dw d^{-1}) was estimated by multiplying the loss of distal blade tissue (cm) with the distal biomass (g dw d^{-1}) found for each blade (Fig. 2). Loss of dissolved matter was not measured. The net production per blade was estimated by subtracting the biomass erosion from the basal biomass production individually for each harvested blade.

Density and biomass

In order to obtain an estimation of the population productivity, standing stock measurements were carried out at two different times, December 1996 for late spring and May 1997 for autumn. The productivity (g produced m^{-2}) for each season was estimated relating the mean of individual blade production (g/d^{-1}) with the mean density of blades per m^2, as in *Ecklonia* (Kirkman 1989). For late spring the mean blade production included the values obtained during October, November and December, where as productivity estimation for autumn included April, May and June averages. These were thought to be good indicators for the periods of the year in which other extreme population characteristics could be expressed, considering the seasonal pattern observed in growth and reproduction for *Lessonia* spp. (Tala *et al*. 2004; Tala & Edding 2005; Vega *et al*. 2005). The productivity estimation is only based in blade production and does not include the production of stipes and holdfast biomass. For perennial algae, like *Lessonia*, the total biomass of stipes and holdfasts is a product of growth over the entire life of the plant, and measurements of their growth and productivity is reliant on knowledge of the age of the thallus. Although, annual productivity has also been estimated by observation of seasonal variations in standing stock biomass, this method is useful mainly for annual species, and is employed at the end of their maximal growth period (Littler & Murray 1974; Murthy *et al*. 1986).

Standing stock samples of both species were obtained randomly within homogeneous sectors of vegetation, at the same level as the tagged plants, using three-sided quadrants measuring 1 m square, allowing to place among holdfasts and stipes of the plants (*L. trabeculata* $n = 7$; *L. nigrescens* $n = 4$). During each sampling, all plants found in each quadrate were removed and transported to the laboratory for measurement. The number of plants per square meter of substratum was used as a measure of population density, where a plant was considered to consist of a group of stipes with blades emerging from a common holdfast. Blade density (blades m^{-2}) and stipe density (stipes m^{-2}) were also recorded. The population biomass (kg plants m^{-2}) was separated into blade biomass (kg blades m^{-2}) and stipe + holdfast biomass (kg m^{-2}). At the individual level, plant weight (kg), blade weight per plant (g) and number of blades per plant were recorded. Due to the large size of the plants, the dry weight was obtained by first air drying for 5 days followed by drying for 72 h at 60°C.

To compare *Lessonia* productivity with that of other Laminariales, productivities were converted to organic matter and organic carbon content using blades, collected at the same time of the standing stock measures ($n = 10$ for species and sampling time). The organic matter (OM) was obtained as ash free dry weight (AFDW) by ashing 1-g samples of dry tissue in a muffle furnace at 500°C for 6 h. Organic carbon per dry gram of alga was determined using the dichromate titration method (Gaudette *et al*. 1974).

Data analyses

The experimental design corresponded to repeated-measures, where the monthly observations of daily production were not independent. These measures were always made on the same 20 tagged plants, with the month factor repeated among all plants. Since in all cases the assumption of sphericity (Mauchly test) was not met, potentially exceeding Type I error (Zar 1999), multivariate analysis of variance (MANOVA) was employed (SPSS 10.0) with $\alpha = 0.05$. MANOVA has been suggested for analysis of experimental designs with repetitive measurements without depending on an assumption of sphericity (Zar 1999). The independent variable was species of *Lessonia* (with two levels), and the dependent variables were daily rates (g d^{-1}) of production and erosion, in successive time intervals. The MANOVA determines significant differences between species over all time intervals together, and it does not indicate what the pairwise differences are over the time. Variances were significantly different among groups (Box's Test, $P < 0.05$). Therefore, the Pillai-Bartlett V statistic was used because it is robust against moderate heterocedasticity when the design is balanced or nearly so (Johnson & Field 1993). In order to generate a balanced design, the analyses included only the months in which simultaneous measurements on both species and for all the 20 tagged plants occurred (Nov, Dec, Jan, Feb, Apr, July, and Oct). A linear regression model was used to describe the relationship between the individual production and sizes of blades.

Differences in mean density, biomass and plant characteristics between the two sampling periods (spring and autumn) were tested with Student's *t*-test for each *Lessonia* species independently. The mean values always present ±1 standard error.

RESULTS

The blades of both species showed marked seasonal production and erosion rates (Fig. 3). The maximum production was observed in the austral spring (Oct–Dec) with over 0.03 g dw d^{-1} for *Lessonia nigrescens* and over 0.04 g dw d^{-1} for *L. trabeculata*. The production decreased towards the autumn and winter months (Fig. 3). While in *L. nigrescens* the minimum production rates extended towards the winter months, in *L. trabeculata* the blades showed a progressive increase from the end of autumn (Fig. 3). *Lessonia trabeculata* and *L. nigrescens* produced an annual mean of 0.026 ± 0.003 g dw d^{-1} and 0.010 ± 0.003 g dw d^{-1}, respectively, showing a significant difference between the two species (Pillai-Bartlett $V = 0.890$, $F_{7,32} = 37.014$, $P < 0.001$), caused mainly by the higher values observed in *L. trabeculata* during spring (Fig. 3).

Erosion from the distal portion of blades showed a similar seasonal pattern, with greater values during spring and summer for both species (Fig. 3). Also, *L. trabeculata* blades had significantly higher erosion (Pillai-Bartlett $V = 0.927$, $F_{7,32} = 58.468$, $P < 0.001$) than those from *L. nigrescens*, with annual means of 0.013 ± 0.002 g dw d^{-1}, and 0.002 ± 0.0003 g dw d^{-1}, respectively. Though the mean erosion rate never exceeded the mean production rate (Fig. 3), the net production showed the lowest values mainly between late summer and winter, which coincided with a negative change in the blade length in both species (Fig. 4). Moreover, the difference between *Lessonia* species tends to disappear with the higher erosion rate in *L. trabeculata* blades, with an annual net production mean of 0.008 g dw d^{-1} for *L. nigrescens* and 0.012 g dw d^{-1} for *L. trabeculata* (Fig. 3).

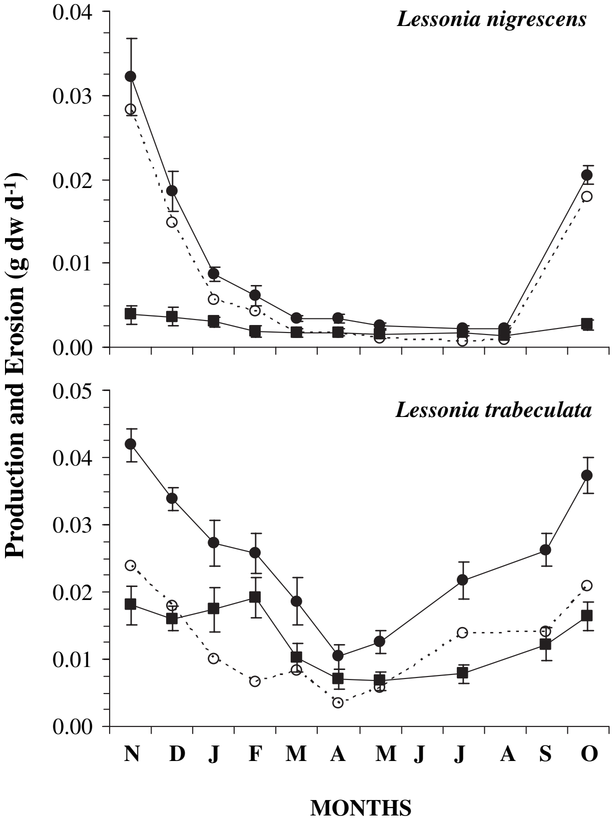


Fig. 3. Seasonal variation of production (solid circle with solid line), erosion (solid square with solid line) and net production (empty circle with dashed line) in blades of *Lessonia nigrescens* (upper) and *Lessonia trabeculata* (lower), between November 1996 and October 1997. The daily means (±SE) are shown in dry biomass units.

Although blades with greater lengths and weights showed higher production ($P < 0.01$), the coefficients of correlation were low, especially for *L. trabeculata* (Fig. 5). The tagged plants showed slight size variation over the year-long study period, and the increases were produced by the growth of the smaller plants, especially *Lessonia nigrescens* (Table 1). No relationship (Spearman rank correlation, $P > 0.05$) was observed between the initial sizes of the tagged plants and the production of blades recorded during the study period.

Table 1. Mean sizes (± SD) and range of tagged *Lessonia nigrescens* and *Lessonia trabeculata* plants at the beginning and end of the study period (time measured = 12 months; $n = 20$)

Characteristic	*L. nigrescens* Initial	*L. nigrescens* Final	*L. trabeculata* Initial	*L. trabeculata* Final
Total length (cm)	94.6 ± 37.3 (15–158)	111.8 ± 39.7 (16–170)	189.3 ± 22.7 (135–220)	184.9 ± 19.6 (145–210)
Holdfast diameter (cm)	15.8 ± 7.8 (1–39)	20.5 ± 9.1 (2–42)	25.9 ± 6.1 (14–37)	28.6 ± 6.8 (16–39)
Stipes per plant (n°)	13 ± 8 (4–46)	12 ± 9 (5–48)	3 ± 2 (1–7)	3 ± 2 (1–7)
Dichotomy per stipe (n°)	4 ± 2 (1–7)	5 ± 2 (1–11)	8 ± 3 (4–14)	10 ± 4 (4–18)

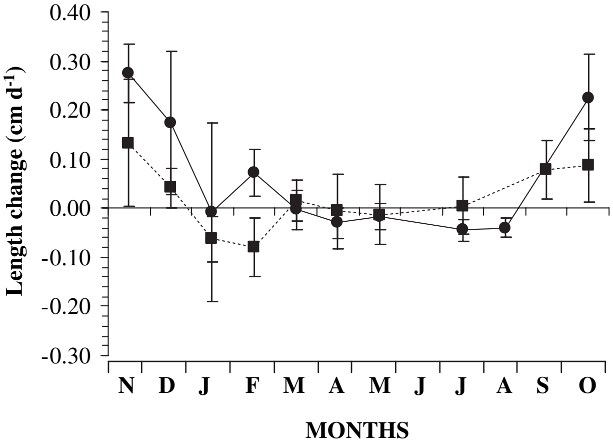


Fig. 4. Seasonal change of blade length in *Lessonia nigrescens* (solid circle with solid line) and *Lessonia trabeculata* (solid square with dashed line), between November 1996 and October 1997. The daily means are shown.

The standing stocks, with respect to density and biomass, were similar in spring and autumn for both species (Table 2; Student's *t*-test $P > 0.05$). In spite of this, the biomass distribution between stipe + holdfast and blades showed a slight change, with higher stipe + holdfast biomass during autumn, changing from c.a. 65% to 72% (Table 2). A tendency towards increase in the number of blades per plant was observed between spring and autumn, especially in *L. trabeculata* (Table 2). Also, the plant characteristics did not show significant differences between seasons in either *Lessonia* (Table 2). Only the organic matter for *L. trabeculata* ($t = 7.379$, d.f. = 18, $P < 0.001$), and carbon contents for *L. trabeculata* ($t = 4.591$, d.f. = 18, $P < 0.001$) and *L. nigrescens* ($t = 7.311$, d.f. = 18, $P < 0.001$) showed significant differences between the two sampling periods, with higher values during spring (Table 2).

The population densities of *Lessonia nigrescens* and *L. trabeculata* were similar, but clear differences were observed in stipe and blade densities, and in the number of blades and stipes per plant, with constantly greater values for *L. nigrescens* (Table 2). However, *L. trabeculata* showed higher values in all of the biomass characteristics evaluated in the population and the blades (Table 2). Nevertheless, blades of *L. nigrescens* had significantly higher OM (autumn $t = 3.266$, d.f. = 18, $P = 0.004$) and carbon content (spring: $t = 16.305$, d.f. = 18, $P < 0.001$; autumn: $t = 4.597$, d.f. = 18, $P < 0.001$) than those of *L. trabeculata* (Table 2).

In spite of the slight differences between net production in the *Lessonia* species in both seasons, at the population level, considering blade density, the differences were inversed and marked by the greater values reached by *L. nigrescens* mainly during spring (Table 3). Finally, relating the productivity to organic matter and carbon (Table 2), the net productivity during spring was estimated at 27.03 g OM m^{-2} d^{-1} and 11.46 g C $m^{-2}d^{-1}$ for *L. nigrescens,* and 6.93 g OM m^{-2} d^{-1} and 2.46 g C $m^{-2}d^{-1}$ for *L. trabeculata*, values which decreased in autumn to 1.78 g OM $m^{-2}d^{-1}$, 0.66 g C $m^{-2}d^{-1}$ for *L. nigrescens,* and 1.07 g OM $m^{-2}d^{-1}$ and 0.42 g C m^{-2} d^{-1} for *L. trabeculata*.

DISCUSSION

A clear seasonal pattern in biomass production was found in both species of *Lessonia*, showing a significant reduction towards austral late spring that continues until late winter in *L. nigrescens* and until the end of autumn in *L. trabeculata*. This pattern in Chilean *Lessonia* is consistent with blade (Edding & Tala 2003; Tala & Edding 2005), stipe (Santelices 1982) and thalli (Santelices *et al.* 1980) elongation rates, and with the growth pattern of other morphologically simple and complex Laminariales (Chapman & Craigie 1978; Gagné & Mann 1981; Kirkman 1984; Brown *et al.* 1997; Fairhead & Cheshire 2004). Species defined as 'seasonal anticipators' (*sensu* Kain 1989) should show slower growth than would be allowed by photosynthesis

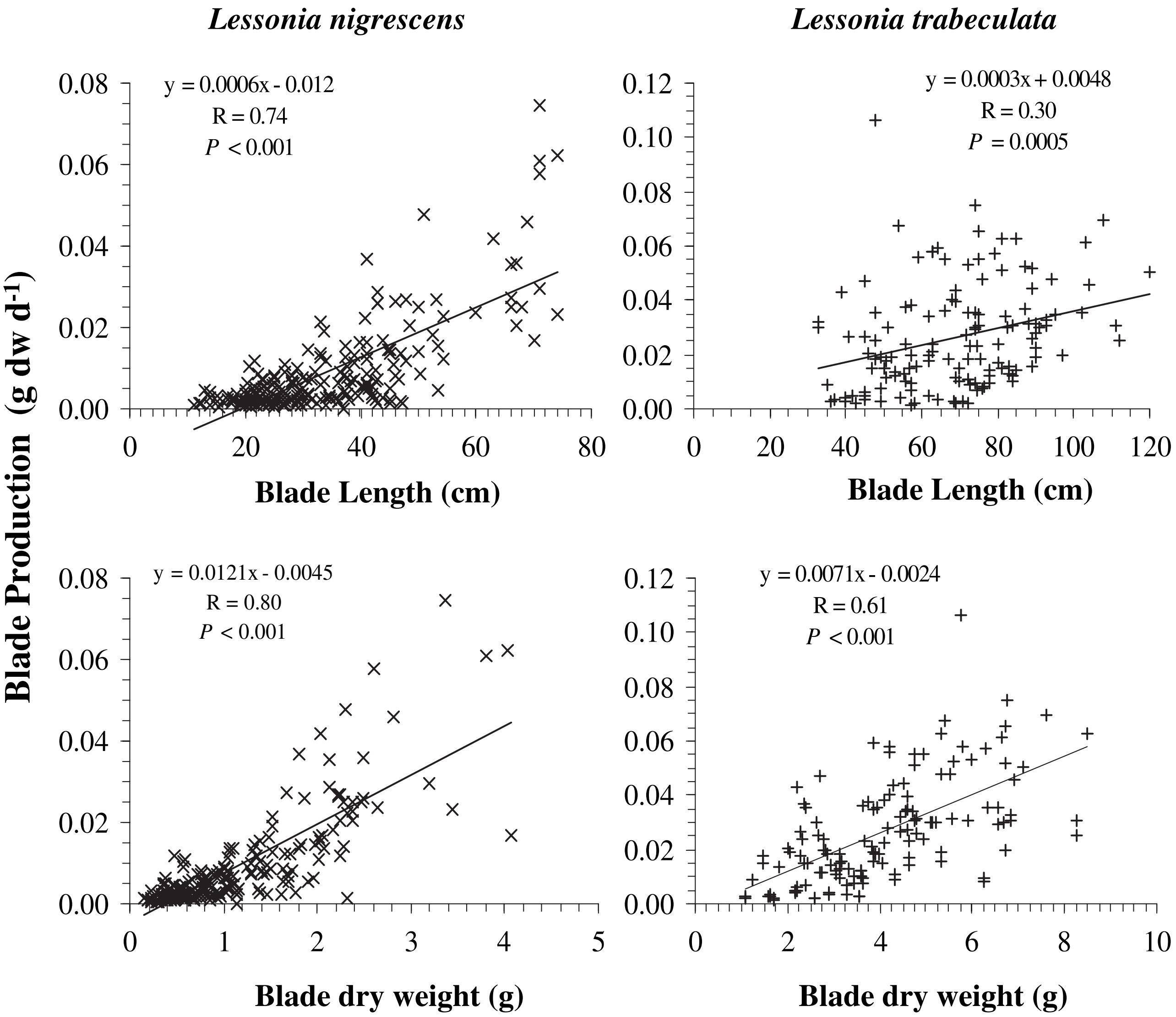


Fig. 5. Relationship between size of blades (length and dry weight) and blade production (g dw d^{-1}) in *Lessonia nigrescens* (left) and *Lessonia trabeculata* (right).

when irradiance is maximal, and an important accumulation of organic photosynthetic reserves for the next period of growth, beginning in winter when light is low but nutrient availability increases (Chapman & Craigie 1978; Kain 1989; Fairhead & Cheshire 2004). In the south of Chile, photosynthesis in *Lessonia nigrescens* should show slight changes throughout the year, in which fluctuations in nutrients would not be sufficiently great so as to limit the growth. Moreover *L. nigrescens* showed a poorly defined annual pattern for organic components and for its energetic content (Westermeier & Gómez 1996), and, as was observed in the present study, a similar organic matter content in the blades between spring and autumn, suggesting that there may be another factor besides the availability of nutrients which influences the productive cycle of this intertidal species. A factors, such as the midday summer levels of UV-B, which are high enough to produce stress and photoinhibition (decrease of Fv/Fm) in intertidal macroalgae (Gómez *et al.* 2004; Huovinen *et al.* 2006), and null development of microscopic life cycle stages of *Lessonia* (Véliz *et al.* 2006). Unfortunately, no comparable information is available with respect to seasonal variation in organic components or photosynthetic activity for *Lessonia trabeculata*, but this subtidal species showed seasonal differences in the organic matter and carbon content in the blades, which may indicate differential seasonal photosynthetic patterns. The low productivity attained by *Lessonia trabeculata* may have been related to the lower content of organic material and organic carbon per blade when compared with blades of *L. nigrescens*. Tip blade erosion, lower in

Table 2. Density, biomass and plant characteristics of *Lessonia nigrescens* and *Lessonia trabeculata* sampled during December (austral late spring) and May (autumn)

	Lessonia nigrescens Spring	Autumn	*Lessonia trabeculata* Spring	Autumn
Density				
Plants (n° m^{-2})	6 ± 1	8 ± 3	5 ± 2	5 ± 2
Stipes (n° m^{-2})	135 ± 48	115 ± 38	8 ± 4	10 ± 1
Blades (n° m^{-2})	2112 ± 1360	2374 ± 1255	527 ± 151	645 ± 156
Blades per plant (n°)	351 ± 129	300 ± 114	123 ± 64	150 ± 81
Biomass				
Plants (kg dw m^{-2}) [kg ww m^{-2}]	1.62 ± 0.44 [12 ± 3]	2.23 ± 0.60 [12 ± 4]	4.55 ± 1.05 [17 ± 4]	5.78 ± 0.75 [21 ± 2]
Stipes + holdfast (kg dw m^{-2}) [% dw]	1.02 ± 0.38 [11.6]	1.59 ± 0.47 [17.4]	2.99 ± 0.73 [38.4]	4.19 ± 0.74 [39.4]
Blades (kg dw m^{-2}) [% dw]	0.59 ± 0.08 [21.2]	0.64 ± 0.25 [21.3]	1.57 ± 0.39 [17.3]	1.59 ± 0.26 [15.1]
Blades per plant (g dw)[% dw]	99.09 ± 6.74 [21.2]	86.21 ± 44.89 [17.6]	484.84 ± 160.45 [17.6]	361.50 ± 148.58 [15.4]
Blades				
Individual weight (g dw) [% dw]	0.28 ± 0.13 [17.6]	0.36 ± 0.16 [19.9]	3.32 ± 1.17 [15.5]	2.51 ± 0.41 [14.4]
OM per g dw blade (%)	64.25 ± 5.50	63.52 ± 8.89	62.91 ± 2.79	53.91 ± 2.79
C per g dw blade (%)	27.23 ± 1.07	23.44 ± 1.92	22.32 ± 0.69	21.21 ± 0.75
Plant characteristics				
Weight per plant (kg dw) [% dw]	0.27 ± 0.04 [13.7]	0.29 ± 0.12 [18.3]	1.04 ± 0.47 [26.6]	1.28 ± 0.40 [26.0]
Total length (cm)	80.61 ± 14.06	71.81 ± 10.05	194.19 ± 38.28	205.24 ± 25.97
Holdfast diameter (cm)	12.26 ± 3.91	13.76 ± 1.67	15.23 ± 3.04	18.58 ± 5.49
Stipes per plant (n°)	22 ± 5	15 ± 3	2 ± 1	2 ± 1
Dichotomy per plants (n°)	4 ± 1	4 ± 1	10 ± 4	14 ± 3

The plant morphology included holdfast, stipes and blades. The values showed are means^{+}-standard error. (dw, dry weight; ww, wet weight).

Table 3. Productivity estimations for the populations of *Lessonia nigrescens* and *Lessonia trabeculata* studied. Daily values per blade (production and erosion) are means from monthly mean, and these are presented as dry (dw) and wet (ww) biomass. Spring includes October, November and December means; autumn includes April, May and June means

	L. nigrescens Spring	Autumn	*L. trabeculata* Spring	Autumn
Productivity per blade				
Production (g dw d^{-1}) [g ww d^{-1}]	0.024 [0.140]	0.003 [0.017]	0.038 [0.248]	0.011[0.085]
Erosion (g dw d^{-1}) [g ww d^{-1}]	0.004 [0.020]	0.002 [0.008]	0.017 [0.128]	0.007 [0.055]
Net production (g dw d^{-1}) [g ww d^{-1}]†	0.020 [0.120]	0.001 [0.009]	0.021 [0.121]	0.003 [0.030]
Population productivity				
Productivity (g dw m^{-2}d^{-1}) g ww m^{-2}d^{-1}]‡	50.06 [295.62]	6.67 [39.62]	19.88 [130.89]	7.39 [54.69]
Erosion (g dw m^{-2} d^{-1}) [g ww m^{-2} d^{-1}]§	7.98 [41.22]	3.87 [19.44]	8.87 [67.32]	4.42 [35.34]
Net productivity (g dw m^{-2}d^{-1}) [g ww m^{-2}d^{-1}]¶	42.07 [254.40]	2.80 [20.18]	11.01 [63.58]	1.98 [19.35]

†(Production) – (Erosion); ‡(Production per blade) (mean number of blades m^{-2}); §(Erosion per blade) (mean number of blades m^{-2}); ¶(Net production per blade) (mean number of blades m^{-2}).

L. nigrescens and higher in *L. trabeculata*, also would influence by a decrease in the net production, with negative blade length changes mainly between summer and the beginning of winter. The increase in tissue erosion in spring–summer could be related to post-reproductive events (Tala *et al*. 2004), as well as temperature and augmented light radiation (Kirkman 1984; Novaczek 1984; Brown *et al*. 1997).

In *Lessonia*, a tendency towards increased production was observed as an enlargement in blade size, although with a high degree of individual variability. However, no clear relationship was observed between the initial size of the tagged plants and the productivities of their blades. The effect of the size of the blades on growth and production within a given population could depend on the size structure, biomass and density of plants within natural populations, as a result of competition (mainly for light) between smaller and larger plants during active growth (Schiel & Choat 1980; Creed *et al*. 1998; Scrosati 2005). *Lessonia* is a morphologically complex genus where it is possible to find several stipes in one plant (more than two per plant) with different levels of dichotomies (more than three per stipe). There are plants with many blades and varied density, size and/or age. It may be expected that younger blades at higher dichotomy levels, as well as larger blades that have a better opportunity to receive light and nutrients, would show greater productivity than older or smaller blades at lower dichotomy levels. Also, lower productivity would be expected in plants with high individual densities of blades, mainly due to self-shading. An analysis of the morphologic architecture of *Lessonia* would be necessary to understand how biomass production is related to the size of blades within the same plant and between plants on a stand. Observations of *L. trabeculata* cultivated on long lines suggest that morphology of the whole plant is related to water movement and to the area that the holdfast can cover (Edding & Tala 2003). Moreover, the different density/biomass distributions on the thallus (blades *vs* stipes + holdfast) between the *Lessonia* species might indicate differential hydrodynamic adaptation to intertidal and subtidal habitats that would affect algal productivity.

The productivity given in the present study is the first record for representatives of the genus *Lessonia* on the southeast Pacific coastline, and it falls within the values for other kelps (Mann 1972; Field *et al*. 1977; Gerard & Mann 1979; Novaczek 1984; Kirkman 1989; van Tussenbroek 1993; Fairhead & Cheshire 2004). Also, the growth rates are within ranges reported for both species where blades were not harvested (Edding *et al*. 1990; Escobar 1994; Edding & Tala 2003). Although there is little variation in the standing stock, a seasonal change is detected in the population productivity given mainly by individual blades changes in the rates of production and erosion. The levels of abundance in large Laminariales are maintained throughout the year with only individual seasonal variability in growth and reproduction (van Tussenbroek 1993; Buschmann *et al*. 2004; Tala *et al*. 2004; Vega *et al*. 2005). The differences between the *Lessonia* species depended on the seasons, where higher productivity in the *L. nigrescens* stand occurred mainly in spring, while in autumn the differences disappeared. The reduced variation observed in *Lessonia* standing stock (density and biomass) as well as the morphological measurements can be explained by the perennial nature of this plant and its long-lived sporophytes, which after reaching a certain size realize the production or replacement biomass mainly with old and new blades. For the studied population, the similar densities between spring and autumn suggest that continually the plants are dislodged, mainly by water movement, without a distinct peak in the year, generating little variation in the population structure. Nevertheless, in certain coastal areas of north and central Chile there is significant loss of *Lessonia* biomass which is carried to the beaches throughout the year. Local environmental conditions would be important in determining local population dynamics that influence algal productivity.

The only study that compares productivity estimation models with real productivity was made on *Laminaria longicruris*, a simple Laminariales (Gagné & Mann 1987). Models which use exponential relationships between size and weight (Power Model and Chordal Model) could overestimate productivity by between 80 and 100%, while the models based on the distribution of biomass in the blades (Constant Biomass Model and Blade Biomass Model) could give an overestimation of 20% (Gagné & Mann 1987). In spite of overestimations in biomass models, the main advantage of the Constant Biomass Area Model is that productivity estimates are obtained from measurements of individual production, which means that the error is independent of the blade size, and errors in the field are minimal since the blades are harvested and measured in the laboratory (Mann & Kirkman 1981; Gagné & Mann 1987). Nevertheless, a weakness is that many thallus and/or blades are required to carry out the destructive sampling. Also, the amount of particulate and dissolved material lost from the blades is unknown, such that the average weight per unit length does not represent the weight of tissue recently produced (Gagné & Mann 1987). However, as was shown in *Ecklonia radiata*, the productivity estimated by the biomass method can result in large underestimates of annual productivity rates, and net productivity (as O_2 evolution) on its own will overestimate the biomass production if it is assumed that all assimilated carbon is incorporated into biomass (Fairhead & Cheshire 2004). As mentioned above, the productivity estimation was based on blade growth. The production of the holdfasts and stipes were intentionally excluded because of the perennial nature of the plant and the impossibility of determining age. The possible grazing of tagged blades during their period of measurement is not considered either. Both factors would contribute to an underestimation of the overall *Lessonia* productivity. Taking into consideration the strengths and weaknesses of any model, the Area of

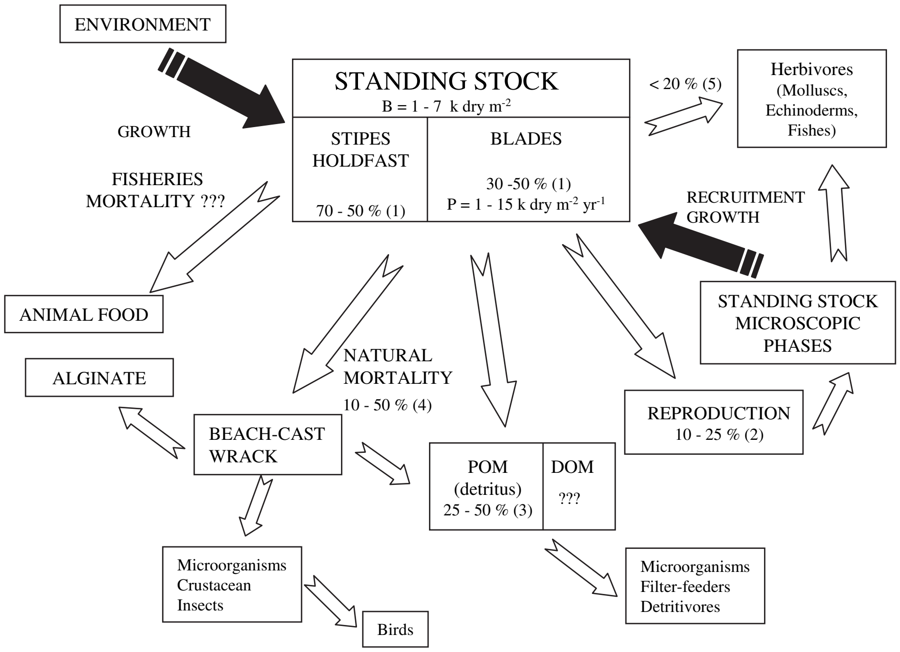


Fig. 6. Preliminary semi quantitative conceptual model of the fates taken by the *Lessonia* biomass produced based on the present study and data from the literature. Arrows going toward the compartment of *Lessonia* standing stock represent factors that favor increases in biomass. Arrows exiting the main compartment indicate loss and destination of the algal biomass. References: (1) present study; (2) Tala *et al.* (2004); (3) Tala and Edding (2005); (4) Edding (1998); (5) Pizarro (1981). B, dry biomass per surface; DOM, dissolved organic matter; P, net annual productivity; POM, particulate organic matter.

Constant Biomass Model was useful to the study of production in *Lessonia*, because it allowed the use of erosion estimates as distal biomass loss values in blades. For the optimal development of these perennial species a compromise would have to exist between the assimilated carbon and the multiple biomass fates/uses through the time.

Similar to the Laminariales of the Northern Hemisphere, which have been well studied, the *Lessonia* spp. constitutes an important genus in the coasts of the Southern Hemisphere, and shows comparable ecologic and economic functions and services (Santelices *et al.* 1980; Vásquez 1992; Vásquez & Fonck 1993; Edding *et al.* 1994; Edding & Tala 2003; Ortiz 2003). A semiquantitative conceptual model of fate of the biomass produced by *Lessonia* based on present and previously published data is shown in Fig. 6. Of the total biomass, about 50% is represented by stipes and holdfasts, which anchor the plant to substrate and produce spatial heterogeneity for the refuge and reproduction of many invertebrates and fish (Edding *et al.* 1994). Between 10 and 25% of the blade biomass is used directly into reproductive events (Tala *et al.* 2004), which include a step obligated by a microscopic phase responsible for the sexual reproduction and subsequent recruitment. *Lessonia* is an important food source for herbivores, in both macroscopic and microscopic phases of the life cycle (Pizarro 1981; Edding *et al.* 1994; Martínez & Santelices 1998). About 25% of the *Lessonia* blade biomass may be lost as particulate material (Tala & Edding 2005). A fraction of kelp detritus may be used within the coastal zone by detritivores and filter feeders, and another fraction may be exported towards pelagic and abyssal areas, later to be re-incorporated to the coastal system by events such as upwelling (Field *et al.* 1977; Mann 1988; Kirkman & Kendrick 1997; Vásquez *et al.* 1998). It forms an important and continuous source of food for filter feeders, especially in zones with a marked seasonal phytoplankton productivity. The portion of dissolved material lost by macroalgae is difficult to quantify *in situ*, and would contribute to the organic particulate matter (Mann 1988). Considering the investments in reproduction (Edding *et al.* 1993; Tala *et al.* 2004), population abundance and size (Camus & Ojeda 1992; Edding *et al.* 1994; Edding 1998; this study), mortality in *Lessonia* should be higher in the first stages of development and diminish towards adult stages. Data obtained in northern Chile allows the estimation that between 10 and 50% of the population biomass is lost as wrack cast onto supralittoral beaches (Edding 1998). During the drift and cast ashore, the macroalgal biomass contributes to dissolved and particulate matter, recycling nutrients and the plant is occupied by small organisms (bacteria, crustaceans, and insects) that feed on decomposing organic material, which in turn serve as food for coastal birds (Kirkman & Kendrick 1997). These zones constitute important areas for the harvest of Chilean kelps by the alginate industry over the last 30 years (Vásquez & Fonck 1993; Edding *et al.* 1994; Edding 1998). Moreover, Chile has experienced an increasing development of herbivore cultures, mainly the introduced abalone (*Haliotis* spp.) that use fresh kelp as food. Predicted demand for kelp is about 5–10% of the animal body mass per day. Therefore, to produce 1 ton of abalone, with sizes between 50 and

70 mm, about 50 k of fresh kelp blades per day are required. Hand harvesting is now a new factor of mortality into *Lessonia* populations not yet quantified.

One of the main reasons for developing and applying a model for *Lessonia* productivity was to have a tool that allows the description and quantification the effect of perturbations, like El Niño, non-regulated exploitation, or pollution within kelp populations. Considering the complex system that *Lessonia* constructs in the coastal shores, changes in its populations would cause a response in the entire community.

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