

Population biology of *Durvillaea antarctica* and *Lessonia nigrescens* (Phaeophyta) on the rocky shores of southern Chile

Renato Westermeier¹, Dieter G. Müller², Iván Gómez¹, Pedro Rivera¹, Hedwig Wenzel¹

¹Instituto de Botánica, Facultad de Ciencias, Universidad Austral de Chile, Casilla 567, Valdivia, Chile

²Fakultät für Biologie der Universität Konstanz, D-78434 Konstanz, Germany

ABSTRACT: The *Lessonia nigrescens*–*Durvillaea antarctica* belt is a characteristic feature of the lower intertidal zone along the Chilean coast. This study describes the dynamics of the *Lessonia*–*Durvillaea* assemblage in an exposed locality of southern Chile. Abundance, spatial and temporal distribution, reproductive periods and response to experimental pruning were quantified. The results revealed differences in population dynamics between species. *L. nigrescens* had low recruitment, but a longer life expectancy. In contrast, *D. antarctica* had great temporal fluctuations in abundance, which were associated to massive recruitment during the warmer seasons. It occupied zones where old *L. nigrescens* individuals were dislodged by wave action. Replacement of *D. antarctica* by *L. nigrescens* was not seen. Regeneration from pruned plants of the 2 species was evident during the first months, but subsequently, deterioration of the regenerated parts was seen, leading to the degeneration and detachment of the whole plant. Thus, for management plans, the total removal of old individuals would be preferable.

KEY WORDS: Population biology · Seaweed · *Durvillaea* · *Lessonia*

INTRODUCTION

Durvillaea antarctica (Cham.) Hariot and *Lessonia nigrescens* Bory form a conspicuous belt in a lower intertidal rocky shore of the Chilean coast southward from 30° S (Guiler 1959, Westermeier 1980, Santelices 1981, Westermeier & Rivera 1986).

Comparative studies in central Chile (Santelices et al. 1980, Ojeda & Santelices 1984) have shown that the competitive interaction of both species seems to follow the community structure model proposed by Connell (1975) and Menge & Sutherland (1976), with *Lessonia nigrescens* persisting in areas of high wave exposure due its morphological adaptations while *Durvillaea antarctica* persists because of its high reproductive rate, rapid growth, and rapid replacement. The population ecology of these species is not known for southern Chilean communities, nevertheless, some data on geographical distribution revealed that the *Lessonia*–

Durvillaea belt suffers local variations, mainly in its vertical limits (Westermeier & Rivera 1986).

During recent years, humans have heavily exploited populations of *Durvillaea antarctica* and *Lessonia nigrescens* in accessible areas (Santelices et al. 1980, Westermeier 1987, Castilla & Bustamante 1989). In 1989, the annual landing of *L. nigrescens* reached 62 723 t, harvested mainly in central and northern Chile, while the annual harvest of *D. antarctica* reached 1040 t (Sernap 1989).

These facts highlight the need to understand the population dynamics of these species from southern Chile in order to provide information for management programs. With this in mind, our study provides quantitative data on spatial and temporal changes in distribution and abundance, and reproductive phenology, as well as morphology. Finally, we report on the effect of experimental pruning on regeneration and survival of plants.

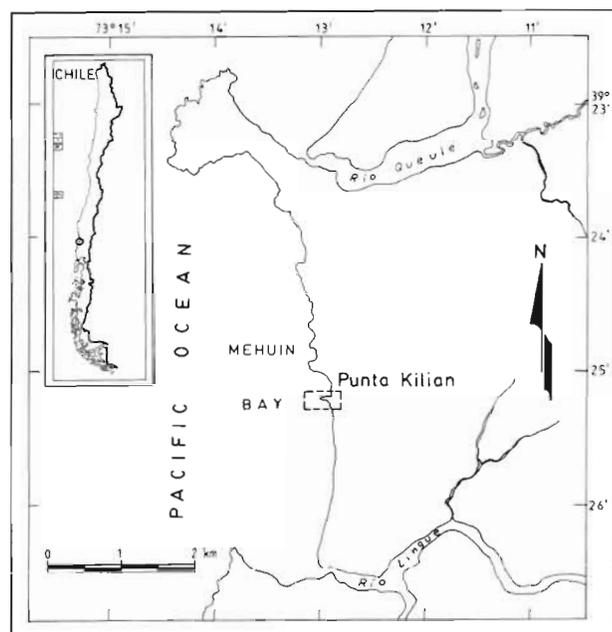


Fig. 1. Mehuin Bay in southern Chile showing the Punta Kilian site

MATERIAL AND METHODS

Abundance and distribution patterns. The study was conducted between April 1985 and September 1987 along the exposed rocky shore of Mehuin (Punta Kilian, 39° 24' S, 73° 14' W). This area (Fig. 1) has been protected from human interference since 1978.

To evaluate the temporal and spatial distribution of *Lessonia nigrescens* and *Durvillaea antarctica* kelps, 2 slightly inclined platforms of 42 m², which were exposed to different wave impact, were selected. These areas were divided into 42 permanent 1 m² quadrats and the total number of plants within every quadrat was monitored seasonally. Evaluation of wave force was indirectly made by measurement of the erosion of plaster of Paris blocks, according to the method described by Doty (1971).

Reproductive phenology. Studies on reproductive state of both *Lessonia nigrescens* and *Durvillaea antarctica* were carried out monthly taking random samples from a less exposed platform. Data on total density of plants inside the platform were also taken, which were related to the percentage of reproductive individuals. No sampling in the more exposed area was performed because initial evaluations in Punta Kilian indicated negligible changes in reproductive phenology attributable to wave exposure. The determination of reproductive maturity was done by examination of sections of the sori (*L. nigrescens*) and conceptacles (*D. antarctica*).

Morphometric relationships and size structure. To determine the temporal changes in morphometric parameters, 20 plants from each *Lessonia nigrescens* and *Durvillaea antarctica* belt were marked. Because of the low life expectancy of the individuals that inhabit more exposed sites, the marked plants were selected from the less exposed platform. Holdfast diameter, stipe length and frond size were measured throughout the study period. Seasonal determinations of dry weight were performed from 15 individual samples of the 2 species from the same site (less exposed). Dry weight was determined separately for holdfast, stipe and fronds. These measurements were made to provide regression data (Sokal & Rohlf 1969).

To evaluate temporal incidence of the different size classes, monthly changes in the abundance of *Lessonia nigrescens* and *Durvillaea antarctica* were determined based on 3 size categories and using the maximum holdfast diameter.

Experimental pruning regeneration and mortality. Considering that *Lessonia nigrescens* is an alga with multiple stipes arising from a solid holdfast, while *Durvillaea antarctica* has only one, we designed an experiment evaluating the comparative capacity of regeneration of the stipes after an experimental cutting.

Fig. 2 shows the harvesting scheme. *Durvillaea antarctica* was cut in the transition zone between stipe and leafy frond, whereas *Lessonia nigrescens* was pruned at the first dichotomy of the stipe. This experiment was carried out at different seasons with groups of 20 plants from a site with moderate wave impact. Similar numbers of plants were used as a control group. Regeneration was evaluated by detection of

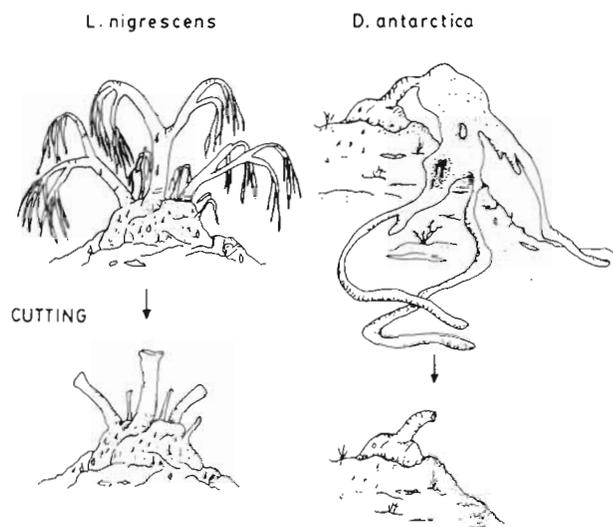


Fig. 2. *Lessonia nigrescens*, *Durvillaea antarctica*. General morphology of 2 kelps showing the experimental pruning

shoots on the pruned stipes and monthly changes in holdfast diameter and length of pruned stipes were recorded. Additionally, 30 young plants of both species from the same area were used for the evaluation of mortality and life expectancy.

RESULTS

On the more exposed rocky platform, *Durvillaea antarctica* showed a strong seasonality, with greater abundance during January and May 1987, reaching maximum values between 26 and 30 plants m^{-2} (Fig. 3). Nevertheless, *D. antarctica* was absent from most quadrats. In contrast *Lessonia nigrescens* ex-

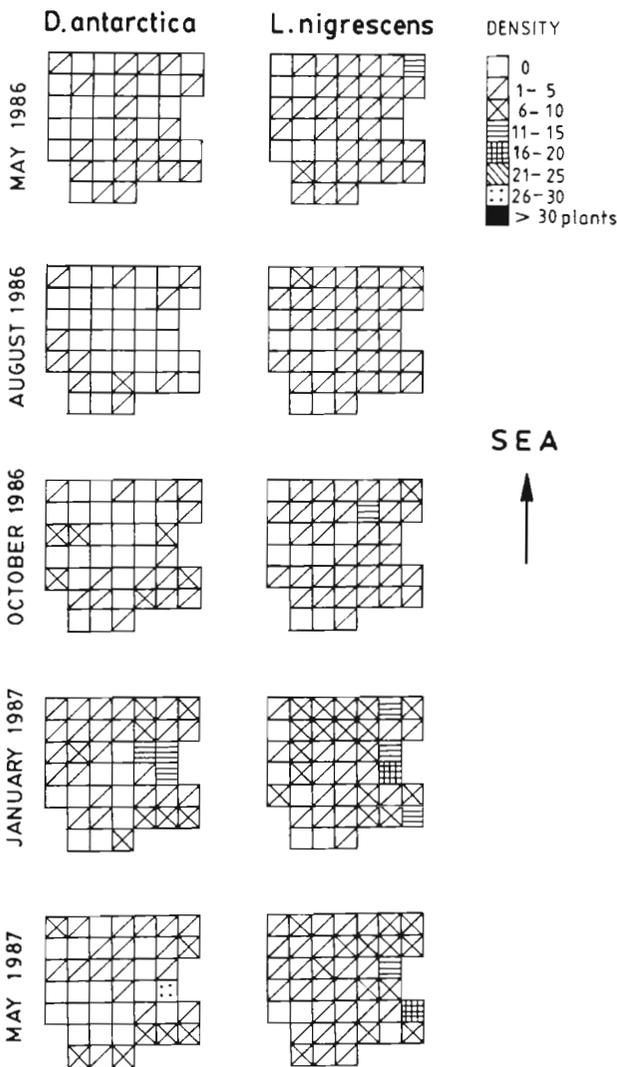


Fig. 3. *Durvillaea antarctica*, *Lessonia nigrescens*. Seasonal and spatial variations in abundance of kelp on the more exposed rocky platform

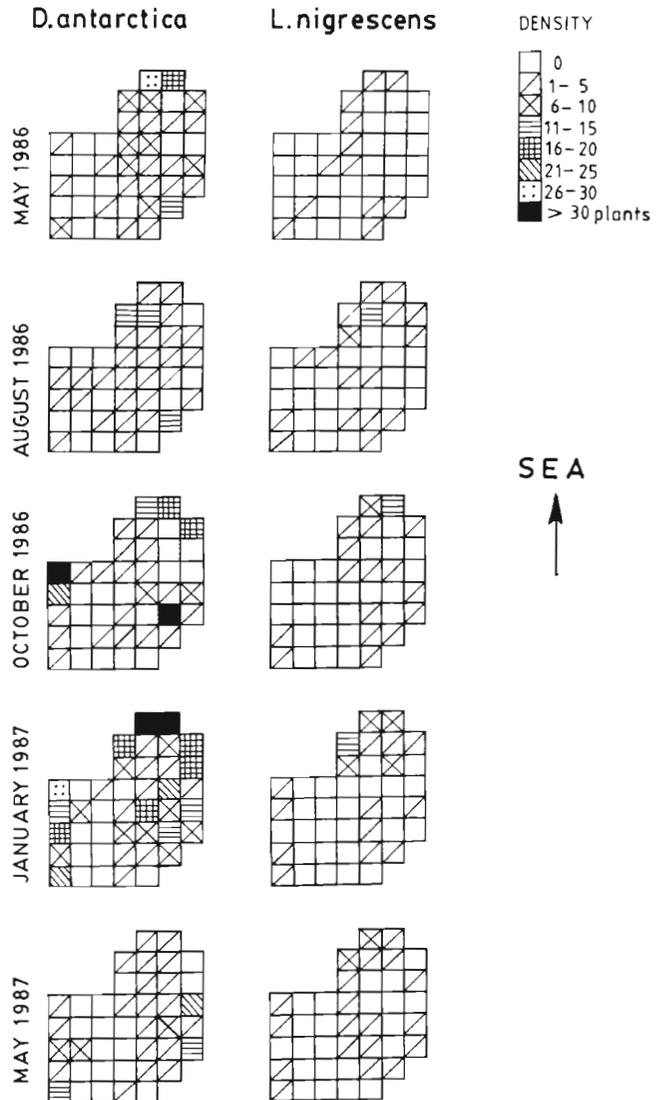


Fig. 4. *Durvillaea antarctica*, *Lessonia nigrescens*. Seasonal and spatial variations in abundance of kelp on the less exposed platform

hibited a more stable temporal abundance, which increased during January and May 1987 to values close to 20 plants m^{-2} . In this area *L. nigrescens* dominated and showed a more homogeneous cover than *D. antarctica*.

Durvillaea antarctica was more abundant in the less exposed site (Fig. 4). This species reached values greater than 30 plants m^{-2} and extended its distribution limit during October 1986 and January 1987, occurring principally in the periphery of the site. *Lessonia nigrescens* also occurred in the marginal areas, but did not enlarge its range. Its abundance was reduced, with maximal values of 11 and 15 plants m^{-2} in January 1987.

Relationship between abundance and reproductive phenology

Durvillaea antarctica showed a strong seasonal pattern of abundance, with 2 peaks of greater abundance, first in summer-autumn 1986 and next during summer 1986-1987 (Fig. 5). In this species, the number of reproductive plants had a high negative correlation ($r = -0.82$, $p < 0.05$) with abundance. Apparently, the high recruitment rates seen in *D. antarctica* included a great number of young individuals, which do not share in reproduction. On the other hand, abundance of *Lessonia nigrescens* fluctuated less and there was no significant relationship with reproduction ($r = -0.11$, $p > 0.05$).

Morphometric parameters

Morphologically, *Lessonia nigrescens* is well adapted to high wave exposure. Its solid holdfast, strong stipes, and small dichotomously branched fronds show high resistance to mechanical forces (Köehl

1986). In contrast, in *Durvillaea antarctica*, the large proliferate frond is connected to a smaller holdfast by a short, slender stipe. This was further confirmed by the analysis of temporal variation in the morphometric parameters (Fig. 6), frond length being the more variable morphological characteristic. In *D. antarctica*, fronds show a strong variation between individuals (15 to 230 cm) and between months throughout the year, but no clear seasonal pattern was found. Probably, the morphological changes of the frond in *D. antarctica* are regulated by meristoderm activity versus destruction of the apical zones of the frond which appears to be caused by multiple agents. On the other hand, *L. nigrescens* attains a maximum frond length of 50 cm with lower monthly variations. In May and June 1985, frond length of *L. nigrescens* declined, coinciding with zoospore release. This suggests that morphological shape could be related to reproductive state at some times.

The regression analysis (Table 1) indicates that in *Durvillaea antarctica* there is a high correlation between frond weight and total weight of the plant ($r = 0.99$, $p < 0.05$). Likewise, a significant direct relation-

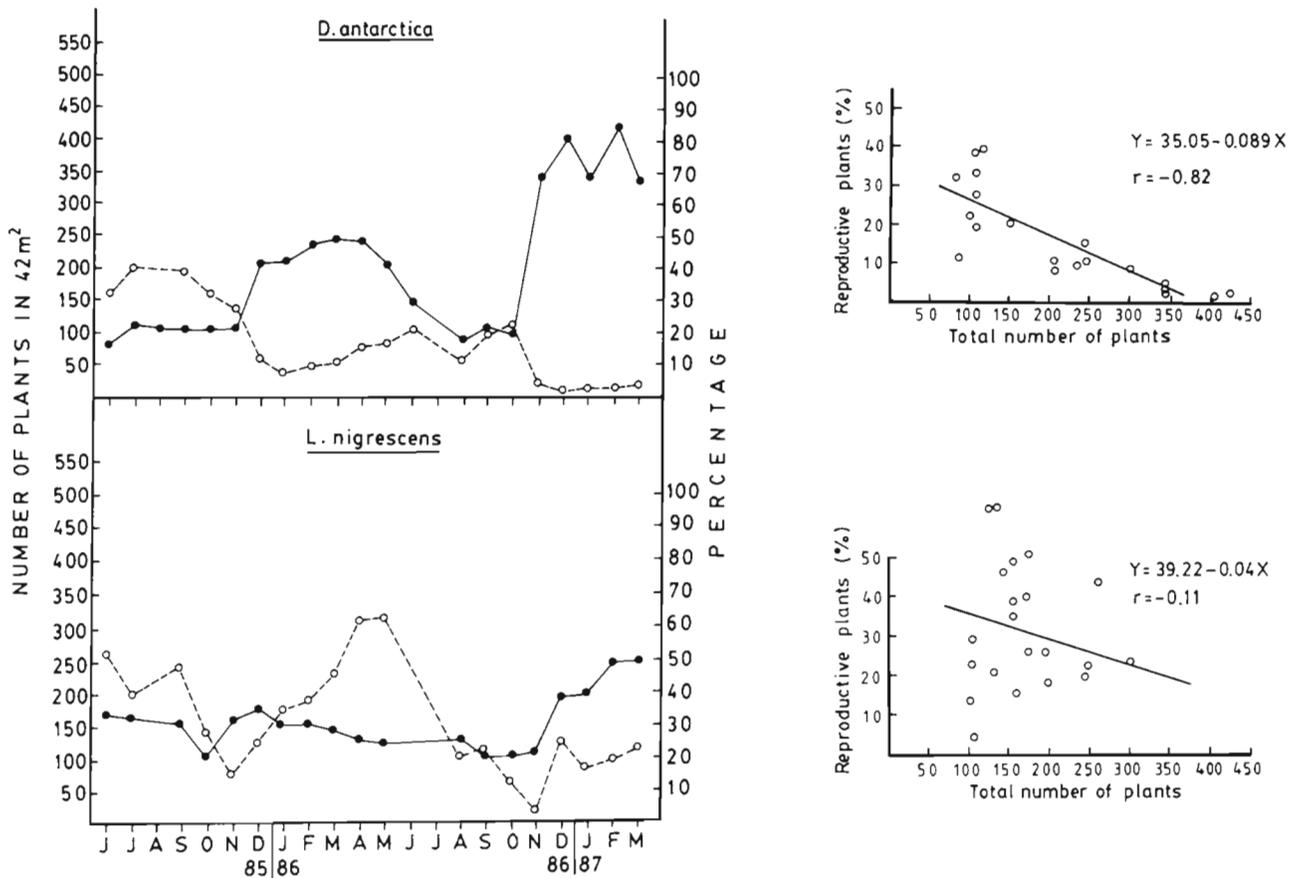


Fig. 5. *Durvillaea antarctica*, *Lessonia nigrescens*. Monthly changes in total number of plants (●) and relative percentage of reproductive plants (○), as well as the statistical relationship between plant density and reproductive percentage

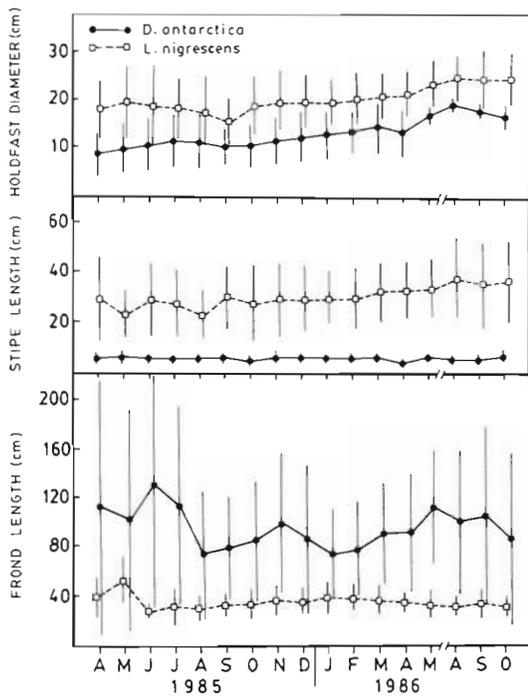


Fig. 6. *Durvillaea antarctica*, *Lessonia nigrescens*. Monthly changes in morphometric characteristics of 2 species of kelp

Table 1. *Durvillaea antarctica*. Relationship between different morphometric parameters. n = 84

Variables y vs x	Equation	Correlation coefficient (r)
Fronde weight vs: Total weight	$y = -16.94 + 0.94x$	0.99**
Holdfast weight vs: Total weight	$y = 8.53 + 0.04x$	0.83**
Holdfast diameter vs: Holdfast weight	$y = 6.25 + 0.17x$	0.73**
Total weight	$y = 7.48 + 0.008x$	0.70**
Fronde weight	$y = 7.66 + 0.009x$	0.69**
Stipe diameter	$y = 3.47 + 3.35x$	0.58**
Fronde length	$y = 5.97 + 0.02x$	0.55**
Fronde length vs: Total weight	$y = 103.49 + 0.20x$	0.70**
Fronde weight	$y = 107.32 + 0.21x$	0.70**
Stipe diameter vs: Fronde weight	$y = 1.59 + 0.001x$	0.48**
Total weight	$y = 1.57 + 0.001x$	0.48**
Fronde length	$y = 1.42 + 0.0026x$	0.36*
Stipe length	$y = 1.51 + 0.041x$	0.20 ^{ns}
Stipe length vs: Stipe diameter	$y = 6.06 + 0.18x$	0.24*

*p < 0.05; **p < 0.01; ns: not significant

Table 2. *Lessonia nigrescens*. Relationship between different morphometric parameters. n = 83

Variables y vs x	Equation	Correlation coefficient (r)
Fronde weight vs: Total weight	$y = 7.31 + 0.29x$	0.95**
Holdfast weight vs: Total weight	$y = 8.84 + 0.20x$	0.88**
Stipe weight	$y = 20.88 + 0.39x$	0.86**
Fronde weight	$y = 19.02 + 0.59x$	0.79**
Number of stipes	$y = 51.79 + 2.48x$	0.21*
Stipe weight vs: Fronde weight	$y = 5.47 + 1.42x$	0.87**
Holdfast diameter vs: Total weight	$y = 9.71 + 0.008x$	0.81**
Holdfast weight	$y = 10.03 + 0.03x$	0.76**
Stipe length	$y = 7.90 + 0.31x$	0.56**
Fronde length	$y = 7.79 + 0.16x$	0.47**
Number of stipes	$y = 8.82 + 0.21x$	0.44**
Fronde length vs: Fronde weight	$y = 28.41 + 0.037x$	0.41**
Number of stipes vs: Total weight	$y = 18.40 + 0.006x$	0.32*
Fronde length	$y = 23.56 + 0.06x$	-0.085 ^{ns}
Stipe length	$y = 20.84 + 0.03x$	0.031 ^{ns}

*p < 0.05; **p < 0.01; ns: not significant

ship between the holdfast weight and total weight was found (r = 0.83). The other morphometric characteristics show lower correlation coefficients. A similar pattern was shown by *Lessonia nigrescens* (Table 2), with the variations of frond weight and holdfast weight being directly proportional to the total plant weight (r = 0.95 and r = 0.88, p < 0.05). The stipes of *L. nigrescens* are strongly integrated in the morphology of the thallus, and their weight correlates significantly with the frond weight and the holdfast weight (r = 0.87 and r = 0.86, p < 0.05, respectively). It must be emphasized that the number of stipes showed little statistical relationship with the remaining morphometric parameters, the highest correlation being the holdfast diameter (r = 0.44).

Monthly changes in holdfast size classes

Temporal changes in size structure (Fig. 7) indicate that the smaller individuals have a high incidence in the population. In *Durvillaea antarctica*, plants larger than 8 cm exhibit a density of up to 40 plants on 42 m²; nevertheless, throughout the study period, no significant variations were seen. The size class <8 cm

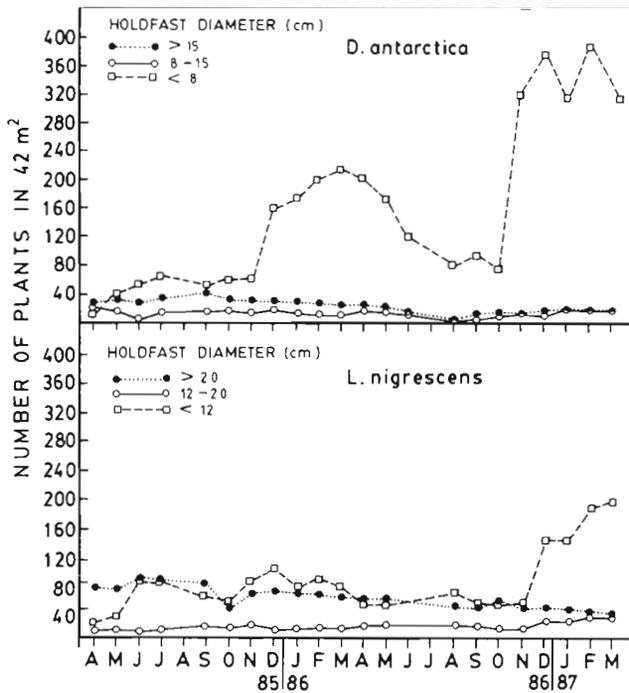


Fig. 7. *Durvillaea antarctica*, *Lessonia nigrescens*. Monthly changes in density for 3 size classes of kelp. Intervals correspond to maximum holdfast diameter

showed clear predominance, with a peak in summer-autumn 1986 and a peak in summer 1987. This is associated with massive recruitment, reaching an abundance close to 390 plants on 42 m² at the end of the study. Unlike *D. antarctica*, the size structure of *Lessonia nigrescens* was more homogenous during the study. It was seen that size classes ranging between 12 and 20 cm were highly represented, reaching a maximum abundance in June 1985 (autumn) of 83 plants on 42 m². The size class <12 cm showed small seasonal variation during the large part of the study, but towards the end, the number of young plants increased, reaching a maximum value of 190 plants on 42 m².

Experimental pruning and mortality

It was clear that *Durvillaea antarctica* undergoes the more drastic mortality after pruning, higher than 73% in the 3 seasons (Fig. 8). In contrast, most *Lessonia nigrescens* mortality occurred in autumn and spring and was lower than 30%. The control also showed a mortality level similar to pruned plants. Regeneration was very high 30 d after pruning, mainly in *D. antarctica*. In autumn it reached 100% of plants regenerated, while *L. nigrescens* in the same time did not show

regeneration. Later, in winter, the regenerative capacity decreased in both *D. antarctica* and *L. nigrescens*. Finally, it was observed that regenerated shoots deteriorated and the plant began to detach.

DISCUSSION

The results of the present study in southern Chile indicate that the distributions of *Durvillaea antarctica* and *Lessonia nigrescens* are similar to those in central Chile. Although there was some overlap during the warmer months, a different distribution within the sites was seen. In this sense, *L. nigrescens* occupies the wave-battered sectors of the platforms, with densities of more than 20 plants m⁻² in some areas. Santelices (1981) postulates that at exposed intertidal levels, distribution patterns are mainly determined by the morphology of the algae. The morphological differences between the studied species constitute a major regulatory factor for the structure and dynamic of the *Lessonia-Durvillaea* belt. In Mehuin, *D. antarctica* occurs preferentially on the periphery of less exposed rocks, which is consistent with the results of Hay (1977) for *D. antarctica* from New Zealand. In contrast, *L. nigrescens*, with a morphology much better suited to wave impact, is most abundant in exposed areas. The distribution limits are more stable in *L. nigrescens* due to its lower recruitment and mortality, while in *D.*

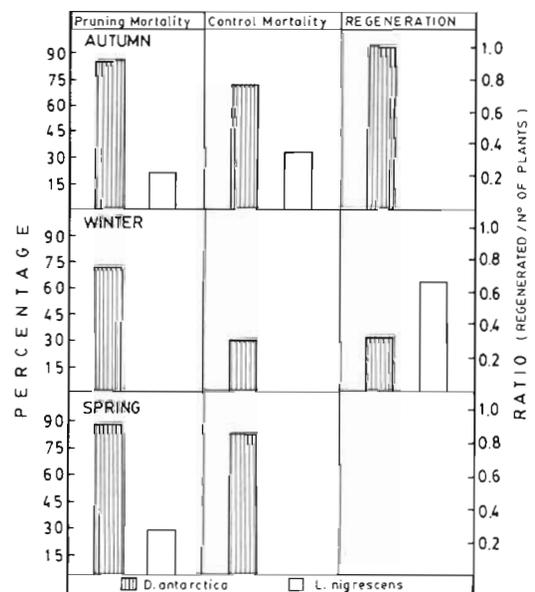


Fig. 8. Response of *Durvillaea antarctica* and *Lessonia nigrescens* to experimental cutting. Bars represent values of mortality and regeneration after 5 mo. Regeneration was calculated as regenerated plants divided by the total number of plants

antarctica, the abundance is more variable, expanding its lower limit during summer (the period with lowest wave action).

Population structure of *Durvillaea antarctica* is determined principally by young individuals (in this study determined by holdfast diameter classes), which constitute more than 80% of the population during summer-autumn. This pattern suggests the existence of recruitment processes associated with plant density. For example, Cheshire & Hallam (1988a) postulate that in *D. antarctica* reproductive potential must be stored in an inflated density of young plants until a gap in the canopy allows fast growth. *Lessonia nigrescens*, in contrast, presents a more stable population structure, as only 1 massive recruitment event occurred (summer 1987). According to Cheshire & Hallam (1989), the alteration of generations (heteromorphic life cycle) occurring in laminarian algae versus its absence in fucalean algae determines the differences in population structure. Probably, this factor could explain the differences found in the *Lessonia-Durvillaea* assemblage from Mehuin. In central Chile, Santelices & Ojeda (1984) relate the low recruitment rate of *L. nigrescens* to space-dependent factors, indicating that after removal of adult plants, high recruitment could be expected. This should be associated with age composition of the population. Thus, taking into account the analysis by Cheshire & Hallam (1989), the more exposed habitats, common in central Chile, contain a high number of low vitality, young plants and the population has high recruitment rates. On the other hand, the southern Chilean populations are dominated by old individuals with high vitality and, therefore, decreased turnover rates.

Wave action has been frequently recognized as a major factor regulating the morphology and life span of these kelps (South & Hay 1974, Santelices et al. 1980, Köehl 1986, Cheshire & Hallam 1988b). This effect should be seen in a seasonal pattern. Nevertheless, no temporal variation in morphological characteristics was found in our study. Holdfast and stipes are not subject to temporal changes and frond length does not show a clear seasonal pattern. Seemingly, other factors such as extreme desiccation (Schonbeck & Norton 1978, Druehl & Green 1982, Hawkins & Hartnoll 1985, Cheshire & Hallam 1988a, b) or mechanical damage during low tide could cause losses in the distal parts of the thallus. Another alternative explanation comes from recent studies on infection by slime moulds. This fact has been reported in *Durvillaea antarctica* in southern Chile (Aguilera et al. 1988) and *D. potatorum* from Australia (Cheshire & Hallam 1988b). Since this agent causes necrosis in distinct zones of the thallus, there may be a relationship with population mortality or at least with plant morphology.

Further experimental studies are necessary. On the other hand, morphological changes in *Lessonia nigrescens* can be caused by the limpet *Scurria scurra*. According to Santelices et al. (1980) and Muñoz & Santelices (1989), this organism has a pruning effect, mainly on the largest stipes, preventing detachment by wave shock. The *Lessonia-Scurria* interaction was common at our sites, but not evaluated.

Several workers have discussed the influence of human predation on the population dynamics of *Lessonia nigrescens* and *Durvillaea antarctica*. Santelices et al. (1980) postulate that human interference is not a predominant selective factor in the *Lessonia-Durvillaea* belt at exposed areas, refuting Guiler's (1959) prediction that removal of *D. antarctica* by algal collectors prevents the competitive displacement of *L. nigrescens*. Castilla & Bustamante (1989) and Bustamante & Castilla (1990) demonstrated that the standing crop of *D. antarctica* in central Chile can be reduced by intensive human activity. Likewise, in southern Chile, Westermeier & Chacana (unpubl. data) compared 2 areas with different levels of human access and found the absence of *D. antarctica* in the sector which is open to humans. However, no one has yet measured the effects of the biomass reduction of *D. antarctica* on the biomass of *L. nigrescens* at those localities. Thus, although there seems to be no question of the effect of human predation on the population dynamics of *D. antarctica*, we still lack data on the direct or indirect effects of such predation pressure on the population of *L. nigrescens*.

Our pruning data are in agreement with those reported by Santelices et al. (1980), who observed initiation of fronds, mainly in *Lessonia nigrescens*. However this did not happen in all stipes, and the plants later detached. Likewise, *Durvillaea antarctica* responded positively to cutting, with numerous blade-shoots arising from the stipe. Nevertheless, after 3 mo they began to deteriorate and, like in *L. nigrescens*, caused the death of the plant. Although high mortality after pruning was evident, losses of the control plants were also considerable, mainly when the environmental conditions were more extreme. This confirms the results of Santelices et al. (1980), who claim that human action is not a determinant in exposed areas. Observations comparing the traditional harvesting technique employed by algal collectors and the cutting model applied in our study indicate the suitability of the removal of entire plants including the holdfast. Thus the harvesting strategy should consist of total removal of adult individuals after their reproductive period, winter-spring for *L. nigrescens*, and summer for *D. antarctica*. In this way, plants harvested are those strongly subject to natural loss, and new space is provided for massive recruitment; for management pur-

poses, other variables, such as seasonal variation in chemical contents, need to be considered. Studies carried out in southern Chile (Westermeier 1987, Westermeier et al. 1987) indicate high levels of alginic acid in autumn and spring for *L. nigrescens*, while *D. antarctica* has high values in summer and winter. Thus, the integration of population data with temporal chemical variation, as well as internal and external marketing demands, will make possible the development of a management scheme for the littoral areas of Chile.

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