

# LESSONIA

MARIO E. EDDING, ERIKA A. FONCK and JUAN E. MACCHIAVELLO  
*Departamento de Biología Marina, Facultad de Ciencias del Mar, Universidad  
del Norte, Casilla 117, Coquimbo, Chile*

## 1. Introduction

*Lessonia* spp. are the most conspicuous brown macroalgae occupying the littoral zone in cold temperate waters of the southern hemisphere. The plants produce high biomass and extensive cover in exposed and semi-exposed rocky shores (Edding and Cardemil 1979b; Santelices 1982a). *Lessonia* spp. contain high percentages of alginates and other primary materials of high commercial value in the world seaweed market.

*Lessonia* became an important resource in South America after the early suggestion by Llaña (1948b) that it was a potential source of alginic acid; Etcheverry (1958) suggested methods of harvesting commercially exploitable stocks of algae in Chile near Valparaíso. The potential utilization of *Lessonia* in Perú has been recognized by Acleto (1981, 1986). Chile is the only place where natural *Lessonia* beds are commercially exploited. Santelices (1982a) proposed a biological basis for the management of *L. nigrescens* as a renewable resource in the intertidal zone of central Chile.

The world exploitation of alginophytes rose by 104% between 1970 and 1983 to 2,297,926 tons (Jelvez *et al.* 1986). Although this increase was supported by artificial cultivation of *Laminaria* in Japan and China (Tseng 1981), natural populations are subject to stress due to exploitation, as in the case of *Lessonia nigrescens* and *Lessonia trabeculata* living along the coast of central and northern Chile. The only available data on standing stock of *Lessonia* are those for *L. nigrescens*, between Arica (18°29'S) and Loa River (21°26'S) estimated to be about 13,000 tons (Gonzalez 1977). Lopehandia (1979) reported 65,741 tons between Arica and Chañaral (26°21'S). Santelices and Lopehandia (1981) estimated that the *L. nigrescens* total standing stock in northern Chile, from Arica to Caldera (28°S), could reach 96,000 tons. Recent data obtained after an evaluation of *L. nigrescens* along the Chilean coast (Red Algas Marinas Chile, 1990) sown an average biomass of 10 kg m<sup>-2</sup>, with a pick of 72 kg m<sup>-2</sup> in front of Coquimbo). The data concerning *L. trabeculata* are those of Concepcion where Pizarro (1981) found an average biomass between 15 to 70 kg m<sup>-2</sup> with a density of 0.4 plants m<sup>-2</sup>; later Villouta and Santelices (1984) working in Los Molles (32°15'S) found 10.3 kg m<sup>-2</sup> at 5 m depth, with lower biomass towards shallow and deeper waters. The average density was 2.1 plants m<sup>-2</sup> at 2 m depth. Alveal (1986) discussed the extreme importance of allowing recovery of presently overexploited natural beds of *Lessonia* in northern Chile.

In spite of the ecological and economic importance of *Lessonia* there are few published data concerning its biology. The number of described species of *Lessonia* has increased during the last decade due to interest in plants collected in South America



and New Zealand. Understanding of the *Lessonia* life history has been advanced by recent experimental cultures of some of these species in the authors' laboratory. Some effects of nutrients, light, and temperature have also been examined in controlled conditions. The knowledge of natural compounds present in *Lessonia* tissues is fragmentary primarily because of taxonomic confusion regarding species analyzed. Interesting ecological studies have been carried out relating to *Lessonia* which promise to be valuable for the understanding of its biology. For example, the role of these algae in the intertidal zone has been studied through observations of invertebrate associations in its holdfasts (Cancino and Santelices 1981, 1984). Other field experiments have determined interactions between *Lessonia* and its associated flora and fauna (Santelices *et al.* 1980; Santelices 1982a; Villouta and Santelices 1984).

## 2. Taxonomy

*Lessonia* Bory, 1825.

Sporangial thalli erect, perennial. Massive holdfast of branched fused or unfused chapters, with one to several terete to complanate stipes, forking and flattening into paired blades, these produced by a split originating in intercalary meristematic region of blade and progressing towards the apex of the frond. This splitting undergoes an additional six to ten divisions. Blades linear to lanceolate, with or without marginal teeth. Unilocular sporangia forming sori in ordinary blades. Vesicles absent.

The genus *Lessonia* is represented by 8 species:

1. *Lessonia flavicans* Bory (1825).
- Lessonia fuscens* Bory, 1826;
- Lessonia ovata* Hooker and Harvey 1845;
- Lessonia frutescens* Skottsberg 1907;
2. *Lessonia nigrescens* Bory (1826).
- Chordaria spicata* Suhr 1839;
- Laminaria scissa* Suhr 1841;
- Lessonia suhrii* J. Agardh 1841;
- Lessonia berterovana* Montagne 1842;
- Lessonia nigrescens f. montagnei* Skottsberg 1921.
3. *Lessonia variegata* J. Agardh (1877).
- Lessonia brevifolia* J. Agardh (1894).
4. *Lessonia corrugata* Lucas (1931).
5. *Lessonia vadosa* Searles (1978).
- Lessonia nigrescens f. lacunifera* Skottsberg 1921.
6. *Lessonia trabeculata* Villouta and Santelices (1986).
- Lessonia fuscens* Kim 1971;
- Lessonia flavicans* Alveal 1970.
8. *Lessonia adamsiae* Hay (1987)

## Key to the species of *Lessonia*

- 1 Frond surface conspicuously rugose with parallel longitudinal ribs, running the length of the frond, *Lessonia corrugata*
- 2 Width of the frond, 3–5 cm, 6–16 ribs *Lessonia adamsiae*
- 2 Width of the frond, 7–11 cm, 15–35 ribs
- 1 Frond surface smooth.
- 2 Blades and stipes with lacunate cortex.
- 3 Cortical lacunae with or without trabeculae, subtidal, *Lessonia trabeculata*
- 3 Cortical lacunae without trabeculae.
- 4 Blades with uniform pigmentation
- 5 Shallow subtidal, 0.5–2 m, width of the medulla up to 50  $\mu$ m in the blade. *Lessonia vadosa*
- 5 Subtidal, 1–22 m, width of the medulla up to 80–130  $\mu$ m in the blade. *Lessonia brevifolia*
- 4 Blades with irregular pigmentation *Lessonia variegata*
- 2 Blades and stipes with solid cortex.
- 3 Holdfast with strongly fused haptera, fronds 1–4 cm wide, 10–16 cell layers in cortex, cortical cells polygonal, intertidal, *Lessonia nigrescens*
- 3 Holdfast with unfused haptera, fronds 6–39 cm wide, 5–8 cell layers in cortex, cortical cells rectangular, subtidal, *Lessonia flavicans*

Taxonomic characteristics used to delimit the species of *Lessonia* are mainly morphological aspects defined subjectively such as color and presence of marginal denticulations on the frond, or characters with a wide range of variability, such as the number of stipes, stipe shape and frond dimensions that usually overlap partially or totally between species (Table 1). Consequently, the poor delimitation of specific ranges produced continuous confusion within the genus *Lessonia*. Searles (1978) in his review of the genus *Lessonia* in South America, Villouta and Santelices (1986) in their description of *Lessonia trabeculata* in central Chile and Hay (1987) in his description of *Lessonia adamsiae* at The Snarcs, add morphological, anatomical and ecological characters that clarify the identity of the plants present in the study areas. The plasticity of the phenotype in *Lessonia*, which is similar to other genera in the order, make it necessary to study the variation of these plants at a population level which consider morphological, anatomical, physiological, genetic and ecological characters.

## 3. Morphology

### 3.1. General

The general morphology of *Lessonia* corresponds mainly to observations of the sporophyte which follows the typical Laminaracean pattern (Lucas 1931; Etcheverry 1951; Lindauer *et al.* 1961; Searles 1978). The sporophyte present a massive holdfast with haptera that may be fused or unfused (Figs 1 b, d; 2 b). The holdfast of *L. nigrescens* may reach 45 cm in diameter in protected areas of northern Chile (Edding and Cardemil 1979a), while in central Chile, Vasquez and Santelices (1984)



Characters	<i>L. trabeculata</i>	<i>L. corrugata</i>	<i>L. variegata</i>	<i>L. vadosa</i>	<i>L. flavicans</i>	<i>L. nigrescens</i>	<i>L. brevifolia</i>	<i>L. adamsiae</i>
<b>Holdfast Shape and structure</b>	Massive, asymmetric and irregularly shaped, 13–20 cm height; when young haptera are free or only partially fused	Strong and scutiform, spreading	Massive, woody, brittle; dichotomously branched haptera	Dissected, with unfused dichotomously branched haptera	Dissected with unfused, profusely branched haptera	Massive, conical or hemispherical mound of tightly fused haptera	More-or-less hapteroid	Massive, asymmetrical, a coalescence of holdfast, basal branches and haptera
<b>Stipes Number</b>	1–29 (47)	100	up to 100	1–2 (4)	1–2	up to 20	1–2 (4)	5–15
<b>Elasticity</b>	Rigid	V. flexible	Flexible	Rigid	Rigid	Flexible	Rigid	Rigid
<b>Shape</b>	Terete or subterete, flattening to the top	Subterete at base, flattening to the top	Oval or irregular at base, flattened distally	Oval-terete	Oval-terete	Base terete, flattening to the top	Terete to subterete	Terete at base, oval distally
<b>Diameter</b>	(–)	2–4 cm	4 cm	(–)	5 cm	4 cm	(–)	(–)
<b>Cortex</b>	Lacunate; lacunas with multicellular filaments, sometimes branched, which originate from the lacunes walls	Solid	Solid	Spherical or ellipsoidal lacunae	Solid	Solid	lacunate	lacunate
<b>Branching pattern</b>	Dichotomously or subdichotomously in the uppermost portions. 3–4 times furcate to mid portions	Dichotomous (6 dichotomies), cuneate widening of the stem below each dichotomy	Forking from the base, 6–7 times at narrow angles. Twisted branches	Dichotomously or subdichotomously branched	Dichotomously or subdichotomously branched	Dichotomously branched	Dichotomous (3–4 dichotomies)	Dichotomous (4–5 dichotomies)
<b>Fronds Shape</b>	Linear or linear lanceolate	Linear ensiform.	Linear-lanceolate	Linear-lanceolate	Lanceolate	Linear	Ovalate	Linear, fragile
<b>Size</b>	9–86 mm wide in undivided blades, 17–124 mm wide in splitting blades	91 cm length, 2.5 cm wide	60 cm length, 1–7 cm wide	(8)12–68(89) cm length, 2–6(9) cm wide	17–86 (100) cm length, (3)6–39(41) cm wide	(0.8)1–3.5(4) cm wide	9.8–12.3 cm length, 2.5–3.1 cm wide	0.5–1.5 m length, 70–100 mm wide
<b>Margins &amp; general appearance</b>	Smooth or dentated	With alternate spines, 5 mm long with broad bases. Surface rugose with 5 or more parallel longitudinal ribs	Distantly papillated. Surface smooth or longitudinally wrinkled	Dentated	Denticulated	Finely dentated	Glandulated. With microscopic superficial verrucosities	Dentate, with little teeth 15–30 mm distant

Table 1. Cont.

Characters	<i>L. trabeculata</i>	<i>L. corrugata</i>	<i>L. variegata</i>	<i>L. vadosa</i>	<i>L. flavicans</i>	<i>L. nigrescens</i>	<i>L. brevifolia</i>	<i>L. adamsiae</i>
<b>Surface</b>	smooth	corrugated	smooth	smooth	smooth	smooth	smooth	corrugated
<b>Color</b>	Brown	Olive with a greenish tinge	Light yellow to olive-yellow or olive-green	Brown	Dark brown	Dark green, almost blackish	Dark brown	(–)
<b>Paraphyses length (μm)</b>	42–59	(–)	80 with a hyaline hat 20 μm wide	52.7–66	54.4–64.7	18.1–75.4	(–)	(–)
<b>width (μm)</b>	5–8	(–)	(1)*	5.5–7.8	5.6–9	1.3–5.7	(–)	(–)
<b>Sporangia length (μm)</b>	43 ± 4.7	(–)	50–65	29–43.5	34.8–46.4	43.5–55.1	(–)	50–60
<b>width (μm)</b>	5.8–8.7	(–)	10	4.4–7.3	8.7	5.8–8.7	(–)	6–7
<b>Meristoderm cell layers</b>	2–3	1	1	1–2	1–2	2–3	1	1
<b>Cortex</b>	Lacunate, with trabeculae	Lacunate	Lacunate	Lacunate	Solid	Solid	Lacunate	Lacunate
<b>cell layers</b>	7–15	6–8	7–10	5–8	5–8	10–16	7–10	4–6
<b>Medulla width (μm)</b>	Polygonal cells Up to 50	(–)	(–)	Polygonal cells Up to 50	Rectangular cells Up to 25	Polygonal cells Up to 100	(–)	(–)
<b>Habitat</b>	Subtidal 0.5–20 m	Subtidal 1–10 m	Subtidal 1–15 m	Subtidal 0.5–2 m	Subtidal 2–20 m	Intertidal +1 to –1 m	Subtidal 2–25 m	Subtidal 1–22 m
<b>Sources</b>	(1)	(2,6)	(3,6)	(1,4,6)	(1,4,6)	(1,4,6)	(5,6)	(6)

Sources: (1) Villouta and Santelices (1986); (2) Lucas (1931); (3) Lindauer et al. (1961); (4) Searles (1978); (5) Agardh (1894); (6) Hay (1987).

(1)\* E. Villouta (pers. commun.); (–) No available data.



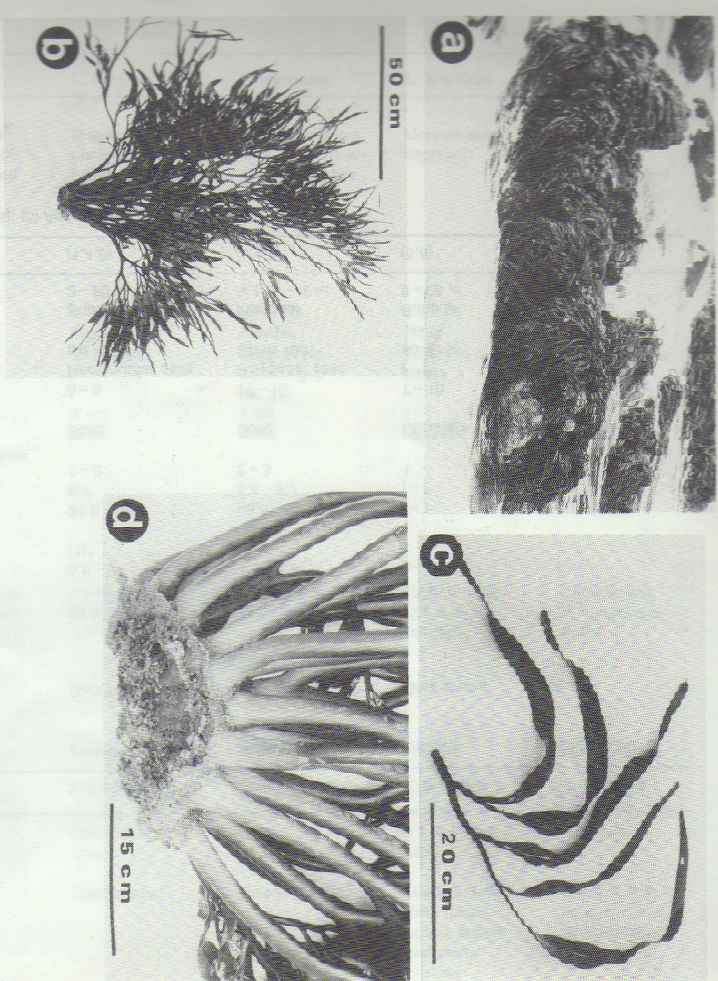


Fig. 1. *Lessonia nigrescens*: a) typical exposed rocky shore in Coquimbo; b) plant habit; c) fronds and branching pattern; d) multichambered holdfast with fused haptera and numerous stipes.

reported values between 17–35 cm in holdfast diameter. The holdfast diameter in *L. trabeculata* changes according to depth. Villouta and Santelices (1984) found that the average diameter increased from 18.9 cm at 2 m depth, up to 24.1 cm at 5 m depth. Below 5 m the holdfast diameter decreased, reaching an average of 14.4 cm at 15 m. The stipes are generally terete, flattening toward the top, presenting a dichotomous branching pattern (Figs 1 b, c; 2 b–c). The number of stipes is variable, ranging between 1 and 100. *Lessonia* blades grow from a basal meristem that produces linear to lanceolate fronds with smooth to denticulate margins (Figs 1 c; 2 d). Gonzalez (1977) found that between Arica (18°29'S) and The Loa River (21°26'S) the highest frequency in *L. nigrescens* frond length was 100 cm (Fig. 3). In the case of *L. adamsiae*, Hay (1987) found that the fronds may reach up to 150 cm in length.

Villouta and Santelices (1984) found that *L. trabeculata* showed a proportional growth in the different parts analyzed. Vasquez (1991) determined that number of stipes and its length to the first dichotomy can be used as an indicator of water movement, exposure and predation by benthic herbivorous. There are positive correlations ( $P < 0.01$ ) between holdfast diameter and frond length, and total weight and holdfast weight. Also Edding and Cardemil (1979a) found that there is a positive correlation ( $P < 0.05$ ) between holdfast diameter and total length in *L. nigrescens*. Table 2 shows morphometric relationships found in individuals of *L. trabeculata* and *L. nigrescens* from populations located in central and northern Chile.

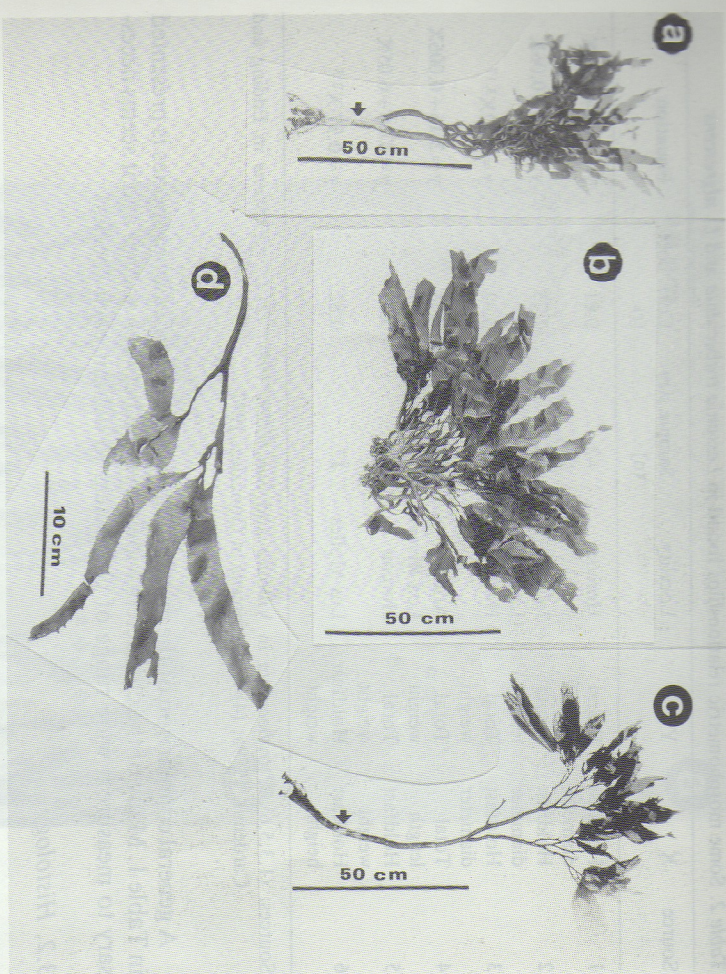


Fig. 2. *Lessonia trabeculata* habit: a, c) old plants with single stipes showing grazers marks indicated by arrows; b) younger plant showing holdfast with unfused haptera and several stipes; d) blades with marginal denticulations.

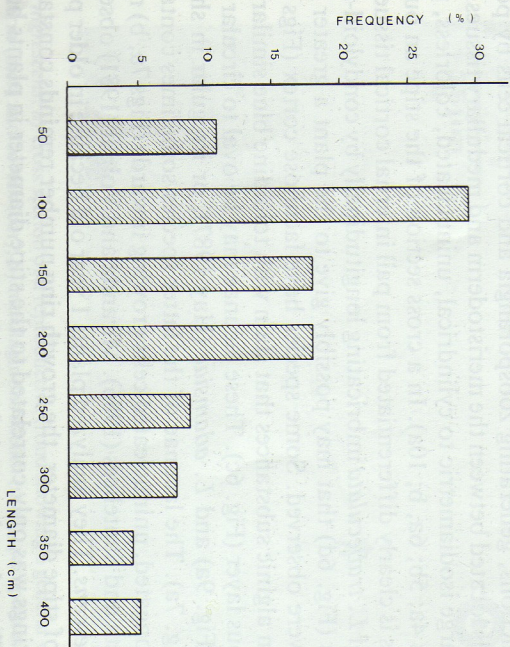


Fig. 3. Frond length of *L. nigrescens* intertidal population from northern Chile. After Gonzalez (1977).



Table 2. Some morphometric relationships found in *Lessonia trabeculata* and *L. nigrescens*.

Source	X	Y	Locality	Sample size (n)	Corr. coeff. (r)	Equation
1	Holdfast diameter	Fronde length	Horton	42	0.81	$y = 19.6 + 4.68x$
2	Holdfast diameter	Fronde length	Liquique-Loa River	62	0.73	$y = 4.06 + 0.06x$
3	Holdfast diameter	Total weight	Horton	28	0.93	$y = 0.12x^{1.17}$
4	Total length	Total weight	Arica-Loa River	306	0.84	$y = 2.16 + 0.006x$
5	Holdfast weight	Total weight	Horton	25	0.95	$y = 87.6 + 6.05x$
6	Holdfast height	Holdfast weight	Los Molles	17	0.82	$y = 0.97x^{2.5}$

Sources: (1,3,5,6) *L. trabeculata* in Villouta and Santelices, 1984; (2) *L. nigrescens* in Edding and Cardemil, 1979a; (4) *L. nigrescens* in Gonzalez, 1977.

A general comparison of the morphology between the *Lessonia* species is presented in Table 1. Many of the characters widely overlap between species and it seems necessary to measure a wide range of characters to delimit each species.

### 3.2. Histology

The microstructure of *Lessonia* can be clearly observed through histological sections of the plant. *Meristoderm*: is the most external tissue, structured by one or several layers, rectangular to cuboidal cells with one nucleus and many phaeoplasts (Figs 5a; 6b; 9b; 10a). Meristoderm is continuous throughout the entire plant and is covered externally by a mucilaginous sheath. This tissue displays both meristematic and photosynthetic functions, generating zoosporangia and cortical cells by periclinal divisions. *Cortex*: is located between the meristoderm and medullary tissues. In the frond is formed of large isodiametric to cylindrical, uninucleated, colorless, parenchymatous cells (Figs 4a; 5b; 6a, b; 10a). In a cross section of the stipe an outer cortex of pigmented cells is clearly differentiated from pail internal cortical tissue (Hay 1987). Cortical cells of *L. trabeculata* imbricating longitudinally by condyloid-shaped cellular projections (Fig. 6d) that may possibly give to the plant a greater resistance to wave action, were observed. Some species have lacunose cortex (Figs 6c; 9a). The lacunae contain alginic substances that stain with toluidine blue similar to the external mucilaginous layer (Fig. 6c). These lacunae may be oval to circular in section as in *L. vadosa* (Fig. 9a) and *L. adamsiae* (Hay 1987), or irregular in shape as in *L. trabeculata* (Fig. 7a). The lacunae of the latter species sometimes contain branched filaments of elongated, uninucleated cells growing inwards (Figs 7a, b) named trabeculae by Villouta and Santelices (1986). Miranda and Voight (1981) observed growth rings in *L. nigrescens*. They analyzed plants 1 year old because in older plants in spite of an increase of stipe diameter, the growth ring number reminds constant; the number of growth rings was only correlated to the stipe diameter in plants between 1 and 1.5 years old. They also observed that tide level, season and exposure to wave action may affect growth ring formation and the frond length-weight relationship. *Medulla*:

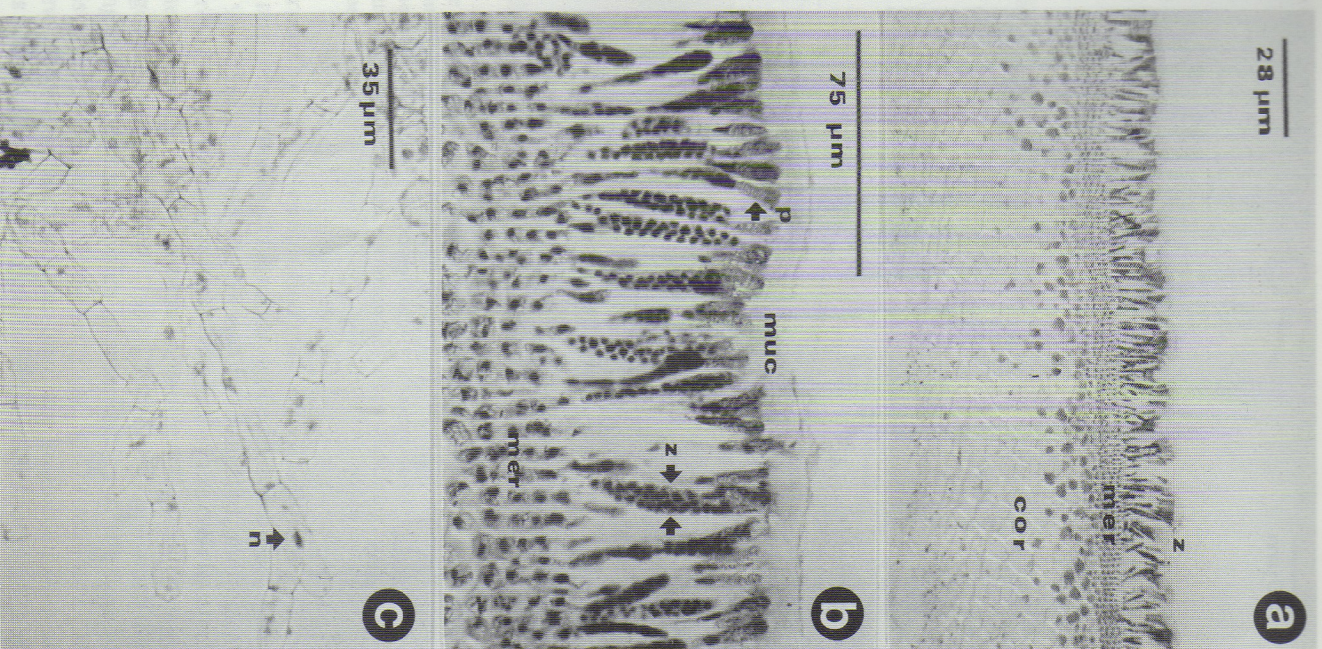


Fig. 4. *Lessonia nigrescens*: a) cross section of a reproductive frond showing a general view of zoosporangia (z), meristoderm (mer) and cortex (cor); b) mucilaginous sheath (muc), paraphyses (p), zoosporangia (z) and multilayered meristoderm (mer); c) sterile female gametophyte with uninucleate cells (n).



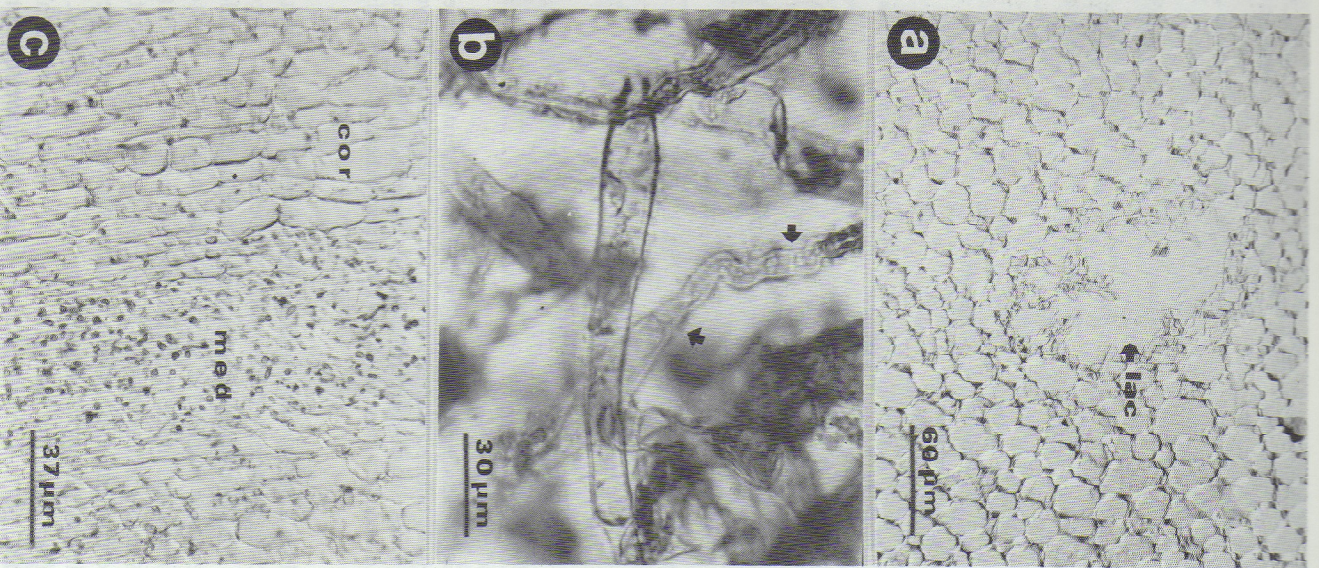


Fig. 7. *Lessonia trabeculata* stipe: a) cortex showing lacune (lac) traversed by multicellular and sometimes branched filaments which arise from the surrounding cortex; b) detail of lacune filaments showing inter-cellular septa (arrows); c) longitudinal section of cortex (cor) and medulla (med).

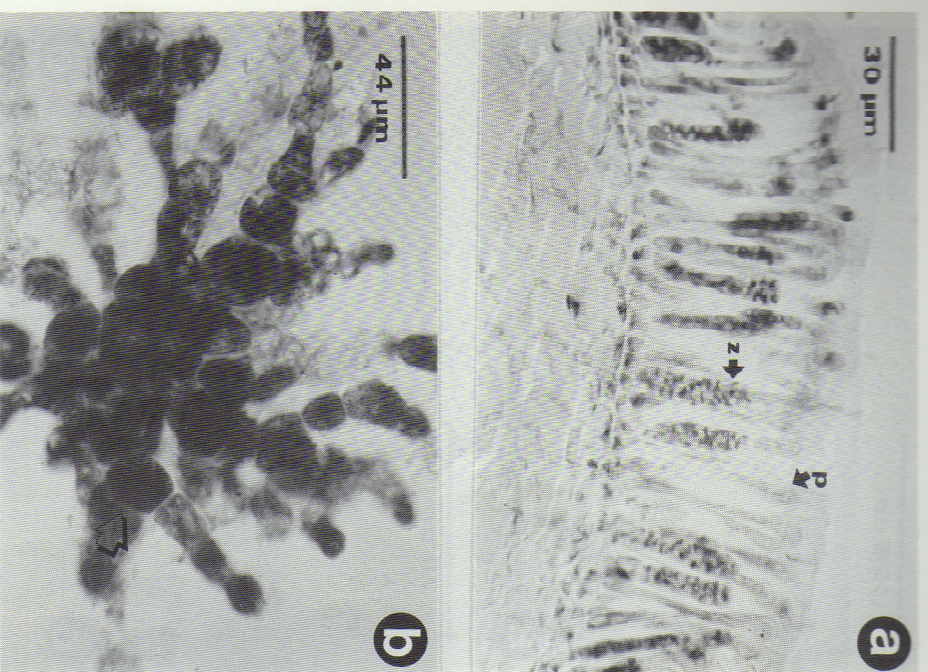


Fig. 8. *Lessonia trabeculata*: a) sori cross section showing the disposition of paraphyses (p) and zoosporangia (z); b) female gametophyte with oogonia (arrow).

mann and Santelices 1982; 3.7–5.5 µm in *L. adamsiae*, Hay 1987). The meiospores are biflagellate (Hoffman and Santelices *op. cit.*) with a parietal phaeoplast, with stigma and without pyrenoids (Asensi *op. cit.*). The size of the sporangia is similar among the species in the genus *Lessonia* (Table 1).

**Gametophyte:** branched, microscopic, uninucleated, haploid, dioecious filaments (Fig. 4c). The females have larger cells than the males. The oogonia are spherical to pear-shaped and larger than the other filament cells (Fig. 8b). After fertilization the sporophyte may remain attached to the female gametophyte and rapidly starts its development. The delicate male filaments develop antheridia which are conical, with only one antherozoid (Elcheverry 1951) bearing unequal flagella (Asensi *op. cit.*).



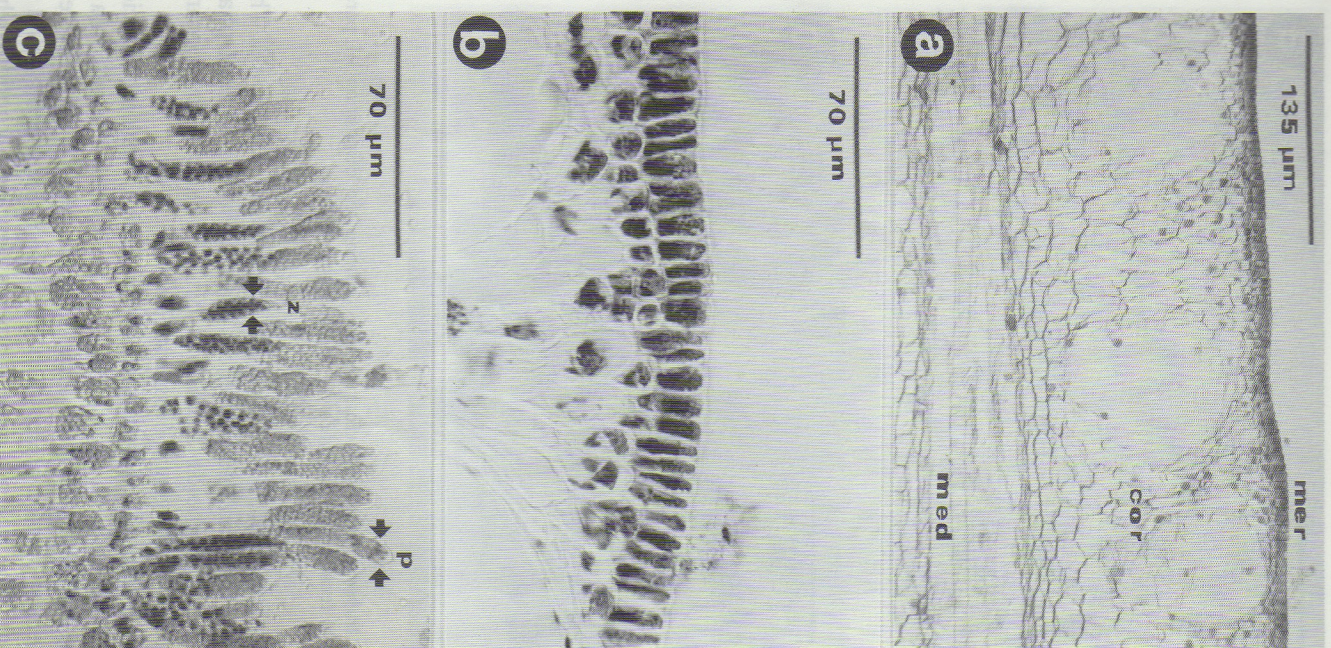


Fig. 9. *Lessonia vadosa* frond: a) general view of meristoderm (mer), lacunated cortex (cor) and medulla (med) in cross section; b) meristoderm; c) transverse section of a sorus, paraphyses (p) and mature zoosporangia (z).



Fig. 10. Cross section of *Lessonia flavicans* frond: a) meristoderm; b) sorus; c) cortex (cor) and medulla (med) showing trumpet cell (arrows).



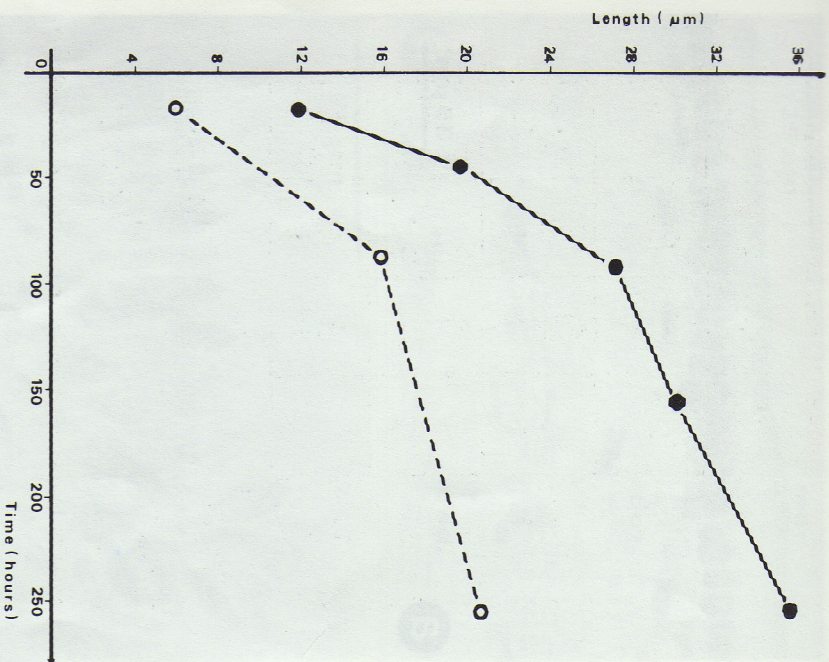


Fig. 11. Differences between *L. nigrescens* gametophyte growth, cultured in static (○) and dynamic (●) systems. After Olivari, 1974.

#### 4. Reproduction and life history

The life history of *Lessonia* is fundamentally similar to that of *Laminaria*, *Desmarestia* and *Macrocystis* all of which have sporic meiosis and alternation of free-living, diploid, sporophytic and haploid, gametophytic generations that correspond to the diplobiontic life cycle type (Bold *et al.* 1980).

The sporophyte of *Lessonia*, as well of other kelps, are large, complex, perennial plants which are dominant in the life cycle, whereas the gametophytes are microscopic, few celled, branching filaments and relatively ephemeral.

There are few data concerning the life history of *Lessonia*. Asensi (1973) described the life cycle of *Lessonia*, based on culture of '*Lessonia fuscescens*'. Seales (1978), however concluded that Asensi (1973) was working with plants of two species (*L. vadosa* and *L. flavicans*). Olivari (1972, 1974) studied the life cycle of *L. nigrescens* and found that the growth of gametophytes in circulating water systems was higher than in static systems (Fig. 11). Hoffmann and Santelices (1982) observed the effect of irradiance and nutrients on the development of gametophytes and gametogenesis. The minimum time required for the gametophytes to reach fertility was 14 days. The

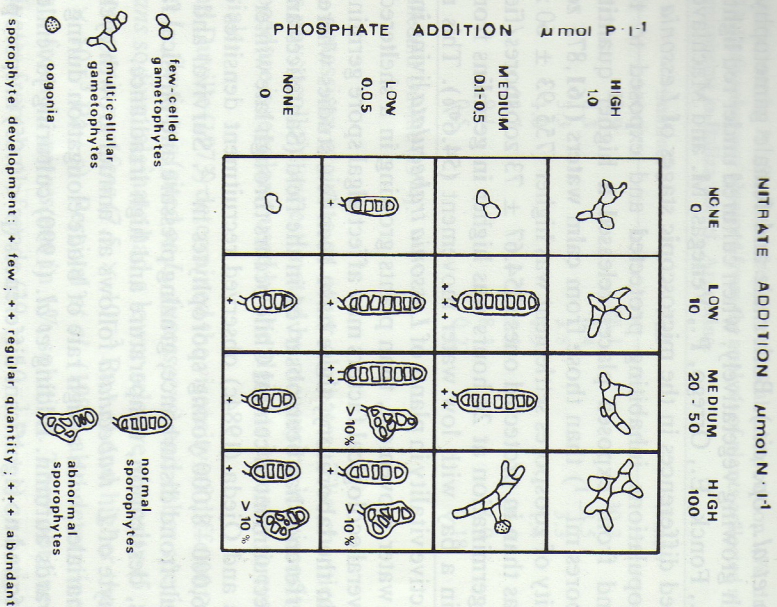


Fig. 12. Effect of different nutrient proportions (N:P) on the development of *L. nigrescens* cultured in the laboratory. After Hoffmann *et al.*, 1984.

zoospores settled down within 2 days and germination began 24 hours after spore settlement. Later Hoffmann and Camus (1986) observed *L. nigrescens* zoospores (5–30  $\mu\text{m}$  diameter) settled slower than *Gelidium linguatum*, *Iridaea ciliata* and *L. laminarioides* whose spore diameter ranged between 20 and 30  $\mu\text{m}$ . It is possible to distinguish between males and females approximately 6 days after settlement. Avila *et al.* (1985) studied the interaction of light and temperature on the development of the meiospores of *L. nigrescens*. They found that spore germination was independent of the culture conditions tested. Hoffmann *et al.* (1984) tested the effect of different concentrations of nitrate and phosphate on the microscopic stages of *L. nigrescens*. It was found that there were different nutrient requirements depending on the stage of development (Fig. 12). Hoffmann *et al.* (*op. cit.*) concluded that nutrient application was a process requiring precise conditions. When no phosphate was added, there was almost no differentiation of sporophytes, independent of nitrate concentration. The most appropriate conditions for sporophyte development were 0.05–0.1  $\mu\text{mol P l}^{-1}$  and 10–20  $\mu\text{mol N l}^{-1}$ . After fertilization the zygote elongates and divides anisotropically, producing a uniseriate filament composed of a few cells. After several anisotrophic divisions a monostromatic blade with a rhizoid at the base is formed. Later, perianth divisions give shape to a polystromatic blade with an elongated mor-



phology (Avila *et al.*, *op. cit.*). Both male and female gametophytes may remain sterile, although growing vegetatively, when cultured under red light in the laboratory. Eddings, M., Fonck, E., Orrego, P., Venegas, M. and Machiavello, J., (unpublished), observed differences in the microscopic stages of *Lessonia trabeculata* collected from populations inhabiting protected and exposed to the wave action localities. Frond from exposed places released a higher quantity of zoospores (319,662 zoospores ml<sup>-1</sup>) than those from calm waters (161,875 zoospores ml<sup>-1</sup>). Also the quantity of zoospores settlement was higher (755.93  $\pm$  60 zoospores/field) in exposed areas than in protected ones (254.67  $\pm$  73 zoospores/field). Finally, the percentage of germination at 24 hours was higher in germlins from exposed areas (91.2%) than in a bay with low water movement (54.6%). This results suggest a higher reproductive vitality in plants of *Lessonia trabeculata* living in an environment with an active water movement, than plants growing in a sheltered environment.

Although several ecological factors may affect algal spore germination and subsequent growth in the laboratory, there have been few studies where grazing and intraspecific interference has been observed in the field (Santelices and Ojeda 1984c). *L. nigrescens* recruitment in central Chile occurs through late winter to the following fall. Santelices and Ojeda (1984c) observed recruitment densities of *L. nigrescens* ranging from 6,000–8,000 young sporophytes m<sup>-2</sup>. Survival and growth was dependent on adult frond disturbance, grazing pressure and physical factors such as tidal differences, desiccation, temperature and high irradiance.

The sporophyte of *L. trabeculata* follows an annual growth cycle similar to that of other Laminariales, with a high rate of blade elongation during the summer and decreasing towards autumn. Eddings *et al.* (1990) culturing juvenile sporophytes of *L. trabeculata* found no significant differences ( $p < 0.05$ ) in sporophyte blade linear growth at different depths. Eddings *et al.* (*op. cit.*) observed that the largest frond elongation growth rate was  $7.5 \pm 1.6$  mm d<sup>-1</sup> at 3 m depth during March.

## 5. Biochemistry

The few available data on chemical composition suggests that chemically *Lessonia* does not differ in great measure from other Laminariales. About 90% by weight consists of water and the remaining 10% is composed of organic matter and mineral salts. The principal organic compounds of *Lessonia* are alginic acid, a water-insoluble polysaccharide made up of uronic acids; fucan, a water-soluble sulfated polysaccharide formed of L-fucose; and mannitol, an hexahydric alcohol, the primary photosynthetic product that differs from the two former compounds in its soluble nature and for being linked to proteins and free aminoacids.

### 5.1. Alginic acid

This compound constitutes part of the cell wall and intercellular matrix. It is an heteropolymer formed of alpha-L-guluronic and beta-D-mannuronic acids joined by 1,4 glucoside linkages. The molecular function is based on its ability to form very strong gels with divalent cations (Larsen 1978).

The extraction of alginic acid is done by alkaline treatment, producing salts as

Table 3. Seasonal variation in *L. flaviicans* fronds chemical composition (% dry weight), March 1972–November 1973. Each value was obtained from the analysis of plants collected monthly during each season (southern hemisphere) in Baliza Sorrel, Argentina.

Compounds	Summer	Fall	Winter	Spring
Ash	28.9	26.1	30.3	35.4
Potassium	8.3	6.4	8.5	11.7
Sodium	3.3	3.8	3.3	3.5
Total nitrogen	1.0	1.5	1.4	1.7
Alginic acid	28.7	25.5	26.6	27.2
Mannitol	9.1	8.3	1.0	2.0
Iodine	0.5	0.27	0.18	0.36

Modified from Duville and Duville (1974).

sodium alginate, potassium alginate or other alginates. The chemical and physical properties of this phycocolloid are estimated by measuring its viscosity in a standard solution; this procedure is regularly used by the alginate industry to evaluate the quality of raw materials.

Krivoruchko and Duville (1973) determined the viscosity of different concentrations of alginates from *L. flaviicans* (cited as *L. fuscicentis*) and other species. A 1% solution of *L. flaviicans* sodium alginate had a lower relative viscosity ( $5 \times 10^{-3}$  Pa + s) than that of *Macrocystis pyrifera* ( $7.5 \times 10^{-3}$  Pa + s) and higher than *Desmarestia carpaestipe* ( $2.5 \times 10^{-3}$  Pa + s). Percival *et al.* (1983) also determined the viscosity of sodium alginate from *L. nigrescens* in 1% solution. They obtained much higher viscosities in alginates from both fronds ( $39 \times 10^{-3}$  Pa + s) and stipes ( $267 \times 10^{-3}$  Pa + s). The differences between *Lessonia* species may be a specific character, although the utilization of unstandardized methods can produce great differences between measurements made at different laboratories. It is known that alginic acid easily undergoes hydrolysis in neutral or alkaline solutions, causing chain shortening (Krivoruchko and Duville 1973). On the other hand, frond and stipe yields within species may demonstrate significant seasonal differences. Duville and Duville (1974) obtained maximum yields from *L. flaviicans* during summer and spring (28.7 & 27.2%) (Table 3) and determined that stipes had the higher amounts of alginic acid (29.4%) (Table 4) as was also shown by Percival *et al.* (1983) for *L. nigrescens*. Santelices (1982a) working with *L. nigrescens* found that gel content in holdfasts varied seasonally with two peaks, one in spring and a second in fall. A similar tendency was found in the fronds with maximum content in fall and late spring. In fronds as well as in holdfast there was a reduction in alginic acid production during November, December and January. Alginate percentages can also vary depending upon the extraction procedure. Percival *et al.* (*op. cit.*) obtained 23.5% from stipes and 16.5% from fronds applying a sequential alkaline treatment, but using direct alkaline extraction, they obtained 41% and 34% in stipes and fronds respectively; in all cases the stipes yield the maximum alginic acid concentrations. Matsushiro and Zambrano (1989) obtained Alginic Acid, with a sequential method, from blades, stipes and holdfast of *Lessonia trabeculata* with a yield of 23, 34 and 35% respectively. The lower percentages produced by the sequential procedure are owed to the fact that the previous acid extraction preferentially removes mannuronic acid units from the alginates.



Table 4. Variation of the chemical composition in *L. joffeana* based on % dry wt (\*) and % ash wt (†).

Compounds	Holdfast	Stipe	Frond
Alginate acid (*)	22.9	29.4	25.3
Aluminium (#)	1.1	0.1	0.5
Antimony (#)	0.05	0.05	—
Ash (*)	24.0	20.0	27.2
Barium (#)	0.4	0.4	0.4
Boron (#)	0.01	0.01	0.03
Calcium (#)	8.0	7.3	3.1
Chromium (#)	0.05	0.05	0.05
Copper (#)	0.05	0.05	0.01
Iron (#)	0.3	1.0	0.5
Lead (#)	0.05	0.05	—
Magnesium (#)	1.0	1.0	1.0
Manganese (#)	0.01	0.01	0.01
Mannitol (*)	4.8	6.2	2.7
Nickel (#)	0.0005	—	—
Phosphorus (#)	—	—	1.0
Potassium (#)	23.9	21.9	20.9
Silica (#)	1.0	0.6	0.1
Silver (#)	0.0003	0.0003	0.0005
Sodium (#)	6.1	10.6	9.1
Strontium (#)	0.1	1.0	0.5
Tin (#)	0.003	0.003	—
Titanium (#)	0.005	0.005	0.001
Vanadium (#)	0.005	—	—
Zirconium (#)	—	0.01	—

(—) No available data.

Modified from Duville and Duville (1974).

Alginates are constructed of three types of polymer blocks, homopolymeric blocks composed of either polymannuronic acid or polyguluronic acid and heteropolymeric blocks consisting of both monomers, all in alternated sequence (Haug *et al.* 1966). The alginate monomer proportion, mannuronic acid: guluronic acid (M:G), affects its physical properties. With more G block content there is an increase in gel strength (Larsen 1981). Haug *et al.* (1969), found that cell wall alginates are rich in polyguluronic acid, while intercellular matrix alginates are richer in polymannuronic acids. The only data for *Lessonia* are those of Percival *et al.* (1983), on *L. nigrescens* stipes in which was found a relative proportion of 1.8 (M/G) and Matsuhira and Zambrano (*op. cit.*) in which was found a proportion of 1.98 for the lamina, 1.03 for the stipe and 1.83 for the holdfast; the higher amount of mannuronic acid in the holdfast may be due to the presence of an abundant intercellular matrix. But, the exact role of the alginic acid in the algae is still dubious and Matsuhira and Zambrano (*op. cit.*) suggested new structural studies on the homopolymeric and heteropolymeric blocks constitution and at the same time to study other polysaccharides in the cell wall as fucan and cellulose.

## 5.2. Fucan

Villarroel and Zanjungo (1975) and Zanjungo (1979) communicated that fucan is the most abundant water soluble polysaccharide in *L. trabeculata* (cited as *L. flavicans*). This fucan has approximately 35.5% L-fucose, a carbohydrate composed of alpha glucosidic linkages and sulphated radicals primarily with axial localization at C2. The relationship of sulfate to fucose was 1:1; this indicated that all of the fucose might be monosulfated. Galactose and xylose which are present in *L. nigrescens* fucoidans (Percival *et al.* 1983, 1984), were not found in *L. trabeculata*. The authors determined that *L. trabeculata* fucan is formed of about four 4-0-sulphate-1-fucopyranose units linked between them with 1-2 or 1-3 alpha glucosidic linkages and with another L-fucopyranose unit, sulfated at C3 or C2.

Percival *et al.* (1983) extracted fucose from the stipes together with haptera and also from the fronds of *L. nigrescens*. In both hydrolyses, galactose and xylose were found in addition to fucose, mannose, and glucuronic acid. Polymeric materials were essentially similar, with differences due to a greater quantity of uronic acid in stipe fucoidan, specially notable when hot acid treatment was used in the extraction procedure (29% in stipes and 17% in fronds) (Table 5). In later work, Percival *et al.* (1984) determining fucan composition, finding 60% carbohydrate, 9% sulfate, 26% uronic acid, 11.4% protein, 10% moisture and 12% ash. Analyzing material of *L. nigrescens* obtained by partial fucoidan hydrolysis, Percival *et al.* (1984) found a glucoromannan structure with alternate units of both monosaccharides, and more than six adjacent galactan residues. Some of the glucuronic acid residues were linked with fucose and nearly all fucose and xylose residues were on the periphery of the macro molecule. The polymeric soluble material and the insoluble product of algae partial hydrolysis contained proteins as well as carbohydrates, suggesting that proteins and carbohydrates were in close association and are separated with difficulty.

## 5.3. Mannitol

Mannitol has been found in *L. flavicans* by Duville and Duville (1974) cited as *L. fuscenscens*, and in *L. nigrescens* by Percival *et al.* (1983). Besides specific variation mannitol percentages may change depending on the part of the plant used for extraction and on seasonality. *L. nigrescens* had 140 mg mannitol in the stipes and 81 mg in fronds from 30 g samples of each (Percival *et al.*, *op. cit.*) and *L. flavicans* had 4.8% in the holdfast, 6.2% in the stipes and 2.7% in fronds (Table 4) reaching maximum frond yields in summer and autumn (Duville and Duville *op. cit.*) (Table 3).

## 5.4. Proteins, amino acids and other constituents

Duville and Duville (1974) determined 1.0 to 1.7% nitrogen content in *L. flavicans* extracts as coming from proteins and free amino-acids. Previously Quilhot (1970) determined a 7.87% protein (dry weight) content in *L. nigrescens*, also Percival *et al.* (1984) obtained proteins from frond and stipe fucan of the latter species (Table 5).

The great proportion of *Lessonia* amino acids are protein constituents with few remaining in a free state. Quilhot (1970) found more amino acids as protein constituents than as free amino acids (Table 6). The amino acids determined in both groups



Table 5. Yields and constituents of the fucan from the aqueous and acidic sequential extracts of *L. nigrescens* 30 g (dry wt) samples.

	Slips, hot water	Fonds, hot water	Slips, hot acid	Fonds, hot acid
Fucan dry wt (mg)	224	212	156	178
Carbohydrate (%) <sup>1</sup>	62	63	53	46
Uronic acid (%) <sup>1</sup>	20(32)	16(25)	29(55)	17(37)
Sulphate content (%) <sup>1</sup>	11(18)	13(20)	6(11)	7(15)
Protein content (%) <sup>1</sup>	10.3	11.5	5.8	6.3
Sugars present:				
Fucose <sup>2</sup>	5.2	3.2	4.55	6.7
Xylose <sup>2</sup>	1.0	1.0	1.0	1.0
Mannose <sup>2</sup>	1.4	1.6	0.7	0.5
Galactose <sup>2</sup>	0.9	1.6	1.0	trace

<sup>1</sup> Percentage calculated from fucan sample dry weight. Figures in parentheses calculated on carbohydrate content; <sup>2</sup> Approximate molar proportion of the constituent monosaccharide sugars. Modified from Percival et al. 1983.

Table 6. Free amino acids and protein amino acids present in 10 mg samples of *L. nigrescens* ( $\mu$  moles / 100 mg dry wt<sup>-1</sup>).

Amino acids	Free amino acid concentration	Amino acids in proteins
aspartic acid	2.42	4.6
cysteic acid	0.09	0.11
glutamic acid	1.53	6.65
alanine	2.82	6.53
beta-alanine	0.04	—
arginine	trace	0.62
cysteine	—	trace
phenylalanine	0.02	2.74
glycine	0.17	6.72
histidine	0.03	0.92
homoserine	—	0.1
isoleucine	0.03	3.22
leucine	0.03	4.82
lysine	0.1	5.52
methionine SO <sub>2</sub>	.09	1.06
proline	0.12	3.29
serine	0.4	3.47
tyrosine	0.04	1.43
threonine	0.3	4.17
tryptophane	trace	trace
valine 0.07	5.35	—
amides	0.84	—
amino acids unidentified	—	0.01
Total of free amino acids ( $\mu$ moles)	9.14	61.33

(—) No available data. Modified from Quilhot, 1970.

are basically the same as those found in animal and plant proteins, excepting citrulline and choline which were absent in *L. nigrescens* and homoserine that is only found as a protein constituent (Table 6). Homoserine was discovered for the first time in seaweed extracts.

Potassium is the most abundant mineral element in *Lessonia* and in seaweeds in general. Potassium ranges from 6.4 to 11.7% dry weight in *L. flavicans* (Duville and Duville 1974). Variations within this range are affected by seasonality (Table 3) and also depend on the locus within the plants (Table 4).

Sodium and calcium are the second most abundant mineral elements in *L. flavicans* (Table 4), and they experienced the same kind of variations as potassium. Other elements like aluminium, antimony, phosphorus and magnesium were found in smaller quantities and also some heavy metals, such as nickel, chromium, lead and arsenic have been described for *L. flavicans* (Duville and Duville 1972), *L. nigrescens* and *L. trabeculata* (Santa Maria, I., Gonzalez, M. and Flores, H., unpublished (Table 7)).

## 6. Ecology

### 6.1. Distribution

*Lessonia* is confined to the southern hemisphere, between Ancón (11°30' S) in Peru and the circumpolar islands (Fig. 13). The northern limit of *Lessonia* corresponds to the species *L. nigrescens* which is found intertidally along the Peruvian coast (How 1914; Schweigiger 1964). Santelices (1982b) suggested that the temperate Pacific coast of South America is a zone of uneven contribution of tropical and subantarctic floras. This area of the Pacific coast is under the influence of the Humboldt current and a subtropical convergence where tropical waters overflow the colder subantarctic current in addition to the coastal upwelling. These upwelling areas were defined by Santelices and Abbott (1978) as being responsible for the presence of *L. nigrescens* north of the subtropical convergence. Catastrophic events such as 'El Niño' (Dayton and Tegner 1984), which is defined as the presence of anomalous warm water coastal waters (Barber and Chavez 1983; Barber et al. 1985; Barber and Chavez 1988) can produce temporal variations in this limit. The El Niño of 1982–83 caused the northern limit of *L. nigrescens* to be restricted to Taltal (25°40' S). This natural catastrophe mainly affected the intertidal populations of *L. nigrescens* along 2,400 km coast, exterminating most of the standing stock. Personal observations made at 8 intertidal stations between Iquique (20°13' S) and the Loa River (21°26' S), indicated the presence of only one individual of *L. nigrescens*. This phenomena suggested that the distribution of *L. nigrescens* may depend on disturbances such as El Niño or other poor understood factors (Paine 1986).

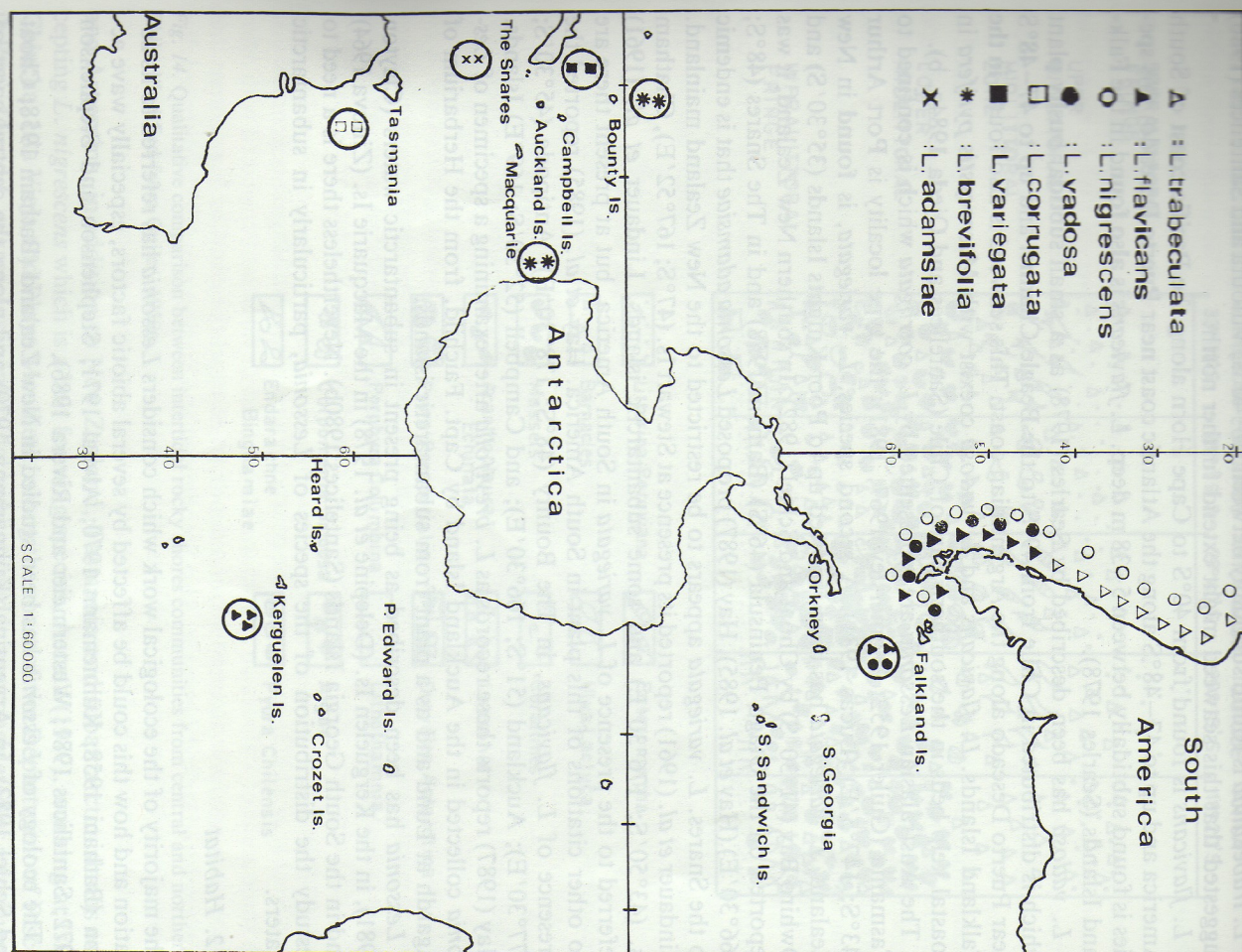
*L. nigrescens* was also found in the Atlantic coast up to 47°45' S by Kühnema (1970). The southern limit of *L. nigrescens* in South America was given by Westmaier and Rivera (1986), corresponding to the Diego Ramirez Islands. Asensi (1990) suggested that *L. nigrescens* is found in the Falkland Islands and South Georgia. Later, Searles (1978) excluded records of this plant from the Falklands, South Georgia, Heard, and Kerguelen Islands.



Table 7. Heavy metals present in *L. nigrescens* and *L. trabeculata* in mg kg<sup>-1</sup>.

Species	Locality	Date	Cu	Cr	Zn	Ni	Pb	Cd	As	Humidity (%)
<i>L. nigrescens</i>	Caleta Mansa (31°40'S)	04/86	1.36	0.26	2.77	1.09	0.85	1.11	17.7	69.1
<i>L. trabeculata</i>	Caleta Mansa	04/86	1.10	0.09	2.27	0.56	0.99	0.86	4.3	70.4
<i>L. nigrescens</i>	Valparaíso (33°02'S)	07/86	1.8	0.2	26.2	0.23	0.16	0.1	3.24	78.9
<i>L. nigrescens</i>	Caleta Mansa	09/86	0.37	0.24	0.69	2.55	1.56	0.83	—	77.9
<i>L. trabeculata</i>	Caleta Mansa	09/86	0.55	0.28	0.64	2.31	0.89	0.79	—	82.2

(—) Data not available. Samples taken on 04/86 are the average of 3 replicates. Samples taken on 07-09/86 are the average of 2 replicates. After Santa María, I., Gonzalez, M. and Flores, H. (unpublished).

Fig. 13. World distribution of *Lessonia* species.



*L. trabeculata* is found subtidally between 20–40°S; Villouta and Santelices (1986) suggested that this seaweed might extend further north.

*L. flavicans* is found from 40°S to Cape Horn along the Pacific coast of South America and up to 47–48°S along the Atlantic coast near Puerto Deseado; this species is found subtidally between 5–38 m deep. *L. flavicans* is also found in the Falkland Islands (Searles 1978).

*L. vadosa* has been described by Searles (1978) as a small subtidal bushy plant which is distributed in Chile from 49°S to the Beagle Channel and up to 47–48°S near Puerto Deseado along the Argentinian coast. This seaweed is also found in the Falkland Islands. *L. flavicans* and *L. vadosa* coexist with *Macrocystis pyrifera* in coastal kelp beds in the southern part of Chile (Santelices and Ojeda 1984a, b).

The Australasian *Lessonia* are represented by *L. corrugata* which is confined to Tasmania (Guiler 1952; Womersley 1967, 1981); the type locality is Port Arthur (43°S; 147°5'E) (Lucas 1931). A second species, *L. variegata*, is found in New Zealand. *L. variegata* has been reported up to Poor Knights Islands (35°30'S) and Owhiro Bay (41°30'S) by Choat and Schiel (1982). In southern New Zealand, it was reported on the Otago Peninsula (46°S) (Batham 1958) and in The Snares (48°S; 166°30'E) (Hay et al. 1985). Hay (1987) proposed *Lessonia adamsiae* that is endemic to the Snares. *L. variegata* appears to be restricted to the New Zealand mainland. Lindauer et al. (1961) reported its presence at Stewart Is. (47°S; 167°52'E), Chatham Is. (43°50'S; 176°30'E) and some subantarctic islands. Lindauer et al. (1961) referred to the presence of *L. variegata* in South America, but at present there are no other citations of this plant in South America. Hay et al. (1985) reported the presence of *L. flavicans*, in The Bounty (48°S; 178°30'E); Antipode (45°30'S; 177°30'E); Auckland (51°S; 166°30'E); and Campbell (52°30'S; 169°E) Islands. Hay (1987) reports these records as *L. brevifolia* after examining a specimen of *Lessonia* collected in the Auckland Island by Capt. Faichild, from the Herbarium of Agardh at Lund and as a plant from subantarctic islands.

*Lessonia* has been described as being present in subantarctic waters (Clayton 1981), in the Kerguelen Is. (Delepine et al. 1978) in the Macquarie Is. (Zimova 1964) and in the South Georgia Islands (Santelices 1980b). Nevertheless there is a need to restudy the distribution of the species of *Lessonia*, particularly in subantarctic waters.

## 6.2. Habitat

The majority of the ecological work which considers *Lessonia* has referred to its zonation and how this could be affected by several abiotic factors, especially wave action (Batham 1958; Kühnemann 1970; Alveal 1971; Stephenson and Stephenson 1972; Santelices 1981; Westemeier and Rivera 1986).

The ecology of *Lessonia* has been studied in New Zealand (Batham 1958; Choat and Schiel 1982), in Argentina (Kühnemann 1970) and along the central coast of Chile (Guiler 1959a, b; Cancino and Santelices 1984; Vasquez and Santelices 1984).

*Lessonia* spp. are found in a wide variety of habitats and their ecological importance has been established in several studies. Its conspicuous presence in the most exposed sites was described as equivalent to areas colonized by *Posidonia* in California (Santelices and Abbott 1978). *Lessonia* is commonly a kelp forest forming species in the subtidal zone of rocky shores along the coast of central and southern Peru, Chile

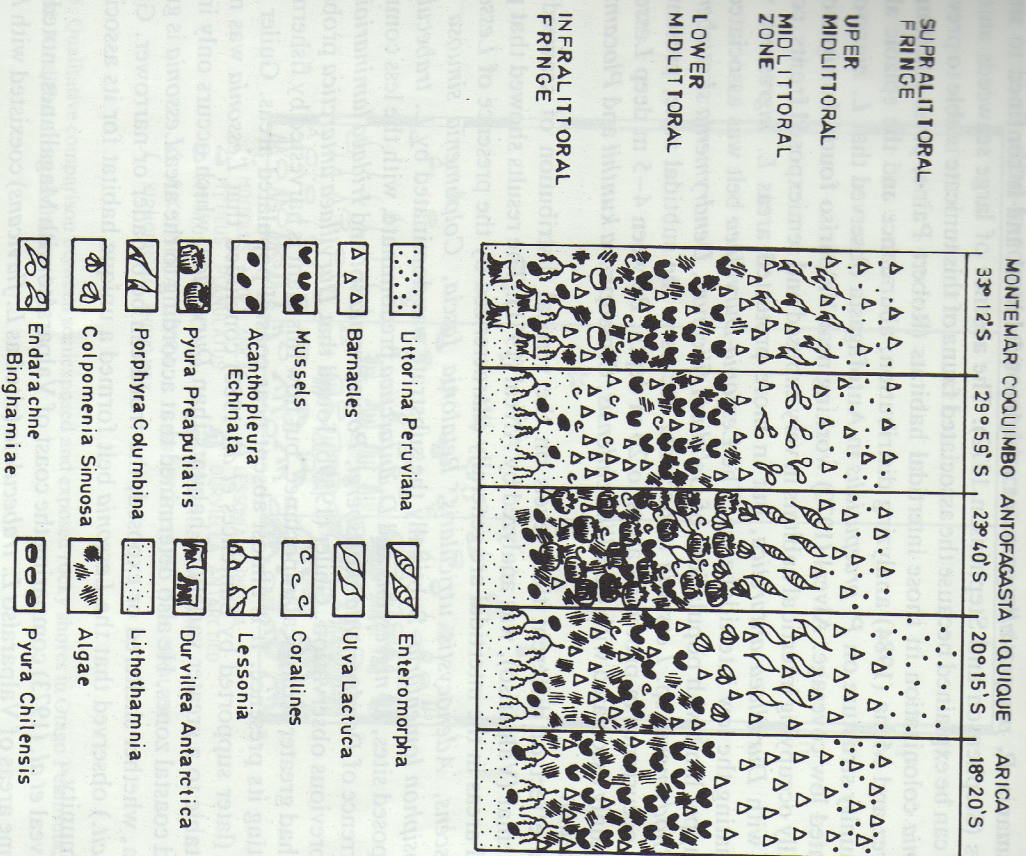


Fig. 14. Qualitative comparison between intertidal rocky shore communities from central and northern Chile. Modified from Guiler, 1959a.

and Argentina, in addition to New Zealand, Tasmania and subantarctic islands excepting *L. nigrescens* which is a belt forming species. Acosta (1977), working at Isla Chinchua, Isla Vieja and Playa Mendieta, along the coast of the Department of Pisco in Peru, found *L. nigrescens* in intertidal habitats and it was considered as a frequent species. Guiler (1959a) described the main invertebrates and seaweeds associated to the zonation found in Valparaíso, Coquimbo, Antofagasta, Iquique and Arica (Fig. 14). Guiler (op. cit.) found that *Lessonia* was replaced by *Pyrua praeputialis* only in Antofagasta. A similar situation has been observed along the southern coast of Africa, where *Pyrua stolonifera* grows tightly packed, outcompeting the larger seaweeds



in Tasmania *P. praeputialis* grows at a higher tidal level and is confined to small clumps (Stephenson and Stephenson 1972). The absence of large seaweeds among *Pyura* can be explained because the associated fauna of this tuminate is able to prevent *Lessonia* colonization in those intertidal habitats (Robert Paine, pers. commun.). Ramirez and Mena (1984) analyzing distribution, abundance and the epizoeic algal community structure on *P. praeputialis* in Antofagasta observed that *L. nigrescens* presented low coverage. Alveal (1970) working near Valparaiso found *L. nigrescens* typically occupying intertidal habitats in very exposed and semiprotected fronts, coexisting with *Durvillaea antarctica*, but in more protected areas *L. nigrescens* was dominating the low intertidal zone. The *Lessonia*-*Durvillaea* belt was associated in their upper limit with populations of *Gelidium filicinum*, *Dendrymenia skottsbergii*, and *Rhodomyenia* sp. *Lessonia trabeculata* occurs in the subtidal zone, presenting broad occurrence in protected areas to 20 m depth. Between 4–5 m deep *Lessonia* was mainly associated with *Corallina chilensis*, *Glossophora kunitzii* and *Plocanium violaceum*.

The effect of different tidal levels on the vertical distribution of seaweeds in Montemar (Valparaiso), was analyzed by Alveal (1971). The results showed that protected areas in the intertidal are generally characterized by the presence of *Lessonia nigrescens*, *Adenocystis utricularis*, *Petalonia fasciata*, *Copomenia sinuosa* and *Scytosiphon lomentaria*. Subtidally the substrate was dominated by *L. trabeculata*. In exposed sites, *L. nigrescens* and *D. antarctica* predominate, with the less common occurrence of *Dendrymenia skottsbergii*, *Polysiphonia* sp. and *Iridaea laminarioides*. In a previous observation, Guiler (1959b) found that *Durvillaea antarctica* probably once had greater ecological importance, but now this plant is harvested by fisherman, affecting its presence. It is almost absent near coastal populated areas. Guiler (*op. cit.*), (later supported by Santelices *et al.* 1980) concluded that *Lessonia* was more adaptable to a greater variety of habitats than *Durvillaea*, which occurs only in exposed coastal zones. He also determined that according to the area *Lessonia* is growing in, whether sheltered or exposed, the frond can be broader or narrower. Guiler (*op. cit.*) observed that the *Lessonia* belt formed a unique habitat for its associated community.

Alveal *et al.* (1973) comparing the coast of Valparaiso with Magallanes, noted that in some areas of Valparaiso *L. trabeculata* (cited as *L. flavicans*) coexisted with *Macrocystis integrifolia* down to 10 m in depth, in contrast the coast of Magallanes that was explored lacked *Lessonia*. Also Stephenson and Stephenson (1972) observed that along the southern coast of Chiloe Island in the infralittoral fringe of wave-swept shores, the main kelp *D. antarctica* was more abundant than *Lessonia*, which grows just below it. Westermaier and Rivera (1986) characterized the intertidal rocky shores of Valdivia (39°S), Osorno (40°S), Llanquihue (41°S), Chiloe (42°S) and the Diego Ramirez Islands (53°S). They found that along the exposed shores of Valdivia *L. nigrescens* and *D. antarctica* occur at the same tidal level, coexisting with *Codium dimorphum* and *Mesophyllum* spp. In protected zones both plants are absent. A similar situation was observed in Osorno. In Chiloe *L. nigrescens* is associated with *Polysiphonia*, *Ulva rigida*, *Rhizoclonium* and *Mesophyllum* in exposed sites. In the Diego Ramirez Islands *L. vadosa* and *Desmarestia* sp. form the lower limit of the intertidal zone. Westermaier and Rivera (1986) concluded that along exposed rocky shores the zonation is variable and that morphology rather than species is the

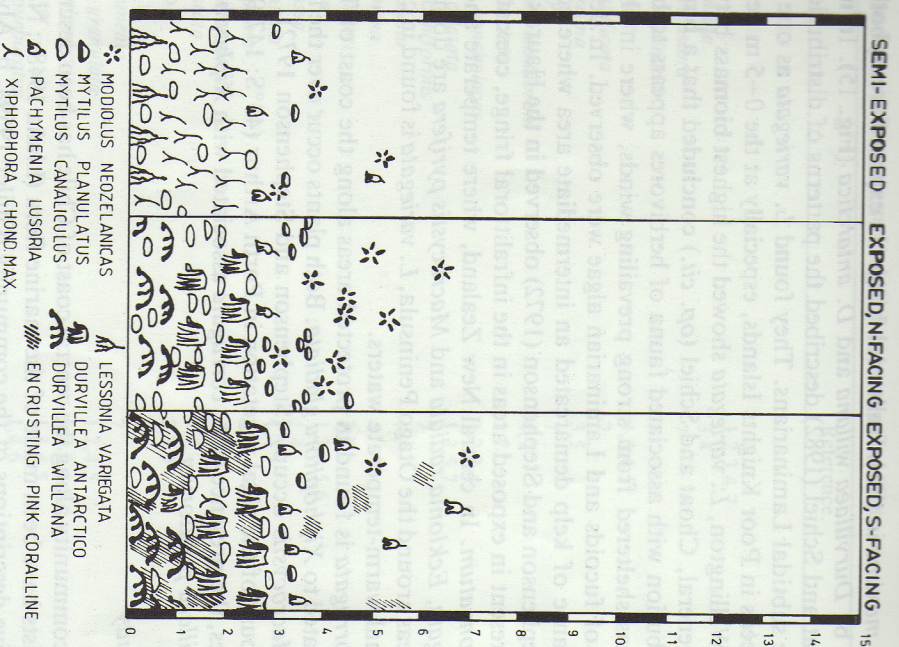


Fig. 15. Qualitative comparison between semiprotected and exposed rocky shores in Otago Peninsula, New Zealand. Modified from Batham, 1958.

dominant factor affecting changes in composition of temporally variable intertidal belts.

Kühnemann (1970) in Puerto Deseado and Barrales and Lobban (1975) in Chubut, both localities from the Atlantic coast of Argentina, described seaweed communities which included *Lessonia*.

The description given by Kühnemann (*op. cit.*) emphasizes morphological aspects of the coast in Rio Deseado, although he found *L. nigrescens* and probably *L. flavicans* and *L. vadosa* along most intertidal and subtidal habitats, associated with *Durvillaea antarctica*, *Macrocystis pyrifera*, *Desmarestia tabacoides*, *Desmarestia herbacea*, *Gigartina skottsbergii* and *Iridaea undulosa*.

Oliver (1923), found that *L. variegata* was associated with *Xiphophora* and *Durvillaea* in exposed situations along the coast of New Zealand. Batham (1958) observed the ecology of the rocky shores in Papanui, Otago Peninsula, in southern New Zealand. In semiprotected areas, *L. variegata* was associated with *Xiphophora chon-*



*drophylla* var. *maxima* in the infralittoral fringe. In exposed areas, both macroalgae were replaced by *Durvillaea willana* and *D. antarctica* (Fig. 15). In northern New Zealand, Choat and Schiel (1982) described the patterns of distribution and abundance of large subtidal Laminarians. They found *L. variegata* as one of the major subtidal seaweeds in Poor Knights Islands, especially at the 0–5 m depth range. In Owhiro Bay, Wellington, *L. variegata* showed the highest biomass between 0–25 m in depth. In general, Choat and Schiel (*op. cit.*) concluded that a bimodal pattern of algal distribution with associated fauna of herbivores appears to be the characteristic of areas sheltered from strong prevailing winds, where in shallow waters mixed stands of fucooids and Laminarian algae were observed. In deeper water, a higher abundance of kelp demarcated an intermediate area where echinoids were dominant. Stephenson and Stephenson (1972) observed in the Hauraki Gulf that *L. variegata* is present in exposed areas in the infralittoral fringe, coexisting with *Carpophyllum elongatum*. In central New Zealand, where temperate and cold waters mix, *L. variegata*, *Ecklonia radiata* and *Macrocystis pyrifera* are dominant species. In exposed areas around the Otago Peninsula, *L. variegata* is found in cold temperate and transitional warm-temperate waters.

*Lessonia corrugata* is found in protected areas along the coast of Tasmania and may be associated to *Xiphophora gladiata*. Both plants occur over the level that *Durvillea* and *Macrocystis* occupy (Stephenson and Stephenson 1972). Cribb (1954), giving an account of the algal vegetation in Porth Arthur (43°S, 147.9°E) found on exposed shores, the presence of *L. corrugata* associated with *Xiphophora billardieri* or with *Durvillea potatorum*.

### 6.3. Community

The seaweed community along the central coast of Chile has been described by several authors. Lists have been made of the marine flora (Llaña 1948a; Navas 1965), as have qualitative descriptions of the community (Guiler 1959a, b; Alveal 1971) and quantitative approaches to the description of the community (Romo and Alveal 1977; Santelices 1980a, 1981; Santelices and Vera 1984).

The contamination due to an oil spill from a merchant ship in the central coast of Chile gave Santelices *et al.* (1977) the opportunity to quantify the intertidal community where *L. nigrescens* had a coverage of 20.37% and a biomass of 1,152 g m<sup>-2</sup> in exposed rocky habitats of Caleta Horcón (32°S).

Factors affecting community organization in the intertidal rocky habitats of central Chile were analyzed by Cancino and Santelices (1981), who observed the patterns of holdfast colonization by invertebrates and the effect of holdfast morphology in structuring such communities. They compared the community of invertebrates living in the holdfast of *L. nigrescens* with those of *Durvillea antarctica* and they found that the multichambered holdfast of *L. nigrescens* allowed the permanence of the first colonizers in the community without species replacement in late successional stages, while in unichambered holdfasts, the process of colonization was predictable according to the species replacement. Later, Cancino and Santelices (1984) concluded that the holdfast of *L. nigrescens* fulfills the following roles: a) an exclusive habitat for some invertebrates; b) available substrate for settlement and nursery grounds for many species of invertebrates (Table 8); c) shelter against the wave disturbance and

Table 8. Marine fauna living in *Lessonia* spp. holdfast and among holdfasts.

Species	Reference
<b>Mollusca</b>	
<b>Gastropoda</b>	
<i>Tegula atra</i>	1,2,3,4,7
<i>Tegula radentata</i>	3,4
<i>Tegula quadrata</i>	7
<i>Agatholoma ordinaria</i>	7
<i>Prisogaster niger</i>	1,3,4,5
<i>Tricolina umbilicata</i>	7
<i>Diloma nigerina</i>	3,5
<i>Nassarius gayi</i>	7
<i>Crassidabrum crassidabrum</i>	4,7
<i>Mitrella unifasciata</i>	1,7
<i>Concholepas concholepas</i>	1,2,3,4
<i>Calappa trochiformis</i>	1,3,5,7
<i>Kelia tumesiana</i>	7
<i>Collisella zebirina</i>	4
<i>Siphonaria lessoni</i>	3,5
<i>Scutaria scurra</i>	1,3,4,5,6
<i>Fissurella crassa</i>	1,4
<i>Fissurella limbata</i>	1,4
<i>Fissurella maxima</i>	1,4
<i>Fissurella latimarginata</i>	1,4
<i>Fissurella costata</i>	1,4
<i>Fissurella</i> sp.	2,3,5
<b>Pelecypoda</b>	
<i>Entodesma cuneata</i>	7
<i>Brachidontes granulata</i>	1,2,4,5
<i>Semimytilus digosus</i>	1,2,3,4,5,6
<i>Aulacomys ater</i>	1,3,4,5
<i>Perumytilus purpuratus</i>	1,4,6
<b>Polychaetophora</b>	
<i>Chiton cunninggii</i>	3,5
<i>Toncia atra</i>	4
<i>Toncia</i> sp.	2,3,5
<i>Chaetopleura peruviana</i>	2,3,4,5
<i>Acanthopleura echinata</i>	1,2,3,4,5
<i>Calistochiton viviparus</i>	3,5
<i>Chiton granosus</i>	2,3,4,5
<i>Enoplochiton niger</i>	1,4
<b>Arthropoda</b>	
<b>Crustacea</b>	
<i>Allopetrolisthes angulosus</i>	2,3,5,7
<i>Allopetrolisthes punctatus</i>	3,5,6
<i>Allopetrolisthes spinifrons</i>	1
<i>Petrolisthes violaceum</i>	3,5
<i>Petrolisthes tuberculatus</i>	2,3,4,5
<i>Liopeolisthes nitra</i>	3,5,7
<i>Plumnotes perlatas</i>	1,5,7
<i>Pisoides edwardsii</i>	5
<i>Sinulphus spinifrons</i>	3,4,5,7
<i>Amphoroidea</i> type	3,5
<i>Pachetodes grossimanus</i>	1,2,3,4,5,7



Table 8. Cont.

Species	Reference
<i>Talepus marginatus</i>	7
<i>Pachicheles chilensis</i>	3,5
<i>Talepus dentatus</i>	3,4,5
<i>Homalaspis plana</i>	3,5,7
<i>Paraxanthus barbigier</i>	7
<i>Pinnotheres politus</i>	7
<i>Gaudichaudia gaudichaudii</i>	3,5
<i>Acanthocyclus gayi</i>	2,4,6
<i>Acanthocyclus husslerii</i>	3
<i>Acanthocyclus</i> sp.	5
<i>Austromegabalanus psittacus</i>	2,4,5,7
<i>Norobalanus psittacus</i>	5
<i>Balanus flosculus</i>	2,4,5
<i>Balanus laevis</i>	4,7
<i>Chthamalus citrinus</i>	1,2
<i>Chthamalus scabrosus</i>	1,3,4,5
<i>Pagurus compilis</i>	7
<i>Pagurus villosus</i>	7
<i>Rhynchonetes typus</i>	3,5
<i>Rhynchonetes</i> sp.	7
<i>Amphipoda</i>	
<i>Amphipoda</i>	5
<i>Echinodermata</i>	
<i>Asteroida</i>	
<i>Patiria chilensis</i>	5
<i>Stichaster striatus</i>	1,2,3,4,5,6
<i>Helaster helianthus</i>	1,4,5
<i>Meyensister gelatinosus</i>	7
<i>Athyonidium chilensis</i>	4
<i>Ophiacis chilensis</i>	1,4
<i>Echinoidea</i>	
<i>Tetrapygus niger</i>	1,3,4,5,7
<i>Loxechinus albus</i>	1,3,4,5
<i>Holothuroidea</i>	
<i>Parallus mollis</i>	1
<i>Chordata</i>	
<i>Ascidacea</i>	
<i>Pyura chilensis</i>	3,5,7
<i>Coelenterata</i>	
<i>Anthozoa</i>	
<i>Phymacis clematis</i>	2,3,4,5
<i>Anthothoe chilensis</i>	3,5
<i>Actinia</i> sp.	1
<i>Annelida</i>	
<i>Polychaeta</i>	
<i>Pinagmatopoma moerchi</i>	6
<i>Nereis</i> sp.	1,7
<i>Halosydna parva</i>	7
<i>Boccardia chilensis</i>	7
<i>Polychirus</i> sp.	7
<i>Marphysa</i> sp.	7
<i>Lumbrineris</i> sp.	7
<i>Dodeacaria</i> sp.	7

Sources: (1) Edding and Cardemil 1979b; (2) Cancino and Santelices 1984; (3) Santelices 1982a; (4) González 1977; (5) Vasquez and Santelices 1984; (6) Santelices *et al.* 1980; (7) Villouta and Santelices 1984.

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Table 9. Main Epiphytes and Parasites (\*) usually found on *Lessonia* spp.

Species	Locality
<b>Seaweeds</b>	
<i>Acrochaetium polysporum</i>	Peru (10)
<i>Acrochaetium catenulatum</i>	Chile (11)
<i>Pilayella novaezealandica</i>	Argentina (7); N. Zealand (6)
<i>Ulva lactuca</i>	Chile (11)
<i>Euteromorphia compressa</i>	Chile (11)
<i>Byopsis rosae</i>	Chile (12)
<i>Boshtella orbigniana</i>	Argentina (1)
<i>Melobesia</i> sp.	Argentina (1)
<i>Grateloupia</i> sp.	Argentina (1)
<i>Ectocarpus confervoides</i>	Argentina (1)
<i>Ectocarpus constanciae</i>	Argentina (1); Chile (3), (11)
<i>Feldmannia chitoncola</i>	Argentina (1)
<i>Heceloneima stewartensis</i>	Chile (11)
<i>Entocladia</i> sp.	N. Zealand (6)
<i>Myrionema patagonicum</i>	Chile (5)
<i>Anthyrtamion elegans</i>	Argentina (1)
<i>Pterothamnion</i> sp.	Chile (11)
<i>Pterosiphonia dendroidea</i>	Chile (3)
<i>Goniotrichum elegans</i>	Chile (11)
<i>Erythrotrichia foliiformis</i>	N. Zealand (4)
<i>Erythrocladia</i> sp.	Chile (5)
<i>Pobysiphonia</i> sp.	Chile (11)
<b>Invertebrates</b>	
<i>Alcyonidium polyorum</i>	Argentina (1)
<i>Terebratella dorsata</i>	Argentina (1)
<i>Membranipora tuberculata</i>	Chile (12)
<i>Celeporella (celeporella)</i>	
<i>retiformis</i>	Chile (12)
<i>Hippothoa bougainvillei</i>	Chile (9)
<i>Gaimardia trapezina</i>	Argentina (1)
<i>Scurria scurra</i>	Chile (5) (8)
<i>Amphoroidea typa</i>	Chile (5)
<i>Talepus dentatus</i>	Chile (12)
<i>Talepus marginatus</i>	Chile (8)
<b>Veretebrates</b>	
<i>Schroederichthys chilensis</i> (eggs)	Chile (12)
<i>Sympteria brevicaudata</i> (eggs)	Chile (12)
<b>Fungi</b>	
<i>Thalassoscypha lessoniellae</i> (*)	Chile (2)

Sources: (1) Kuhnemann 1970; (2) Kohlmeier 1981; (3) Alveal *et al.* 1973; (4) South and Adams 1990; (5) Santelices *et al.* 1983; (6) Lindauer *et al.* 1961; (7) Boraso 1973; (8) Gonzalez 1990; (9) Viviani 1977; (10) Dawson *et al.* 1964; (11) Collantes and Echeverry 1980; (12) this work.

major predators. Vasquez and Santelices (1984) found 49 taxa of invertebrates living in the *L. nigrescens* holdfast. Most of these were juveniles. Also, oviferous females were continuously observed, confirming the role of the holdfast as shelter for mature females.



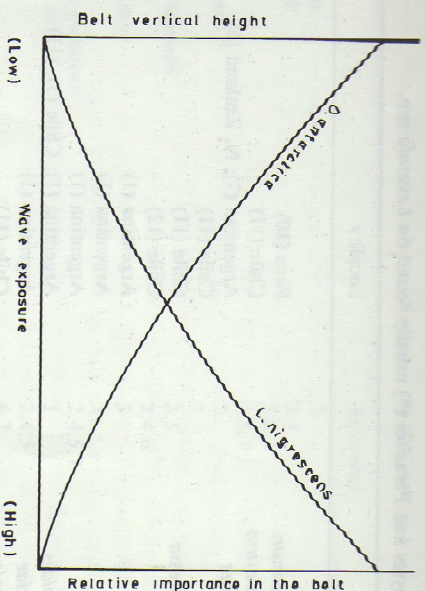


Fig. 16. Model of interaction between *Lessonia nigrescens* and *Durvillaea antarctica* in central Chile. After Santelices, 1981.

The fronds of *Lessonia* provided shelter for invertebrates that depend heavily on this algae, and substrate for several seaweeds and fish eggs (Table 9).

Santelices *et al.* (1980) found that *L. nigrescens* appears to be a plant better adapted to placed with strong surge, where this alga is the dominant competitor (Ojeda and Santelices 1984). Complete space monopolization by *L. nigrescens* is prevented by adaptations of *Durvillaea antarctica*, especially by its quick settlement in areas with free available space. The adaptation of these species cause them to interact along the intertidal zone (Fig. 16).

There are few studies on the structure of subtidal communities where *Lessonia* is present. Villouta and Santelices (1984) described subtidal kelps of *L. trabeculata*. The highest biomass and holdfast diameter was found at a depth of 5 m, where its density was almost 2 plants  $m^{-2}$ . Several organisms associated with the holdfast are presented in Table 8. Pizarro (1981) studied the effect of grazing on a population of *L. trabeculata* in Concepción. In this research it was suggested that the upper limit of this population was determined by the herbivore density. At the other extreme, the lower limit was established by the decrease of light.

The kelps that live along the Chilean coast present interesting differences when they are compared to kelp communities in other latitudes (Schiel and Foster 1986). *Lessonia* is the dominant species on the northern and central Chilean coast. Along the southern coast of Chile, *L. vadosa* and *L. flavicans* coexist with *Macrocystis* (Santelices and Ojeda 1984a, b). *L. flavicans* and *L. vadosa* are part of the second strata of the *Macrocystis pyrifera* forest in Isla Navarino (53°S, 72°W); this is similar to the situation found by Barrales and Lobban (1975) studying the kelp *M. pyrifera* in Chubut, Argentina. When the canopy of *M. pyrifera* was removed, *L. flavicans* decreased its biomass suggesting that this condition was unfavorable for *L. flavicans*. Villouta and Santelices (1984) concluded that *Lessonia* should be recognized as a dominant genus in the temperate waters of the southern hemisphere. The food webs in South American kelp forest are simpler than in other known kelp communities. Dayton *et al.* (1973) found that *Lessonia* kelp beds do not have an ecological analog in northeastern Pacific genera.

There are few data concerning invertebrates that prey on *Lessonia*. Miran (1973), observing the feeding behaviour of *Aplodactylus punctatus* in San Anton (33°35'S), found that almost 100% of the stomachs were full of *Lessonia* the year around. Their diet was based almost entirely on *Lessonia* which is dominant on rock bottoms. Pizarro (1981), working with *L. trabeculata* near Concepción, described the activities of several herbivores: the gastropods *Tegula tridentata* and *Tegula cadirocostata*, the crustaceans *Talitrus marginatus* and *T. dentatus* and the fish *Aplodactylus punctatus*. In laboratory food preference experiments was found that *T. tridentata*, and both *Talitrus* had *L. trabeculata* as a second food preference after *Desmarestia* and among *Tridacta*, *Ulva*, *Grateloupia*, *Trematocarpus*, *Gymnogo grus* and *Dendrymenia*. When the diet of *A. punctatus* was analyzed *L. trabeculata* presented a low relative importance. Santelices *et al.* (1983) observed that *nigrescens* is the regular food of the sea urchin *Tetrapygus niger*, but, the zooids *Lessonia* are able to survive after passing through the sea urchin digestive tract. A similar situation has been studied by Santelices and Correa (1985) working with several herbivores where over 25% of the species tested survived the digestion of the herbivores. Vasquez *et al.* (1984), observing distributional patterns and diet of for species of sea urchins in the kelp forests of Puerto Toro (55°S, 67°W), found that *L. flavicans* and *L. vadosa* were preyed on only by *Loxechinus albus*. Nuñez and Vasquez (1987) observed that the main item in *Aplodactylus punctatus* diet was *trabeculata*. Fuentes and Gomez (1987), determining the feeding activities *Aplodactylus punctatus* in the coastal waters of Coquimbo, found that *Lessonia* was 10% of the weight of 47 analyzed stomachs. Benavides *et al.* (1987) observed that *L. nigrescens* was not affected in its chemical composition or in its caloric content when digested by *A. punctatus*. Fuentes (1987) also found that *Medialuna anciata* a generalist fish, feeds on *Lessonia*. In none of these studies are there observations that prove a modification of the biota by grazing fish or invertebrates.

Owen *et al.* (1984), culturing abalone in Coquimbo, found that *Haliotis rufescens* is able to feed on *L. trabeculata* (cited as *L. flavicans*) and *L. nigrescens*, although young juveniles grew best when presented in with a mixed diet of macro and microgae. In feeding experiments, *H. rufescens* fed only on *L. nigrescens* attained high growth rates than when fed on *L. trabeculata*.

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