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Ecological effects of harvesting *Lessonia* (Laminariales, Phaeophyta) in central Chile

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Abstract

Lessonia nigrescens and *L. trabeculata* are economically important canopy-forming kelps in Chile. Experimental harvesting of stipes above the first dichotomy reduces stipe movement and inter-stipe friction, allowing the development of a heavy epiphytic load and increased grazing. Complete stipe removal leads to holdfast death as neither species is able to simultaneously regenerate all stipes. The invertebrate fauna inside the holdfast does not respond to upper canopy changes, but mortality does occur in partial or complete plant removals. Kelp removal also affects inter-plant distances, results in increased access of grazers to the outside and inside of kelp holdfasts, reduces recruitment of other algal species, and modifies the morphology of *L. trabeculata* such that the plants become more susceptible to removal by water movement.

Introduction

Two species of *Lessonia*, *L. nigrescens* Bory and *L. trabeculata* Villouta et Santelices, are regularly exported from Chile as raw materials for alginate production. *Lessonia* exports started in northern Chile in 1978, and by 1981 they reached a maximum annual volume of 10000 t (dry). Exports varied between 1983 and 1985 seemingly as a result of the 1983 El Niño phenomenon. *Lessonia* gathering has since extended into central and southern Chile, and export volume has gradually increased.

Lessonia nigrescens is the dominant organism (cover and biomass) in the low intertidal-shallow subtidal boundary on wave exposed rocky areas along most of temperate Pacific South America (Santelices *et al.*, 1980). *Lessonia trabeculata* forms extensive subtidal kelp beds on rocky bottoms in areas exposed and semi-exposed to heavy surge (Villouta & Santelices, 1984, 1986; Vásquez, 1989). These types of subtidal habitats are those most commonly found along northern and central Chile (20° to 40° S) and, therefore, this is the most important area for kelp harvesting.

Gathering of *Lessonia nigrescens* is done either by removing entire plants or by cutting the stipes just above the holdfast. Gathering of subtidal *L. trabeculata* generally is restricted to plants cast ashore, although subtidal harvesting by divers has been reported in a few places.

As with many other kelps, individuals of both species reach large sizes (up to 4 m long, 50 cm holdfast diameter) and form dense beds. They increase environmental heterogeneity, modify water motion and determine the light regimes in the understory (Santelices & Ojeda, 1984; Vásquez, 1989). *Lessonia* also serves as habitat for a large variety of invertebrates (Cancino & Santelices, 1981, 1984; Vásquez & Santelices, 1984; Villouta & Santelices, 1984, 1986) that use the seaweed as exclusive habitat, nursery ground, a refuge from waves or predation, or shelter for reproductive adults or for oviparous females and their embryos. Careless harvesting is likely to adversely affect not only the productivity of seaweed populations but also the diversity of associated invertebrates and algae.

In this study we review, integrate and compare the experimental evidence related to the ecological effects of harvesting on *Lessonia* and on the community associated with it.

Materials and methods

The effects of cutting stipes either above the first dichotomy or 2 cm above the holdfast and of removing the entire plant were compared. Comparisons included changes in the plants and in the associated communities. In the plants, regeneration capacity, mortality rates, morphological changes and recruitment were measured. In the community, changes in the fauna living in and the fauna and flora living around the holdfast of *Lessonia nigrescens* were also measured.

Studies of the intertidal populations of *Lessonia nigrescens* were done in Los Molles (32° 14′ S, 71° 33′ W) between 1980 and 1981. Studies with *Lessonia trabeculata* were carried out in a subtidal (4–12 m deep) bed at Playa El Frances (30° 08′ S, 71° 26′ W) between 1987 and 1988. Details of the experimental designs and results gathered have been published elsewhere (Santelices, 1982; Santelices & Ojeda, 1984; Ojeda & Santelices, 1984; Vásquez, 1989). In this study we have included published and unpublished results especially important to understanding general patterns.

Results and discussion

Effects on the Lessonia individuals

Removal of upper canopy

Cutting the stipes of *Lessonia* either above the first dichotomy or just above the holdfast resulted in high mortality in both species (Fig. 1). Cutting the stipes above the first dichotomy resulted in a reduction of the inter-stipe friction; without this friction between stipes and their fronds, a heavy load of epiphytes developed on some of the abscissed stipes. The cut stipes of *L. nigrescens* do not move and can thus be reached and consumed by sea urchins (*Tetrapygus niger*). In the case of *L. trabeculata*, sea urchins, snails (*Tegula tridentata*) and fishes (*Aplodactylus punctatus*) attacked the abscissed stipes. It is not surprising, therefore, that mortality reached 50–60% in both species five to six months after experimental cutting. In these experiments all experimental plants disappeared within 8–10 months, but mortality of control plants during the experimental time never rose beyond 30–35% (Fig. 1B).

Cutting the stipes just above the holdfasts also resulted in 100% mortality in both species (Fig. 1A). A few, small holdfasts of *Lessonia nigrescens* generated a few, erected stipes after harvesting. However, these new stipes as well as the holdfast surface soon became covered with epiphytes or were consumed by snails (*Tegula atra*) or sea urchins (*Tetrapygus niger*). Thus, the removal of the upper-canopy in either of the two species was equivalent to a delayed removal of the whole plant.

Removal of the whole plant

Removal of whole plants resulted in increased inter-plant distances. In both species the most significant effects resulting from these increases was from the increased access of grazers to the holdfast and to areas between holdfasts. In the case of *Lessonia nigrescens*, this greatly decreased juvenile recruitment. High juvenile recruitment usually occurs in openings of 1 to 2 m between holdfasts (see Fig. 6, Santelices & Ojeda, 1984). Larger vegetational discontinuities suffer in-

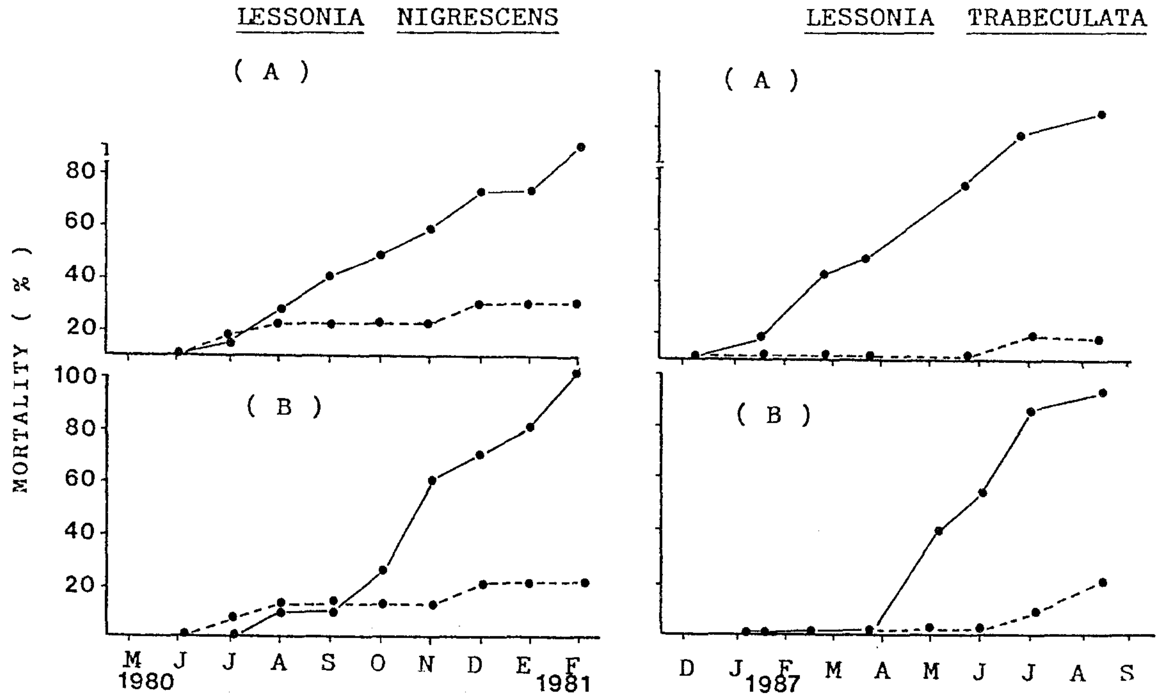

Fig. 1. Mortality of experimental populations of *Lessonia nigrescens* and *L. trabeculata* under alternative harvesting systems. (A) Experimental cut at the base of the stipe (N = 50); (B) Experimental cut above the first dichotomy (N = 50). (——) Experimental, (– – –) Control (N = 50)

creased grazing effects and decimation of recruits. Smaller inter-holdfast distances result in greater disturbance by adult thalli, and in mature undisturbed *L. nigrescens* belts (3 to 4 individuals m^{-2}), recruitment does not occur.

In *Lessonia trabeculata* beds, reductions in plant density from 3 to 0.5 m^{-2} resulted (Figs. 2A, 2B) in significant increases in sea urchins (*Tetrapygus niger*) and snails (*Tegula tridentata*) in experimental areas. Due to increased grazing, stipe number in experimental areas decreased about 50% (Fig. 2C). This appeared to cause increased elongation of a few stipes, which, by the end of the experiment, had fewer but longer stipes than control plants (Figs. 2C, 2D). Reduction in stipe number and length decreases stipe flexibility. These morphofunctional changes, together with grazing on the holdfast, weaken the resistance of individuals to drag forces and increase mortality from water movement.

A morphological study of *Lessonia trabeculata* plants cast ashore indicated that elongated plants with one or a few apically branched stipes were most commonly cast ashore.

Effects on communities

Effects on the fauna inside the holdfast

Studies of the holdfast fauna have been done only for *Lessonia nigrescens*. The irregularly shaped, open holdfast of *L. trabeculata* does not host a similar diversity of invertebrates.

Removing the apical canopy, either a few centimeters above the holdfast or at the level of the first dichotomy, did not cause changes in the invertebrate community living inside the holdfast of *Lessonia nigrescens* (Fig. 3). Measurements of the total number of individuals or of the number of individuals per species as a function of holdfast diameter (Figs. 3A, 3B), as well as measurements of the number of invertebrate species or of the total invertebrate biomass as a function of holdfast volume (Figs. 3C, 3D), did not produce any

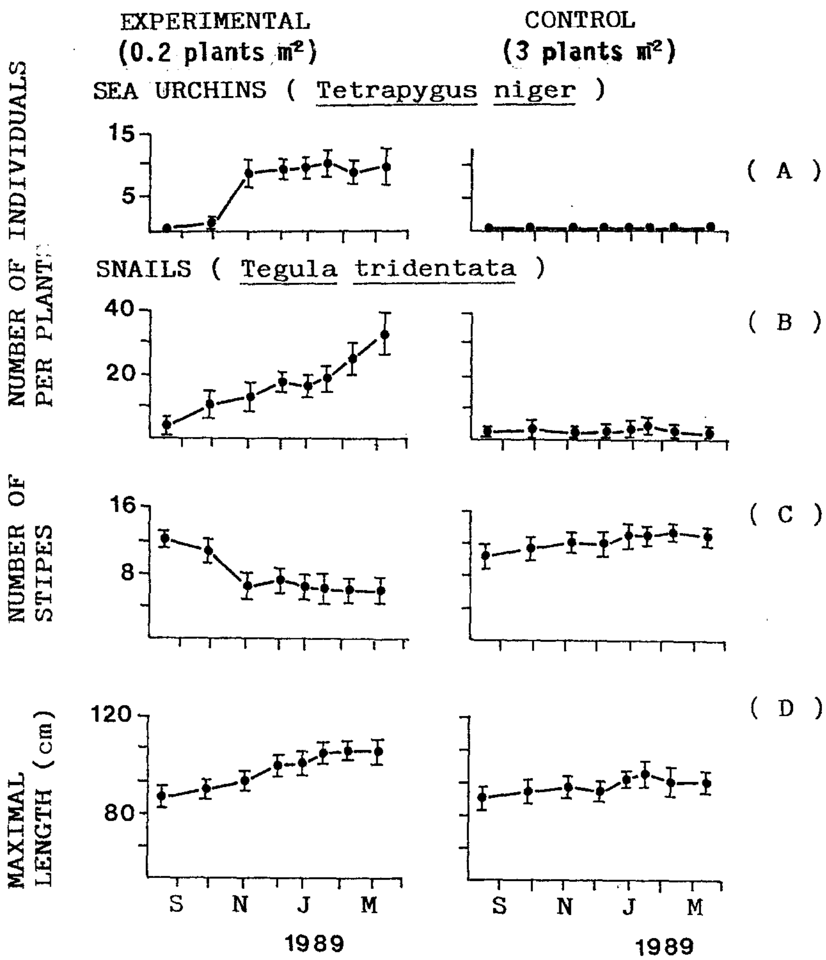

Fig. 2. Effects of experimental plant removals on grazer densities and plant morphology in a subtidal *Lessonia trabeculata* bed. (X + 2 SE; $N = 18$).

statistically significant differences (Mann-Whitney U Test; Kolmogorov-Smirnov Two Sample Test) between experimental and control populations. These results suggest (Santelices, 1982) that the invertebrate fauna inside the holdfast is not affected by the alternative harvesting methods, and invertebrates do not abandon the holdfast of experimentally abscissed plants. But, due to increased mortality of entire plants caused by harvesting, this faunistic component will be lost under any of the three alternative harvesting practices used.

Effects on the associated flora in presence of grazers

As mentioned previously, removal of adult plants of *Lessonia nigrescens* or *L. trabeculata* substantially changed the plant-spacing pattern, exposing the plants and substratum to increased grazing effects and creating barren grounds. In beds of both species, these barren grounds have persisted for several years unless the grazers were removed.

No natural removals of large numbers of sea urchins have been observed in intertidal areas dominated by *Lessonia nigrescens*; some of these barren grounds have persisted for the last 10 years. In subtidal beds of *Lessonia trabeculata*, some barren grounds can be repopulated (Vásquez, 1989). During seasons of reduced water movement, and especially in rocky environ-

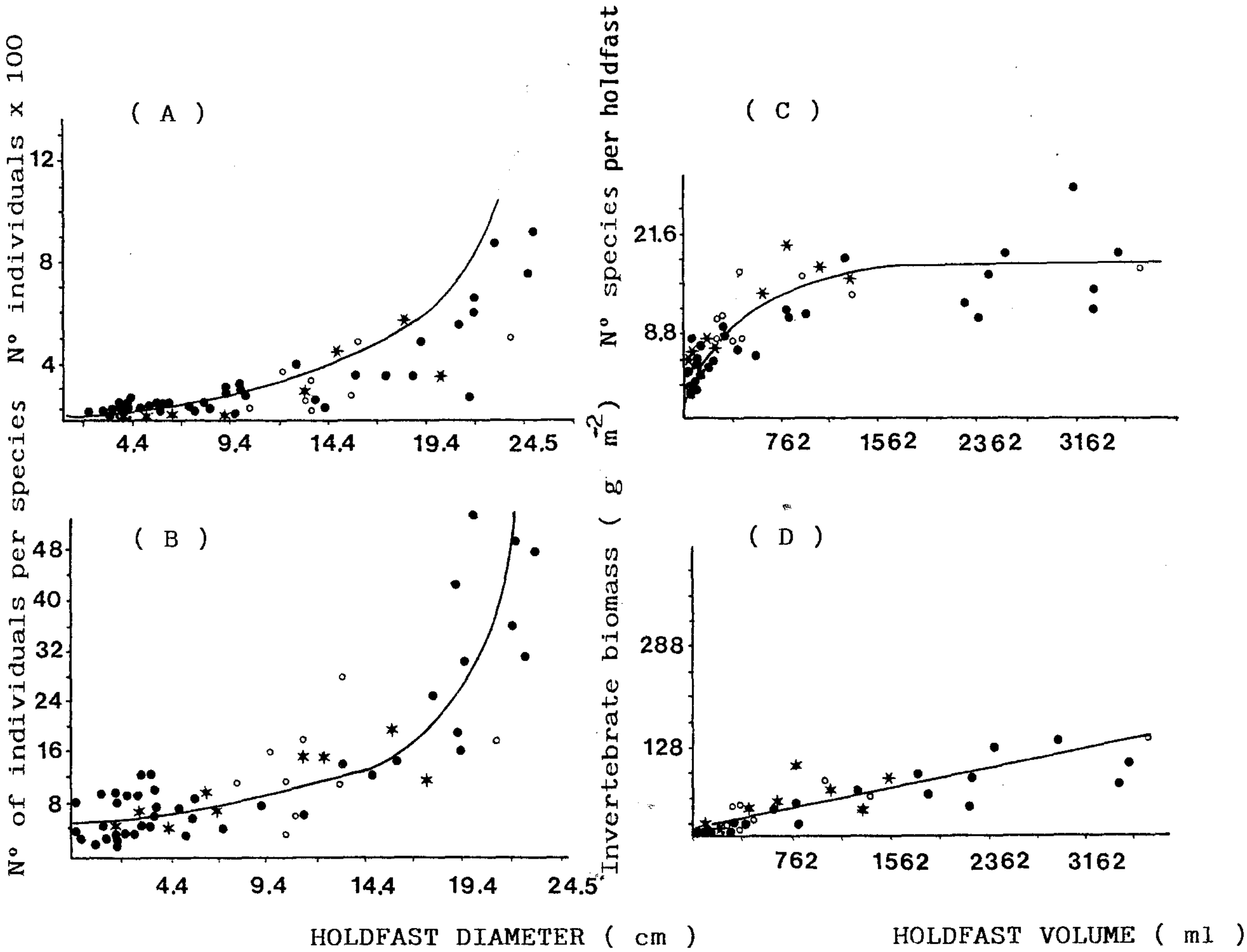

Fig. 3. Pattern of invertebrate distribution in holdfasts of *Lessonia nigrescens*. Experimental harvested and control populations showed no significant differences in patterns of distribution, the number of individuals as a function of holdfast diameter (A–B), the number of invertebrate species, or invertebrate biomass, as a function of holdfast volume (C–D). (●) Control, (O) experimental removal at the base of the stipes and (★) experimental removal above the first dichotomy.

ments occasionally influenced by sand, the polychaete *Phragmatopoma moerchi* can settle on these barren grounds. The growth and expansion of polychaete colonies provide refugial areas for recruitment of several different types of organisms (e.g. the Rhodophyta *Gelidium chilense* (Montagne) Santelices et Montalva, the Phaeophyta *Glossophora kunthi* (C. Agardh) J. Agardh, and juveniles of *Lessonia trabeculata*). These areas may persist, revert to a sea urchin dominated barrens, or become dominated by kelps. Seemingly, the density of the stipes of these juveniles kelps, their early fertility, and the movement of peripheral stipes induced by water movement result in further colonization of these barren grounds by *Lessonia trabeculata*.

Effects on the associated flora in absence of grazers

The ecological effects of removing *Lessonia nigrescens* where there are no grazers varied according to the season when removal was performed.

In central Chile, pure or mixed populations of the non-calcareous, crustose green alga *Codium dimorphum* Svedelius and of the cushion-forming species *Gelidium chilense* dominate the zone immediately above the *Lessonia nigrescens* belt. If the kelps are removed in winter, some opportunistic algae, such as species of *Ulva*, *Codium* or *Gelidium*, can temporarily invade the newly exposed rocky surface. However, *L. nigrescens* is fertile during winter, and the sporophyte can settle on bare rock or crevices among plants of *Gelidium* or *Codium* spp. By fast growth and expansion of their holdfasts, these juvenile kelps either overshade or overgrow the smaller species.

The above situation changes drastically when removals are done in summer because *Lessonia nigrescens* is fertile only during winter. Summer removal of the kelp is followed by a rapid occupation of the substratum by *Ulva* and *Enteromorpha* spp., followed by steady increment in cover by mid-intertidal algae such as *Gelidium chilense* (Ojeda & Santelices, 1984). *Gelidium chilense* is able to extend from mid-intertidal levels into the *Lessonia* belt. Thus, summer removal of *L. nigrescens* allows for four to five months of invasion and growth of *G. chilense*, free from its competitive dominant. Settlement of *L. nigrescens*, expected to occur in winter, did not occur in these experiments due to the monopolization of the primary substratum by *G. chilense* (Ojeda & Santelices, 1984).

Equivalent experimental results are lacking for *Lessonia trabeculata*-dominated beds. However, as *L. trabeculata* is fertile all year and can recruit and colonize vacated substrata as long as grazers are absent (Vásquez, 1989), it is unlikely that seasonality would have a major effect on recolonization of this species.

Conclusions

Experimental studies of *Lessonia nigrescens* and *L. trabeculata* have revealed several ecological effects of harvesting that ought to be considered when managing wild stocks of these species. In both kelps, the removal of the upper canopy eventually leads to death of the plants. The invertebrate fauna does not abandon the holdfast of pruned *L. nigrescens*. Therefore, both partial and complete plant removal has similar mortality consequences for the kelp and for the invertebrate fauna associated with the kelp.

The most important population effects of removal are the increments in inter-plant distances and the resulting increasing access of grazers to the kelp holdfast and to inter-holdfast surfaces. Increased grazing reduces recruitment of both *Lessonia* species and modifies the morphology of *L. trabeculata*, rendering individuals of the latter species more susceptible to being removed by water movement.

Kelp removal in the absence of grazers should be performed at the season of maximum fertility. Time delays between kelp removal and onset of fertility may lead to permanent occupation of the space by other algal species.

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