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The role of grazers in the zonation of intertidal macroalgae of the Chilean coast

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The role of herbivores in maintaining the pattern of zonation of macroalgae in the mid-intertidal community of semi-exposed shores was studied during 8 months (January to September 1979). Herbivores were totally removed every 15 days from a semi-exposed intertidal rocky wall, while another wall served as a control. Percent cover of algae was measured at two month intervals. Herbivore removal resulted in a disruption of the pattern of zonation. *Iridaea boryana* and *Gymnogongrus furcellatus* expanded the width of their belts into the zone initially occupied only by *Ulva rigida* and *Lithophyllum* spp. We conclude that herbivory is the basic mechanism which maintains the limits between the zones of these macroalgae in southern Chile.

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Роль фитофагов в поддержании определенного характера распределения многоклеточных водорослей в литоральных сообществах полуобнаженного берега исследовали в течение 8 месяцев (с январи по сентябр 1979 г.). Фитофаги полностью изымались через каждые 15 дней с полуобнаженной скалистой стенки, а другая стенка служила контролем. Определяли % покрытия водорослями через 2-месячные интервалы. Изъятие фитофагов привело к нарушению характера пространственного распределения. *Iridaea boryana* и *Gymnogongrus furcellatus* расширили свои границы внедрением в зону, ранее занимаемую лишь *Ulva rigida* и *Lithophyllum spp.* Мы сделали вывод, что фитофаги - основной механизм поддержания границ между зонами, занимаемыми этими многоклеточными водорослями в южном Чили.

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Introduction

Several different algal floras are found in the southeastern Pacific Ocean along the coast of Chile (Santelices 1980). The region near Valdivia, 39°–42° S, is characterized by a zone of red alga, *Iridaea boryana* (Setch. and Jardn.) Skottsb., at mid-intertidal levels on rocky shores (Jara and Moreno 1982). This alga, considered the ecological equivalent of *Chondrus* in the northern hemisphere, forms a canopy 10–15 cm in height, beneath which several species of algae form an "obligate understory" (sensu Dayton 1975).

The experimental studies of Jara and Moreno (1982) demonstrated that predation by the small pulmonate gastropod, *Siphonaria lessoni* Blainville, has an important effect on the organization of this community. Predation by *S. lessoni* weakens the fronds of *Iridaea boryana* and subsequent wave action reduces its cover. However, because *S. lessoni* is not capable of affecting the crustose phase of *Iridaea,* it does not determine the intertidal distributional limits of this alga.

Jara and Moreno (1982) observed that during periods of sand accretion in the rocky intertidal, certain consumers trying to avoid to be covered by the sand, move from lower intertidal to mid levels. The most important of these is *Fissurella picta* Lamarck. These consumers appear to determine the lower limit of *Iridaea boryana* and to allow the development of a low intertidal algal assemblage of calcareous algae (*Lithophyllum* spp.) and *Ulva rigida* (C. Ag.) Thuret.

Experimental studies on the patterns of algal zonation in other parts of the world suggest that the borders between zones are determined by competition (Lubchenco 1980, Schonbeck and Norton 1980, Santelices 1981) or predation (Lubchenco 1980). If general models of the organization of intertidal communities (e.g. Paine 1977) can be applied to the Chilean coast, we should find in the absence of herbivores, that macroalgal distribution is regulated by competition. This study is an attempt to answer which mechanisms maintain algal zonation on the semi-exposed rocks in Mehuín, Chile.

Materials and methods

Study site

This experiment was conducted in the marine reserve, Punta Kilian, of the Austral University at Mehuín (39°24′S, 73°13′W). Climatic characteristics of the area are described by Jara and Moreno (1982). The experimental wall is semi-protected from wave action, 4 m high, 13 m wide and is divided in the middle by a 20 cm wide crevice. Both halves front on a large channel at the bottom of which sand accumulates during summer months.

According to Oliva (1967) 4 zones of macroalgae are found in semi-protected areas. The highest zone is found higher than 2 m above mean lower low water and is characterized by the seasonal appearance of *Porphyra columbina* on top of barnacles (*Chthamalus scabrosus* and *C. cirratus*). Between two and one meters above lower low water is the zone of *Iridaea boryana,* below which there is a zone of calcareous algae (*Lithophyllum* spp. with *Ulva rigida.* Finally, below mean low water is a zone of *Macrocystis pyrifera* which in this region of the Chilean shore can extend down to 8 m in depth (Moreno and Sutherland 1982).

Experimental design

We removed herbivores from a portion of the wall every 15 d for 8 months (January to September 1979). Species removed were *Fissurella picta* and other herbivores of lower density: *Chiton granosus* Frembly, *Tegula atra* (Lesson), and *Collisela zebrina* (Lesson). These were also removed from a buffer zone between the removal area and the neighboring non-manipulated area. The removal zone and its control were 3 m in width.

In the removal and control areas we measured the width of the *Iridaea boryana* zone in 8 fixed positions. We also measured algal percent cover in three permanent quadrats of 1 m^2 located in what initially was the zone of calcareous algae and *Ulva rigida.* On each quadrat we superimposed 81 regularly spaced points. When an alga was present but did not fall under any point we arbitrarily assigned it a value of one percent.

Statistical analysis

The 8 replicate measurements of the width of the *Iridaea boryana* zone in both treatments were compared with a student's t-test, after first verifying the equality of variances according to Snedecor and Cochran (1980). The percent cover estimates were analysed with a Kolmogorov-Smirnov test to determine their statistical distribution. Since some values were bimodal, all data were transformed with an angular transformation according to Sokal and Rohlf (1969). The mean abundance of each species in the exclusion and control was then compared with one-way analysis of variance.

Results

Herbivore exclusion

The grazers in this community are large; *Fissurella picta* ranges from 2 to 6 cm while *Chiton granosus* which is much less abundant, attains lengths of 4 cm. The latter species, however, is carnivorous as well as herbivorous since its principal food is barnacle larvae (Jara 1980), and thus our results are basically due to the removal of *Fissurella picta.* Following *Fissurella* removal in January 1979 there was a rapid increase in the width of the zone of *Iridaea boryana* (Fig. 1), and from April through September this increase was significant when compared to the control area. The slight decreases in the width of

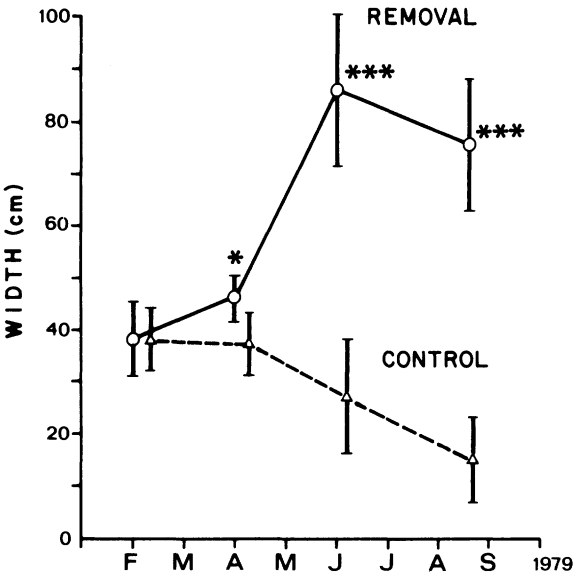

Fig. 1. Width of the *Iridaea boryana* zone during the herbivore removal experiment. Asterisks indicate a significant difference between treatments (t-test, *P < 0.05; ***P < 0.001).

Iridaea zone in both areas after June is due to wave action from winter storms (Fig. 1).

In the removal area, *U. rigida* initially increased in abundance overgrowing calcareous algae (Fig. 2A). After April *Ulva* decreased in density in both areas, but *Iridaea boryana* came to dominate the lower zone only in the removal area (Fig. 2A,B). Two other important events occurred with the removal of *Fissurella picta*. *Porphyra columbina* was present through June in the removal area while it disappeared from the control area by April (Fig. 2A,B). In addition *Gymnogongrus furcellatus* appeared in the removal area but not in the control area. *Gymnogongrus furcellatus* reached values of 12% cover and formed a new zone above the level of *Macrocystis pyrifera*.

Discussion

The removal of *Fissurella picta* permitted *Iridaea boryana* to expand down into the area originally occupied by *Ulva rigida* and calcareous algae. However, there was little evidence of subsequent competitive exclusion in this lower zone in spite of the fact that *Iridaea boryana* is the competitive dominant of mid-intertidal levels (Jara and Moreno 1982); more algal species were present in greater abundance in the absence of herbivores.

Paine's (1977) model on the role of predation in maintaining species diversity predicts two phenomena: 1) at low predator densities species diversity is reduced because of the development of a competitive dominant and 2) at high predator densities diversity is reduced because of overexploitation. In the latter case only algae with efficient anti-predatory defenses, e.g. calcareous algae, can coexist with their consumers (Paine and Vadas 1969). In our study both phenomena were seen, at higher levels on the wall, grazing pressure from *Fissurella picta* is reduced and *Iridaea boryana* dominates space up to a level determined by its resistance to desiccation. Its lower limit is determined by the grazing activities of *Fissurella picta* and in the lower zone only *Litophyllum* sp. and *U. rigida* can coexist with *Fissurella*. *Fissurella* grazing activity is probably reinforced by *Tegula atra* and the bulldozing action of *Chiton granosus*. The ephemeral life history of *U. rigida* and the calcareous morphology of *Lithophyllum* serve as anti-herbivore devices in this zone. The removal of consumers demonstrates that this area can be invaded by algae from higher *(Iridaea)* and lower *(Gymnogongrus)* levels. There are no physical limitations on the

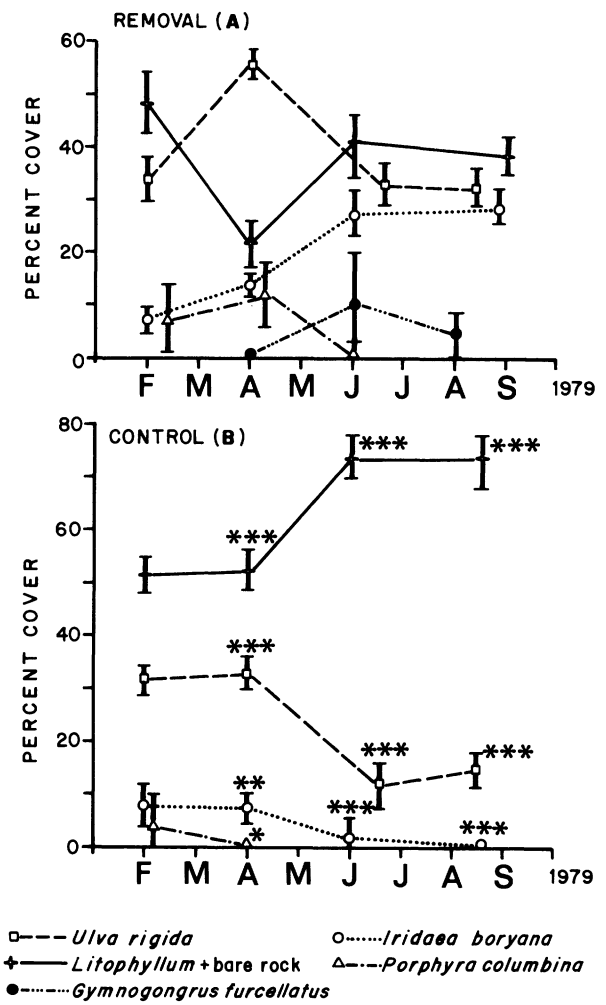

Fig. 2. Abundance of the main macroalgae during the experiment. Mean percent cover and their SD are shown. A. Effect of herbivore removal and B. the control plots. Asterisks indicate a significant difference between treatments (One way ANOVA, *P < 0.05; **P < 0.01; ***P < 0.001).

survival of these species in the area usually dominated only by calcereous algae and *Ulva*. It is not clear whether or not *Iridaea boryana* would eventually dominate this lower zone in the continued absence of herbivores.

In the herbivore removal experiment of Jara (1980) the increase in the canopy of *Iridaea boryana* at mid-intertidal levels created conditions such that *Gymnogongrus furcellatus* and *Macrocystis pyrifera* both from the subtidal, were able to recruit and grow. In our experiment *Gymnogongrus furcellatus* also recruited, suggesting that its absence from the mid-intertidal is a result of the action of herbivores. In contrast, in the southern hemisphere *Macrocystis pyrifera* escapes from herbivores (Moreno and Sutherland 1982), but seems to require moister conditions that were present on the experimental wall.

The tidal level occupied by *Iridaea boryana* in the south of Chile is occupied by crustose algae (*Codium dimorphym* and *Gelidium* sp.) in central Chile, where they form a continuous cover due to their low growing fronds and coalescent morphology. These structures form a cushion that could be an efficient anti-herbivore mechanism (Santelices 1981). *Iridaea boryana* in central Chile lives in the mid-upper intertidal. The experimental removal of *Codium dimorphum* permit the recruitment of *I. boryana* and other intertidal algal species in the new space. Then, Santelices (1981) suggests that competition for space is the factor controlling the lower limits of *Iridaea boryana,* in spite of the fact that the roles of key-hole limpets (*Fissurella* spp.) and black sea urchin *(Tetrapigus niger)* remains unknown in this community.

On the New England coast Lubchenco (1980) found that the removal of *Chondrus* permitted the establishment of *Fucus* spp., algae more common at higher intertidal levels. While this demonstrated that the limit between zones was maintained by competition, she also showed that the lower limit of *Chondrus* was determined by sea urchin *(Strongylocentrotus droebachiensis)* grazing in areas where these were common. Schonbeck and Norton (1980) concluded that competition among fucoid algae determined algal zonation patterns in the isle of Cumbrae, Scotland. However, these authors observed that differential grazing by molluscs could confer a competitive advantage to some algae (*Ascophyllum* and *Fucus*).

There seems to be a consensus that patterns of algal zonation are maintained by biological factors and are not necessarily related to tidal levels as was supposed for many years (e.g. Stephenson and Stephenson 1972). The exception is the upper limit of high intertidal algae where desiccation plays the most important role. The present study has shown that in the region near Valdivia, herbivory plays a fundamental role, determining not only the abundance but also the presence or absence of algae in the different belts.

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