Hydrobiologia 151/152: 313–328 (1987)
M. A. Ragan and C. J. Bird (eds)
Twelfth International Seaweed Symposium

Biological bases for management of *Iridaea laminarioides* Bory in southern Chile

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Key words: seaweed, *Iridaea laminarioides*, harvesting, regeneration, resource management

Introduction

The harvest and export of *Iridaea laminarioides* Bory, the dominant species in the intertidal communities in southern Chile, have increased significantly in the last five years, reaching 15% of the total Chilean production of marine algae in 1985. Of this 15%, 48% is harvested from the X Region (SERNAP, 1985).

The biology of the species has been studied by Hannach & Santelices (1985) and Westermeier *et al.* (1985); its rôle in intertidal communities of southern Chile has been examined by Jara & Moreno (1983) and Moreno & Jaramillo (1983).

This paper analyses the productivity of *I. laminarioides* populations, evaluating the standing stock, growth rate, effects of pruning, and phenology to determine effective management policies for the resource.

Materials and methods

The study was carried out at Mehuín (39°24′S, 73°14′W), province of Valdivia. Here, two zones were chosen: Punta Kilian and, one km away, Punta Pichicuyín (Fig. 1). Two sampling stations were chosen at Punta Kilian. Station 1 is located on a rocky platform semi-exposed to the waves and where the algae experience strong grazing. Station 2 corresponds to rocks protected from the waves, with less grazing but where there is great erosion and sand accretion. Station 3 was placed at Punta Pichicuyín in a semi-exposed rocky platform with little grazing action.

Every fortnight from March 1984 until December 1985, data on the following parameters were recorded for the three stations: standing stock, phenology and regeneration of pruned thalli and of crust discs. Results are expressed as the average value of each of the parameters.

Abundance: The standing stock of *I. laminarioides* was determined in summer (December), autumn (March), winter (June) and spring (September) by sampling a 2500-cm^2 area (four replicates). The algae were removed with a spatula and placed in labelled plastic bags. In the laboratory, the epiphytes were washed off with seawater and the thalli were separated according to length. Thalli were weighed (wet weight) and then dried to constant weight in a drying chamber (5 d, 60 °C). The standing stock of reproductive thalli was determined from the same samples, separating the different stages macroscopically.

The cover was quantified for 21 months using a 2500-cm^2 quadrat with 100 regular spots.

Phenology: 1.20 × 1.20-m areas, each divided into nine 400-cm^2 squares, were used in determining phenology. The cover of cystocarpic, tetrasporic and sterile and male gametophytes together was quantified using a 400-cm^2 quadrat with 100 regular spots.

Pruning experiment: Thalli of different length in 4-cm^2 areas were pruned at the laminar base each season. Length ranges were 0–5, 5–10 and >10 cm. Ten plants, each with 7 and 15 thalli per

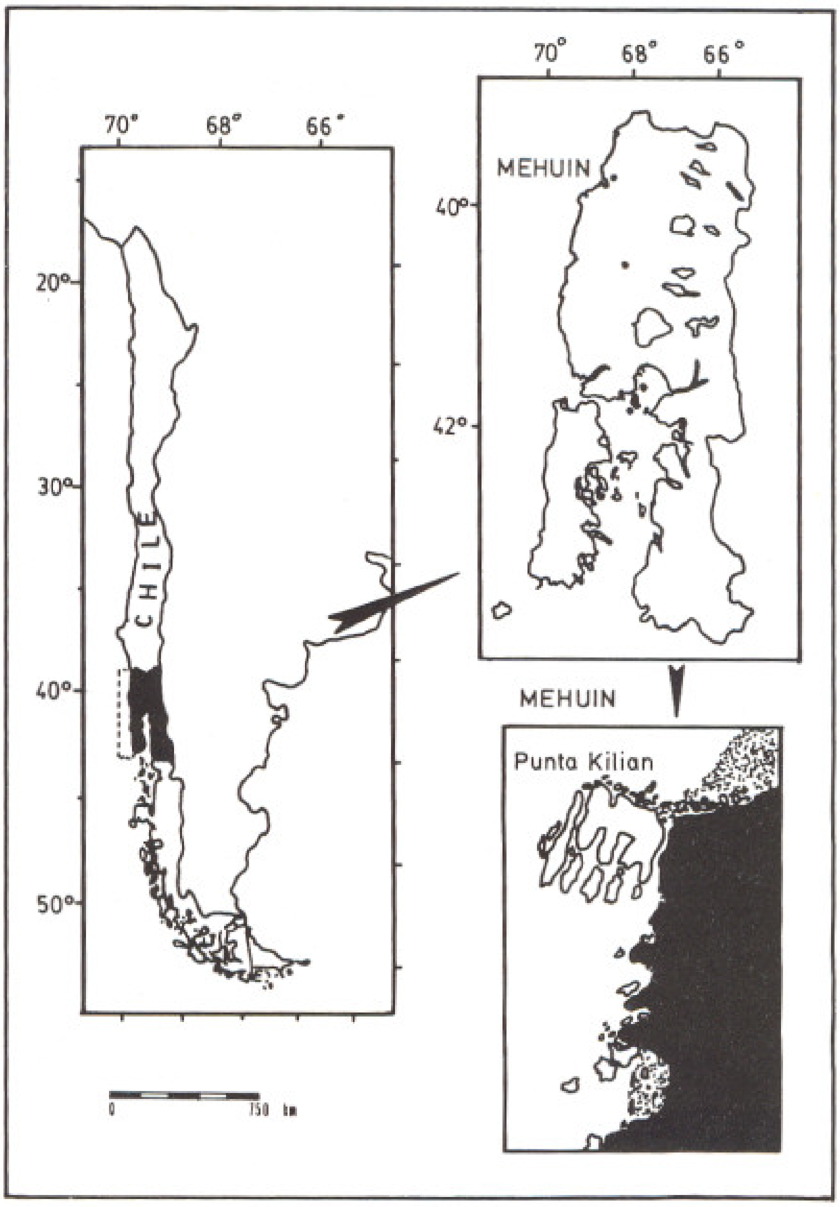

Fig. 1. Location of study in southern Chile.

plant and with a corresponding control, were pruned each season. Thallus regeneration was measured according to the respective growth.

Crust-disc regeneration experiment: Results from the pruning experiments led us to experiment with regeneration of the crust-disc. From April 1985 to April 1986, thalli were cut at the disc level. The regeneration (production) according to number of thalli arisen was determined. The cumulative percentage of production was derived from the monthly increases, and distribution of total production (%) throughout the year was estimated. To study the canopy effect on the production of the new thalli, these were removed every fortnight from one group of plants while thalli of the other group were left untouched.

Thallus development from crust discs experiment: Crusts were tagged, and a quantification of the number of arisen thalli was made. One of the treatments consisted of the monthly removal of the newly sprouted fronds; in the second treatment, crusts were not manipulated, serving thus as a control.

Results

Abundance

Maximum values for biomass (Fig. 2a) were obtained at all stations in autumn (March). Station 1 presented the highest value ($800\ g \cdot m^{-2}$). It was followed by stations 2 ($480\ g \cdot m^{-2}$) and 3 ($350\ g \cdot m^{-2}$). These values represent summer (December to February) production. During the winter and spring months, the biomass decreases at the three stations. No significant quantitative or seasonal differences were observed between stations 2 and 3. Station 1 presented a different situation: the winter (June) value was $280\ g \cdot m^{-2}$ whereas in spring (September) the plants disappeared. In December, the biomass increased to $380\ g \cdot m^{-2}$ at stations 2 and 3. At station 1, the situation remained the same as in September when no plants were present.

Algal abundance estimated by cover (Fig. 2b) decreased gradually at stations 1 and 2 from March to December 1984. From August 1985 onward, there was a total absence of *I. laminarioides* at station 1. At station 2, the abundance fluctuated from 5 to 15% from January to November 1985. The behavior at station 3, on the other hand, agrees with the standing stock in that there was a greater abundance between September and February, decreasing to 20% cover towards the winter months.

At stations 1 and 2, the total number of $thalli \cdot m^{-2}$ (Fig. 3) showed a different behavior from that of the biomass, while at station 3 the number of thalli showed the same cycle as that of standing stock and cover. The density of thalli was different at the three stations: 2400–4900 (station 1), 700–3400 (station 2) and 1800–4200 $thalli \cdot m^{-2}$ (station 3).

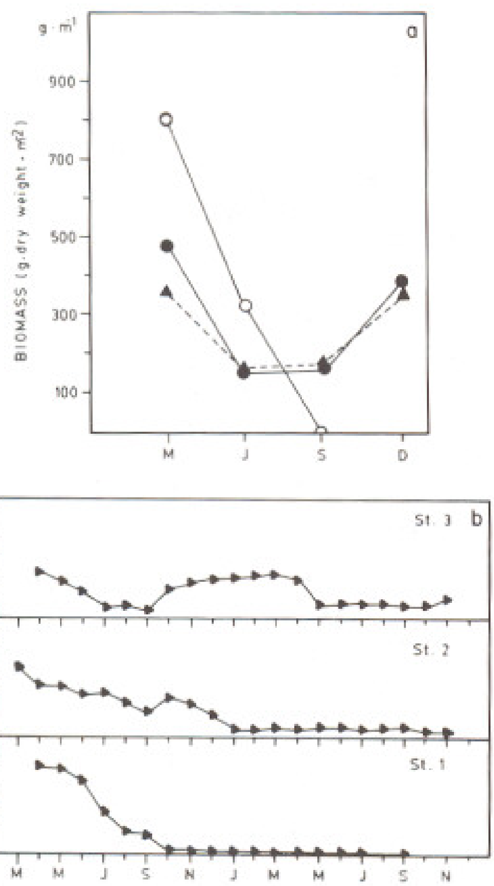

Fig. 2. a) Seasonal variation in standing stock: o —— o Station 1; ● —— ● station 2; ▲ – – ▲ station 3; b) Monthly changes of percent cover.

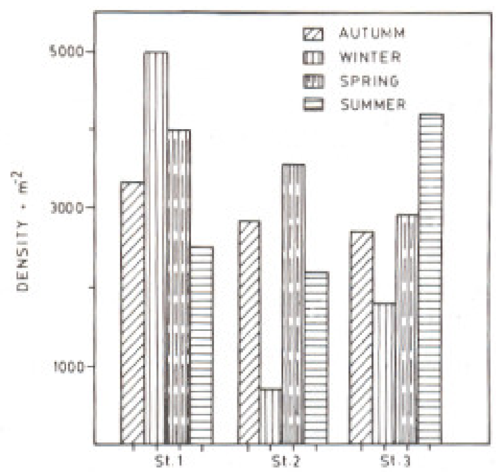

Fig. 3. Seasonal density of cover.

The seasonal distributions of lengths of the thalli (Fig. 4a) at the three stations show that the most abundant length was 0–3 cm (50%) while thalli >9 cm are scarce (<10%). Intermediate lengths (3–6 cm) do not exceed 25%. The peak of production of thalli occurs in spring when 0–3 cm thalli reach their highest abundance. The longer thalli are most abundant towards autumn, in correspondence with the biomass at that season.

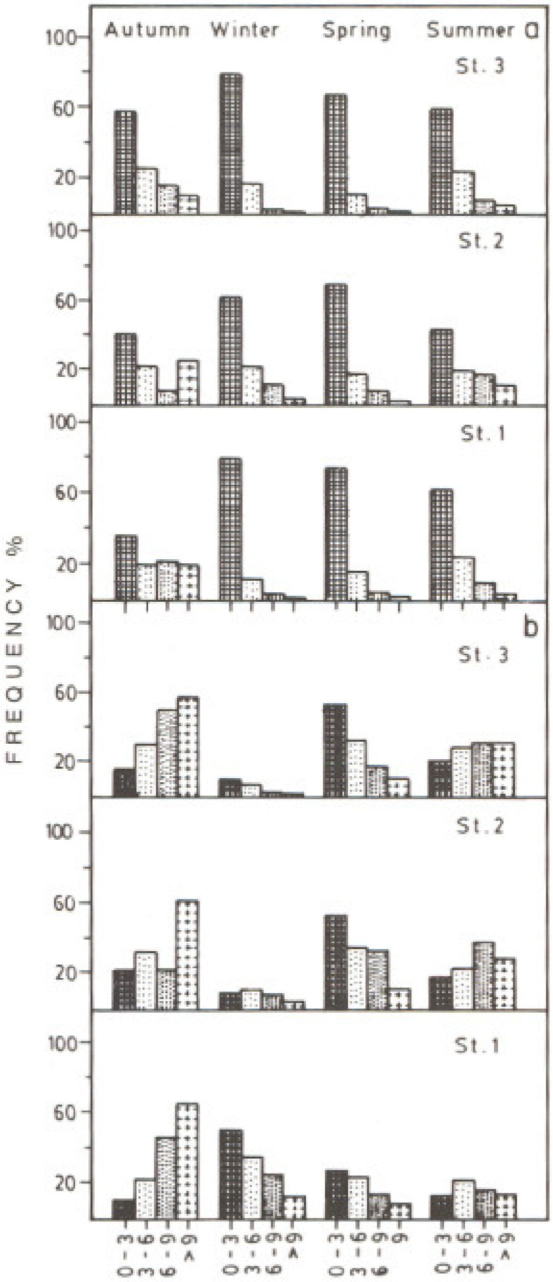

Fig. 4. a) Proportions of thalli in different length-classes by season, expressed as percentage of total number of thalli; b) Seasonal variation of lengths of thalli.

When the yearly cycle of production of thalli is analyzed (Fig. 4b), one can see that growth of thalli was greatest in spring and summer; highest values were obtained in autumn (>50% of the thalli >9 cm long). In winter (June–July) the number of thalli decreases at all lengths considered.

Phenology

Tetrasporophyte and carposporophyte reproductive stages are present all year round at densities of 60 to 360 thalli·m^{-2} (Fig. 5); sterile plants and gametophytes together were present in the greatest density, between 600 and 4400 thalli·m^{-2}. There is greater density in winter and lesser in spring and summer; at stations 1 and 3, this density gradually decreases towards winter. A different pattern was observed at station 2 with alternating densities throughout the year.

The carposporophytes showed a different pattern at each of the sampling stations. Thus in autumn, station 1 showed its greatest density (340 thalli·m^{-2}), and this gradually decreased towards summer. Station 2 showed in autumn and summer its greatest density, whereas the lowest densities, 50–55 thalli·m^{-2}, occur in winter and spring.

Sterile plants and male gametophytes together showed a different seasonal cycle at each station. At station 1, maximum abundance was in winter (4400 thalli·m^{-2}) and the minimum occurred in summer (2500 thalli·m^{-2}). At station 2, the maximum was detected in spring (3200 thalli·m^{-2}) and minimum in winter (550 thalli·m^{-2}). Maximum density at station 3 appeared in summer (3900 thalli·m^{-2}) and the minimum in winter (1500 thalli·m^{-2}). Thus all stations differ with regard to densities of thalli and seasons of maximum and minimum abundance.

The reproductive thalli represent from 40 to 50% of the total biomass (Fig. 6a). There are no significant differences in the abundances of the different reproductive stages; there are, however, differences

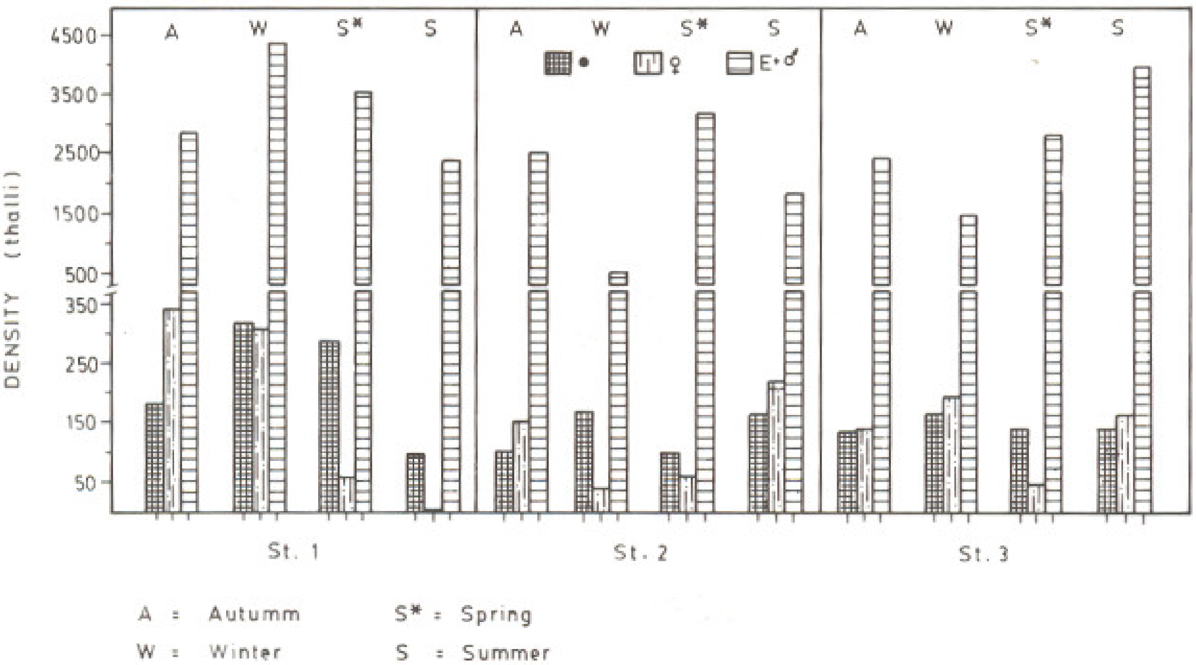

Fig. 5. Seasonal changes of densities of reproductive thalli per m^2: sterile and male (E + ♂), cystocarpic (♀), tetrasporic thalli (●).

in the densities of reproductive thalli. Seasonal abundances of the different reproductive stages, expressed as percent cover, reinforce the pattern described above. The amount of reproductive thalli does not surpass 30%, while the sterile plants and male gametophytes together can reach 50% during the months of greatest abundance.

Regeneration of thalli pruned at the laminar base

Regeneration was slowest after the autumn pruning for all three length-classes of thalli three months post-treatment. The thalli at station 3 had regrown the most by five to six months after pruning. On the other hand, the 0–5 cm thalli at station 1 had reached only 85% regeneration, when between June and July, the thalli split and only the crust discs remained. Contrary to this, thalli at station 3 continued to develop and by the end of 12 months had reached 190% development (Fig. 7). Six months after pruning, the 5–10 cm thalli had reached maximum regeneration (40% at station 1), while at station 3, the maximum (180% regeneration) was reached nine months post-treatment. Thalli of >10 cm at station 1 showed maximum regeneration after six months; after 12 months, regeneration at station 1 was 100% and at station 3, 110%.

The mortality of thalli pruned in autumn, when maximum development is being reached, is low (Fig. 7b). At station 1, there was 30% mortality, while stations 2 and 3 there was none. After the point of maximum development, mortality in pruned thalli increases considerably, reaching 70% at stations 2 and 3; these remain latent, with only the stipe and a small laminar portion. At station 1, mortality was 100%; only the crust discs remained.

Results of the winter pruning are shown in Fig. 8a: no regeneration was observed, four months after treatment, at any station and for any size-class. After the winter months, there was a great development of thalli to 190% regrowth at station 2, 100% at station 3 and 70% at station 1. Thalli of 5–10 cm reach their maximum development one or two months after the 0–5 cm thalli. The greatest percentage of regeneration was seen at station 3 (210%). Regrowth at station 1 was 100%, at station

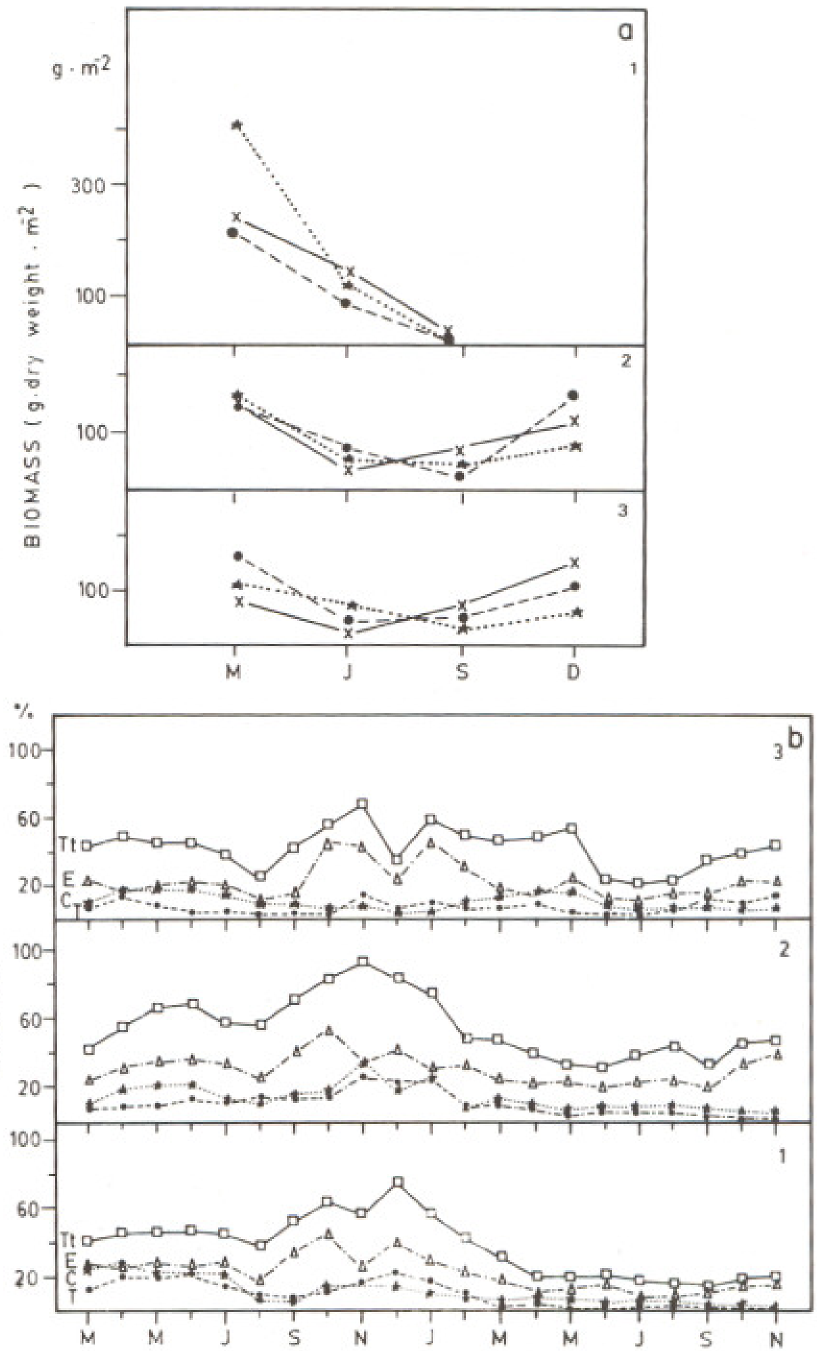

Fig. 6. a) Seasonal changes in standing stock of dry matter in reproductive thalli: ★ – – ★: ♀; ×——×: E + ♂; ●——●: ⊕; b) Monthly variation of percent cover by reproductive and total thalli: Tr: total; E: sterile and male; C: cystocarpic; T: tetrasporic thalli.

2 only 50%. Thalli >10 cm reached their maximum regeneration during the same months as those of 5–10 cm. However, the regeneration percentages were different.

Thalli pruned in winter did not show mortality during the periods of rapid regeneration (Fig. 8b). Once maximum development was reached, mortality increased: 85% at station 1, 60% at station 2 and

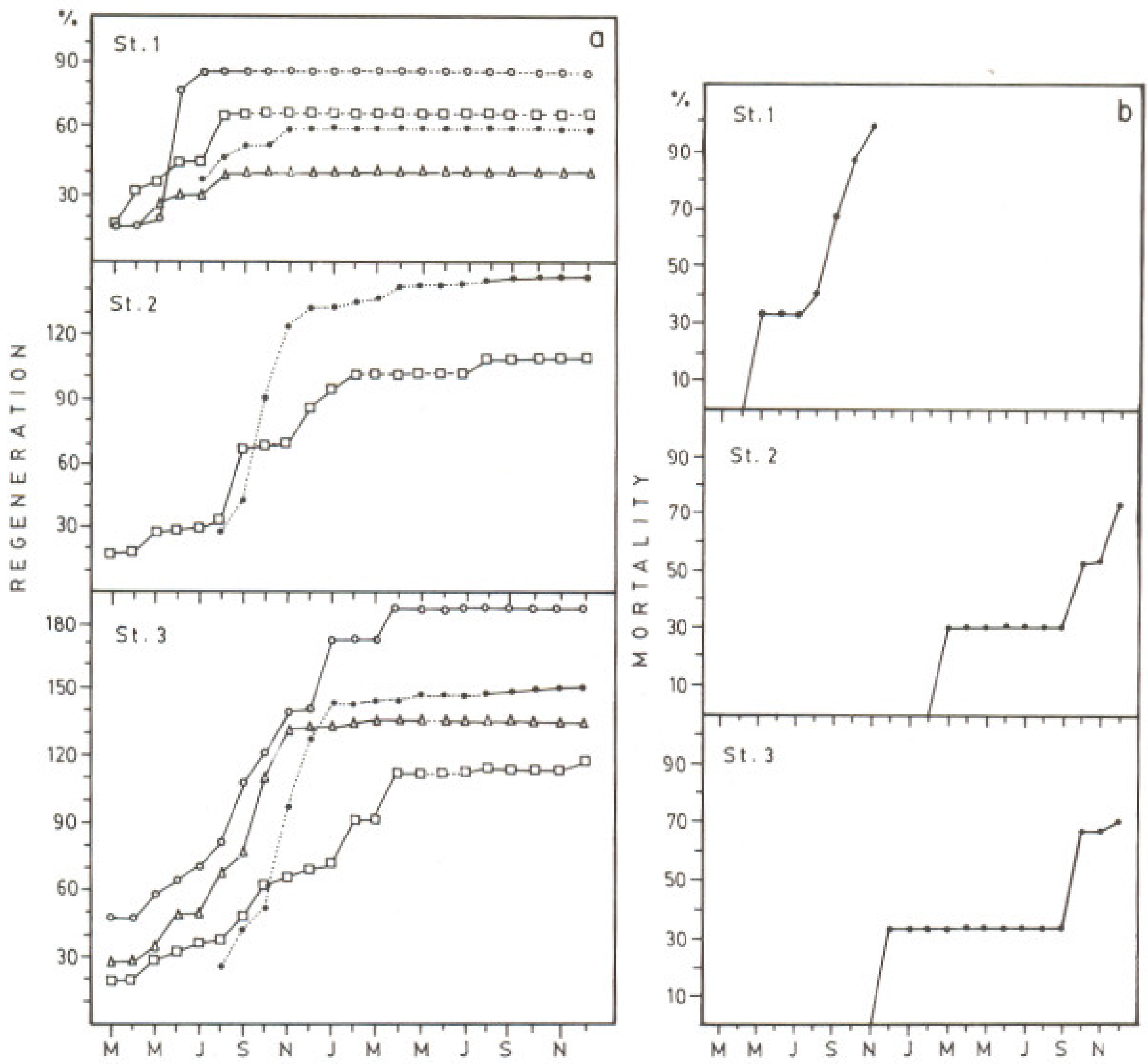

Fig. 7. Net regeneration accumulated (percent) from pruned thalli (a), and mortality in autumn (b): ○——○: Thalli 0–5 cm; △——△: thalli 5–10 cm; □——□: thalli 10 cm; ●---●: control.

40% at station 3.

Regeneration of thalli pruned in the spring (Fig. 9a) shows that the 0–5 cm thalli reached their maximum development (50% at station 1) by five months after treatment. However, regeneration at station 2 and 3 was 90 and 130%, respectively. Sixteen months post-pruning, thallus lengths were 100 and 165% at these same two stations. Interestingly, once 90% regeneration was reached at station 1, development slowed. Thalli of 0–5 cm sustained development to the end of the experiment, at station 1 reaching 70% regeneration and at stations 2 and 3, 140%. The same occurred with 0–5 cm thalli, regeneration being rapid for six months, then slowing. Pruning of thalli >10 cm was done only in spring at station 3, since thalli of this size were not then present at other stations. Maximum development (110%) was attained ten months after treatment.

Mortality of thalli pruned in spring (Fig. 9b) resembled that for autumn and spring at stations 1 and 2, only with higher percentages. Mortality at station 3 reached 40% in the period of rapid regeneration. This pattern was maintained constant

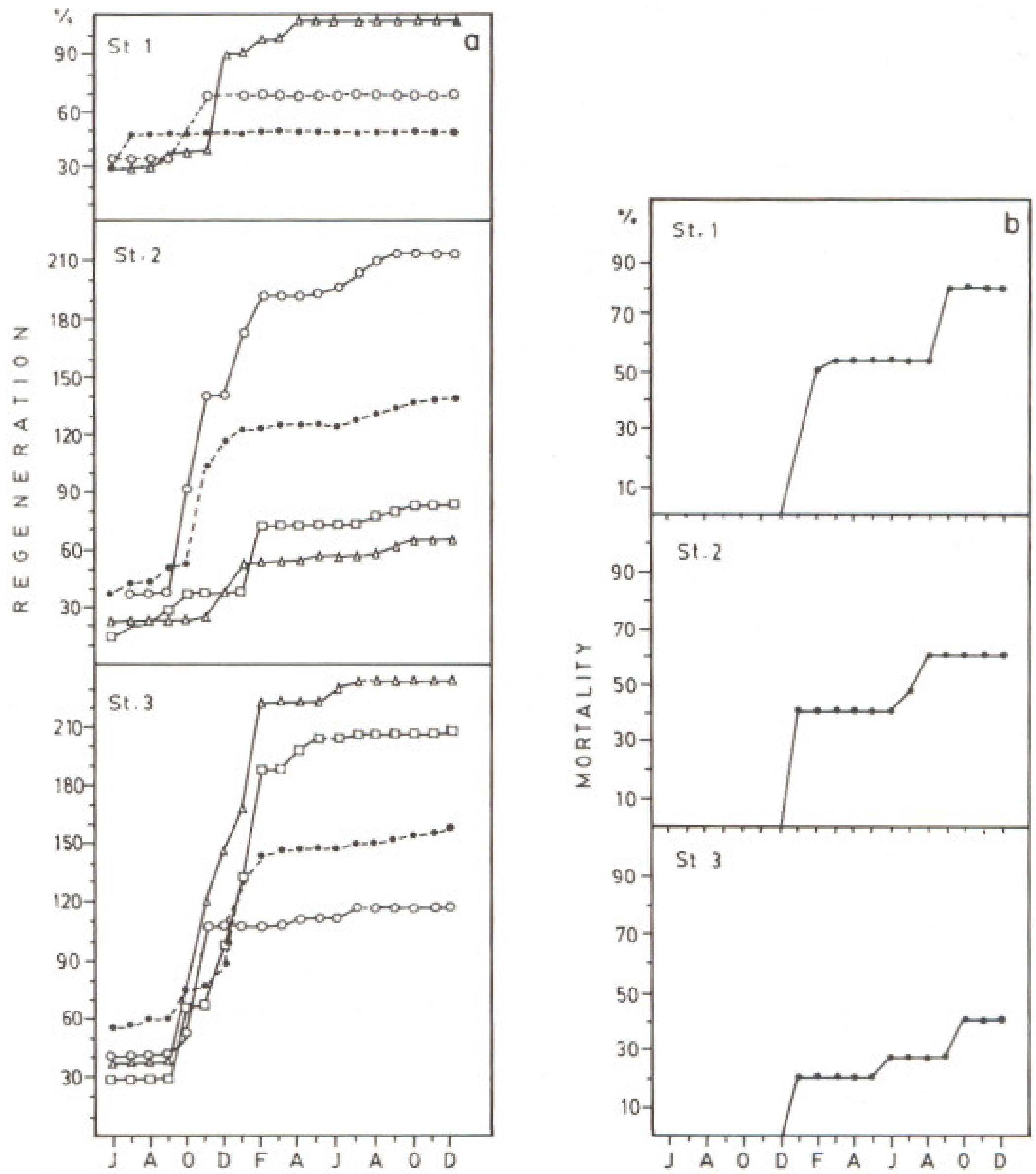

Fig. 8. Net regeneration accumulated (percent) of pruned thalli (a) and mortality in winter (b). o —— o: thalli 0–5 cm; △ —— △: thalli 5–10 cm; □ —— □: thalli 10 cm; ● --- ●: controls.

for four months, after which mortality increased drastically (to 80%) in winter when regeneration is slower.

Figure 10a shows the regeneration of thalli pruned in summer (December). Thalli of 0–5 cm did not regenerate. Six months post-pruning, 90% regeneration was obtained at stations 2 and 3. However, at station 2 regeneration ceases while at station 3 it continues, reaching 95% in the last six months of observations (December 1985). The 5–10 cm thalli at station 1 developed rapidly in the first three months post-pruning, reaching 70% regeneration. Thalli at stations 2 and 3 developed more slowly, reaching maxima of 80–90% in seven months. Regenerations of thalli >10 cm was investigated only at station 2; maximum development

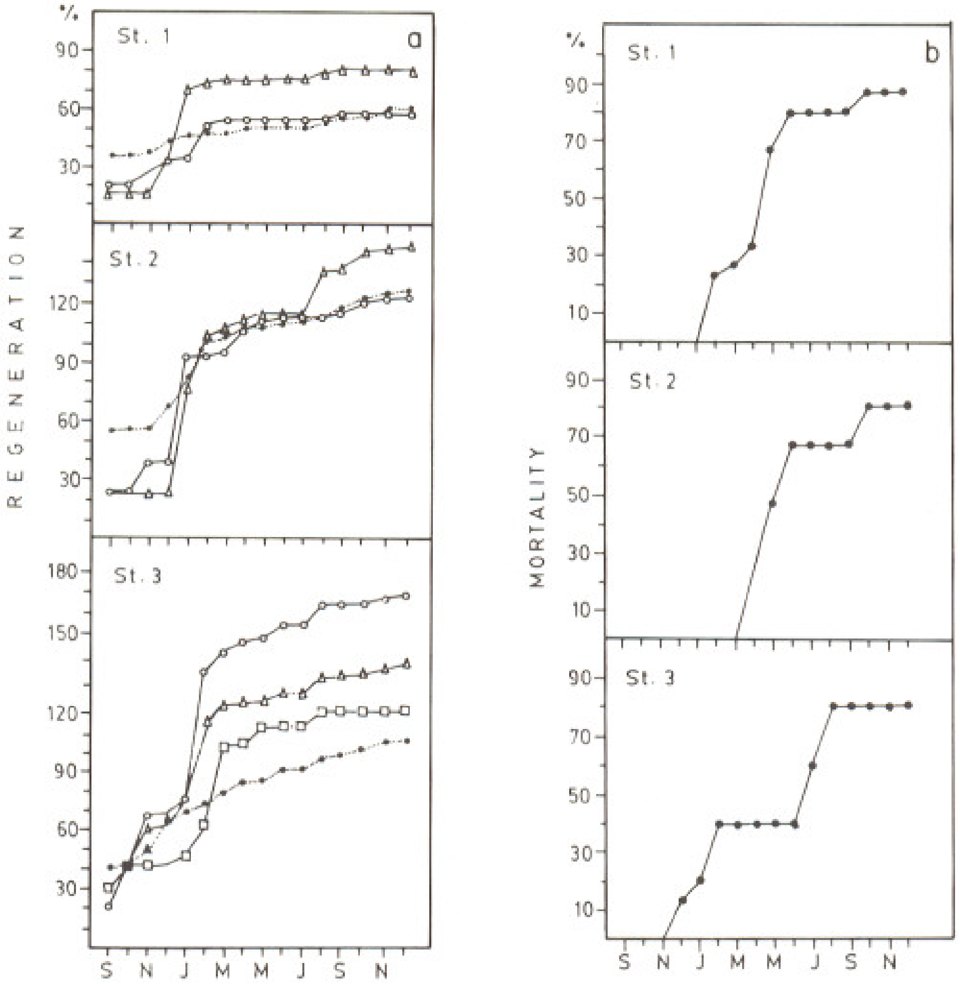

Fig. 9. Net regeneration accumulated (percent) of pruned thalli (a) and mortality in spring (b). ○——○: thalli 0–5 cm; △——△: thalli 5–10 cm; □——□: thalli 10 cm; ●---●: controls.

(100%) was reached after nine months.

The mortality of pruned thalli (Fig. 10b) during the months of rapid regeneration was high in the three stations, reaching 55% at station 1, 50% at station 2 and 80% at station 3.

Regeneration of thalli pruned at the disc

Figure 11a presents variations observed at stations 2 and 3 in the total number of thalli remaining after the treatment with and without removal of formed thalli. At station 2, for the treatment without removal, the total number of thalli formed increases in spring and at the beginning of summer (November–December) to a total of approximately 35. Afterwards, the number of thalli decreases with fluctuations. The periodic-removal experiment gave, at both stations, a sustained increase in the total number up to September–October (station 2, 40; station 3, only 17). In following months, thalli decreased to 5–10 at station 2 and to nil at station 3 in February. For the control group, maximum thallus production was found at both stations in spring and summer, with 112 thalli at station 2 and 80 at station 3. Considering the accumulated net production (Fig. 11b), 100% was reached in 2–3 months, and eventually 350% (station 2) and

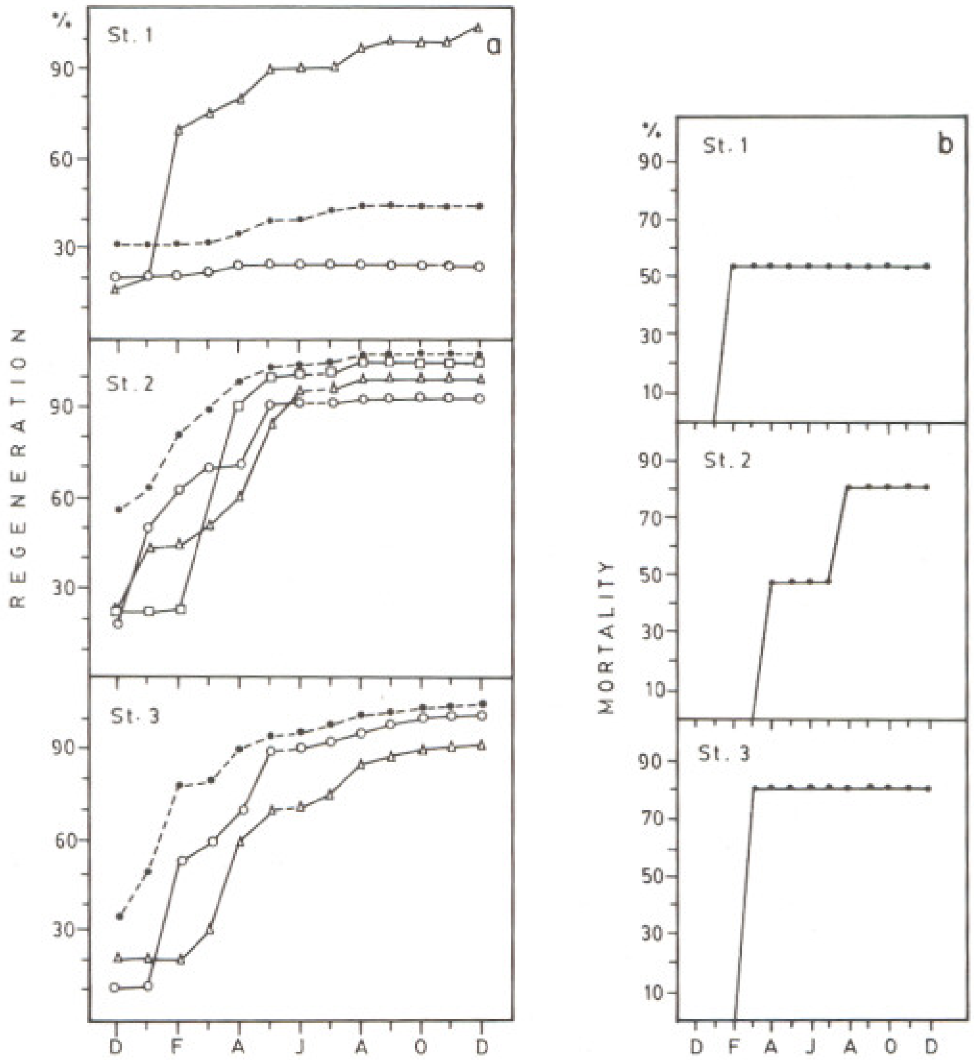

Fig. 10. Net regeneration accumulated (percent) of pruned thalli (a) and mortality in summer (b). ○——○: thalli 0–5 cm; △——△: thalli 5–10 cm; □——□: thalli 10 cm; ●– – ●: controls.

250% (station 3) of the net value was attained. The accumulated net production reached by the control group was less than 230% and 140% for stations 2 and 3, respectively. There was a strong increase in the summer (December–March). During the removal experiments, production was distributed irregularly at both stations (Fig. 11c). At station 2, the maximum value (25%) occurred in June, whereas in the experiment without removal of thalli there was a more homogeneous production with the maximum (25%) being reached during September–October.

During the winter prunings (Fig. 12), the non-removal treatment produced, at both stations, similar maxima of 50–60 thalli in November–December. The removal group also showed maxima in November–December, but thallus numbers were lower. Thereafter there was a decrease in number of thalli, especially at station 2.

By three months post-treatment, accumulated net production had already reached 100% of the monthly increase. This increased considerably during the following months, and reached 270% and 350% in ten months. The situation in the control

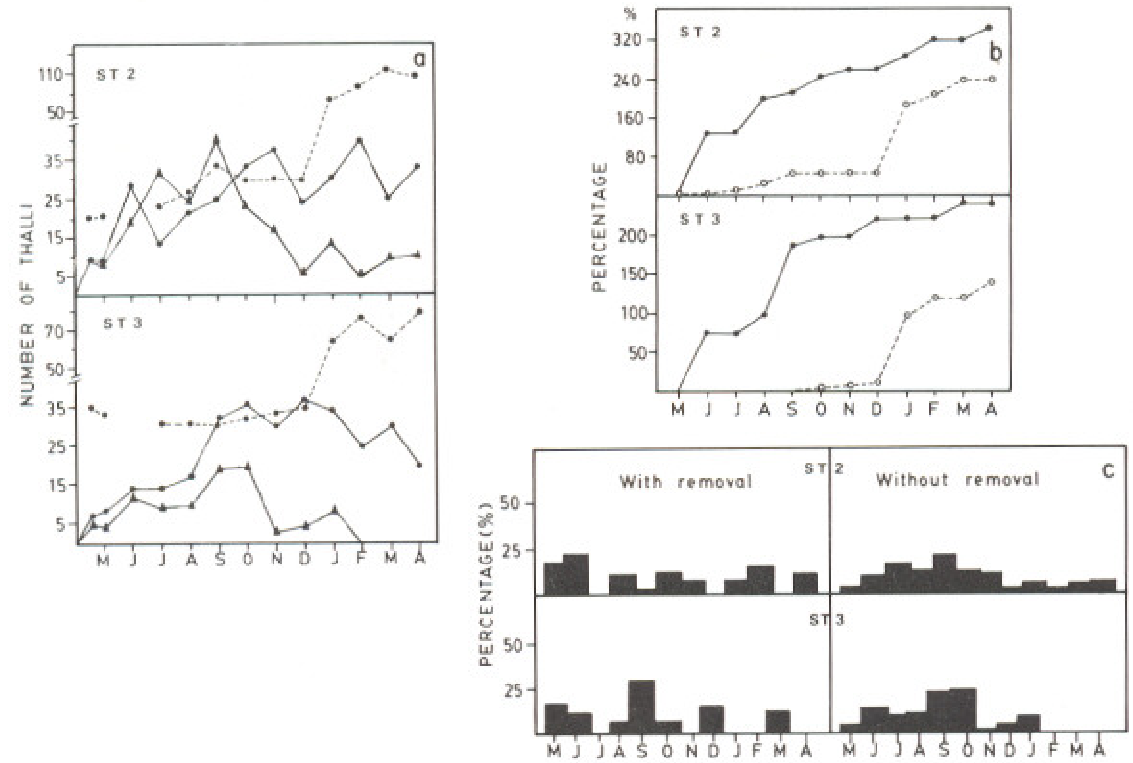

Fig. 11. a) Monthly changes of number of thalli pruned at the crust dics level in autumn. ●--- ●: treatment control; ▲——▲: treatment with removal at thalli; ●——●: treatment without removal of thalli, in station 2 (St 2) and station 3 (St 3); b) Net accumulated percentage of regeneration. o--- o: control; ●——●: without removal, in station 2 (st 2) and station 3 (St 3); c) Monthly changes in number of thalli produced, expressed as percent of total. Station 2 (St 2) and station 3 (St 3).

groups resembles the results obtained in the autumn experiments; during the summer (January–March) these reached 180% and 120% at stations 2 and 3, respectively. The monthly distribution of thallus production for the different treatments is shown in Figure 12c. In the treatment with removal, the greatest percentage of thallus formation occurred in December (48%) at station 2, and in November, with similar values, at station 3. In the experiments without thallus removal, the highest production also occurred in November–December, but did not exceed 25%. Thallus formation was more homogeneous, as has already been observed in the autumn treatment.

Figure 13a shows the results obtained in the spring pruning. The total number of thalli in the non-removal treatment increased progressively until nearly 50 thalli were present at the end of the summer at stations 2 and 3. In the plants with removal at station 2, the same result as for the other treatments was found (Fig. 13b). At station 2, cumulative production in six months was 60% while the control group reached nearly 200% in March–April. Completely different results were recorded at station 3, where at the end of two months, there was an accumulated net of 180%, reaching 280% at the end of the experiment. The control treatment exhibited the same tendency as before (autumn and winter), *i.e.,* the highest net thallus formation occurred in summer and early autumn. The monthly distribution in the numbers of thalli produced is shown in Figure 13c. Plants in the removal experiments showed a maximum production in January at both stations 2 and 3, with those at station 2 showing the highest production (50%). In the removal experiments, thallus for-

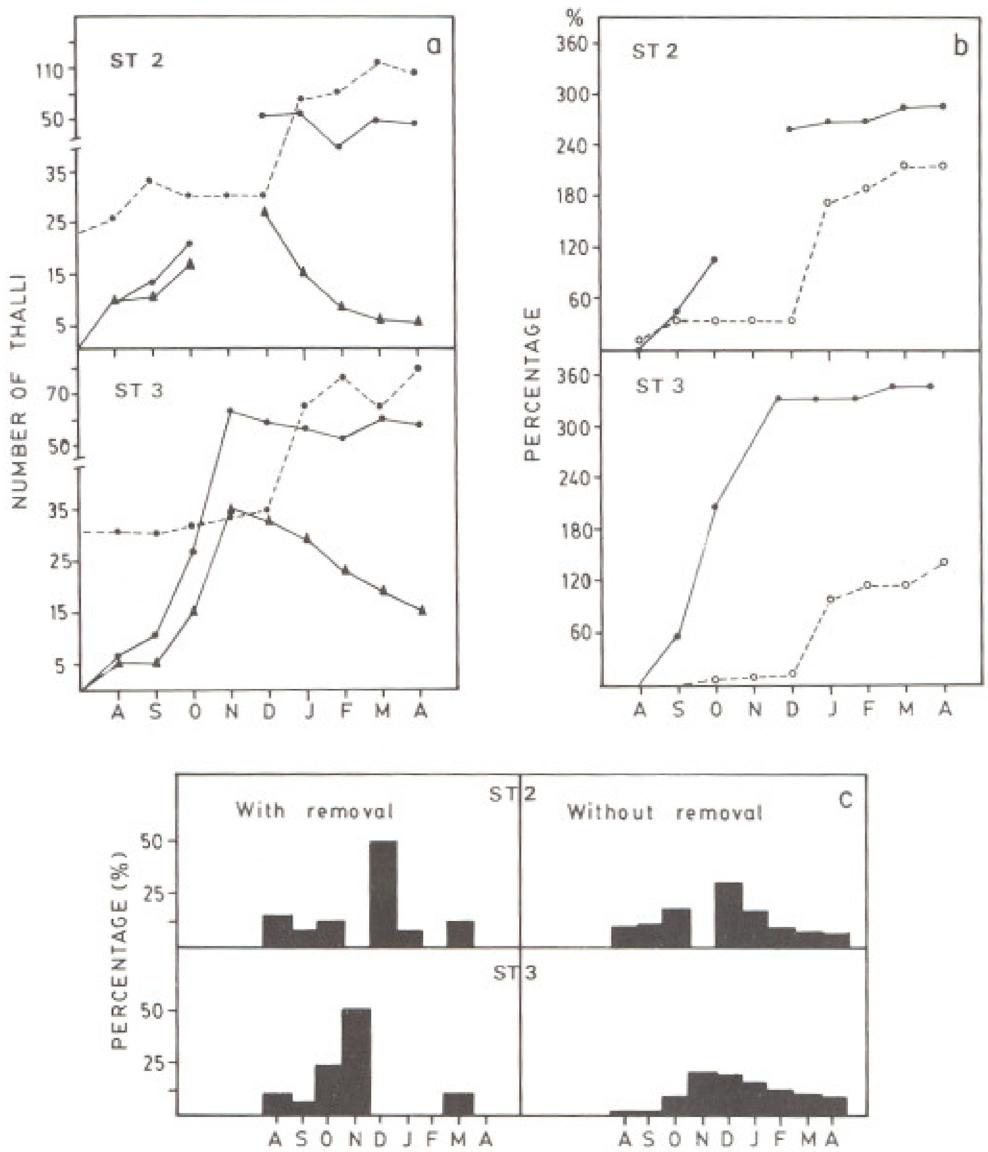

Fig. 12. a) Monthly changes of number of thalli pruned at the crust disc level in winter. ●--- ●: treatment control; ▲—— ▲: treatment with removal thalli; ●—— ●: treatment without removal of thalli, in station 2 (St 2) and station 3 (St 3); b) Net accumulated percentage of regeneration: ○--- ○: control; ●—— ●: without removal, in station 2 (St 2) and station 3 (St 3); c) Monthly changes in number of thalli produced, expressed as percent of total. Station 2 (St 2) and station 3 (St 3).

mation was also homogeneous; the maximum (25%) was recorded in January–April.

Thallus development from crust discs

Figure 14a shows the density of thalli in the removal treatment. This density increases gradually from August to December, when it reaches a maximum of 22 thalli·cm^{-2}. Subsequently there is variability between 15–22 cm^{-2}. Thallus formation was greatest (about 25%) in November, December and March (Fig. 14b).

In the control group (Fig. 15a) the density of thalli was significantly lower. The greatest density was found in summer, and the month with the

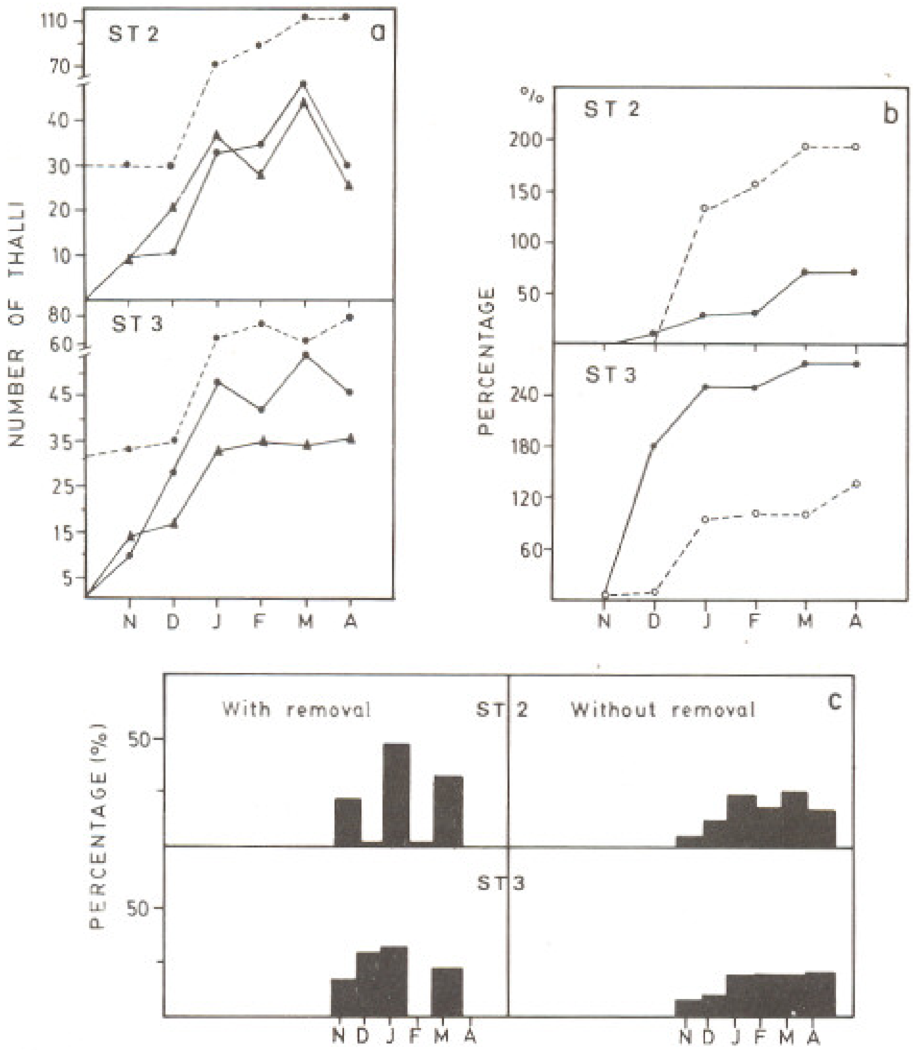

Fig. 13. a) Monthly changes of number of thalli pruned at the crust disc level in spring. ●--- ●: treatment control; ▲—— ▲: treatment with removal of thalli, ●—— ●: treatment without removal of thalli, in station 2 (St 2) and station 3 (St 3); b) Net accumulated percentage of regeneration: ○--- ○: control; ●—— ●: without removal, in station 2 (St 2) and station 3 (St 3); c) Monthly changes in number of thalli produced, expressed as percent of total. Station 2 (St 2) and station 3 (St 3).

highest (6.5 thalli$\cdot$cm^{-2}) was February. June, October and November were the months with the greatest contributions to numbers of thalli (Fig. 15b).

An inverse relation was observed between the number of thalli produced and their size, in both treatments (Figs. 11–14). Thus a greater number of thalli allows the formation of a canopy, which hinders the growth of new thalli form the crust disc.

Discussion

Temporal differences in maximum biomass-covered area and thallus densities indicate that, at the three sampled sites, the main production happens at different times; this suggests that the populations are regulated by different factors. Thus, at station 1, the major biomass occurs near the end of summer (March), whereas the main density of thalli comes in winter. The lack of coincidence between

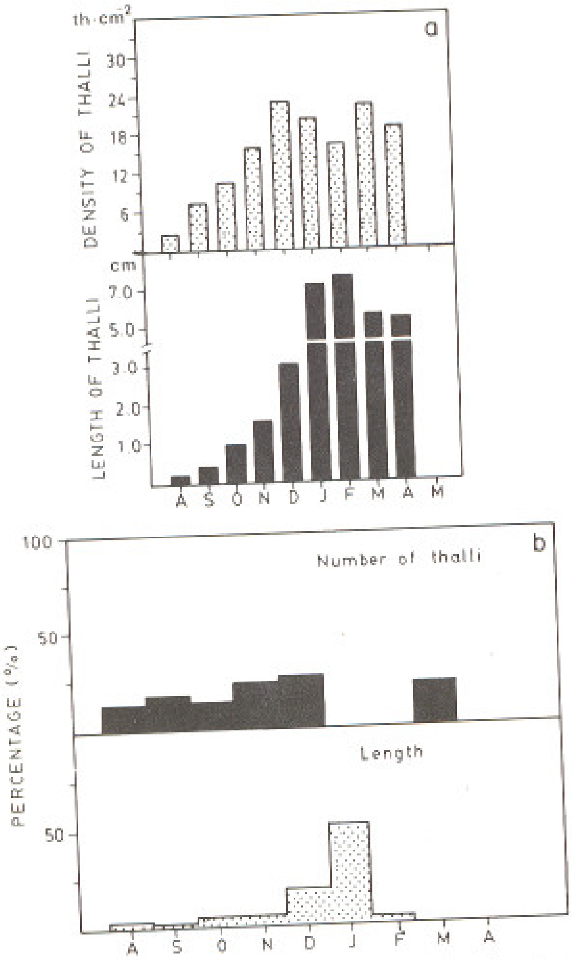

Fig. 14. a) Monthly production of thalli arising from basal crust disc. Treatment with removal of thalli, expressed by length (cm) and density of thalli (th·cm^{-2}); b) Monthly changes of number and length of thalli produced, expressed as percentage of total thalli produced over the year.

biomass and thallus density occurs because at the end of autumn the thalli are longer than 9 cm, whereas in winter the smaller size (0–3 cm) is abundant. As Haug & Jensen (1954) and Westermeier (1982) found for other macroalgae and Westermeier *et al.* (unpubl.) for *Iridaea laminarioides,* the high percentage of protein found in winter is directly related to the presence of young thalli. At stations 2 and 3, on the other hand, the relationship between biomass and thalli density is direct, with maxima in spring and summer. The greatest production of thalli is centered in spring, and the thalli reach their largest size in summer. These differences in production are explained by the results obtained by Jara (1980), Moreno & Jaramillo (1983), Jara & Moreno (1984) and Moreno *et al.* (1984), who demonstrated the importance of herbivory on the abundance of *I. laminarioides,* with the absence of herbivores allowing the dominance of this species after competition with other algae for the monopolization of space and light.

Looking at the results of the pruning experiments, the major productivity is centered in spring and summer, independent of factors regulating the population. It is then that the thalli show greatest growth. Production of thalli from the disc is directly related to density and size. Thus, pruning experiments at the disc level show that these have scant recuperation but originate new thalli which show great development.

The life cycle of *I. laminarioides* is triphasic with alternating isomorphic generations (Candia, 1983). In the southern Chilean populations the three phases are present, without a clear domination by any one. However, the cystocarpic phase is predominant in Central Chile (Hannach & Santelices, 1985). These differences are related to these communities being regulated by different factors, with the presence of a crust disc allowing continuous production of cystocarpic, tetrasporic, and(or) male gametophytic thalli which mature after five to six months. On the other hand, the continuous liberation of propagules allows the regeneration of new thalli. The presence of complex life cycles with stages and(or) heteromorphic phases allows a species to have different life strategies (Lubchenco & Cubit, 1980; Dethier, 1981). In spite of possessing an isomorphic life history, *I. laminarioides* should behave as a species with a heteromorphic life history owing to the presence of the crustose disc.

Based on these results we suggest that the harvest of *I. laminarioides* should be restricted to thalli of larger size to allow the continuous renewal of thalli. Spring and summer months are most favorable for harvest.

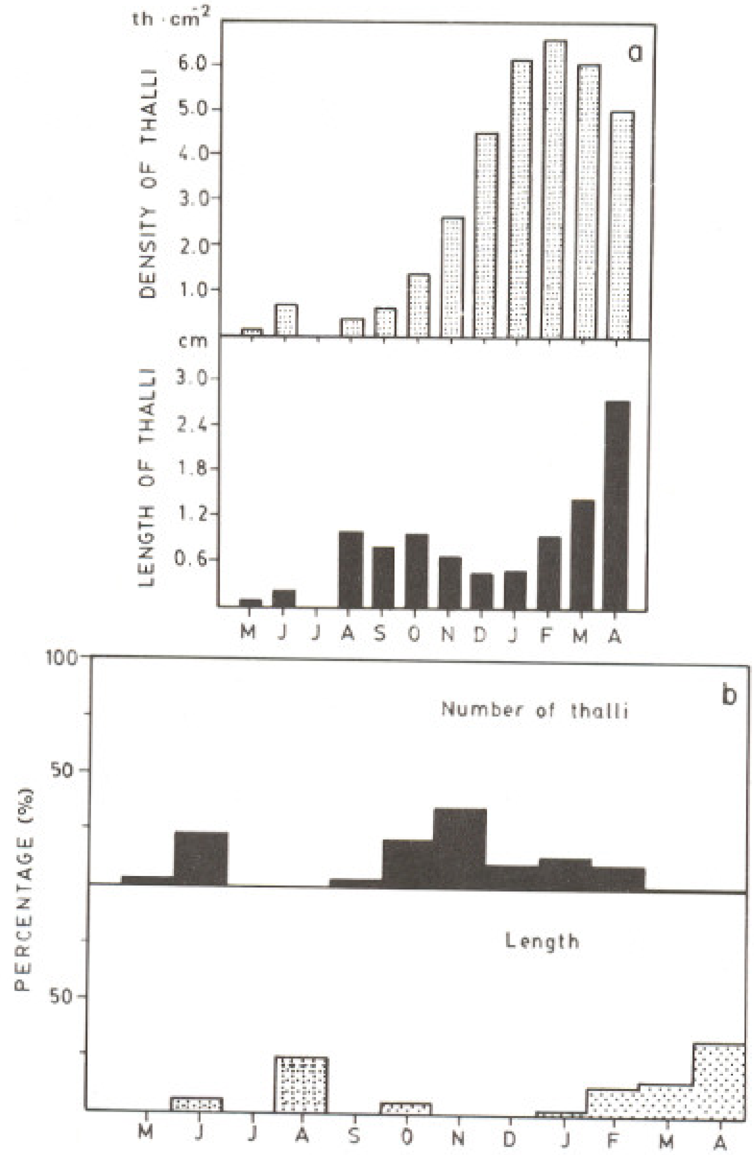

Fig. 15. a) Monthly production of thalli arising from basal crust disc. Treatment control (without removal), expressed by length (cm) and density of thalli (th · cm $^{-2}$); b) Monthly changes in number and length of thalli, expressed as monthly percentage of total thalli produced over the year.

Acknowledgements

This research was done with financial support of the Organization of American States (OAS) through Project CHI-01/84-85 and Dirección de Investigación y Desarrollo of the Universidad Austral de Chile, Grants S-82-37 and RS-82-37. D. Patiño, R. Heitzer, V. Guaiquil, L. Berkoff and G. Peruzzo have greatly contributed during the execution of this study.

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