Competitive Algal Community Organization in Exposed Intertidal Habitats from Central Chile

B. Santelices, S. Montalva and P. Oliger

Departamento de Biología Ambiental y de Poblaciones, Instituto de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Casilla 114-D, Santiago, Chile

ABSTRACT: Measurements of cover in the field indicate that most of the lower intertidal wave-exposed habitats of Central Chile are dominated by the colonial, non-calcareous, crustose chlorophyte *Codium dimorphum*. Summer bleaching of the *C. dimorphum* colonies results in reduction of cover below the 1.5 m intertidal level and disappearance from levels above the 1.5 m mark. This, in turn, results in seasonal distributional changes in mid and upper intertidal species. Field removal experiments indicate that *C. dimorphum* is able to overgrow, exclude and therefore limit the lowermost extent of most other intertidal species. Recovery of *C. dimorphum* and the course of successional events thereafter (followed during 41 months) are affected by seasonal bleaching and grazing. Herbivore exclusion experiments indicate that grazing plays a major role in the seasonal reduction of cover of *C. dimorphum* after initial summer bleaching of the colony. These results are discussed in view of presently accepted hypotheses on intertidal algal zonation, intertidal community structure, successional events and ecological adaptation of non-calcareous crustose algal morphologies.

INTRODUCTION

Studies thus far conducted on intertidal algal zonation in Central Chile are restricted to qualitative descriptions of species distribution and zonation patterns (Guiler, 1959a, b; Alveal, 1970, 1971; Stephenson and Stephenson, 1972; Alveal et al., 1973) with little understanding of the role of climatic and biological factors on zonation and community organization.

Presently accepted models of intertidal community dynamics (Connell, 1975; Menge and Sutherland, 1976) predict little effect of competitive interactions as structuring factors of natural communities in the presence of predators, except when species with escape mechanisms to predations or grazing are involved. Although direct experimental evidence is missing in some cases, large sizes, calcareous cell wall inclusions, chemical defenses, fugitive life histories and crustose habits all have been suggested to be potentially important antiherbivore mechanisms in benthic algae (Paine and Vadas, 1969; Paine et al., 1979; Vadas, 1979; Littler and Littler, 1980). Competitive interactions are therefore expected among these species, as Dayton (1975) found to be the case among large-sized lower intertidal kelps along the Pacific coast of North America. The pertinent literature, however, is inade-

quate for us to estimate how widespread and important these exceptions could be in the organization of marine intertidal systems. Indeed, Menge and Sutherland (1976) have recognized that a key refinement to their proposed model of community organization will be an in-depth examination of the regulation of primary producers.

Most of the space in the middle and lower intertidal levels of rocky, wave-exposed habitats in Central Chile is occupied by the colonial, non-calcareous crustose chlorophyte *Codium dimorphum* Svedelius. This study provides observational and experimental evidence indicating that *C. dimorphum* is one of the key organisms at these intertidal levels. We first studied the seasonal distributional changes of the *C. dimorphum* belt and the effects of these changes on the vertical distribution of other algae. Then we examined algal community changes following *C. dimorphum* removal. Finally we experimentally evaluated the role of crust integrity as a grazing escape mechanism and its importance as a factor organizing this intertidal algal community. In so doing, we describe, for the first time, successional events in intertidal habitats of temperate Pacific South America, evaluate the tenability of several general hypotheses on intertidal algal zonation (Doty, 1946; Connell, 1961; Lubchenco, 1980) and

examine some of the ecological adaptations of non-calcareous, crustose algal morphology. So far as we are aware only Paine et al. (1979), and more recently Lubchenco and Cubit (1980) and Slocum (1980), have experimentally attempted to determine some of the ecological properties of this type of algal morphology.

Study Area

The study area at Pelancura is located 5 km north of Port San Antonio in Central Chile (33° 35′ S Lat.; 71° 38′ W Long; Fig. 1). It consists of rocky platforms receiving the full force of storm-generated waves and experiences the direct effect of onshore waves. The zonation pattern of these exposed rocky habitats is similar to the patterns described by Guiler (1959b);
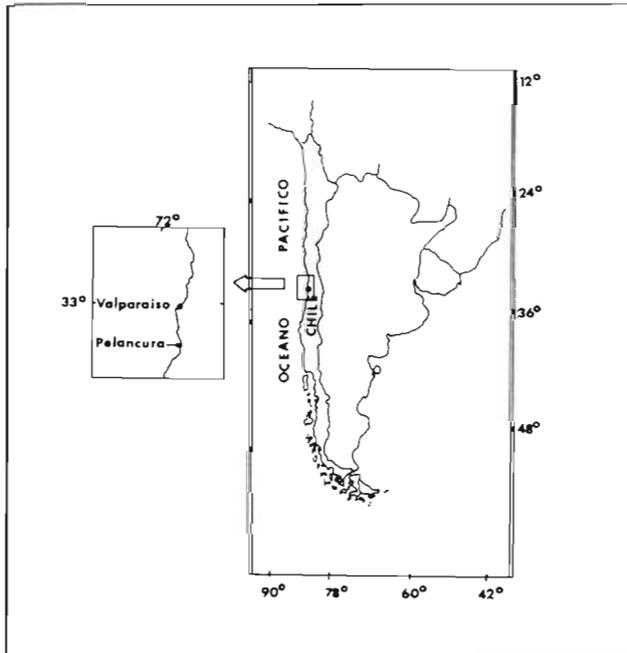

Fig. 1 Location of study sites in Central Chile

Alveal (1970) and Stephenson and Stephenson (1972) for other exposed localities in Central Chile. The sublittoral fringe is characterized by 2 species of large, kelp-like Phaeophyta (Lessonia nigrescens Bory and Durvillea antarctica [Chamisso] Hariot). A 50–100 cm wide zone of Codium dimorphum normally occurs immediately above the L. nigrescens – D. antarctica association while the middle and upper intertidal are characterized by pure or mixed populations of Perumytilus purpuratus (Lamarck), Chthamalus spp. and several filamentous or frondose algae such as Ulva rigida (C. Agardh) Thuret, Iridaea boryana (Setchell and Gardner) Skottsberg, Enteromorpha compressa (Lin-

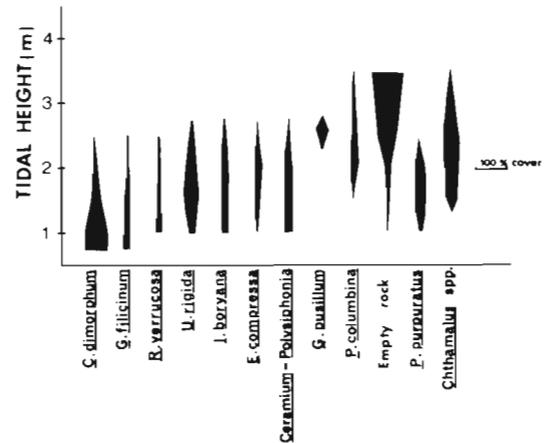Fig. 2. Zonation pattern above the Lessonia nigrescens – Durvillea antarctica belt in exposed rocky intertidal habitats of Central Chile. The zonation pattern represents average cover values of 144, ¹/₄ m² quadrats measured during a 13 month sampling program. See methods for further details

naeus) Greville and Porphyra columbina Montagne (Fig. 2). Much free primary space ('Empty rock' in Fig. 2) normally occurs at the middle and upper intertidal levels in these exposes habitats. No free primary space is normally available at the lower level of the C. dimorphum belt. Although Gelidium filicinum Bory is locally abundant, the C. dimorphum colonies normally extend as a continuous, flatgreen cover at this level.

MATERIALS AND METHODS

Temporal changes in space occupancy by benthic macro-algae and sessile macro-invertebrates were determined monthly with reference to tidal height. Two permanent transects (1 m wide each) extending from the upper intertidal to the Lessonia nigrescens – Durvillea antarctica belt were initially established at the study site. The distance between the transects was 4 m, their total extent 4–6 m. Six square quadrats (¼ m²) were systematically sampled along each transect at 0.5 m intervals. Vertical height of each quadrat with respect to the mean low water level (MLWL) was determined using stadia rod, inclinometer and predictions of tidal heights of the locality (Anonymous, 1976, 1977, 1978, 1979). Each quadrat had 81 points at 5 cm intervals which were used to measure cover values of intertidal organisms by the point intercept method. Percent cover values were averaged for those quadrats within each 0.25 m tidal height interval. Overall percent cover values for each species were calculated as the grand mean of all 0.25 m interval averages. Sampling was repeated monthly from October 1976 to October 1977.

To test for the effects of *Codium dimorphum* removal on intertidal algal community structure, six 625 cm^2 permanent quadrats were established in May 1976 on rocky surfaces at the level where *C. dimorphum* had the highest cover values (between 0.5 and 1.5 m above MLWL). The portion of the *C. dimorphum* colony inside the quadrat was manually removed and the rocky surface throughly scraped with an iron spatula and wire brushes. Colonization and species turn-over were followed monthly in these experimental plots up to October 1979. Pertinent comparisons with 6 undisturbed, previously marked control plots were performed monthly. A similarity index (Bray and Curtis, 1957) was used to measure the monthly degree of average change in the experimental plots. In general, low similarity values between the experimental plots and control plots indicate invasion of upper intertidal algae into the experimental plots. In contrast, high similarity values between the experimental plots and the *C. dimorphum* control quadrats were taken to indicate space recovery by *C. dimorphum* colonies and exclusion of other intertidal algae from the experimental plots. The Bray and Curtis' similarity index was selected to allow for pertinent comparisons with recent recolonization studies at an approximately similar latitude on the Pacific coast of North America (Murray and Littler, 1978).

As the study progressed, field evidence indicated that crust integrity reduced the susceptibility of *Codium dimorphum* colonies to herbivores. Crust discontinuities might allow time for the recruitment or migration of herbivores which would reduce the growth rate of the colony and slow down the recovery rates of newly vacated surfaces. To test for this hypothesis, removal experiments were repeated at the level where *C. dimorphum* had dominance using six 100 cm^2 removal quadrats. Three quadrats, randomly selected, were protected from herbivores (*Siphonaria lessonii* Blainville, *Collisella zebrina* [Lesson]; *Tegula atra* [Lesson] and *Chiton granosus* Frembly) with metalic exclusion nets (cages with no roofs); the other 3 quadrats being used as control of herbivore effects on growth rates of *C. dimorphum* colonies. The area of the cleared surface covered by the regrowth ot the *C. dimorphum* colony after a given period was measured in the field using plastic sheets and planimeter and then calculated as the percent of the original surface. Measurements were performed in the 3 replicates for each experimental condition at irregular intervals during the 6 first months after *C. dimorphum* removal. To test for interactive effects of grazing with abiotic seasonal events, independent sets of experiments were started at 2 different times of the year. One was set early in the fall (May, 1979) and extended through winter and early spring (October, 1979). A second set was started early in spring (September 15, 1979 and lasted up to late summer (March, 1980).

RESULTS

Temporal Changes in Vertical Distribution of Intertidal Algal Species

Seasonal variation of *Codium dimorphum* includes both total vertical extent and percent cover values for a given vertical level (Fig. 3). During winter, the species can reach up to 2.5 m above MLWL while its upper vertical limit does not extend beyond the 1.5 m level during late spring and summer. In the vertical distance between 0.5 and 1.5 m above MLWL, *C. dimorphum* forms a permanent belt with percent cover values ranging from 35 % in January to 62 % in July (Fig. 3). *Gelidium filicinum*, the other permanent species at this level, normally has lower percent cover values (maximum: 20 % in January).

During late spring and summer, the borders and the surface outgrows of the *Codium dimorphum* colonies start to bleach. Above the 1.5 m level much of the *C. dimorphum* belt disappears and the space is occupied by a diverse group of upper intertidal algal species such as *Ulva rigida*, *Iridaea boryana*, *Ceramium* sp., *Polysiphonia* sp. and *Enteromorpha compressa*. Below the 1.5 m level, the continuous *C. dimorphum* belt can become locally discontinuous and irregularly shaped. Individual colonies can now be recognized, many of them also with bleached borders. *Iridaea boryana*, *Ulva rigida* and *Ralfsia verrucosa* (Areschoug) J. Ag. are the primary space users after summer reduction of *C. dimorphum* below the 1.5 m level. The inverse relationship found between percent cover values of *C. dimorphum* and other benthic algal at different intertidal levels are shown in Fig. 4. Only the negative correlation between *C. dimorphum* and other algae cover values found 1 m above MLWL is statistically significant ($p \ll 0.01$).

The middle and upper shore levels (above 1.5 m MLWL) are dominated by invertebrates: *Perumytilus purpuratus* (Lamarck), *Chthamalus cirratus* Darwin and *Chthamalus scabrosus* Darwin; their vertical extent varies little throughout the year. *Ulva rigida*, *Iridaea boryana*, *Enteromorpha compressa* and *Porphyra columbina* are also important as primary space users (Fig. 3). Although a given thallus of any of these algal species does not persist at this level through the year, each species continuously occupies space through successive generations. Much free space is available for algal growth through most of the year (from 5 % in September to 25 % in December at 2 m above MLWL and 60 % in October to 90 % in January

at 3 m above MLWL). This is the reason why the negative correlations between *C. dimorphum* and other algae (Fig. 4) have no statistical significance at higher intertidal levels.

In summary, the 13 months of study on space utilization patterns at the exposed intertidal rocks of Pelancura indicate that: (a) *Codium dimorphum* is the dominant species at the level immediately above the *Lessonia nigrescens – Durvillea antarctica* belt; (b) space occupied by the *C. dimorphum* colonies below the 1.5 m intertidal level is reduced during the summer, and the species also disappears from the levels above the 1.5 m mark; (c) under these circumstances, other middle upper intertidal algal species, especially

Ulva rigida and *Iridaea boryana*, can extend their vertical distribution substantially, modifying their lower limits of intertidal algal zonation.

Experimental Removal of *Codium dimorphum*

The average percent cover values of several intertidal organisms found at different successional times during the 41 months of study are shown in Fig. 5. In total, 16 algal and 2 sessile invertebrate species occurred in the experimental plots; all of them are normally inhabitants of the upper intertidal. During the first months, diatoms and blue green algae invaded the
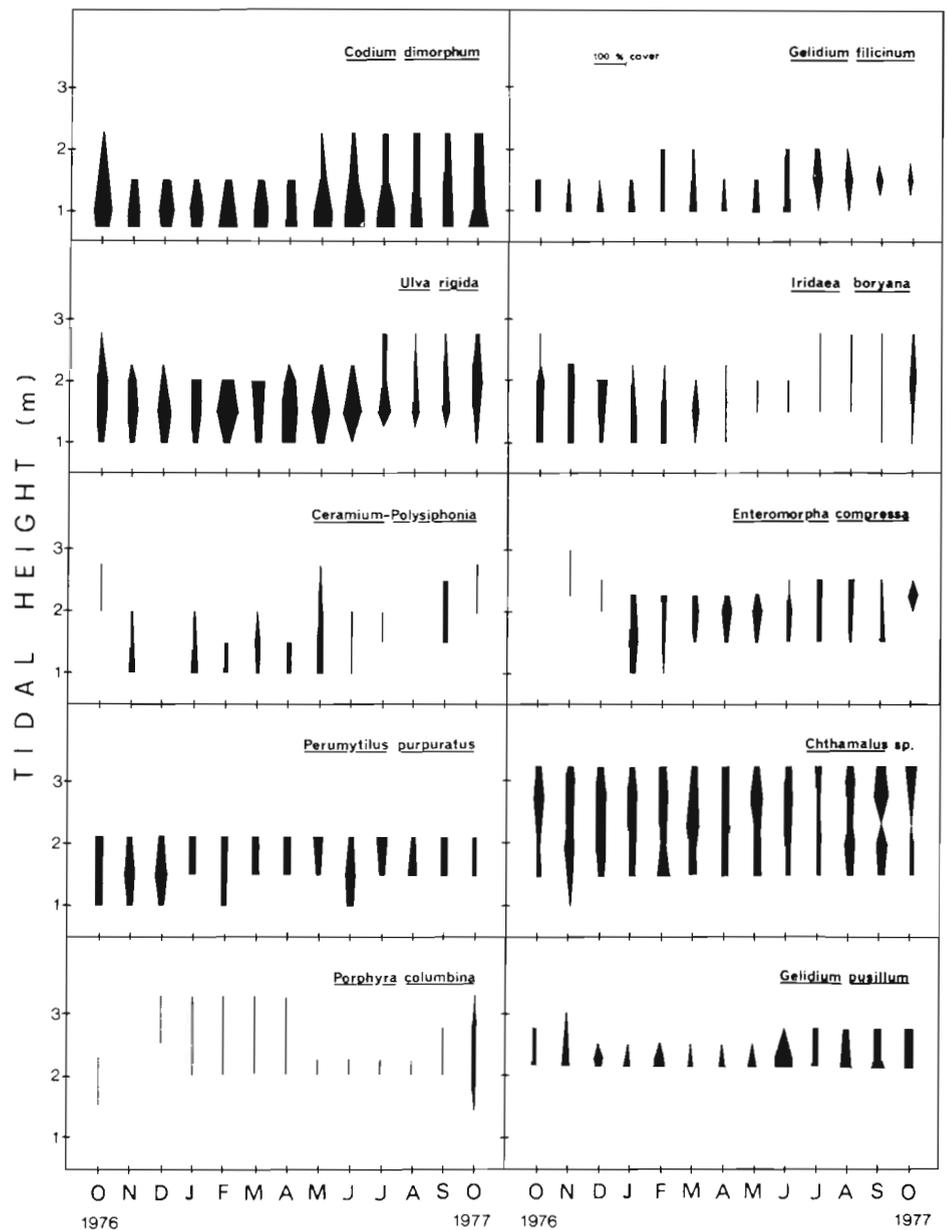

Fig. 3. Temporal changes of percent cover of the commonest intertidal species of algae and sessile invertebrates found on exposed rocky intertidal habitats of Central Chile at the Pelancura study site
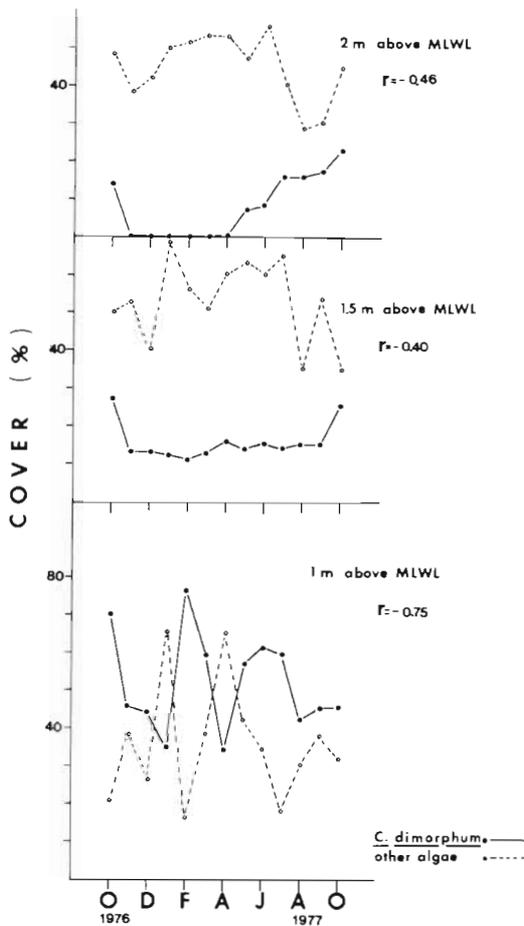
Fig 4. *Codium dimorphum* and other intertidal benthic algae in exposed rocky intertidal habitats of Central Chile. Correlation values equal or above 0.553 and 0.684 are significant at 5 % and 1 % levels respectively

quadrats covering 100 % of the rocky surface. These organisms were rapidly replaced by *Polysiphonia* sp., *Porphyra columbina*, *Ulva rigida* and *Iridaea boryana*. *Codium dimorphum* and small individuals of *Gelidium pusillum* (Stack.) Le Jolis appeared as early as 8 months after clearing the *C. dimorphum* dominated space. Eleven months after removal (April, 1977) *C. dimorphum* had recovered an average of 5 % of the rocky surface. No further changes in *C. dimorphum* cover values occurred up to October 1977. However, seasonal bleaching started affecting the colonization process at this time and new, empty primary space was produced by summer die-back of the borders of the colony of *C. dimorphum*. For November 1977, *C. dimorphum* covered on an average only 20 % of the surface of the experimental plots, decreased to 10 % during December, and disappeared during February 1978 (Month N° 21).

Seasonally-affected successional events were followed for the next 20 months, at which time the experi-

ments were discontinued, with no evidence of *Codium dimorphum* increasing its average percent cover. Only on 2 occasions during the whole study (April-October 1977 and December 1978) were the *C. dimorphum* percent cover values close to the values normally found at this level of the beach. These values, however, were later reduced by bleaching of the *C. dimorphum* colonies.

A similar conclusion is obtained when similarity values (Is) are calculated (Fig. 6) comparing the community structure of the removal plot with the lower intertidal *(Codium dimorphum)* control plots. The increase in average of *C. dimorphum* percent cover in the experimental plots during most of the year 1977 results in high similarity values between the experimental plots and the control plots. The summer bleaching of the *C. dimorphum* colonies during October-December 1977 affected the experimental plots more intensely and produced a major decrease in the average *C. dimorphum* percent cover. The Is values between the experimental and the control plots, therefore, decreased and reached zero similarity for January 1978. For most of 1978 the Is values remained quite low, rising again the next spring (December 1978) and then decreasing. The Is values found between March and October 1977 are essentially similar to Is values found between March and October 1979.

Growth and persistence of *Codium dimorphum* in the experimental plots (e. g. between April and October 1977; May-September 1978) occurs at seasons with reduced solar radiation and temperature (Fig. 6). Die back of *C. dimorphum* colonies occurs at times of increased solar radiation and temperatures and extreme low water level (e. g. November 1977 – March 1978; January 1979 – May 1979). Only on one occasion (December, 1978) did the experimental *C. dimorphum* removal quadrats evidence high growth rates at times of high solar radiation and increased water temperature. At that time, however, the monthly average day time extreme low tide level was above 0.35 cm thus allowing growth of the experimental *C. dimorphum* colonies. A similar relationship occurred in February 1976 (Fig. 4 and Anonymous, 1976). Therefore, the seasonal bleaching of *C. dimorphum* seems regulated by an interaction of at least 3 climatic factors: solar radiation, seawater temperature and day time low tide.

In summary, these removal experiments show that: (a) Within a year after removal, all upper and middle intertidal algal species and 2 of the 3 invertebrate species can occupy the newly vacated space which is dominated by extensive *Codium dimorphum* colonies under undisturbed conditions. (b) The recolonization pattern indicates that *C. dimorphum* can replace these species. However, recovery of *C. dimorphum* is strongly affected by bleaching of the borders of the

colonies and even 41 months after removal, *C. dimor-phum* was unable to recover its original value. (c) On at least 2 occasions during these 41 months (April to October 1977, December 1978), experimental *C. dimorphum* cover values were close to the undisturbed *C. dimorphum* values (highest Is values). Climate permitting (e. g. a delayed summer), it is likely that regrowth of *C. dimorphum* could completely cover that vacated space.

Experimental Studies on Grazing

The removal experiments indicated that free primary space is available during the first months after *Codium*

dimorphum removal (Fig. 5). Field observations imply that the average number of grazers seemingly increased after *C. dimorphum* removal, concentrating and browsing in the newly created edges of the colony. Fig. 7 compares growth rates (as percent of the originally emptied surface covered by *C. dimorphum* regrowth) on removal plots with and without herbivores exclusion, at 2 times of the year. If the growing borders of *C. dimorphum* are protected by exclusion meshes, recovery rates are faster. The effect, however, is most pronounced and statistically significant ($p \ll 0.01$) in the experiment started in early spring. In that case, *C. dimorphum* recovery rate progressed fast
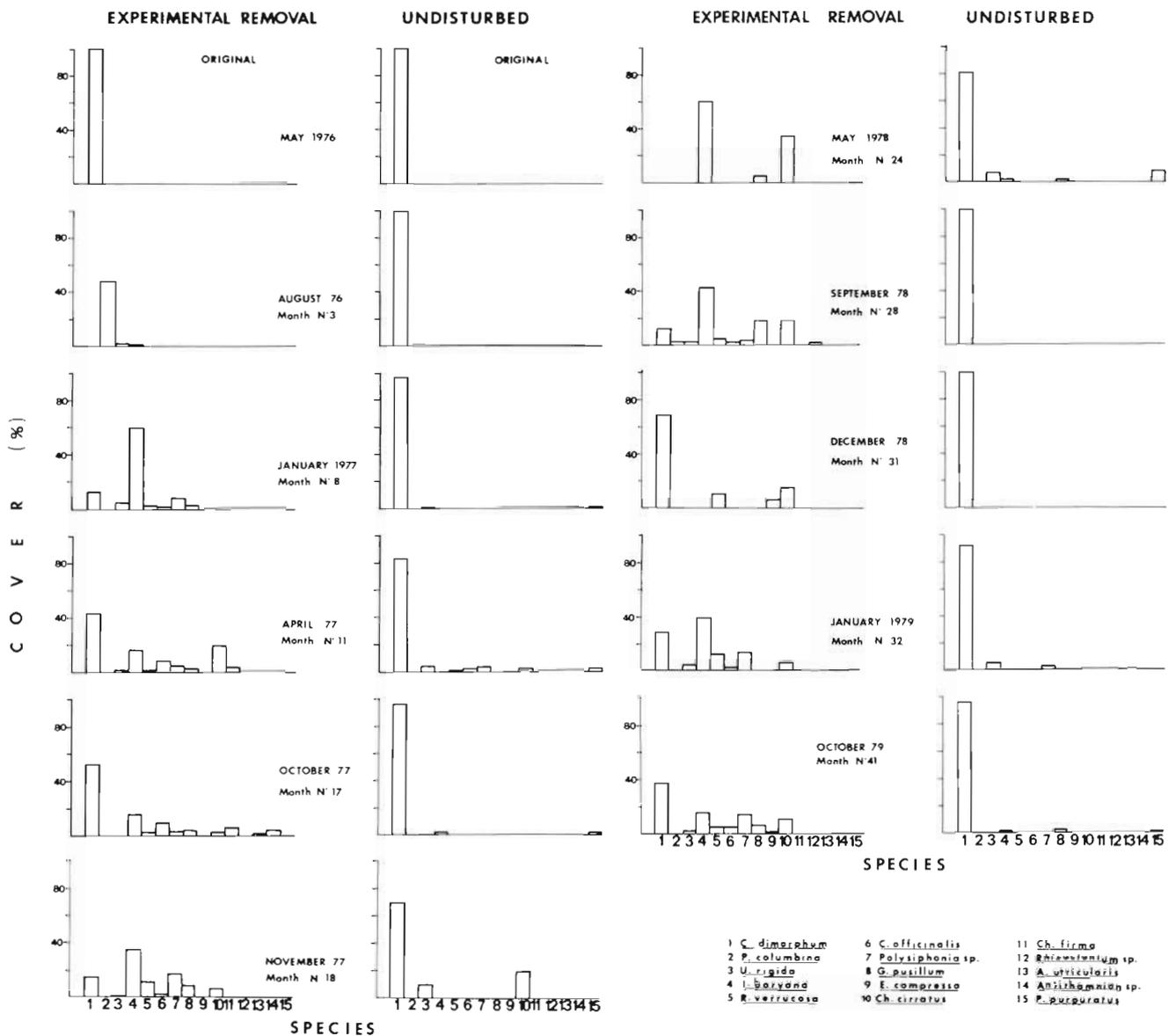

Fig 5. *Codium dimorphum* removal experiments. Species turn over in experimental and control plots at selected months during the 41 month study period. Percent cover estimates the mean from six 625 cm² quadrats for both removal and control plots. *Scytosiphon lomentaria* and *Bryopsis rhizophora* were occasionally found in the removal plots (Months 6 and 9 respectively)
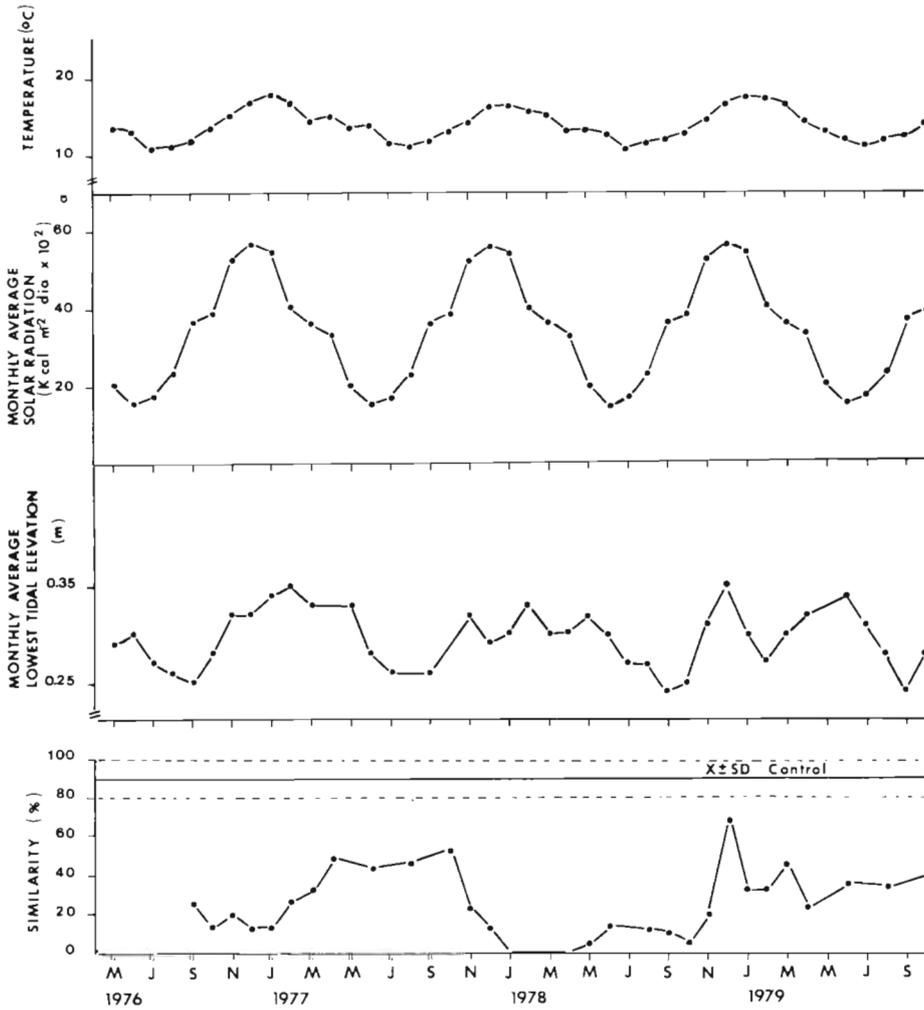
Fig. 6. *Codium dimorphum* removal experiments. Temporal changes in similarity index value (Is) between experimental plots (removal) and control plots. $\overline{X} \pm$ S. D.: average Is of control plots over the whole study plus standard deviations

up to November 1979, after which time seasonal bleaching occurred. Reductions in *C. dimorphum* cover values during late summer strongly affected the quadrats without herbivore exclusion meshes and only slightly the quadrats with exclusion mesh, suggesting that an important part of the reduction of *C. dimorphum* percent cover values during summer could be due to grazing after initial bleaching of the colony borders. Field observations indicate that bleaching disrupts crust continuity creating new borders for

grazer attack. Browsing from the borders of the colony reduces total *C. dimorphum* cover during this time of the year.

DISCUSSION AND CONCLUSIONS

Even though the problem of zonation patterns of intertidal organisms has been known since Lamouroux (1824) remarked on the phenomenon, much of the
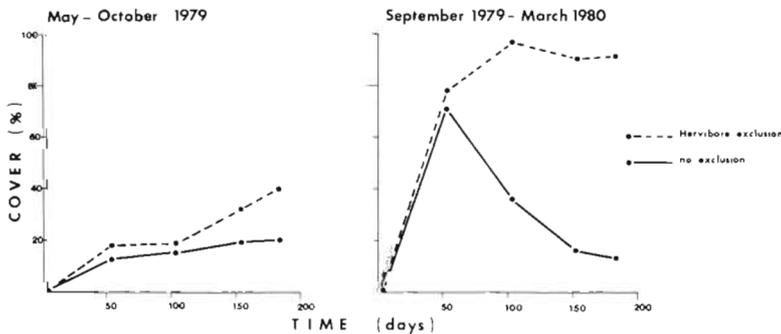

Fig. 7. *Codium dimorphum*. Comparative growth rates in removal experiment, protected or unprotected from grazing

literature has been concerned with its description rather than its explanation. This is especially true for Pacific South America where most studies have been descriptive. Since the pioneer studies by Connell (1961), zonation patterns in general are recognized to be the result of the effects of physical and biological factors: lower limits of organisms are, in general, set by biological factors, while physical parameters such as desiccation are important in the determination of the upper limits of organisms. Recently, however, Lubchenko (1980) has reviewed the evidence concerning upper limits, among other reasons because Cubit (1975) had found that grazing could have a significant role in the determination of upper rocky intertidal limits of benthic algae. The results gathered in this research point to the effects of an interaction of at least 3 types of factors (climate, predation and competition) in the determination of relative importance and upper limits of *Codium dimorphum* in the intertidal habitats of Central Chile. During spring and summer, increased light intensity and temperatures, coupled with increased frequency of extreme day-time low tides, bleach the *C. dimorphum* colonies disrupting crust continuity and creating new borders susceptible to grazer attack. Percent cover of *C. dimorphum* is thus reduced in the lower intertidal levels of the belt and the plant completely disappears from the middle intertidal levels. During fall, winter and early spring decreased light intensity and temperature, and reduced frequency of extreme day-time low tide allows *C. dimorphum* growth. Its cover increases in the lower intertidal and extends as discrete, discontinuous patches, into the middle intertidal. The invasion of upper levels of the *C. dimorphum* belt by this species at this time of the year probably results from a superior competitive ability with respect to other algal species. In the same manner it dominates successional events after its removal from the low intertidal.

There are not yet enough data available to explain what determines the lower limit of the *Codium dimorphum* zone in Central Chile. As mentioned earlier, in exposed habitats the lower limit of the *C. dimorphum* zone coincides with the *Lessonia nigrescens – Durvillea antarctica* zone. Previous studies (Santelices, 1979; Santelices et al., 1980) and ongoing research point to a multiple interaction where grazing on *C. dimorphum*, and the effects of desiccation and predation on juveniles of *L. nigrescens* are all factors to be considered. In an analogous way, the present results also indicate that the lower limits of other frondose intertidal algae (especially *Ulva rigida* and *Iridaea laminaroides*) are determined by the upper limit of *C. dimorphum* and therefore also by a complex of several, biotic and abiotic factors.

The findings on *Codium dimorphum* allow an evaluation of some of the presently accepted general theory explaining organization of biological communities. Menge and Sutherland (1976) have proposed a general, simple model, critically evaluating the roles of competition and predation as structuring agents. Their model predicts little effect of competition on the determination of the importance of organisms of low trophic levels (including the primary producers), except in species with escape mechanisms. In such species, it was proposed that predation could play a major role only during recruitment, thereafter the population numbers being regulated by competition. In other words: after recruitment, populations of algal species
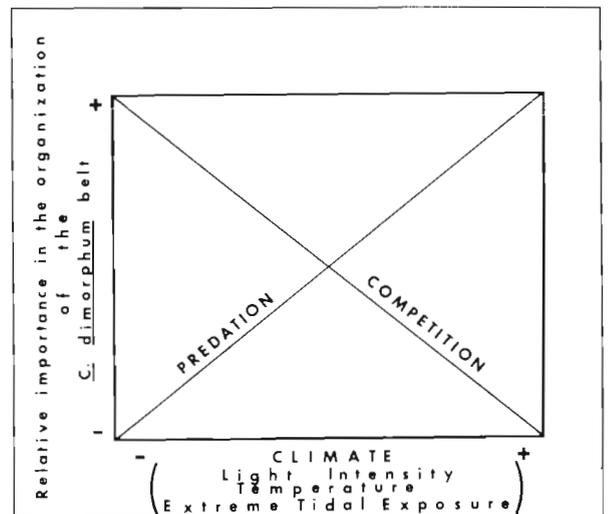

Fig. 8. *Codium dimorphum*. Model predicting the relative importance of climate (light intensity and extreme day time low tide), predation and competition on the growth and vertical distribution of the colonies in exposed intertidal habitats of Central Chile

with escape mechanisms should be expected to function as if they were at a 'relatively' high trophic level and not regulated by herbivores. Our results indeed indicate that *C. dimorphum* colonies should have a 'minimum size', representing the minimum able to tolerate grazing by the middle and upper intertidal grazers of Central Chile. However, from that size up, the importance of predation or competition as structuring agent would depend on climate (light intensity, temperature and extreme day time low tides) as proposed in the model shown in Fig. 8. Crustose habits have been supposed to constitute a grazing escape mechanism in benthic algae (Paine and Vadas, 1969; Paine et al., 1979; Vadas, 1979; Littler and Littler, 1980). However, in *C. dimorphum* crustose growth depends heavily on climate. Therefore, escape is

incomplete, and the Menge and Sutherland (1976) model does not strictly apply to this species.

Sixteen algal species settled in the experimental plots following *Codium dimorphum* removal. Several of them never had been found previously at that tidal level. In essence, many other intertidal species occurring above the *C. dimorphum* level are able to fully colonize and persist in the cleared plots. Their normal occurrence is restricted to the middle and upper intertidal levels and should be interpreted as being due to overgrowth and exclusion by *C. dimorphum* rather than to the effects of physical parameters. These results emphasize the role of competitive interactions in the organization of low intertidal algal communities. So far Burrows and Lodge (1950), Dayton (1975), Lubchenko (1980), Santelices et al. (1980) and Schonbeck and Norton (1980), all have pointed to the occurrence of competitive interactions and evaluated their importance in intertidal algal communities.

As in many other studies on successional events everywhere, diatoms and blue-green algae were the earliest colonizers in all clearing experiments at Pelancura. Most previous studies predicted that the sequence of events in the process thereafter seems to be largely set by seasonality (Northcraft, 1948; Fahey and Doty, 1949; Fahey, 1953; Huvé, 1953; Guiler, 1954; Dayton, 1971; Connell, 1972; Emerson and Zedler, 1978). This is so because different organisms reproduce at different times and their reproductive propagules are more ready to colonize the newly exposed area. In the case of *Codium dimorphum* removal, the time of year is most important, however, in relation to the number of months available for *C. dimorphum* growth before summer bleaching starts. If the growing season for *C. dimorphum* is long enough to recover the newly vacated surface, the continuous crustose cover is nearly completed. If the growing season is too short, *C. dimorphum* does not complete a continuous crustose cover on the vacated surface and is strongly affected both by bleaching and subsequent grazing of the colony borders. Our results show that at least at 2 times (April-October 1977 and December 1978) during the 41 month study the *C. dimorphum* values in the experimental plots were quite similar to those in the control areas.

For the same reasons, size of disturbance patch should be important in successional events after *Codium dimorphum* removal. Previous studies by Moore (1939), Northcraft (1948) and Connell (1972) among others also called attention to this factor. In our case it could be predicted that the larger size of the disturbance, the longer the time needed to recover the vacated surface, and the higher the probabilities of the whole process being affected by seasonality and predation. Size of disturbance probably has, in addition, a close relationship with the type of grazing disturbance that can be overcome by *C. dimorphum*. The size of crust discontinuities produced by small-sized grazers at the level where *C. dimorphum* occurs *(Collisella zebrina, Siphonaria parasitica)* never reach more than 5 cm^2 in surface area and this is probably easily overgrown by *C. dimorphum*. On the other hand, *C. dimorphum* is normally absent from lower tidal levels where larger-sized grazers normally occur (e. g. large chitons such as *Acanthopleura echinata* (Barnes) or sea urchins such as *Tetrapygus niger* or *Loxechinus albus* (Molina). Experimental evidence is missing to test this mutually exclusive relationship, but the data on growth patterns of *C. dimorphum* allow us to predict such a relationship.

Recently, Lubchenko and Cubit (1980) and Slocum (1980), using non-calcareous algal with heteromorphic life histories, have shown that the crustose stages may be adapted to survive in areas or through times of high grazing pressure. Thus, the crustose phase in heteromorphic algae is persistent but susceptible to overgrowth, while the blade-phase is more productive but susceptible to grazing. Paine et al. (1979) further characterized ecological traits of non-calcareous, crustose heteromorphic benthic algae as phases with slow growth, relatively great longevity and persistence, possibly abetted by grazing on encrusting microflora. The life history of *C. dimorphum* is as yet unknown, but there is no evidence of heteromorphic alternation of generation in the genus *Codium* (Bold and Wynne, 1978). It is not surprising then that our results show similarities and differences with the previously described ecological adaptations of crustose heteromorphic algal morphologies. As in the case of these species, *C. dimorphum* can attain great age and probably has low recruitment and mortality rates. In contrast with crustose heteromorphic algae, *C. dimorphum* has a clear capacity to regenerate any part of the crust, has fast seasonal growth and its peripheral tissue seems at least as edible as the central area. Thus, adaptations of *C. dimorphum* include not only ecological traits of crustose heteromorphic algae but some of the adaptation of the fleshy-phase as well. Future studies on non-calcareous crustose algae should indicate whether or not ecological differences between crustose species of algae are related to differences in algal life histories.

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