Patterns of organizations of intertidal and shallow subtidal vegetation in wave exposed habitats of central Chile

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Abstract

Wave-exposed rocky intertidal habitats of central Chile exhibit zonation of algal morphologies rather than strict patterns of species zonation. In low shore areas, there is a vertical sequence of perennial belts of calcareous crusts, kelp-like forms and expanded cushions or non-calcareous crusts. The calcareous crusts are represented by species of *Mesophyllum*, the kelp-like forms include *Lessonia nigrescens* and *Durvillaea antarctica*, while the cushions are represented by *Gelidium chilense* and *G. lingulatum* and the non-calcareous, expanded crusts by *Codium dimorphum*. Thin and thick blades, represented by *Iridaea laminarioides*, *Ulva rigida* and *Porphyra columbia* and filamentous forms including *Ceramium rubrum*, *Centroceras clavulatum* and *Polysiphonia* spp. are more patchy than the lower, perennial belts. They may, however, form distinct temporal monocultures at upper intertidal levels. Upper and lower limits of the various zones are set by interactions of several factors, the relative importance of which can change seasonally. When some of the factors restricting species distribution are experimentally removed, other interactions among factors become limiting.

Within each zone, species are morphologically similar, with the abundance of species being regulated by symmetric competitive interactions. Competition is often asymmetric at the boundaries of zones except when adults of small-sized forms interact with morphologically similar juveniles of larger forms. Irrespective of their extremely different morphologies, the permanent, zone-forming algal species generally combine escape from grazers or defensive adaptations with clear competitive abilities. Nevertheless, there is a clear competitive hierarchy which is expressed in vertical displacements and zonation. The lower-shore habitats could potentially be occupied by any of the different types of algae. Fast growth and large size allow the kelps to occupy this zone pushing the calcareous crust dominated-zone down into shallow subtidal areas and displacing the cushions and fleshy crusts into the low and middle intertidal regions. In turn, these last forms can displace thick and thin foliose forms and filaments to upper levels on the shore. Displaced forms may exist as patches at various levels of the shore.

Introduction

The coastline of mainland Chile is about 4200 km long, extending from Cape Horn in subantarctic waters (55 deg. 58 min. S) to Arica, in the Tropics (18 deg. 20 min.). Coastal topography and cli-mate clearly define different regions along this coastline, each with different types of marine communities (see Santelices, 1989, for a review). Even though the first descriptions of some of these communities were published almost 30 years ago (Dahl, 1953; Guiler, 1959a, 1959b), less

than 50 reports on the subject have been produced thereafter. Emphasis was first placed on qualitative descriptions, then on quantitative descriptions of eulittoral communities, then to explorations of sublittoral habitats and finally to experimental evaluations of the factors regulating community organization. Yet, today there are still extended areas along this coast that have been scarcely explored (e.g. between 18 deg. and 25 deg. S; 42 deg. and 55 deg. S) and whole marine systems whose communities have not yet been scientifically studied. Experimental studies on the factors determining the organization of algal assemblages started in Chile less than 10 years ago. They have been restricted mainly to exposed and semi-exposed rocky eulittoral habitats around 30 deg. S and 39 deg. S and to a few sheltered eulittoral and sublittoral communities of the Beagle area (54 deg. S).

This review summarizes and integrates the information emerging from studies in Central Chile. Results from studies in the Beagle area have not yet provided integrated ideas of community organization. The first part of this review describes the intertidal-shallow subtidal vegetation forming zone or belts on wave exposed rocky surfaces. The second part analyses the experimental evidence gathered so far on the factors determining zones and boundaries between zones in these habitats. The third part focuses on some of the general patterns emerging from these studies.

Intertidal vegetation on wave exposed rocky surfaces

North of Chiloe (41 deg. 29 min. S) the Chilean coastline is fairly continuous, almost straight lined, fully exposed to prevailing winds and waves, with open sandy beaches and few sheltered bays. Wave-exposed rocky surfaces are common habitats along this stretch of coastline and patterns of intertidal zonation have been repeatedly described at various places (Guiler, 1959a; 1959b; Alveal, 1970, 1971; Romo & Alveal, 1977; Santelices et al., 1977, 1980, 1981, Castilla, 1979,

1981; Montalva & Santelices, 1981; Ruiz & Giampoli, 1981; Ojeda & Santelices, 1984). The kelp *Lessonia nigrescens* and the bull kelp *Durvillaea antarctica* form a boundary between the eulittoral and the sublittoral areas (Fig. 1). The extent of this fringe and the relative abundance of these species change with the slope of the substratum and wave impact (Santelices et al., 1980).

Steep, almost vertical, wave-exposed rocks are usually dominated by *L. nigrescens*. Exposed shores with more gradual slopes have kelp beds of *L. nigrescens* with scattered individuals of *D. antarctica*. In more sheltered habitats *D. antarctica* displaces the wave resistant *L. nigrescens*.

When the *Lessonia-Durvillaea* belt is absent, two other algal formations can be found at this level, depending on the type of spatial opening left by the absence of kelp (Ojeda & Santelices, 1984). In small clearings surrounded by individual of *Lessonia nigrescens*, and in the absence of large grazers, large patches of *Gelidium chilense* can be found. In openings where there are abundant grazers, patches of crustose coralline algae and bare rock normally occur. A pink cover of *Mesophyllum* sp normally extends into the sublittoral areas from the lower limit of the kelp holdfasts. Hordes of the black sea urchin *Tetrapygus niger*, large individuals of the chiton *Acanthopleura echinata*, and the black snail *Tegula atra* can be found on the coralline algal assemblages.

The 0.5 to 1.5 m zone, immediately above *Lessonia nigrescens*, is dominated by several algal associations, the relative importance of which correlates with changes in rocky slope, wave exposure and incident light. On vertical walls, and, especially on shaded places, *Codium dimorphum* forms expanded green crusts. These often cover other middle-eulittoral organisms and support a diversity of small limpets (e.g., *Collisella zebrina*, *Collisella ceciliana*, *Siphonaria lessonii*). On more horizontal platforms with good water exchange and greater levels of light intensity, *Gelidium lingulatum*, *G. chilense*, *Laurencia chilense* and tufts of *Corallina officinalis* form the dominant vegetation. *Fissurella crassa* and *F. limbata* are
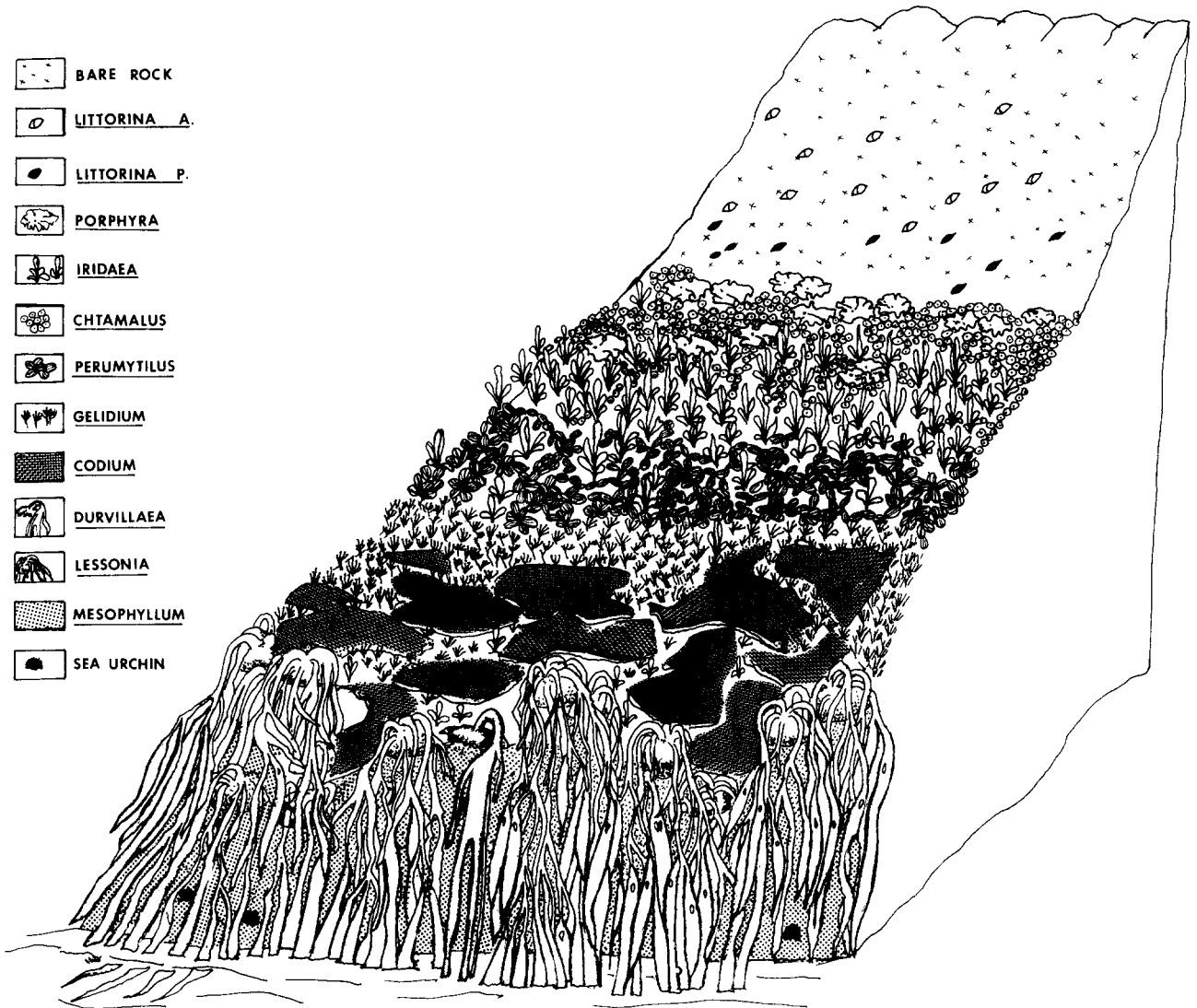
BARE ROCK

LITTORINA A.

LITTORINA P.

PORPHYRA

IRIDAEA

CHTAMALUS

PERUMYTILUS

GELIDIUM

CODIUM

DURVILLAEA

LESSONIA

MESOPHYLLUM

SEA URCHIN

Fig. 1. Diagrammatic representation of the algal species commonly found on wave-exposed, rocky intertidal habitats of central Chile.

common grazers at the lower levels of the eulittoral, whereas *Chiton granosus* extends further up into middle and upper eulittoral areas.

The middle eulittoral zone contains a band of the mussel *Perumytilus purpuratus*, the width of which varies as a function of slope and wave exposure. The uppermost eulittoral levels, and up to 2–2.5 m above MLWL, are dominated by pure or mixed stands of the chthamaloid *Jehlius cirratus* and *Chthamalus scabrosus*, with the former species extending higher up in the intertidal than

the latter one. Several filamentous or frondose algae such as *Ulva rigida*, *Iridaea laminarioides*, *Enteromorpha compressa*, *Centroceras clavulatum* and several species of *Polysiphonia* can be found among mussels, extending to some extent into the barnacle zone.

Above 3 m of tidal elevation the cover of the barnacle *Jehlius cirratus* is much reduced and these crustaceans co-occur with patches of *Porphyra columbina* and aggregations of *Littorina peruviana* and *L. araucana*. Rocky places exposed

to heavy sunlight have, at these tidal heights, patches of dark-red crusts, the commonest of which is *Hildenbrandia lecannellieri*.

If the above pattern of algal distribution is examined considering algal morphologies rather than taxonomic entities, a clear pattern emerges (Santelices, 1981). Three permanent zones and one or several temporal zones can be recognized (Fig. 2). The three permanent components occupy the low shore and are markedly trimodal in size. They include the zone dominated by *Mesophyllum* sp. and other crustose coralline algae, the zone immediately above, dominated by kelp-like seaweeds (*Lessonia-Durvillaea*) and a narrow zone dominated by crustose or cushion-forming algae (*Codium dimorphum* and/or *Gelidium*). The temporal belts include frondose and filamentous forms (*Iridaea laminarioides*, *Ulva rigida*, *Centroceras clavulatum*) which can be found forming patches of variable sizes within permanent belts, or forming horizontally extended monocultures at the uppermost vertical levels. These extended monocultures are generally variable in abundance from time to time and can form distinct belts during some seasons. It is interesting to notice, in addition, that above and below the kelps, the zones are dominated by algal morphologies which exhibit short stature and reduced inter-plant distances. They often form an almost continuous cover with few, if any, spaces among the individual colonies or crusts.

Determination of zones and boundaries

The experimental results so far gathered indicate that, normally, the interactions among several types of factors determine the dominance of one
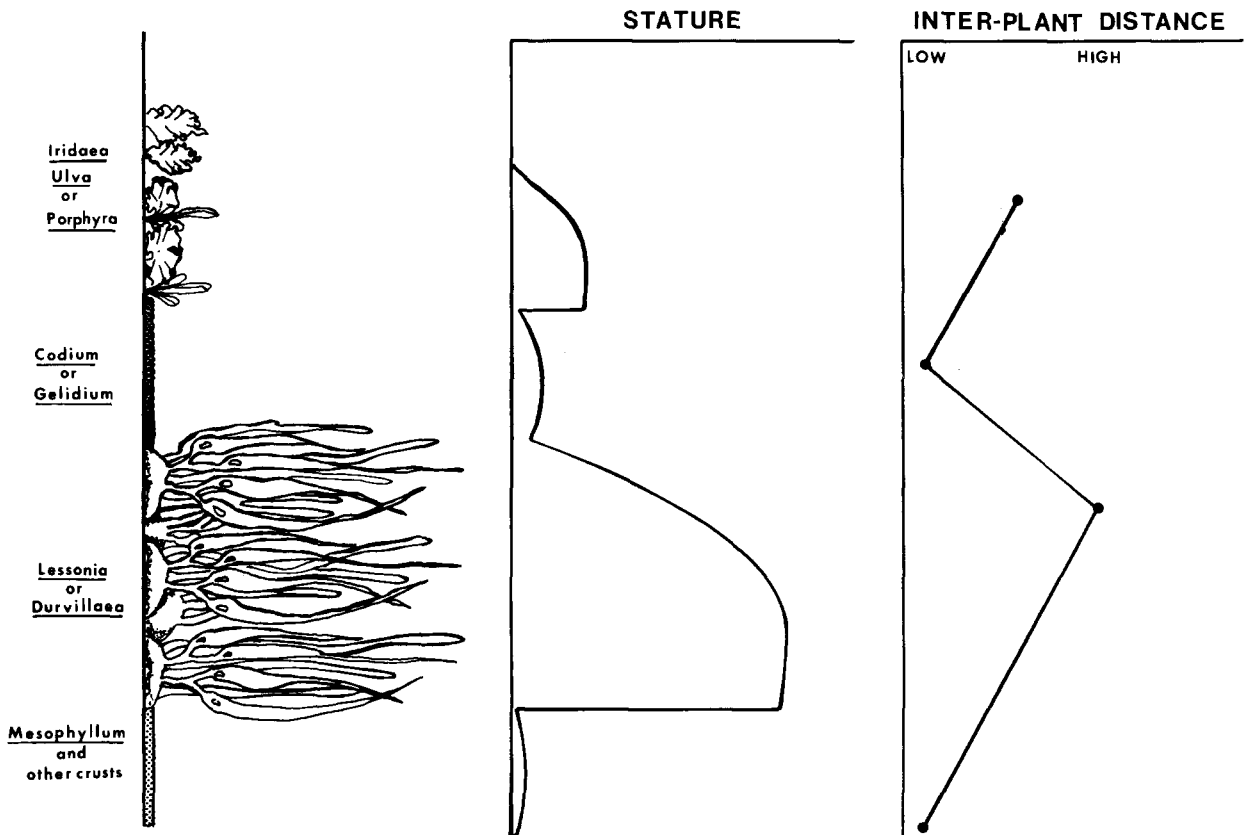

Fig. 2. Diagrammatic representation of the dominant algal morphologies on wave-exposed, rocky intertidal habitats of central Chile. The low shore is occupied by three permanent components markedly trimodal in size and in inter-plant distances. The upper shore contains monocultures of filamentous of frondose forms, variables in abundance from time to time.

or another species at a given tidal level and the boundaries between these zones. Experimental evidence also indicates that much of the physiognomy of the low eulittoral zone is determined by factors regulating juvenile recruitment in the kelp-dominated zone. This analysis will therefore foccus on this particular zone first.

The kelp-dominated zone

Interference by adult plants, and the grazing effects of large-sized subtidal herbivores, completely inhibit recruitment of juveniles within the *Lessonia-Durvillaea* belt (Santelices & Ojeda, 1984). In experiments done between 1981 and 1983 in several localities of central Chile not a single juvenile recruited in the zone where densities of adult (larger than 20 cm of holdfast diameter) were above 3 plants/m². Similarly, no recruitment of kelps was observed in removal plots exposed to grazing by black sea urchins (*Tetrapygus niger*). Twelve months after the beginning of this last experiment, only 2 juveniles of *L. nigrescens* settled at intertidal levels above those normally occupied by the species, and persisted for 2 months, growing to 50 cm long. These two individuals, however, disappeared during the next summer.

Field observational data and experimental results indicate that grazing and interference by adult plants are patchy and mutually exclusive. Barren areas covered with crustose coralline algae and dense aggregations of the black sea urchin are especially common in the intertidal-subtidal pools with frequent water exchange, but not directly exposed to wave action. The opposite is true for adult individuals of *Lessonia nigrescens*. Movement of fronds resulting from water-motion can deter populations of sea urchins away from the kelps, especially during low tides. Recruitment of juveniles of *L. nigrescens* could therefore be expected to occur in areas where these 2 factors counteract each other. This situation corresponds to vegetational openings small enough to have reduced grazing pressure yet large enough to have reduced disturbance by adult plants. Field

measurements in search of such optimal size indicate that vegetational discontinuities of 1.0 to 2.0 m of interholdfast distance have increased juvenile recruitment (Fig. 3). Observations further indicate that the fronds of 2 plants contiguous to a vegetational opening are moved simultaneously in one or another direction by wave action wiping out some of these larger grazers. As a result, there is a roughly triangular area with the hypotenuse formed by the inter-plant distance which is inaccessible to grazers during most of a tidal period (Santelices & Ojeda, 1984). It is difficult to calculate exactly the size of the undisturbed triangular area allowing increased recruitment of juveniles in the field. It is a function of total length of fronds, degree of rocky slope, length of a tidal period, and density and motility of grazers. Field observations also indicate that movement of fronds could limit incursions by grazers into subtidal areas to periods of low tides only. Sea urchins and other grazers can reach these areas during high tides when the fronds of *L. nigrescens* spread almost perpendicular with respect of the substratum and stop rubbing against the rocky surface.

The existance of an optimal inter-plant distance as a requirement for the successful recruitment of juveniles also has been described by Dayton *et al.* (1984) for several California kelps. In the *Laminaria* beds of South Africa, the relationship is slightly different. Velimirov & Griffiths (1979) found patches of *Laminaria* consistently formed of central parts with pregressively smaller individuals towards the margins. A distinct belt of bare rock separated these kelp patches from patches of herbivorous animals. The barren interface between patches was found to be the results of sweeping action by the peripheral plants as these are bent by incoming swells. This sweeping effect provides protection against herbivory and it is a mechanism by which areas suitable for kelp colonization are prepared, allowing existing kelp patches to expand over time.

The requirement for a suitable opening for recruitment is consistent with several other aspects of the biology of *Lessonia nigrescens*. The size of such a discontinuity is within the size likely
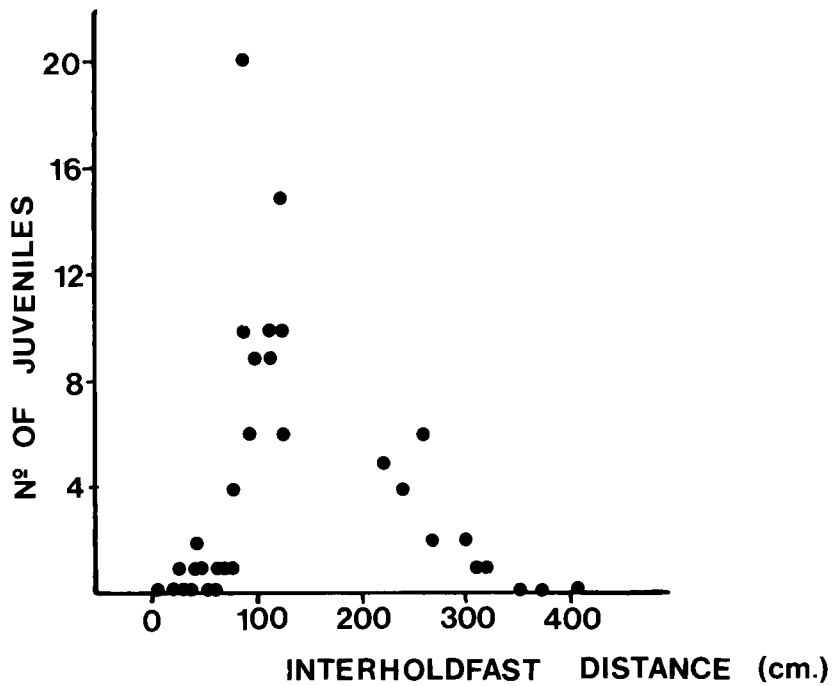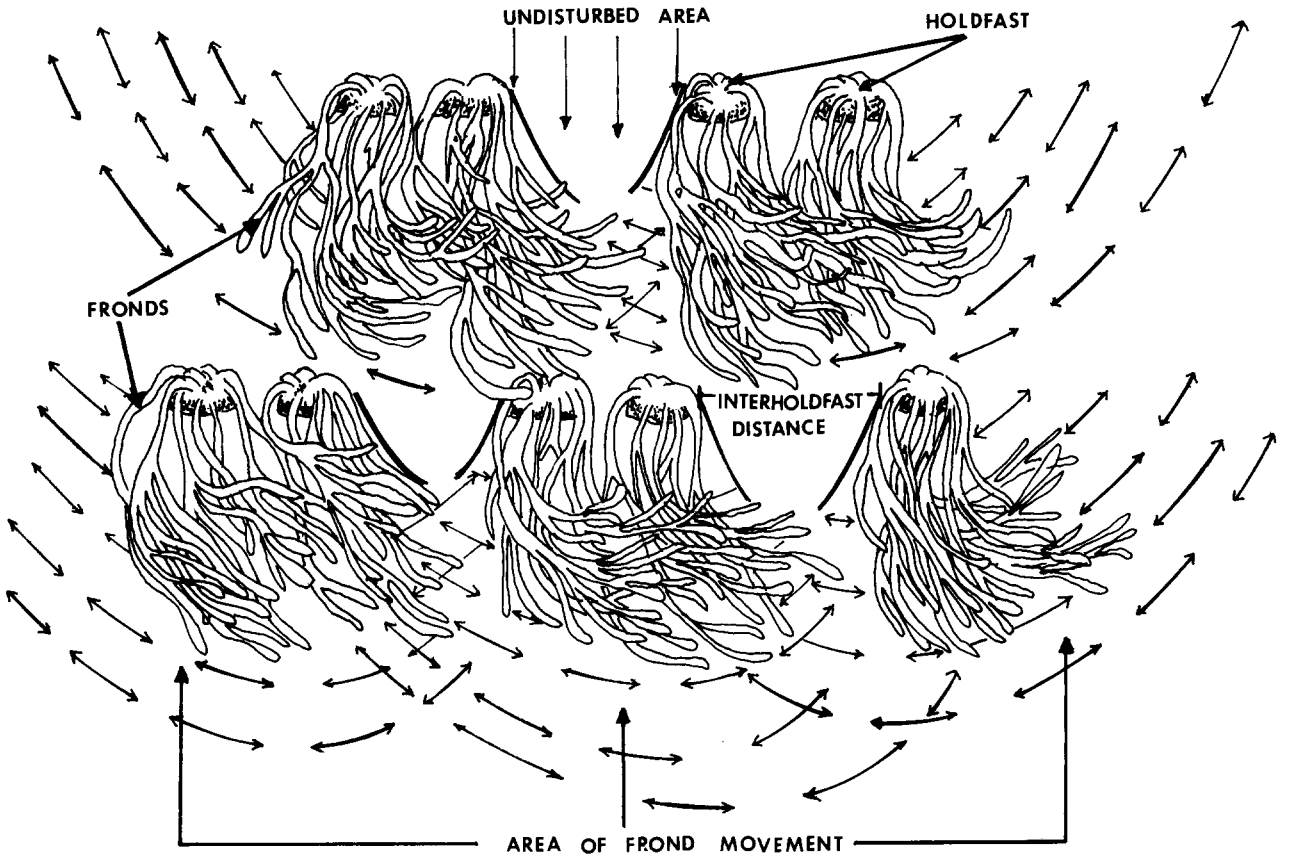
Fig. 3. Diagrammatic representation of vegetational openings within the *Lessonia* belt. Movements of fronds due to waves produce an area for recruitment which has reduced grazing pressure and reduce interference.

to be produced by the detachment of one or a few old, eroded plants. Storms strong enough to remove these plants are much more common in winter, when *L. nigrescens* has maximal fertility (Santelices *et al.*, 1980; Ojeda & Santelices, 1984). The expected outcome of the recolonization following these disturbances should be the settlement of juveniles of *Lessonia nigrescens* within these openings, maintaining the belt in space and time. It is as yet unknown if a similar phenomenon occurs in populations of other kelp species, but Markham (1973), Dayton (1975a) and Smith (1986) have suggested that the seasonal reproductive pattern of species of *Laminaria* and *Hedophyllum* represent adaptive responses to seasonally predictable patches of substratum produced by storms. Thus, the phenomenon seems to be common among kelps.

A most important point emerging from the concept of optimal openings is the intensity of grazing and of competitive interactions occurring within such clearings. Because these areas can be reached by grazers only during some parts of the tidal cycle, grazers can only exert an intermitent pressure in the area, probably less than that commonly described for barren grounds. This would allow a few juveniles to survive and grow to sizes large enough to escape from grazing. Such intermittent grazing would reduce the number of, but not remove all recruits and probably results in less intraspecific competitive interference among juveniles of *L. nigrescens*. This process, which may be the normal way that individuals are replaced within beds of *L. nigrescens*, is not simulated in experiments where all adults plants are removed, exposing the newly vaccated surface either to intense grazing or to strong interspecific interference.

We do not have equivalent information on juvenile settlement of the second species normally found at this tidal level, the bull kelp *Durvillaea antarctica*. There is, however, no a priori reason to expect that this species is also not sensitive to grazing. In central Chile, *D. antarctica* is fertile for most of the year. Settlement of juveniles, however, occurs after removal of large, adult plants by waves and storms (Santelices *et al.*, 1980). This

also seems to be a density-dependent phenomenon. Therefore, probably the requirement of an optimal opening in the canopy also applies to this species, although perhaps such clearings need to be of different dimensions and shapes.

Since *Lessonia nigrescens* and *Durvillaea antarctica* co-occur at the same vertical elevation, and since they have somewhat similar morphologies it is expected that the species composition within the belt might be affected by interspecific interference. Guiler (1959b) discussed this problem, noting that the plants of *D. antarctica* appeared as better adapted to places with intense wave action. Individuals of that species are, however, harvested in variable amounts by fishermen and visitors to the beach. Guiler (1959b) predicted that under undisturbed conditions *L. nigrescens* would be of much less ecological significance due to competitive displacement by *D. antarctica*. Our field studies at places with and without human interference and varying degrees of water movement indicated, however, that *L. nigrescens* had much greater cover than did *D. antarctica* at places exposed to intense wave shock, irrespective of human accessibility (Santelices *et al.*, 1980).

Differences among species in their resistance to wave shock are related to several features. The way the species might apportion the total frond weight to their stipes seems to be very important. *Lessonia nigrescens* has this weight spread over several stipes, while *Durvillaea antarctica* supports all the weight on one or a few stipes. The presence of weak points at which the fronds are broken during storms is also important, especially for *D. antarctica*. Nearly 70% of these plants that are cast on the shore are found broken between the stipe and the holdfast. The presence of the limpet *Scurria scurra*, which apparently has a prunning effect on the largest and heaviest stipes of *Lessonia nigrescens*, prevents the kelp plants from becoming so heavy as to be susceptible to detachment by water drag. In addition, the holdfast of *L. nigrescens* can regenerate pruned stipes within six months after abscission, a capacity not shown by the holdfast of *D. antarctica*.

Complete monopolization of space by *Lessonia*

nigrescens is prevented by a series of adaptations of *Durvillaea antarctica*. Certain morphs of this species are less affected by wave action. Apparently as a result of joint embryo germination and subsequent coalescence of several holdfasts, these plants have several stipes rising from a single holdfast. In this respect, the morphology of *D. antarctica* remaining attached after storms is similar to the morphology of *L. nigrescens* in having a large holdfast with several stipes. This morphological variation of *D. antarctica* allows a population of the bull kelp to persist even in exposed habitats. In addition, boring into algal holdfasts by invertebrates weakens the mechanical resistance of old, eroded plants providing open space where juveniles of either species could settle. *D. antarctica* seems to take greater advantage of this primary space by means of a fugitive life history.

These observations indicate, therefore, that competitive displacement mediated by wave action could be expected within the belt (Fig. 4). Competitive displacement of *L. nigrescens* by *D. antarctica* is likely to occur only in the intertidal-subtidal boundary of sheltered habitats. In most exposed habitats, *D. antarctica* would constantly be removed by water movement. The effect of waves would be greater for plants high in the belt on rocky fronts with a steep slope. During low tides, these blades hang from the rocks exerting strong drag on the stipes as the incoming tides move the blades back and forth. Large plants of *D. antarctica* can be found in shallow subtidal levels of exposed habitats, where the weight of the

Fig. 4. Interactions of factors determining the dominant algal distribution patterns on wave-exposed rocky intertidal habitats of central Chile.

blades is partially supported by the water. Here, the fronds move in an incomplete circle rather than been violently pulled back and forth as in the intertidal-shallow subtidal fringe of wave-exposed habitats of central Chile.

It is interesting to note that the interference interaction between *Lessonia* and *Durvillaea* tends to be symmetric (sensu Connell, 1983), the outcome depending on wave-impact and slope of the shore. This apparently results from two contrasting phenomena. One is the morphological similarity of the two species. It is true that both are mechanically different and react differently to wave impact. *D. antarctica*, however, has the capacity to approach the structural and functional morphology of *L. nigrescens* ant this is especially well represented by the populations of *D. antarctica* remaining attached to the substratum after storms.

The second set of characters allowing for some symmetry in the interaction relates to the life-histories of these species which, in spite of their morphological similarities, differ greatly. *Lessonia nigrescens* is seasonal in its growth and reproduction and has a time delay between the appearence of fertile sporophylls and newly settled young sporophytes. Fertility occurs only after 14 to 18 months of growth of young individuals and at least 50% of the population persists in the field for more than 20 months. *Durvillaea antarctica* has a faster growth rate; a non-seasonal though density-dependent juvenile settlement. Fertility occurs after 6 months of first appearing on the shore and individuals do not live for long in the field. Clearly, morphological similarity can not be used as a good predictor of life strategy.

The boundary between crustose coralline algae and kelps

A pink cover of calcareous crusts, probably one or several species of *Mesophyllum*, normally extends from the kelp-dominated zone into deeper waters. Due to the logistic problems involved in its experimental manipulation, this formation has not been the subject of specific studies yet. Experimental manipulations within the kelp-dominated zone have allowed us to understand the causes of the lower vertical limit of the kelps and the maintenance of the boundary between kelps and calcareous crusts.

Experimental evidence suggests (Santelices & Ojeda, 1984; Ojeda & Santelices, 1984) that the persistence of a calcareous crust depends on grazing (Fig. 4). In the absence of grazers, and depending on the season, crusts may be covered either by kelps, bull kelps or other frondose algae. It should be noted, however, that experimental quadrats completely covered with these pink calcareous crusts exposed to very intense grazing result in a marked reduction of cover of the crusts and in an increase of bare rock (Ojeda & Santelices, 1984). Therefore, the development of a zone covered by calcareous crusts depends on intermediate amounts of grazing, which must be a little more intense than that necessary for recruitment of kelps.

Crustose coralline algae not only form a well-defined zone immediately below the kelp-dominated zone. They can be found as alternative states (sensu Sutherland, 1974) within the kelp-dominated zone in vegetational openings large enough to allow grazers to enter (Fig. 5). Crusts will last while the disturbing agent (grazers) persists. If the grazers are excluded, a variety of frondose algal species will cover the crust and the opening might eventually be covered by juvenile kelps. Therefore, the kelp-dominated zone has the potential to be inhabited by calcareous crusts. The actual boundary between the two zones, results from grazing on the otherwise competitively superior kelp.

Given the above interaction, it is possible to consider how much higher into the intertidal zone the crustose coralline-dominated zone could expand in the absence of kelps or how much deeper the kelp-dominated zone could extend in the absence of grazers. Experimental evidence suggests (Fig. 5) that when these factors are removed other, sometimes unexpected factors, soon restrict the distribution of these two types of algae. In all the experimental removal of kelps close to the middle and upper vertical limits of the
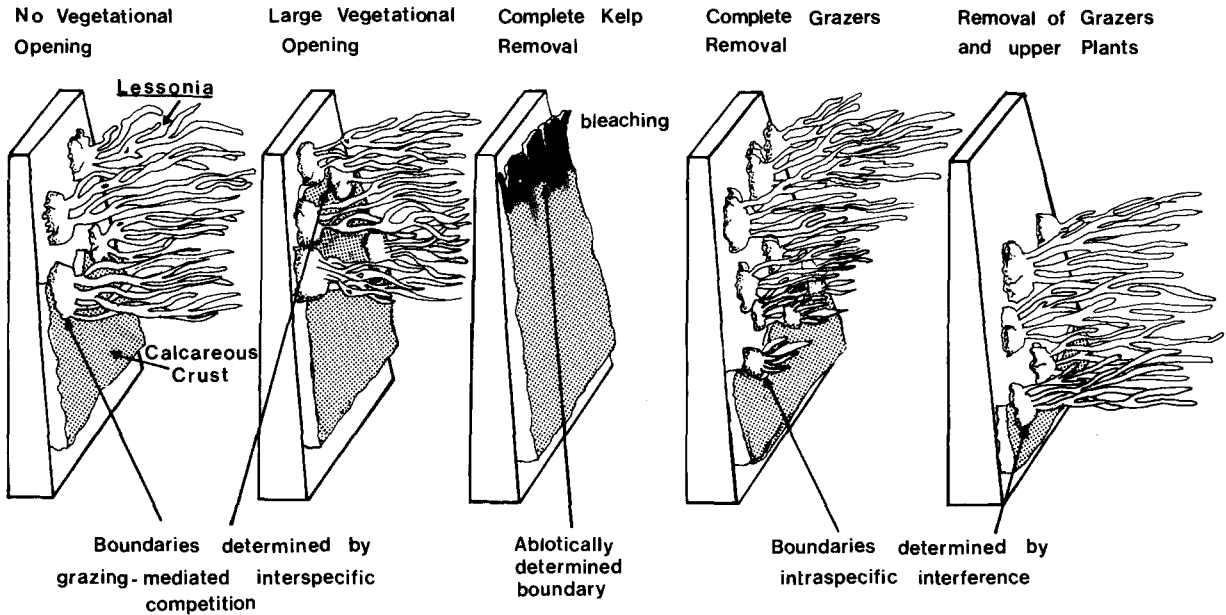
| No Vegetational Opening | Large Vegetational Opening | Complete Kelp Removal | Complete Grazers Removal | Removal of Grazers and upper Plants |

Fig. 5. Some alternative vegetational states often found on the low shore.

kelp-dominated zone (Ojeda & Santelices, 1984) there was bleaching and reduction of the percentage cover of the calcareous crusts, especially during summer. When the kelp recruits reached a large cover (60–80%), the cover of the calcareous crust recovered. Therefore, the crust behaves as an obligate understory species (sensu Dayton, 1975a, 1975b) and it seems to be sensitive to increased light intensity and desiccation. In the absence of kelps, this factor probably limits the vertical extent of the crust into intertidal levels.

In the absence of grazers, the kelps extend subtidally. Individuals that settle into the middle levels of the *Lessonia* zone have fast growth and the growing canopy can significantly reduce the light intensity reaching individuals settled further down the shore. Individuals lower down exhibit reduced growth (Fig. 5) their holdfasts do not increase in size and they are eventually removed by water movement. All juveniles settled at the lowest levels in our experimental plots (Santelices & Ojeda, 1984) disappeared from the shore within 6 months after settlement because of intraspecific competition. In contrast, if the individuals in the middle levels of the *Lessonia* band are also removed, survival and growth rates increased, approaching the values shown by individuals

settled in the middle levels (Santelices & Ojeda, 1984). Intraspecific interference has been shown to regulate population structure of subtidal kelps and other brown algal species (Rosenthal *et al.*, 1974; Black, 1974; Chapman & Goudey, 1983; Santelices & Ojeda, 1984; De Wreede & Klinger, 1987). Yet it has infrequently been considered an important agent regulating the lower boundary of intertidal or subtidal populations. Since the limiting effect of this type of interaction is a function of the light intensity reaching shaded individuals, the lower limit of the kelp could vary according to, among other factors, seasonal changes in light intensity, rocky slope, light reflections produced by water movement and the growth rate of kelp juveniles.

The boundary between kelps and fleshy crusts and cushions

Pure or mixed populations of the non-calcareous, crustose green alga *Codium dimorphum* and of the cushion-forming species *Gelidium chilense* and *G. lingulatum* dominate the zone immediately above the *Lessonia nigrescens-Durvillaea antarctica* association. The factors determining the

boundary here are also seasonally variable. When the primary space in this boundary area is liberated of kelp during winter (Santelices & Ojeda, 1984), *Lessonia nigrescens* recruits to form a 2 m wide band. The uppermost levels of this newly-recruited belt is 30–50 cm above the upper vertical limit of a normal, consolidated kelp zone containing adult plants. Densities of recruits here are 1/3 to 1/2 the values found further below and these young kelps can be found mixed with *Gelidium* or with patches of *Codium*. The tufts of *Gelidium* or the expanded green crusts of *Codium* can temporarily invade the newly exposed rocky surface during the first months after kelp are removed, but juvenile of *Lessonia* can settle on bare rock or crevices among the plants of *Gelidium* and *Codium* and by fast growth and expansion of their holdfasts, either overshadow or overgrowth these smaller-sized species.

Survival and growth-rates of the kelp that settle at the uppermost intertidal levels of recruitment are, however, very low (Santelices & Ojeda, 1984) and between spring and summer they suffer the effects of high light intensity and high temperatures, coupled with day-time low tides. By the end of the summer, most of the uppermost individuals have disappeared. Now and then scattered dwarf kelps could be found at this tidal level in rocky areas with surface irregularities which retain variable amounts of water during low tides.

In these winter experiments (Santelices & Ojeda, 1984; Ojeda & Santelices, 1984), the single or interacting effects of middle intertidal small-sized grazers and *Codium* and *Gelidium* had no effect on the recruitment, growth and survival of the individuals of *L. nigrescens*.

The above situation changes drastically when removals are done in summer, because *L. nigrescens* is fertile only during winter. Summer removal of the kelp is followed by a rapid occupation of the substratum by some opportunistic species, such as *Ulva* or *Enteromorpha*, followed by an steady increment of the cover value of some middle intertidal algae such as *Gelidium chilense*, which in central Chile is reproductive all the year round. This species is able to extend from the middle intertidal levels into the normal limits of the *Lessonia* belt occupying the newly exposed rocky surface. Thus, summer removal of *L. nigrescens* allows for 4 to 5 months of invasion and growth of *G. chilense*, free from its competitive dominant. The settlement of *L. nigrescens* expected to occur in winter did not occur in our experiments due to monopolization of the primary substrate by *G. chilense*. Therefore, the interaction of factors determining this boundary could be either abiotic extremes or interspecific competition, depending on the season when adults are removed (Figs. 4 and 6).
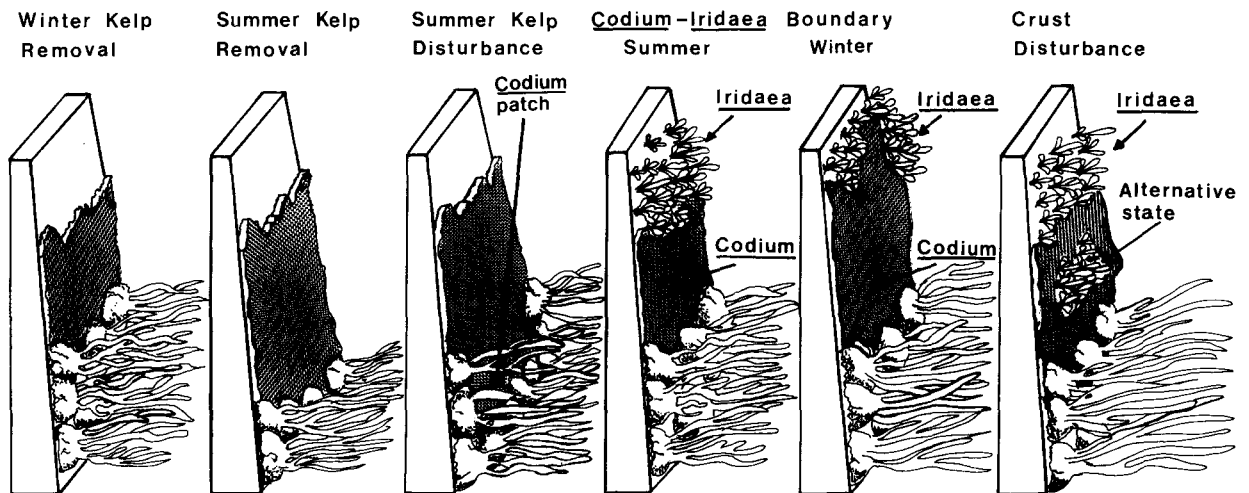
These results stress the importance of inter-

Fig. 6. Some alternative vegetational states often found on the mid- and upper-shore.

ference interactions between adult plants of a species (*Gelidium*) and the juveniles of a different species (*Lessonia*). A similar adult-juvenile interaction was reported by Lubchenco (1980) between *Chondrus* and *Fucus* in New England. As stated previously, the fast growth of the juveniles of *Lessonia nigrescens* and the significant size differences between adult plants of *Lessonia* and *Gelidium* result in a asymmetric competitive interaction. On the other hand, interactions between adult plants of *Gelidium* and the morphologically closer juvenile form of *Lessonia* tends to be more symmetric, and *Gelidium* is able to outcompete *L. nigrescens*.

As in the case of the patches with calcareous crusts, *Gelidium* or *Codium* can be found in the kelp-dominated zone as very persistent alternative states. Normally they are found in clearings surrounded by kelps and devoid of large grazers such as the chiton *Acanthopleura echinata* or the sea urchin *Tetrapygus niger* (Fig. 6). These *Gelidium* dominated patches probably result from the removal of kelp individuals during the summer (Ojeda & Santelices, 1984). Patches of *Gelidium*, however, do not require the continued presence of the disturbing agent to persist. Thus, in our experimental patches (Ojeda & Santelices, 1984) they lasted well over two years after the initial summer removal of *Lessonia*. Their patchy presence in the kelp-dominated zone indicates, in addition, that this part of the shore has the potential to be occupied by these cushions and fleshy crusts but they are vertically displaced by kelp to the zone dominated by cushions and crusts.

In the algae, fast growth and large size have been frequently understood as adaptations limiting herbivory (Connell, 1975; Dayton, 1975a; Lubchenco and Cubit, 1980). Large sizes also provides several other adaptive advantages, such as the ability to overshade or to whisplash other organisms. The fast growth and the large size of *L. nigrescens* certainly facilitated its ability to outcompete *Gelidium* at its upper border and calcareous crusts at its lower boundary. Size seem to be a generally overlooked, yet extremely important factor determining competitive outcomes in the algae.

The accumulated information on the factors determining the extent of the kelp-dominated zone, its species composition and the upper and lower boundaries are integrated in Fig. 4.

The zone dominated by fleshy crusts and cushions

Most of the published information related to this level of the shore in central Chile refers to *Codium dimorphum*. Field studies (Santelices *et al.*, 1981) indicate that the total vertical extent of this species and it percent cover at any given vertical level also varies seasonally. During winter the species can reach higher intertidal levels than during spring and summer. *Codium dimorphum* permanently dominates the low intertidal areas, ranging from 35% cover in summer to 62% in winter. The other permanent species at this level, *Gelidium chilense*, normally reaches less than 20% cover.

During late spring and summer, the border and the surface outgrowths of the *Codium dimorphum* colonies start to bleach and the expanded, continuous green crust can become locally discontinuous and irregularly shaped. Individual, smaller-sized colonies can now be recognized, many of them with bleached borders which then disintegrate leaving empty space between the colonies. Several algae normally found at upper intertidal levels such as *Ulva rigida*, *Iridaea laminarioides*, *Enteromorpha compressa*, *Ceramium sp.* occupy this primary space after the summer reduction of *C. dimorphum* at this level of the shore. Indeed, the seasonally changing covers of *C. dimorphum* are negatively correlated with those of other algae (Santelices *et al.*, 1981). The disruption of crust integrity increased the susceptibility of *Codium dimorphum* colonies to herbivory. A diverse assemblage of small grazers such as *Siphonaria lessonii*, *Collisella zebrina* and *Tegula atra* can be found on the slippery surface of the *Codium* colonies, apparently grazing on the colony surfaces in addition to on epiphytes. When the crust became discontinuous, however, it was observed that larger densities of larger-sized grazers could settled on the newly vacated sur-

face, grazing on the borders of the colony, slowing down the growth rates of the colony and delaying the recovery of the primary substratum.

The above observations motivated experimental work. Removal patches were excavated in the colony to evaluate whether in a different time of the year (late fall) the upper and middle intertidal species could extend into these low vertical levels. In addition, recovery rates of the *Codium* colonies in the presence and absence of grazers were compared. To test for interactive effects of grazing with abiotic seasonal events, independent sets of experiments were started at two different times of the year (fall and spring).

The results of these experiments showed that within a year after removal, all upper and middle intertidal algal species and 2 of the 3 sessile invertebrate species can occupy the newly vacated space which is dominated by extensive *Codium dimorphum* colonies under undisturbed conditions. The colonization processes followed for 41 months after experimental removals indicated, in addition, that *C. dimorphum* could gradually replace and exclude these species. Recovery of *C. dimorphum* was, however, strongly affected by bleaching of the borders of the colonies. Even 41 months after removal, *C. dimorphum* was unable to recover its original abundance.

A comparison of growth rates of algae in the removal plots with and without herbivores indicates that recovery rates where faster where the growing borders of *C. dimorphum* are protected by exclusion meshes. The effect was most pronounced in experiments started in early spring. This suggested that an important part of the reduction of cover of *C. dimorphum* during summer could be due to grazing after initial bleaching of the borders of the colony. Thus, the abiotic extremes during late spring and summer bleaches the colonies, disrupting the crust and creating new borders for attack by grazers. Browsing from the borders of the colony reduces the total cover of *C. dimorphum* during this time of the year.

In spite of the morphological differences from kelp, *C. dimorphum* also appears as a species with a combination of adaptations allowing it to escape herbivory and to have strong competitive

abilities. This combination of biological characters distinguishes this species from other fleshy crusts. Crustose habits of benthic algae have in general been supposed to represent mechanisms for escaping from grazing (Paine & Vadas, 1969; Paine *et al.*, 1979; Vadas, 1979; Littler & Littler, 1980; Lubchenco & Cubit, 1980; Slocum, 1980). The crustose phase in heteromorphic algae is persistent, but susceptible to overgrowth, has slow growth rates and requires grazing to remove the otherwise encrusting microflora. The erect phase, by contrast, is more productive and has faster growth, but is less persistent and susceptible to grazing (Paine *et al.*, 1979; Lubchenco & Cubit, 1980). *Codium dimorphum* combines ecological traits of crustose and fleshy phases. As an expanded crust it has a morphology susceptible to grazing almost exclusively from the border, and the colonies have great longevity and great persistence. In addition, it has a clear capacity to regenerate any part of the crust and has fast, seasonal growth. This combination of characters allows the species to escape herbivory and to outcompete most other intertidal species except kelps. It is important to realize that *Codium dimorphum* is able to escape the grazing effects of only the grazers most common at middle intertidal levels, most of which are small-sized molluscs. It does not seem to have the capacity to escape larger herbivores. This seems to be due to the fact that the size of the grazer-induced patch might affect the successional events occurring after removal of *Codium dimorphum*. The larger the size of the disturbance, the longer the time needed to recover the vacated surface, and the greater the probabilities of the whole process being affected by seasonality and grazing. Small-sized discontinuities in the crust produced by small molluscs such as *Collisella zebrina* and *Siphonaria parasitica* never reach more than 5 cm in surface area. These are probable easily overgrown by *C. dimorphum*. Larger-sized discontinuities, such as those likely to be produced by large chitons such as *Acanthopleura echinata*, large individuals of *Fissurella crassa* or *F. limbata* and sea urchins most likely limit the distribution of *C. dimorphum*. Many of these grazers could perhaps reach the

low intertidal levels dominated by *C. dimorphum* but a combination of factors seems to prevent this. Some of these grazers (e.g. the species of *Fissurella*) are removed by fishermen and visitors to the beach (Moreno & Jaramillo, 1983; Oliva & Castilla, 1986). Some (e.g. sea urchins) can be dislodged by movements of the kelp. When found at these tidal levels, such species are restricted mostly to pools and large rocky crevices. Still some others (e.g. chitons, snails) are apparently stopped in their incursions from subtidal areas by the kelp holdfasts. Even though *C. dimorphum* and kelp might exhibit competitive interactions at the boundary zone, the presence of *C. dimorphum* is at least partially enhanced by the presence of the kelp. These observations suggest that, as in the case of the boundary between kelps and crusts, when the factors primarily restricting distribution are removed (interspecific competition with kelp) other factors (grazing by large-sized herbivores) might restrict distribution. It is expected therefore that even in the absence of kelps, *C. dimorphum* might not be able to extend much further down shore. Perhaps, in the absence of kelp, large grazers coming from subtidal areas might restrict its downward distribution.

We lack equivalent data for *Gelidium*, the other normal inhabitants of this tidal level. The accumulated information indicates that interspecific interference between the morphologically similar *G. chilense* and *G. lingulatum* is important (Montalva & Santelices, 1981) in determining their biomass and fertility.

The boundary between cushions, crusts and fleshy blades

Codium dimorphum reaches the middle intertidal zone during winter but it bleaches and disappears from this level during summer. The space is occupied by algal species normally found at the upper intertidal levels, such as *Ulva rigida*, *Iridaea laminarioides*, *Ceramium* sp., *Polysiphonia* sp. and *Enteromorpha*. Experimental exclusion of herbivores suggests that grazing enhances the reduction of cover of *C. dimorphum* after the initial sum-

mer bleaching of the colony. It can be concluded, therefore, that the interaction of factors determining this boundary also varies seasonally (Figs. 4 & 6). During winter, when the colony grows, the importance of grazing decreases while the importance of interspecific competition increases. During summer, grazing increases in importance after the initial crust is bleached as a result of increased light intensity and temperatures (Santelices *et al.*, 1981).

The Iridaea laminarioides dominated zone

Factors dominating the abundance of upper eulittoral vegetation in these habitats are less well understood due to several factors. The basal parts of some species might be able to perennate while their erect canopies are seasonal. Some species might occupy space through successive generations, while other seemingly replace each other throughout the year. A conspicuous band of the mussel *Perumytilus purpuratus* and barnacles can, in some areas, dominate this zone. The mussel beds host a diversity of small-sized grazers that could locally modify abundance of algae. In addition, the mussels ingest and digest algal spores, modify their settlement patterns and protect the algal germlings from desiccation (Santelices & Martinez, 1988). All these factors tend to confuse our understanding of the processes and patterns organizing the mid-upper intertidal vegetation. Nevertheless, pertinent information is emerging from habitats where some of these species can form spatially or temporally dominant monocultures. This is the case of *Iridaea laminarioides* dominated zone. In wave exposed, rocky habitats this species is normally found living in and around the mussel beds, immediately above the *Codium/Gelidium* dominated band, forming a distinct zone during winter (Hannach & Santelices, 1985). The same species, however, forms a distinct and persistent zone in middle rocky intertidal areas with periodic sand accretion (33° S and 39° S). These plants have a crustose holdfast able to resist grazing by small-sized herbivores (Jara & Moreno, 1984) and being covered by for up to 4–6 months

(Santelices & Norambuena, 1987). The crustose base is able to produce erect blades which are fast growing and highly productive (Santelices & Norambuena, 1987; Westermeier et al., 1987) but sensitive to grazing by large and small molluscs (Jara & Moreno, 1984) and by amphipods (Buschmann & Santelices, 1987).

Fields observations and experiments indicate that different factors in different habitats may set the lower boundary of the Iridaea-dominated zone. As discussed in the previous section, experimental removal of Codium dimorphum permitted the recruitment of I. laminarioides, suggesting that competition for space is the factor controlling the lower limits of Iridaea in these wave-exposed, mid rocky intertidal habitats (Santelices et al., 1981). In Mehuin (39° S), when sand accreted on a rocky shore, certain consumers such as Fisurella picta moved from the low to the middle intertidal (Jara & Moreno, 1984). Experimental removal of these large-sized grazers (Moreno & Jaramillo, 1983) allowed a rapid downward increase in the width of the zone dominated by Iridaea laminarioides. The great cover of I. laminarioides precluded further invasion of the rocky habitats by ephemerals such as Ulva rigida. In later studies, Moreno et al., (1984) reverted the experiment, with a major increase in the density of F. picta. This resulted in dramatic declines in the abundance of this macroalga.

It is interesting to notice that the experimental removal of Fissurella picta not only permitted Iridaea laminarioides to expand down into the area occupied by Ulva rigida and calcareous algae. It also allowed for the development of a band of Gymnogongrus furcellatus at low levels. This is exactly the situation found in the sand-invaded beaches of Matanzas (33° S) where sand persists longer than in Mehuin (39° S). Experimental removal of G. furcellatus from low intertidal levels at Matanzas was followed by a downward extension of I. laminarioides. Like I. laminarioides, G. furcellatus possess a basal crust (the tetrasporic phase) able to resist being smothered by sand, but sensitive to grazing by large-sized herbivores. These results point, once again to the fact that once a primary factor restricting species distribution is removed (e.g. grazing by F. picta), other, secondary factors (competition with G. furcellatus) soon become important.

As in the case of the Gelidium-dominated zone, the relative importance of grazing and competition as structuring agents of the Iridaea laminarioides dominated zone varies seasonally. In areas invaded by sand, where the effects of grazing are reduced, I. laminarioides outcompete other frondose plants such as Ulva rigida and Porphyra columbina. Experimental removal of the apical parts of I. laminarioides allows otherwise strongly seasonal frondose forms to become established (Santelices & Avila, 1986; Santelices & Norambuena, 1987). This is consistent with the findings of Moreno & Jaramillo (1983) that a downward extension of I. laminarioides displaced the band of Ulva rigida. Competitive exclusion is, however, not consistent everywhere. In central Chile, I. laminarioides has a seasonal cycle of growth and reproduction forming its maximal blade cover during spring and summer. Desiccation during summer and the production and release of spores lead to destruction of the thalli, reducing the algal cover during autumn. At these times, Ulva rigida and some filamentous species appear in patches within the Iridaea laminarioides band.

On wave-exposed rocky habitats, the situation is more complex. Here, Iridaea laminarioides normally occur among mussels where the small-sized grazers occurring among mussels eat the settling algal spores and germlings. Some opportunistic species, such as Porphyra and Ulva, escape grazing by fast growth. Others, like Iridaea laminarioides, have longer-lived crusts and seasonally erect fronds. The crust of I. laminarioides is sensitive to herbivory not only by large-sized grazers, such as Fissurella picta (Moreno & Jaramillo, 1983) but also by large densities of small-sized grazers (Santelices & Martinez, 1988), such as those found in mussel bed. The crusts, however, are found in small angles and points of contact among mussels, areas which probably are out of the reach of grazers. Experimental removal of grazers caused increased cover of I. laminarioides in these mussel beds (Santelices & Martinez,

1988). Yet, the alga has a seasonal cycle of carpospore production, allowing the species to reach 100% cover at only a very few times of the year, even in the absence of grazers. Some species such as *U. rigida* or *P. columbina* could be found at other times, forming patches within the *Iridaea*-dominated band.

The above findings are interesting because they suggest two general patterns, also found in the case of *Lessonia* and *Codium*. One is the possibility of other, normally upper intertidal species, occurring as patches within the *Iridaea*-dominated zone. As in the previous cases, these patchy species are excluded from these levels in some seasons, by increased growth of *Iridaea laminarioides*.

The second point refers to the combination of strategies shown by *Iridaea laminarioides* where it is dominant. The basal parts of the plant behaves somewhat as a crust. It has long persistence and can last for three years or more (Hannach & Santelices, 1985). Even though it is sensitive either to large sizes or to large densities of herbivores, the crust is able to resist browsing by small grazers in the densities normally found outside the mussel bed (Jara & Moreno, 1984). The erect part of the plant has a competitive strategy, with fast growth and great production.

We lack experimental evidence on the causes of the upper limits of the *Iridaea laminarioides*-dominated zone. Dwarf, bleached individuals are often observed at this level of the beach and desiccation seems an obvious factor. Indeed, rocky uplifting by about 40 cm during the March 1985 earthquake in central Chile, destroyed all our *I. laminarioides*-dominated experimental sites and pushed the upper limits of our experimental populations downshore by about 40 cm (Santelices & Martinez, 1988). We do not know whether the increased effects of abiotic extremes make these algae more sensitive to grazing, or whether both factors interact in other ways to determine the upper boundary in this zone. Amphipods, another ecologically important type of grazer, become significant at high levels on the shore (Buschmann & Santelices, 1987). They are difficult to manipulate and we do not understand

their roles in these communities. In addition, recent experimental studies have shown (Luxoro & Santelices, in prep.) clear ecological differences between the isomorphic life history phases of *I. laminarioides*. The tetrasporophytic phase is less tolerant to desiccation and is more preferred as a food by numerous grazers in mid- and upper-shore areas than is the cystocarpic phase. Therefore, the upper limit reached by this species in any place could perhaps be determined by the phases of life-history present at that place. This depends on the food preferences of the local grazers.

Other frondose forms

This group is formed by several ephemeral species, such as *Ulva rigida*, *Porphyra columbina*, *Centroceras clavulatum*, *Polysiphonia* sp., which are able to live in clearings at any intertidal level, but often form somewhat predictable temporary monocultures on the upper shore. Interspecific competition with the other low intertidal species and grazing are supposed to restrict these species to these refugial areas. The situation might, however, not be so simple. Experimental caging of upper, cleared rocky habitats in central Chile showed no significant changes during 18 months. Thereafter a thick cover of *U. rigida* and *P. columbina* developed where herbivores were excluded during seasons and at tidal heights that were unexpected for these two species. Therefore, it would not be surprising to find that a complex interaction of factors determines which algae occur at these very high tidal levels.

General patterns

The above results suggest some trends revealed by experimental manipulations, that seem particularly interesting or of general validity for understanding structure and organization of the algal vegetation on wave-exposed rocky intertidal habitats of central Chile. Since the pioneer experimental studies developed by Baker (1909), a growing body of literature is attempting to uncover

ecological determinants of patterns of distribution of intertidal organisms. Because seaweeds are among the competitive dominats on primary space, they have regularly been included in these studies. A number of generalizations dealing with the algae have been formulated so far (see Chapman, 1986 for a review), but in the light of the results of studies in Chile some are in need of further analysis.

Zonation of algal morphologies and the symmetry of competitive interactions

Characterization of patterns of zonation by dominant morphologies seems particularly useful to qualify the often described asymmetric character (sensu Connell, 1983) of competitive interactions. Although some studies might have included ill-designed experiments on competition (see Underwood, 1986 for a review), competitive dominance is a well established phenomenon among intertidal algal associations (Dayton, 1975a; Lubchenco, 1980; Sousa, 1979a, 1979b; Santelices *et al.*, 1980, 1981; Quinn, 1982; Kastendiek, 1982; Santelices & Ojeda, 1984). Several of these studies have suggested that symmetric competition (competition with a reciprocal negative effect of equal magnitude) is rare. Because competition is often asymmetric, approximately linear hierarchies of competitives relationships have been suggested for intertidal organisms (Dayton, 1975a, 1975b; Lubchenco & Menge, 1978; Quinn, 1982).

Our results indicate that asymmetric competitive interactions are common only when they involve two vertically-zoned different morphologies (e.g. kelps versus crusts; crusts versus frondose thalli) but interactions are not necessarily asymmetric when they involve morphologically similar species within a band (e.g. *Lessonia* versus *Durvillaea*; *Ulva* versus *Iridaea*). Under some conditions, each of the species within a zone can outcompete the other, morphologically similar species in the zone. Under other sets of conditions these species could co-occur either as patches or as vertical bands of monocultures

within a given zone, each dominated by a given morphology. Since external morphology represents adaptive compromises for different functions (Neushul, 1972), it is not surprising that similar or approximately similar algal morphologies use the resources in roughly similar ways, originating symmetric competition. Within this framework it is expected that the outcome of this within-zone interaction could be mediated by grazing, the abiotic environment or an interaction between these two factors. Because the number of morphologically close species within a zone can be more than two, and since the relative importance of grazing and physical factors changes in space and time, it is expected that competition reversals and competitive networks could be found when studying the within-zone competitive interactions.

It is hard to know the frequency of this situation elsewhere because most studies have confused intra and inter-zones interactions. The literature contains some suggestive results. More than 25 years ago, Burrows & Lodge (1951, 1953) found that the removal of *Ascophyllum nodosum* in the 'Fucus-dominated zone' allowed the downward extension of *Fucus vesiculosus*-a somewhat morphologically similar species occurring immediately above the band of *Ascophyllum*- and the upward extension of *F. serratus*. In California, Hruby (1976) and Foster (1982) documented strongly asymmetric competitive interaction between *Laminaria* and *Iridaea*, but within the *Iridaea* band there was a grazing-mediated symmetric competitive interaction between *Ulva* and *Iridaea*. Also in California, Dayton (1975a, 1975b) has described competitive displacement between *Hedophyllum* and *Lessoniopsis* which alters according to the amount of wave action. This situation is considered to be similar (Dayton, 1984) to the relation described for *Lessonia-Durvillaea* in central Chile. Some of Sousa's (1979a, 1979b) results represent within-zone competitive interactions mediated either by disturbance (*Gigartina leptorhyncus-G. canaliculata-Rhodoglossum affine*) or grazing (*Ulva-Gigartina*). Even in mid-shore areas of New South Wales, where grazing by molluscs is important (Under-

wood, 1980; Underwood & Jernakoff, 1981), removal of grazers has led to short-time, but potentially symmetric interactions among thin thalli (*Enteromorpha*, *Ulva*, *Porphyra*; Jernakoff, 1983, 1985; Underwood & Jernakoff, 1984).

The above conclusions about symmetry are important when discussing ecological determinism and competitive hierarchies in intertidal habitats. Care should be taken not to extend conclusions obtained from one type of interaction to the other type. For example, Paine (1984) stressed the very strong degree of ecological determinism involved in the competitive exclusion of a large number of fugitive species by the kelp *Hedophyllum sessile*. He also found that the competitive relationships within a guild of coralline crusts (which is essentially a within-band comparison), were much less deterministic, with the possibility of reversals and networks. Both results are consistent with our observations and with the predicted outcome of inter- and within-band competition. Paine (1984), however, extended the conclusions gathered from interactions between kelps and erect thalli to interactions between crusts. He predicted that in the absence of grazers a single-species monoculture would also appear among the crusts. Our results suggest this is not necessarily the case because other factors, such as changes in gradients of abiotic conditions or differences in life-history would prevent monopolization. The example of *Lessonia* and *Durvillaea* is particularly pertinent to this point. A similar morphology does not necessarily mean similar life-history strategies. There are numerous habitats along the gradient of wave action where the fugitive strategy of *D. antarctica* compensates for its mechanically less resistant morphology, allowing for co-existance with *L. nigrescens*. Paine (1984) also suggested that single-species stands are the result of interspecific competition under broadly homogeneous conditions. This implies, by contrast, an extension of conclusions gathered from within-band competitive interactions to the inter-band interactions. In central Chile, *Lessonia nigrescens* does not require broadly homogeneous conditions to form single-species stands. Its fast growth and large size allow the species to monopolize primary space, escaping grazing and outcompeting other, morphologically different species, under broadly heterogeneous sets of conditions.

Algal morphology also seems to explain some of the observed reversals in competitive hierarchy between bands. Such changes have been found in some juvenile-adult interactions (Lubchenco & Menge, 1978; Lubchenco, 1980; Ojeda & Santelices, 1984) apparently because the morphology of the juvenile is similar to that of the adult plant of the competing species.

Ecological characters common to the dominant morphologies

A comparative analysis of the ecologically important characters shown by the group of species forming permanent zones in the low shore indicates that, with the exception of the coralline crustose algae, all of them combine escape from grazers or defensive adaptations with clear competitive abilities. Several authors (Dayton, 1971, 1975a; Lubchenco & Menge, 1978; Lubchenco, 1980) have found similar combination of characters in dominant species elsewhere, but often the analysis has been restricted to only one dominant form. Our results indicate that both morphology and inter-plant distances are of paramount importance. Very different morphologies can be notably successful at various elevations of the shore.

The low shore of wave exposed habitats of central Chile are dominated by large, perennial plants. As it has been reported previously (Dayton, 1971), fast growth and large size are the important characters here. They allow the individuals not only to escape grazing but also to outcompete other, smaller or slower-growing species. Inter-plant distances can vary in different habitats. Among adult plants, inter-plant distances affect the shading of potential (including conspecific) competitors. Among juveniles, inter-plant distances can significantly affect recruitment (via grazing), growth (via intraspecific competition) and persistance of the kelp-dominated zone.

The dominant algal morphology at the low-middle levels of these shores is represented by densely packed cushions and crusts, with little space among individuals. The inter-plant distances are of paramount importance to prevent grazing and perhaps also to prevent desiccation, at least among the filamentous cushions of *Gelidium*. It is interesting to note that Hay (1981) and Taylor & Hay (1984) have found that turfs are more resistant to desiccation and herbivory that are solitary forms. *Codium* adds to those adaptations the capacity to behave as a non-typical crust, growing fast and regenerating new tissues.

The set of adaptations exhibited by *Iridaea* very much approaches those described by Lubchenco (1980) for *Chondrus crispus*. It has a crustose, persistent holdfast able to resist at least some grazing, to perennate and to generate new blades. The erect blades are fast growers and carry the reproductive structures. Thus, different parts of the plant are specialized either in resisting grazing or growing fast. Very clearly these three groups of species have solved the dichotomous, often opposing costs (Littler & Littler, 1980) involved in generating antiherbivorous defenses and in investing resources for new growth. The finding that inter-plants distances, and perhaps other field distributional variables, are of paramount importance points to the need for field experimental work before generalizing on algal morphologies.

Factors limiting distribution

As Chapman (1986) has commented, the experimental evidence gathered over the last 10–15 years has seriously challenged Connell's (1972) conclusion that, in general, the upper shore limits of species distributions are set directly by the physiological environment, while biological interactions set the lower limits. We now know that some upper and lower distributional boundaries are set by predation, competition, abiotic extremes or interactive effects among various factors. Our results generally agree with these present views, but add further complications. Interactions

of factors are probably the rule rather than the exception in our system. Furthermore, the relative importance of these factors as determinants of a given boundary can change spatially or seasonally. In addition, several of our results show that whenever a factor primarily restricting species distribution is removed, other – generally unexpected – factors might restrict distributions. Some of these might even change the sign of the interaction in a short distance along intertidal gradients, as is the case for *Lessonia-Mesophyllum*. All these complexities clearly limit the predictive capacity about zones, boundaries and determinats unless carefully designed experimental work is done. Underwood & Denley (1984) have defined some basic criteria to improve the predictive capacity of the experimental work in these environments.

Competitive hierarchies and contrasting strategies for the use of the space

The study of macroalgal distribution patterns on intertidal shores of wave-exposed rocky habitats of central Chile suggests, as other have already stated (Dayton, 1975a; Lubchenco, 1980), that the low intertidal areas represent better physiological habitats for species occurring further up. These are usually prevented from occurring low down because of competition. Experimental results show that, in our system, the zone inhabited by *Lessonia-Durvillaea* has the physiological conditions appropriate for all of the other algal species. The settlement of these kelp-like species pushes down into the shallow subtidal the calcareous crust-dominated zone. It also pushes into the mid- and upper intertidal regions all other dominat morphologies. The establishment of fleshy crusts and cushions pushes the frondose and filamentous algae further up, a number of these are restricted to the upper shore by the abundance of *Iridaea laminarioides*. Thus, this intertidal shows a rather strict competitive hierarchy among algal morphologies, with predictable upward and downward displacements. Exclusion of a species is normally incomplete. With some

exceptions, displaced species can often be found as patches within other zones. With the exception of coralline crusts, none of the species in a zone with a given morphology are found in other zones further up in the shore. This is so because the interaction of factors determining upper boundaries in this system often include the abiotic environment. With the exception of crustose coralline algae, all species in the system can frequently be found as patches in morphologically different zones located lower on the shore. The permanence of those patches as alternative states within a morphologically different zone has a relation with ranking of morphologies in the competitive hierarchy. For example, patches of *Codium* and *Gelidium* persist longer in the kelp-dominated zone than do algae with a frondose or filamentous morphology. Among other reasons, this is because the blades and filaments can be displaced by *Codium* or *Gelidium*. Nevertheless, frondose and filamentous forms can persist longer in the zone dominated by cushions and crusts that in the kelp-dominated zone and further up they may form temporary monocultures.

The above situation tend to be common in many intertidal systems and it suggests two contrasting strategies in marine benthic algae. One group of species are able to pre-empt and hold substantial quantities of space. The other group is adapted for a patchy occupation of the environment. These two categories do not necessarily coincide with the respective concepts (Littler & Littler, 1980) of late successionist and opportunistics species. Very different life-history strategies can be found among those species that are space-holders. Thus, *Lessonia nigrescens* behaves like a typical late successionist while the life-history of *Durvillaea antarctica* approaches the opportunistic end of the spectrum. Equivalent differences in life-histories are evident when common patch-forming species, such as *Porphyra columbina* and *Ulva rigida*, are compared. *Porphyra columbina* has long, heteromorphic life cycles, with a microscopic phase able to escape grazing and with very precise abiotic requirements for production of spores and formation of erect thalli. *Ulva rigida* has a much simpler, direct cycle. Yet both species

develop an essentially similar patchy use of the environment. While the literature contains sizeable amounts of data referring to adaptations to hold space, relatively less is known of which might be interpreted as specific adaptations for a patchy life style. Some species, such as *Postelsia palmae-formis*, require predictable annual disturbances of some intensity (Paine, 1979) to clear space on the shore. Dispersal over large distances is typical of some of these species (*Ulva, Enteromorpha*) while others have persisting, microscopic stages (*Postelsia, Porphyra*). Strong, genetic differentiation over short distances on the shore occurs in *Enteromorpha linza*, despite the fact that (Innes, 1988) the populations studies were connected by water and no obvious barriers existed to prevent dispersal of microscopic propagules. Future research will probably allow us to understand whether patchy use of the space is in itself an alternative strategy for the algae.

Factors reducing variability of intertidal landscapes

In recent times, intertidal marine ecologists have discovered and become impressed with the great variability in community structure often found in intertidal habitats. In the past the trend was to describe broad zonation patterns which sometimes were forced to fit 'the universal scheme' expected for the region. At present, the trend has reversed and the main emphasis now is on sources of variability. Indeed there are opinions suggesting that intertidal landscapes are mainly made up of patches, without a predictable organization in space and times.

The experimental work on wave-exposed intertidal macroalgae of central Chile had identified two approaches as particularly useful to deal with this problem. One, already anticipated by Paine (1984), consists of using the monocultures as idealized null states or standards against which to measure departures in community structure. The situation often found in central Chile where three permanent and one or several temporary monocultures replace each other in vertical elevation, has been particularly useful to understand the

many individual processes which, collectively, generate the variations in intertidal landscapes.

The second approach consists of identifying hierarchies among the factors that increase or reduce variability. For example, even though up to four morphologically different algal zones can be identified on the vertical gradient of wave-exposed habitats, the total number of vegetational patterns is just a fraction of the total number expected by random combination of these four morphological zones. Some of these patterns have been illustrated in Figs. 5 and 6 and several others have been infrequently observed in the field. Yet the number of existing landscapes are less than 30 and that figure is much less than the total number of potential combinations. The factors reducing variability are numerous and some are of greater importance than others. For example, the competitive hierarchy found among different morphologies and the abiotic control of upward invasions are very important in the system, because they prevent many potential combinations. The existence of secondary, as well as primary, factors restricting species distribution and the changes in sign among competing forms reduce variability further. In general, all factors positively affecting the space-holder species and/or negatively affecting the patchy space users will decrease variability in the system. Identification of these factors will considerably increase our predictive capacity in the organization of intertidal rocky communities.

Acknowledgements

References

Alveal, K., 1970. Estudios ficoecológicos en la región costera de Valparaíso. Rev. Biol. mar., Valparaíso 14: 85–119.

Alveal, K., 1971. El ambiente costero de Montemar y su expresión biológica. Rev. Biol. mar., Valparaíso 14: 85–119.

Baker, S. M., 1909. On the causes of the zoning of brown seaweeds on the seashore. New Phytol. 8: 196–202.

Black, R., 1974. Some biological interactions affecting intertidal populations of the kelp Egregia laevigata. Mar. Biol. 28: 189–198.

Burrows, E. M. & S. M. Lodge, 1951. Autoecology and the species problem in Fucus. J. mar. biol. Ass. U.K. 30: 161–176.

Burrows, E. M. & S. M. Lodge, 1953. Intertidal plant populations with special reference to the genus Fucus. Proc. int. Seaweed Symp. 1: 6.

Buschmann, A. & B. Santelices, 1987. Micrograzers and spore release in Iridaea laminarioides Bory (Rhodophyta: Gigartinales). J. exp. mar. Biol. Ecol. 108: 171–179.

Castilla, J. C., 1979. Características bióticas del Pacífico Sur-Oriental, con especial referencia al sector chileno. Revista de la Comisión Permanente del Pacífico Sur 10: 167–182.

Castilla, J. C., 1981. Perspectivas de investigación en estructura y dinámica de comunidades intermareales rocosas de Chile Central. II. Depredadores de alto nivel trófico. Medio Ambiente 5: 190–215.

Chapman, A. R. O., 1986. Population and community ecology of seaweeds. In J. H. S. Blaxter & A. J. Southward (eds), Advances in Marine Biology, Academic Press, Lond. 26: 1–161.

Chapman, A. R. O. & C. L. Goudey, 1983. Demographic study of the macrothallus of Leathesia difformis (Phaeophyta) in Nova Scotia. Can. J. Bot. 61: 319–323.

Connell, J. H., 1972. Community interactions on marine rocky intertidal shores. Ann. Rev. Ecol. Syst. 4: 169–192.

Connell, J. H., 1975. Some mechanisms producing structure in natural communities: A model and evidence from field experiments. In M. L. Cody & J. M. Diamond (eds), Ecology and Evolution of Communities. Harvard University Press, Cambridge: 480–490.

Connell, J. H., 1983. On the prevalence and relative importance of interspecific competition: Evidence from field experiments. Am. Nat. 122: 661–696.

Dahl, E., 1953. Some aspects of the ecology and zonation of the fauna on sandy beaches. Oikos 4: 1–27.

Dayton, P. K., 1971. Competition, disturbance and community organization. The provision and subsequent utilization of space in a rocky intertidal community. Ecol. Monogr. 41: 351–389.

Dayton, P. K., 1975a. Experimental evaluation of ecological dominance in a rocky intertidal algal community. Ecol. Monogr. 45: 137–159.

Dayton, P. K., 1975b. Experimental studies of algal canopy interactions in a sea-otter-dominated kelp community at Amchitka Island, Alaska. Fish. Bull. U.S.A. 73: 230–237.

Dayton, P. K., 1984. Processes structuring some marine communities: Are they general? In D. R. Strong, D. Simberloff, L. G. Abele & A. Thistle (eds), Ecological Communities: Conceptual Issues and the Evidence. Princeton University Press, Princeton: 181–197.

Dayton, P. K., V. Curril, T. Gerrodette, B. D. Keller, R. Rosenthal & D. V. Tresce, 1984. Patch dynamics and stability of some California kelp communities. Ecol. Monogr. 54: 253–289.

DeWreede, R. E. & T. Klinger, 1987. Reproductive strategies in algae. In J. Lovett-Doust & L. Lovett-Doust (eds), Plant Reproductive Strategies. Oxford University Press, London (in press).

Foster, M., 1982. Factors controlling the intertidal zonation of Iridaea flaccida (Rhodophyta). J. Phycol. 18: 285–294.

Guiler, E. R., 1959a. Intertidal belt forming species on the rocky coast of northern Chile. Papers and Proceedings, Royal Society of Tasmania 93: 33–58.

Guiler, E. R., 1959b. The intertidal ecology of the Montemar area, Chile. Papers and Proceedings, Royal Society of Tasmania 93: 165–183.

Hannach, G. & B. Santelices, 1985. Ecological differences between the isomorphic reproductive phases of two species of Iridaea (Rhodophyta: Gigartinales). Mar. Ecol. Prog. Ser. 22: 291–303.

Hay, M. E., 1981. The functional morphology of turf-forming seaweeds: persistence in stressful marine habitats. Ecology 62: 739–750.

Hruby, T., 1976. Observations of algal zonation resulting from competition. Estuar. coast. mar. sci. 4: 231–233.

Innes, D. J., 1988. Genetic differentiation in the intertidal zone in populations of the alga Enteromorpha linza (Ulvales: Chlorophyta). Mar. Biol. 97: 9–16.

Jara, H. F. & C. A. Moreno, 1984. Herbivory and structure in a mid-littoral rocky community: a case in southern Chile. Ecology 65: 28–38.

Jernakoff, P., 1983. Factors affecting the recruitment of algae in a mid shore region dominated by barnacles. J. exp. mar. Biol. Ecol. 67: 17–31.

Jernakoff, P., 1985. An experimental evaluation of the influence of barnacles, crevices and seasonal patterns of grazing on algal diversity and cover in an intertidal barnacle zone. J. exp. mar. Biol. Ecol. 88: 287–302.

Kastendiek, J., 1982. Competitor-mediated coexistance: interactions among three species of benthic macroalgae. J. exp. mar. Biol. Ecol. 62: 201–210.

Littler, M. M. & D. S. Littler, 1980. The evolution of thallus form and survival strategies in benthic marine macroalgae: field and laboratory test of a functional form model. Am. Nat. 116: 25–44.

Lubchenco, J., 1980. Algal zonation in a New England rocky intertidal community: An experimental analysis. Ecology 61: 333–344.

Lubchenco, J. & J. Cubit, 1980. Heteromorphic life histories of certain marine algae as adaptations to variations in herbivory. Ecology 61: 676–687.

Lubchenco, J. & B. A. Menge, 1978. Community development and persistence in a low rocky intertidal zone. Ecol. Monogr. 48: 67–94.

Markham, J. W., 1978. Observations on the ecology of Laminaria sinclairii (Harvey) Farlow, Anderson et Eaton. Syesis 1: 125–131.

Montalva, S. & B. Santelices, 1981. Interspecific interference among species of Gelidium from Central Chile. J. exp. mar. Biol. Ecol. 53: 77–88.

Moreno, C. A. & E. Jaramillo, 1983. The role of grazers in the zonation of intertidal macroalgae of the Chilean coast near Valdivia. Oikos 41: 73–76.

Moreno, C. A., J. P. Sutherland & H. F. Jara, 1984. Man as a predator in the intertidal zone of southern Chile. Oikos 42: 155–160.

Neushul, M. 1972. Functional interpretation of benthic marine algal morphology. In I. Abbott & M. Kurogi (eds), Contributions to the Systematics of Benthic Marine Algae of the North Pacific. Japanese Society of Phycology, Kobe: 47–73.

Oliva, D. & J. C. Castilla, 1986. The effect of human exclusion on the population structure of key-hole limpets Fissurella crassa and F. limbata on the coast of Central Chile. P.S.Z.N.I.: Marine Ecology 7: 201–207.

Ojeda, F. P. & B. Santelices, 1984. Ecological dominance of Lessonia nigrescens (Phaeophyta) in Central Chile. Mar. Ecol. Prog. Ser. 19: 83–91.

Paine, R. T., 1979. Disaster, catastrophe and local persistance of the sea palm Postelsia palmaeformis. Science 205: 685–687.

Paine, R. T., 1984. Ecological determinism in the competition for space. Ecology 65: 1339–1348.

Paine, R. T. & R. L. Vadas, 1969. The effects of grazing by sea urchins, Strongylocentrotus spp., on benthic algal populations. Limnol. Oceanogr. 14: 710–719.

Paine, R. T., C. J. Slocum & D. O. Duggins, 1979. Growth and longevity in the crustose red alga Petrocelis middendorfii. Mar. Biol. 51: 185–192.

Quinn, J. F., 1982. Competitive hierarchies in marine benthic communities. Oecologia 54: 129–135.

Ruiz, E. & L. Giampoli, 1981. Estudios distribucionales de la flora y fauna costera de Caleta Cocholgue, Bahía de Concepción, Chile. Boletín de la Sociedad de Biología de Concepción 52: 145–166.

Romo, H. & K. Alveal, 1977. Las comunidades del litoral rocoso de Punta Ventanilla, Bahía de Quintero, Chile. Gayana (Misc.) 6: 1–41.

Rosenthal, R. J., W. D. Clarke & P. K. Dayton, 1974. Ecology and natural history of a stand of giant kelp *Macrocystis pyrifera* off Del Mar, California. Fish. Bull. U.S.A. 72: 670–684.

Santelices, B., 1981. Perspectivas de investigación en estructura y dinámica de comunidades intermareales rocosas de Chile Central. I. Cinturones de macroalgas. Medio Ambiente 5: 175–189.

Santelices, B., 1989. Coastal ecosystems of mainland Chile. In P. Nienhuis & A. Mathieson (eds), Intertidal and Littoral Ecosystems of the World. Elsevier Scientific Publishing Co. 24 (in press).

Santelices, B. & M. Avila, 1986. Bases biológicas para maximizar cosecha de 'Luche' (*Porphyra columbina* Montagne) en Chile Central. En R. Westermeier (ed.), Actas del Segundo Congreso Nacional sobre Algas Marinas Chilenas. Universidad Austral de Chile, Valdivia, Chile: 201–211.

Santelices, B. & F. P. Ojeda, 1984. Recruitment, growth and survival of *Lessonia nigrescens* (Phaeophyta) at various tidal levels in exposed habitats of Central Chile. Mar. Ecol. Prog. Ser. 19: 73–82.

Santelices, B. & E. Martínez, 1988. Effects of filter-feeders and grazers on algal settlement and growth in mussel beds. J. exp. mar. Biol. Ecol. 118: 281–306.

Santelices, B. & R. Norambuena, 1987. A harvesting strategy for *Iridaea laminarioides* in Central Chile. Hydrobiologia 151/152: 329–333.

Santelices, B., J. Cancino, S. Montalva, R. Pinto & E. González, 1977. Estudios ecológicos en la zona costera afectada por contaminación del 'Northern Breeze'. II. Comunidades de playas de rocas. Medio Ambiente 2: 65–83.

Santelices, B., J. C. Castilla, J. Cancino & P. Schmiede, 1980. Comparative ecology of *Lessonia nigrescens* and *Durvillaea antarctica* (Phaeophyta) in Central Chile. Mar. Biol. 59: 119–132.

Santelices, B., S. Montalva & P. Oliger, 1981. Competitive algal community organization in exposed intertidal habitats for Central Chile. Mar. Ecol. Prog. Ser. 6: 267–276.

Slocum, C. J., 1980. Differential susceptibility to grazers in two phases of an intertidal alga: Advantages of heteromorphic generations. J. exp. mar. Biol. Ecol. 46: 99–110.

Smith, B. D., 1986. Implications of population dynamics and interspecific competition for harvest management of the seaweed *Laminaria*. Mar. Ecol. Prog. Ser. 33: 7–18.

Sousa, W. P., 1979a. Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. Ecol. Monogr. 49: 227–254.

Sousa, W. P., 1979b. Disturbance in marine intertidal boulder fields: The non equilibrium maintenance of species diversity. Ecology 60: 1225–1239.

Sutherland, J., 1974. Multiple stable points in natural communities. Am. Nat. 108: 859–873.

Taylor, P. R. & M. E. Hay, 1984. Functional morphology of intertidal seaweeds: adaptive significance of aggregate vs. solitary forms. Mar. Ecol. Prog. Ser. 18: 295–302.

Underwood, A. J., 1980. The effects of grazing by gastropods and physical factors on the upper limits of distribution of intertidal macroalgae. Oecologia (Berlin) 46: 201–213.

Underwood, A. J., 1986. The analysis of competition by field experiments. In J. Kikkawa & D. J. Anderson (eds), Community Ecology: Patterns and Process. Blackwell Scientific Press: 240–268.

Underwood, A. J. & E. J. Denley, 1984. Paradigms, explanations and generalizations in models for the structure of intertidal communities on rocky shores. In D. R. Strong, D. Simberloff, L. G. Abele & A. Thistle (eds), Ecological communities: Conceptual issues and the evidence. Princeton University Press, Princeton: 151–180.

Underwood, A. J. & P. Jernakoff, 1981. Effects of interactions between algae and grazing gastropods on the structure of a low-shore intertidal algal community. Oecologia 48: 221–233.

Underwood, A. J. & P. Jernakoff, 1984. The effects of tidal height, wave-exposure, seasonality and rocky-pools on grazing and distribution of intertidal macroalgae in New South Wales. J. exp. mar. Biol. Ecol. 75: 71–96.

Vadas, R., 1979. Seaweeds: an overview, ecological and economic importance. Experientia 35: 429–432.

Velimirov, B. & C. L. Griffiths, 1979. Wave-induced kelp movement and its importance for community structure. Bot. mar. 22: 169–172.

Westermeier, R., P. J. Rivera, M. Chacana & I. Gómez, 1987. Biological bases for management of *Iridaea laminarioides* Bory in southern Chile. Hydrobiologia 151/152: 313–328.