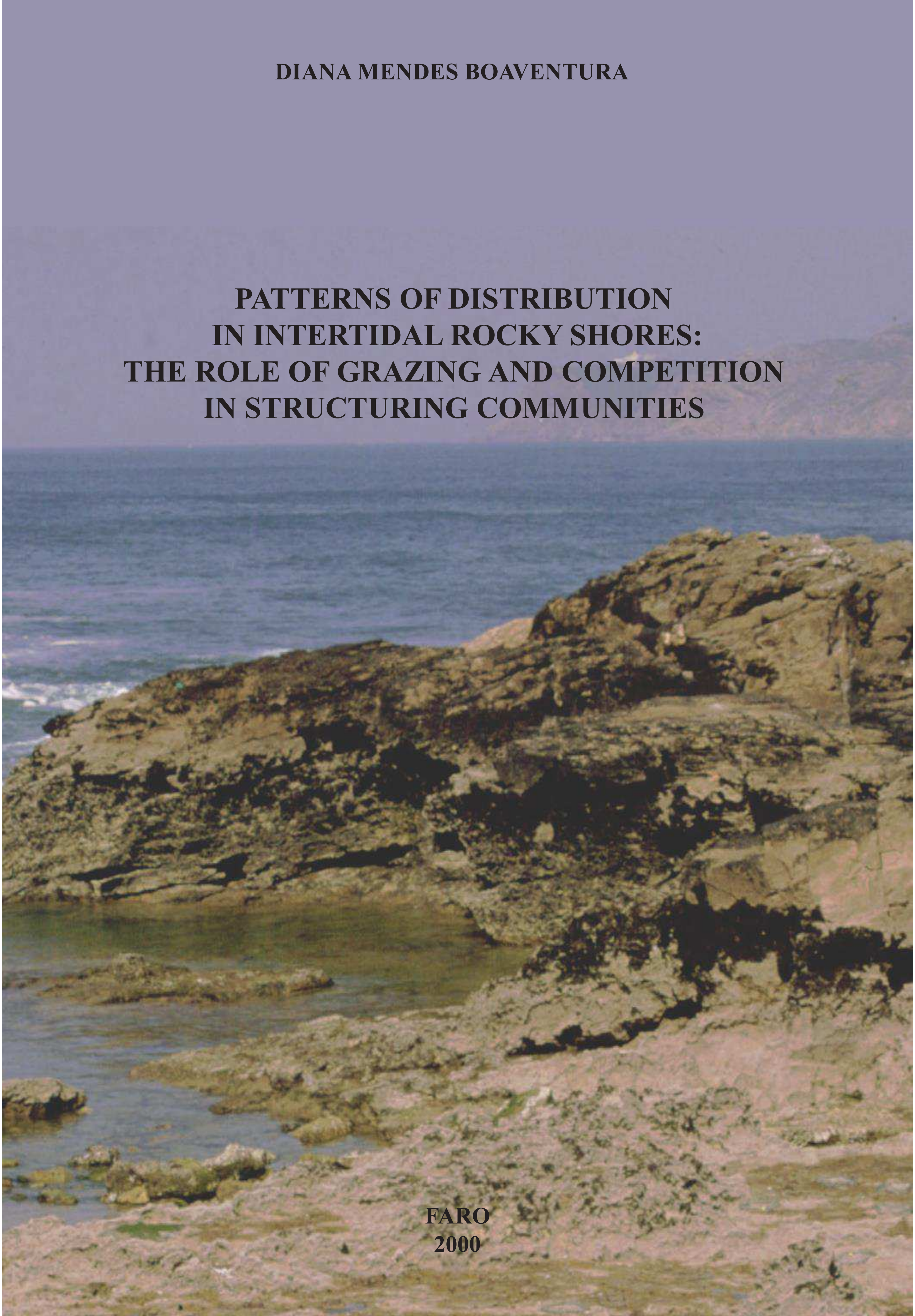

DIANA MENDES BOAVENTURA

PATTERNS OF DISTRIBUTION IN INTERTIDAL ROCKY SHORES: THE ROLE OF GRAZING AND COMPETITION IN STRUCTURING COMMUNITIES

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À memória da minha mãe

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ABSTRACT

Patterns of distribution on rocky shores and the role of grazing and competition as structuring agents of intertidal communities were studied in the present work. The intertidal rocky shore communities of the Portuguese coast have been studied in a scattered way by different authors. Taking into account that Portugal is thought to be a zone of overlap of boreal Atlantic species at their southern limits and more subtropical and Mediterranean species at their northern limits, it is important to study the whole littoral coast. A general description of zonation patterns along the coast and the comparison of distribution patterns of mid-shore organisms were made in this work. In order to test if there is any variation in species distribution and abundance in upper and lower mid-shore zone along the intertidal Portuguese coast, three main regions were studied (north, centre and south). Nine shores were visited in each region and a total of 27 shores were sampled along the Portuguese coast. In each one of the 27 locations, the shore was levelled and a general qualitative description was made, which also aided stratification of subsequent quantitative sampling. Non-destructive quantitative methods were used within upper and lower mid-shore zones. Five replicate quadrats were counted in each of the two mid-shore areas using a quadrat of 50 x 50cm with 49 intersection points. Zonation patterns in Portugal may be seen as mixture of the patterns described for the north east Atlantic coasts and those described for the Mediterranean. The results of this study also confirm the latitudinal variations from north to southern Europe, with animal dominated communities extending further into shelter at more southerly locations. Similarly, southwards, dominance by large brown algae declines low on the shore and red algal turves become more important. Multidimensional analysis and the ANOSIM test have revealed clear differences in the structure of upper and lower mid-shore zone in part due to the number of species found. In general, the upper level exhibited a lower diversity and a higher dominance. Despite the decrease in abundance of several species along the regional gradient (from both North to South and South to North) the differences in the community structure were not as clear as for the vertical gradient. A possible explanation for this is that the increase in complexity of the community from high to low shore is superimposed on the latitudinal changes. Within each level, however, the northern region was considerably different from the south and central regions. SIMPER analysis revealed the species which contributed to the geographical separation of the northern region in relation to the centre and south. It has also given important information on the geographical decline in abundance of species.

A great part of the work in this thesis was devoted to experimental ecology studies on causes of distribution patterns, essentially focussed on the importance of grazing and competition by limpets in intertidal communities. A red algal turf is often found just below the barnacle/limpet zone of many European shores, especially on steep shores of moderate exposure. The hypothesis that grazing by limpets determines the upper limit of distribution of the red algal turf was tested in Portugal and Britain. We also aimed to assess whether the grazing effect is modified by different factors operating at various spatial scales. Grazers were excluded by fences, and there were half-fenced and unfenced controls. Exclusion plots were rapidly colonised by green ephemeral algae in the months immediately after the beginning of the experiment (summer); these algae were later replaced by perennial algae. The percentage cover of turf forming macroalgae showed a significant increase at both locations. Their upper limit of distribution extended more than 50 cm in most of the shore areas. In contrast, control and half-fenced plots remained devoid of algae. After two years, ungrazed areas were mainly colonised by red algal turf (e.g. *Caulacanthus ustulatus, Gelidium* spp*., Laurencia pinnatifida*) in Portugal, while canopy cover (*Fucus serratus* and *Himanthalia elongata*) dominated in Britain. Physical factors acting at both local and geographical scales are likely to explain these differences. However, although physical factors probably have an important influence on the size and abundance of sublittoral fringe macroalgae, the results from this experiment indicate that grazers seem to play a major role in directly setting its upper limits. The community converged rapidly to undisturbed conditions after fence removal. When the algal turf was cleared beneath the “usual” limit of distribution, limpets extended down shore but showed no ability to prevent subsequent colonisation by macroalgae. The upper limit of algal turf seems to be in permanent dynamic balance between the activities of grazers at higher levels on the shore and the rapidity of colonisation and growth of the algae at lower levels, being probably modified by physical factors which favour algal growth or grazing efficiency.

Inter- and intraspecific competitive interactions among the species *Patella depressa* and *Patella vulgata* were analysed on the northern coast of Portugal, where both species co-occur in similar proportions. Increased (x 2, x 4), decreased (x 1/2) and normal densities of limpets were used to test the effects of competition on the growth and mortality of the limpets. Fenced plots of 25 x 25 cm enclosing marked limpets at various densities in plastic coated wire fences (25 x 25 x 4 cm high) were set at a mid tidal level on the shore. Twelve treatments with different combination of densities and species were assigned to the plots, with three replicates of each. Mortality was recorded every fifteen days and growth was measured monthly during the five moths of the experiment. At the end of the experiment limpets were collected for biometry, sex determination and gonad stage evaluation. The availability of food was indirectly assessed by determination of chlorophyll concentration with spectrophotometric analysis of rock chips. Both species of grazing molluscs showed increased mortality and reduced growth and weight in increased density treatments. Limpets in decreased density treatments showed lower mortality and higher growth rate. Although both species could affect negatively the other, there were no significant differences between the effect of *P. vulgata* on *P. depressa* and the effect of *P. depressa* on *P. vulgata* on mortality and length. Results from tissue weight, however, revealed that intraspecific increases in density resulted in a more accentuated reduction of weight than when both species were present. The results were compared with previous studies of competition in grazing molluscs and discussed in relation to the limits of distribution of *P. vulgata* on the Portuguese coast.

Competitive interactions within and between size-classes of the limpet *Patella depressa* were investigated in central Portugal. Experimental enclosures of 25 x 25 cm containing marked limpets were set at a mid tidal level on the shore. Twelve treatments with different combination of densities and size-classes were assigned to the plots, with three replicates of each. Decreased density treatments showed very low mortality and substantially increased growth. Both size-classes of limpets showed increased mortality and reduced growth in increased density treatments. This effect was, however, more accentuated for large than small limpets when fenced separately. Although both size-classes could negatively affect each other, the effect of large limpets on small was greater than the reverse. Large limpets are superior competitors that may modulate the abundance of small limpets on the shore. It is unlikely, however, that they will totally exclude small limpets due to intensity of competition within the large size-class. Niche differentiation and high recruitment at low shore levels are other possible factors that can contribute to reduce the effects of this asymmetric competition between the size-classes.

The present work has revealed that both grazing and competition are major biological factors determining the structure of intertidal rocky communities. This study has also contributed to refute old ideas on the causes of distribution patterns. Notwithstanding the obtained results on grazing and competition further experimentation is needed on other aspects of the ecology of intertidal communities.

RESUMO

A presente dissertação teve por objectivo estudar os padrões de distribuição em povoamentos intertidais de substrato rochoso e a influência da herbivoria e competição na estrutura das comunidades. Em Portugal pouca atenção tem sido dedicada ao estudo das comunidades intertidais de substrato rochoso. A costa portuguesa é uma zona de fronteira biogeográfica para espécies de afinidades atlântico-boreais e temperadas-quentes, sendo por isso fundamental o estudo dos povoamentos ao longo de toda a costa. No presente trabalho foi feita a descrição geral dos padrões de zonação ao longo da costa continental portuguesa e a comparação quantitativa dos padrões de distribuição na zona eulitoral. Com o objectivo de testar se existem variações na distribuição e abundância dos organismos na zona eulitoral superior e inferior ao longo de toda a costa, foram consideradas três regiões principais: norte, centro e sul. Nove estações foram visitadas em cada região, correspondendo a um total de 27 praias amostradas. Em cada uma destas estações efectuou-se uma descrição geral dos povoamentos e o levantamento dos padrões de zonação em relação ao zero hidrográfico. A amostragem quantitativa recorreu ao uso de metodologias não-destrutivas e foi efectuada na zona eulitoral superior e inferior, tendo sido amostrados 5 replicados em cada uma destas zonas. Os padrões de zonação ao longo da costa Portuguesa possuem características descritas para costas Norte Atlânticas e Mediterrânicas. Os resultados do presente estudo confirmam também as variações latitudinais do norte para o sul da Europa, com a decrescente cobertura de algas na zona eulitoral mesmo em locais abrigados. De igual modo também a abundância de algas castanhas diminui na franja sublitoral, sendo substituídas por uma zona de algas vermelhas nas regiões mais a sul. Os resultados da análise multidimensional e do teste ANOSIM revelaram diferenças significativas na estrutura das comunidades da zona eulitoral superior e inferior, relacionadas em parte com o número de espécies existentes. De um modo geral, registou-se uma menor diversidade e maior dominância no nível superior. As diferenças na estrutura das comunidades ao longo do gradiente regional não se revelaram tão evidentes como as referidas para o gradiente vertical, apesar do decréscimo na abundância de variadas espécies ao longo da costa (tanto de norte para sul como no sentido inverso). Uma explicação possível para este resultado é o facto do aumento de complexidade das comunidades do nível superior para o nível inferior prevalecer em relação ao gradiente regional. Considerando cada nível separadamente a região do Norte destacou-se das regiões do centro e sul. A análise SIMPER revelou as espécies que mais contribuíram para esta separação bem como aquelas que apresentam um gradiente de abundância ao longo da costa.

Na presente dissertação estudaram-se ainda as causas de determinados padrões de distribuição recorrendo à ecologia experimental, e focando essencialmente aspectos relacionados com a influência da herbivoria e competição nas comunidades intertidais. Em diversas regiões da Europa é frequentemente encontrado na zona intertidal inferior um "tapete" de algas vermelhas, em especial nas zonas de hidrodinamismo moderado. A hipótese de o limite superior deste tapete de algas vermelhas ser determinado por moluscos herbívoros foi testada em Portugal e Inglaterra. Também se procurou avaliar se o efeito provocado por moluscos herbívoros seria alterado por diversos factores que operam a diferentes escalas espaciais. Os gastrópodes foram excluídos recorrendo ao uso de redes, e utilizaram-se ainda controlos para testar o uso da rede ("meia-rede") e controlos sem qualquer manipulação. As áreas experimentais sem gastrópodes foram rapidamente colonizadas por algas efémeras nos primeiros meses da experiência. Estas algas foram mais tarde substituídas por algas perenes. A percentagem de cobertura de algas vermelhas aumentou significativamente nas duas regiões. O limite superior de distribuição estendeu-se mais de 50 cm na maioria das áreas experimentais. O controlo e "meias-redes" permaneceram desprovidos de algas. Após dois anos do início da experiência, as áreas sem herbívoros eram essencialmente colonizadas por algas vermelhas (e.g. *Caulacanthus ustulatus*, *Gelidium* spp., *Laurencia pinnatifida*) em Portugal, enquanto que em Inglaterra dominavam algas castanhas (*Fucus serratus* e *Himanthalia elongata*). É provável que a acção de factores físicos à escala local e geográfica esteja relacionada com estas diferenças. No entanto, apesar dos factores físicos poderem ser

importantes no tamanho e abundância das algas na zona intertidal inferior, os resultados desta experiência indicam que são os herbívoros que parecem determinar o limite superior destas algas. Após a remoção das redes a comunidade retornou rapidamente às condições iniciais antes da manipulação. Quando áreas de algas vermelhas foram removidas imediatamente abaixo do limite normal de distribuição os herbívoros dirigiram-se para estas áreas mas não impediram a posterior colonização por macroalgas. O limite superior do tapete de algas vermelhas parece estar em permanente equilíbrio dinâmico entre a actividade dos herbívoros nas zonas imediatamente acima do limite e a rapidez de colonização e crescimento das algas nas zonas inferiores, sendo provavelmente alterado por factores físicos que favorecem o crescimento das algas ou a eficácia dos herbívoros.

A competição inter- e intraespecífica entre as espécies *Patella depressa* e *Patella vulgata* foi analisada na costa norte de Portugal. Densidades aumentadas (x 2, x4), reduzidas (x 1/2) e normais foram utilizadas para testar os efeitos da competição no crescimento e mortalidade das lapas. Na zona eulitoral estabeleceram-se áreas experimentais de 25 x 25 cm vedadas com rede plastificada. Doze tratamentos com diferentes combinações de densidades e espécies foram atribuídos a estas áreas, com três replicados por tratamento. A mortalidade foi registada quinzenalmente e o comprimento foi medido mensalmente durante um período experimental de cinco meses. No final da experiência as lapas foram colhidas tendo em vista o estudo biométrico, a determinação do sexo e a avaliação do estado de maturação da gónada. A quantidade de alimento disponível foi avaliada indirectamente através da determinação da concentração de clorofila existente em pequenas amostras de substrato recorrendo à espectrofotometria de absorção. Ambas as espécies sofreram uma maior mortalidade e redução no crescimento e peso nos tratamentos de densidade aumentada. As lapas nos tratamentos de densidade reduzida exibiram uma baixa mortalidade e um maior crescimento. Apesar de ambas as espécies serem capazes de afectar negativamente a outra, não se registaram diferenças significativas entre o efeito de *P. vulgata* em *P. depressa* e o efeito de *P. depressa* em *P. vulgata* na mortalidade e crescimento. No entanto, os resultados do peso revelaram que o aumento intraespecífico de densidade levou a uma redução mais acentuada de peso do que quando ambas as espécies estavam presentes. Os resultados obtidos foram comparados com estudos prévios de competição entre moluscos herbívoros e discutidos em relação ao limite de distribuição de *P. vulgata* na costa portuguesa.

As interacções competitivas entre classes de tamanho, e dentro das mesmas, foram investigadas na espécie *Patella depressa*, na costa central de Portugal. Foram utilizados doze tratamentos com diferentes combinações de densidades e classes de tamanho, com três replicados de cada. Os tratamentos de densidade reduzida mostraram baixa mortalidade e um aumento substancial no crescimento. Ambas as classes de tamanho sofreram um aumento na mortalidade e crescimento reduzido nos tratamentos de densidade aumentada. Contudo, este efeito foi mais acentuado nas lapas de maiores dimensões do que nas menores, nos tratamentos em que as classes de tamanho foram separadas. Por outro lado, apesar de ambas as classes de tamanho afectarem negativamente a outra, o efeito das lapas de maiores dimensões nas menores foi mais forte que o oposto. As lapas de maiores dimensões revelaram ser competidores superiores que podem moderar a abundância de lapas menores na região intertidal. No entanto, a exclusão total de lapas de menores dimensões é pouco provável devido à alta competição existente dentro da classe de tamanho superior. Outros factores como a ocupação de nichos diferentes e o elevado recrutamento em zonas inferiores poderão também contribuir para minimizar os efeitos da competição assimétrica entre classes de tamanho.

O presente trabalho revelou que a herbivoria e a competição são factores biológicos que desempenham um papel muito importante na estrutura das comunidades intertidais. Este estudo contribuiu também para refutar ideias antigas sobre as causas dos padrões de distribuição. Apesar dos resultados obtidos, é necessário prosseguir com o trabalho experimental relativamente a outros aspectos da ecologia das comunidades intertidais.

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CHAPTER 1

General introduction

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GENERAL INTRODUCTION

Why study rocky shores?

The intertidal zone has been of interest for biologists since many years. It can be considered a boundary zone where the transition from an aquatic marine habitat to terrestrial conditions occurs within a restricted area. Therefore any shore is a sharp environmental gradient which is ideal for ecological studies. Additionally it has a great diversity of species, which may be as great or greater than that found in the more extensive subtidal habitats. It should be stressed that this area is an extension of the marine environment and is inhabited almost exclusively by marine organisms. Although plant life is restricted to algae and a few higher plants, examples of most of the major animal groups can be found on the shore. Access to the shore is generally easy and aquatic organisms can be directly observed during low tide without special equipment. Due to all of these features the intertidal zone provides an ideal system for research and education in systematics and taxonomy, ecophysiology, population and community ecology (Connell, 1972; Hawkins & Jones, 1992; Paine, 1994; Raffaelli & Hawkins, 1996; Nybakken, 1997).

Marine intertidal communities are highly productive and have been of interest and use for humans since prehistoric time. Shores are susceptible to a variety of human impacts such as the exploitation of food resources, human settlement, pollution, introduction of new species, coastal zone change or tourism. Coastal development and global climatic changes can have important consequences for shore habitats. Sea level rise as a result of the global warming is an important issue and application of intertidal ecology. Hence, because shores are affected by human impacts and are also more accessible and easier to investigate than other marine systems, they are frequently the subject of biological monitoring and conservation programmes (reviewed in Raffaelli & Hawkins, 1996).

Intertidal rocky shores are particularly easy to study. Many species are sessile and even the mobile animals are generally slow moving. Organisms are taxonomically tractable and relatively short-lived. Their abundance can be easily estimated as percentage cover or density in a non-destructive way, allowing the dynamics of populations or communities to be studied without too much interference. Most importantly, because they are easy to manipulate, they are particularly suitable for an experimental approach. This enables a better understanding of the functioning of rocky shore communities (Paine, 1966, 1994; Connell, 1972; Little & Kitching, 1996; Raffaelli & Hawkins, 1996).

In summary, the richness, the diversity of environmental factors, and the ease of access attracted to this area a considerable amount of scientific attention. This has proved important to produce unifying concepts and models regarding the organisation of marine communities and community ecology in general.

The shore environment

Tides

The study of marine intertidal communities involves the comprehension of the shore environmental conditions, particularly the tides. Tides are certainly an over-riding physical feature influencing intertidal communities by modification of the gradient between the sea and land (see discussion in Raffaelli & Hawkins, 1996).

The periodic, predictable rise and fall of the level of the sea over a given time is called a tide. This is actually a wave of very long wavelength. Its astronomical origin is due to the interaction of the gravitational attraction of the Sun and the Moon on the Earth and the forces generated by the rotating Earth and Moon system. As a result of these forces, the water in ocean basins is pulled into bulges- “two high tides”- in line with the Moon. As the Moon rotates around its common axis with the Earth these tides circle the Earth. The simplest and most common tidal pattern is a semidiurnal one, with two high and low tides each day. The two tides can be of different sizes, which is partially due to the varying declination of the Moon. The effect of the Sun is seen in spring and neap tides. When the gravitational forces of the Sun and the Moon act together, i.e. when Sun, Moon and Earth are directly aligned, tide-raising forces are at a maximum. This occurs at the times of new and full Moon and results in tides of very large amplitude called spring tides. Conversely, when the Moon and Sun are at right angles to the Earth, the gravitational attractions of Sun and Moon act in opposition. Tide-raising forces on the Earth are at minimum resulting in tides of small amplitude called neap tides. Seasonal differences in the amplitude of spring tides are caused by the changing declination of the Sun. The highest spring tides occur at equinoxes, while at the solstices spring tides are at their lowest amplitude (Duxbury & Duxbury, 1993; Little & Kitching, 1996; Raffaelli & Hawkins, 1996; Nybakken, 1997; Thurman, 1997).

Different tidal patterns such as semidiurnal, diurnal and mixed occur in various parts of the world. Variations in the number and in the height of high and low tides per day in different regions are related to complexities caused by several factors. These include, for example, presence of land masses, peculiarities of the ocean basins or the Coriolis force (Raffaelli & Hawkins, 1996).

Despite this enormous variation in the behaviour of tides, they are in general predictable and knowledge of the timing of tides and of mean tidal heights is essential when working on a shore. Tidal heights are measured in relation to a conventional level called chart datum (CD), which corresponds to the lowest astronomical tide. Useful mean heights above this level are the mean values for high and low water of spring and neap tides (MHWS, MHWN, MLWN, MLWS). The mean tidal level (MTL) is the average of these four heights. Extreme water of spring tides (EHWH, EHWL) can also be used for representation of the height above chart datum.

Environmental conditions and adaptations of intertidal organisms

The main feature which tidal regime imposes on the littoral is the alternation of emersion and submersion periods, as irregular in duration and frequency these might be (Lewis, 1964). It can affect the intertidal communities through the duration of exposure to air and time of the day during which it occurs. Additionally, certain rhythms of activity of intertidal organisms are also related to tidal effect (Nybakken, 1997).

Most of the intertidal species evolved from marine ancestors. The marine environment is relatively stable. Salinity is constant and temperature variations are small. Carbon dioxide, water and oxygen needed for photosynthesis and respiration are abundant, and nutrients are readily available being rarely limiting in coastal waters (Hawkins & Jones, 1992). Therefore, from low water to the spray zone the environmental gradient is of increasingly harsh physical conditions, due to greater fluctuations in environmental conditions associated with the increased proportion of time exposure to the air (Hawkins & Jones, 1992; Raffaelli & Hawkins, 1996). Similarly, adaptations of intertidal organisms are intimately related with avoidance or minimisation of the stress of air exposure (Nybakken, 1997).

Intertidal organisms show various mechanisms for avoiding water loss. The simplest mechanism is to avoid heat and air exposure and, therefore, mobile animals (e.g. crabs) may seek for refuge in moist crevices or under algae canopy (Nybakken, 1997). Another mechanism, which is shown by several intertidal algae (e.g. *Porphyra*, *Ulva* and *Enteromorpha*), is to be simply adapted to withstand a severe water loss from their tissues (Kanwisher, 1957). Fucoid algae also seem to lack physiological or structural means to retard water loss (Schonbeck & Norton, 1979). Many other intertidal species, however, possess structural and behavioural mechanisms to prevent desiccation (Newell, 1979; Nybakken, 1997). Sessile animals avoid water loss by closing their shells at low tide. Mussels and other bivalves have the ability to close their valves tightly to prevent desiccation. Barnacles have lateral calcareous plates and aperture plates that when closed cut down water loss. Limpets have a “homescar” into which their shells fit, and where they generally return at low tide. It has been suggested that this close fit would reduce desiccation (Lewis, 1954), but other hypotheses for the advantages of homing behaviour have been reviewed by Underwood (1979). Other gastropods have opercula that completely seal the aperture of the shell (Nybakken, 1997). At low tide there may also exist osmotic problems. A classical example is that of rock pools where salinity may be increased by evaporation or reduced by rainfall (Lewis, 1964; Hawkins & Jones, 1992). The responses of organisms to such phenomenon are generally the same as those observed for preventing desiccation (Nybakken, 1997).

Most of intertidal species conduct their main activities when immersed or immediately after the tide recedes (Lewis, 1964). Many filter feeder animals (e.g. mussels, barnacles) can only feed when immersed. Many grazers and predators also move and forage more efficiently at high tide or nocturnal low tide, when desiccation is less intense. Large mobile predators (e.g. crabs, fishes) will also have a longer feeding time low on the shore (Lewis, 1964; Hawkins & Jones, 1992). Respiration is similarly more effective in the water than in the air. Algae need to be surrounded by water for respiration, photosynthesis and nutrient uptake. The majority of the animals have respiratory surfaces adapted to extract oxygen from the water. There are, however, many adaptations protecting exchange structures and allowing intertidal animals to respire in air (e.g. modified gills, reduction of the gills and formation of a vascularised mantle cavity, anaerobic respiration) (Newell, 1979; Nybakken, 1997). The alternation emersion and immersion periods seem to have induced of activity rhythms in intertidal organisms (Lewis, 1964, Naylor, 1985). The existence of breeding cycles synchronised with certain tides to ensure fertilisation and larval dispersion can be seen as a reproductive adaptation to tidal fluctuations (Nybakken, 1997).

Exposure to wave action is another major environmental gradient in the intertidal zone. It is essentially a horizontal gradient but stress does not occur in a clearly defined direction (Raffaelli & Hawkins, 1996). In general, intertidal organisms can live higher up on the shore in exposed than sheltered conditions. This is mainly due to wave spray on exposed shores, which can minimise desiccation problems, particularly for high shore species. Exposed conditions are favourable for filter-feeders because water movement will provide plenty of suspended food particles. For mobile species, however, problems of dislodgement increase with wave action and foraging may become more difficult. Conversely, siltation can be a problem in sheltered conditions as it may clog the gills of some animals. In extreme shelter conditions the lack of water movement may also restrict the supply of oxygen for both plants and animals, dissolved nutrients for seaweeds and reduce larval supply (Hawkins & Jones, 1992; Little & Kitching, 1996; Raffaelli & Hawkins, 1996).

Both vertical and horizontal gradients can be modified by several factors including the topography and geology of the shore and a variety of biotic influences (Lewis, 1964; Raffaelli & Hawkins, 1996).

Patterns of distribution on intertidal rocky shores

Patterns of distribution of intertidal rocky shore communities have long been studied by marine biologists. Classical descriptive works have focussed on the characteristic distribution of species in horizontal bands- zonation patterns (e.g. Stephenson & Stephenson, 1949, 1972; Lewis, 1964; Pérès & Picard, 1964). This type of distribution pattern is not exclusive of marine ecosystems and may be observed, for example, on terrestrial vegetation on mountain slopes. However, due to the sharp environmental gradient on intertidal rocky shores, zonation patterns are particularly striking and spatial condensed, and have attracted a considerable amount of attention (Russell, 1991). The recognition that shores from different parts of the world had certain biological features in common led Stephenson & Stephenson (1949) to propose an “universal” scheme of zonation for intertidal rocky shores. According to this classification scheme the shore could be divided into three main zones: i) a high shore zone to which they called **supralittoral fringe**, characterised by encrusting lichens, cyanobacteria, small littorinid gastropods and isopods; ii) a mid-shore zone called **midlittoral zone**, dominated by filter-feeders such as barnacles and mussels and; iii) a lower shore zone called **infralittoral fringe**, dominated by red algae and large brown kelps.

In his the extensive study of zonation patterns on the British Isles, Lewis (1961, 1964) used a slightly different terminology. The populations of the coast and shallow seas were divided into littoral and sublittoral zones. The former corresponds to marine organisms which are adapted to or need alternating emersion and submersion periods or spray. Within the littoral zone Lewis (1964) called **littoral fringe** to the top zone and **eulittoral** to the mid-shore zone. The part of sublittoral zone that can be exposed at low tide was called **sublittoral fringe**.

The main difference in the two classifications systems is the used terminology and the extension of the littoral zone. Stephenson & Stephenson (1972) littoral zone corresponded to the zone between extreme high and low water of spring tides, including the infralittoral fringe and part of the supralittoral fringe. They were both, however, based upon biological characteristics and the different zones were not established according to tide levels, though they may be related to them.

A similar approach was adopted for the Mediterranean by Pérès & Picard (1964). These authors proposed a more complex zonation system from coastal to deep oceanic marine zones. None the less, the main zones described for littoral communities were essentially the same as those established in the Stephenson-Lewis approach. Three primary zones each characterised by particular kinds of organisms.

The reference to zonation patterns may be advantageous for comparison of work carried on different parts of the world, or to define the studied area in terms of zone or habitat instead of the precise tidal level (Raffaelli & Hawkins, 1996). The terminology used by Lewis (1964) was adopted in the present work to refer the three major intertidal zones: littoral fringe (high-shore), eulittoral zone (mid-shore) and sublittoral fringe (low-shore).

Factors determining distribution of species on the shore

Interested by the studies on zonation patterns (e.g. Lewis, 1964; Brättstrom, 1980; Norton, 1985; Russell, 1991) marine ecologists tried to explain the causes of the observed distribution patterns. Consequently, they started to analyse the influence of physical and biological factors on marine intertidal communities (e.g. Southward, 1958; Ballantine, 1961; Connell, 1972; Saldanha, 1974; McQuaid & Branch 1984; Hawkins & Hartnoll, 1985) and to perform experimental analyses to understand the functioning of rocky shore communities (e.g. Dayton 1971; Paine, 1974; Menge, 1976; Lubchenco & Menge, 1978; Benedetti-Cecchi et al., 1996). Manipulative studies of community dynamics involved the analysis of physical disturbance and succession on intertidal communities (e.g. Dayton, 1971; Emerson & Zedler, 1978; Sousa, 1979, 1984; Dethier, 1984; Farrell, 1991; Benedetti-Cecchi & Cinelli, 1993; McCook & Chapman, 1997) or experimental investigations on the effects of competition (e.g. Connell, 1961; Branch, 1976; Underwood, 1978a, 1984), grazing (e.g. Lubchenco, 1978, 1980; Hawkins, 1981; Hawkins & Hartnoll, 1983; Benedetti-Cecchi & Cinelli, 1992; Dye, 1993; Benedetti-Cecchi et al., 1996; Jenkins et al., 1999a, 1999b), predation (e.g. Paine, 1966; Menge 1978a,b, 1983; Menge & Lubchenco, 1981) and recruitment (e.g. Thorson, 1966; Denley & Underwood, 1979; Hawkins & Hartnoll, 1982; Kendall et al., 1985; Petraitis, 1990; Menge, 1991, Jenkins et al., 1999c).

Considerable attention has been devoted to the study of vertical distribution of some species on the shore. Early ideas to account for the pattern of zonation and vertical distribution of species were mainly related to physical factors. The concept that critical tidal levels were important determinants of the structure of intertidal communities was first suggested by Colman (1933) and was adopted by several authors for many years (e.g. Doty, 1946; Evans, 1947). Critical levels were calculated from predicted tide tables, based on the examination of a curve of proportion of emersion time throughout the year. These levels were apparently coincident with the upper and lower limits of several intertidal species. However, the concept of critical tidal levels was refuted by Underwood (1978b) after the experimental examination of this hypothesis. He found no evidence that the limits of distribution of species were clumped at any particular levels.

Physical factors have long been thought to be responsible for the upper limits of distribution of most intertidal species (e.g. Baker, 1909; Connell, 1972). Experimental work has shown the importance of aerial exposure and desiccation in controlling the upper limits of distribution of high- and mid-shore fucoid algae (Schonbeck & Norton, 1978). Lower on the shore evidence was provided that physical factors determined the upper limit of some red algae (Lubchenco, 1980; Carter & Anderson, 1991). In contrast, lower limits of distribution have usually been associated with biological factors like competition, grazing or predation (Schonbeck & Norton, 1980; Lubchenco, 1980; Hawkins & Hartnoll, 1985). Experimental investigations of the factors affecting algal zonation in New England rocky shores by Lubchenco (1980) led to the conclusion that competition is the primary determinant of *Fucus* sp. lower limits (affecting presence or absence) and herbivory is of secondary importance (affecting abundance). Interspecific algal competition has also been shown to set lower limits of fucoid algae (*Pelvetia canaliculata* (L.) Decaisne & Thuret and *Fucus* spp.) in the U.K., in several experiments involving both field transplants, exclusion areas and laboratory cultures (Schonbeck & Norton, 1980) and canopy removal (Hawkins & Hartnoll, 1985).

More recently, the importance of biological factors such as grazing and competition have been shown to set upper distribution limits of some species (Underwood 1980, 1985; Sousa et al., 1981; Underwood & Jernakoff, 1981, 1984; Hawkins & Hartnoll, 1985). After the Torrey Canyon oil spill, large-scale kills of limpets due to excessive dispersant application resulted in upward extension of some low shore species (Southward & Southward, 1978). Underwood (1980) demonstrated that upper limit of foliose macroalgae in Australian shores was primarily set by herbivorous molluscs. Thus, the upper limits of these lower algal beds would depend on the grazing of algal propagules by gastropods and only in the absence of grazers physical factors would become important in determining the upper limit of macroalgae (Jernakoff, 1983). Some canopy forming algae have also been induced to extend upwards after the removal of competitor algal species (Hawkins & Hartnoll, 1985).

The role of competitive interactions as structuring agents in marine benthic communities has been intensively discussed on intertidal rocky shores (e.g. Connell, 1961; Dayton, 1971; Haven 1973; Menge, 1976; Underwood, 1978a). Several reviews on the experimental analyses of competition in the field have been published in the last decades (e.g. Connell, 1983; Schoener, 1983; Underwood 1986, 1992). Birch’s (1957) definition of competition as “the process leading to ‘harm’ to individuals when other individuals of the same or different species use the same resources which are in short supply” has been generally adopted in the marine ecological literature (Underwood, 1979, 1992, 1997; Connell, 1983; Hawkins & Hartnoll, 1983).

According to Underwood (1978a, 1992) there are three major reasons why competitive interactions should be well documented for intertidal communities and be regarded with undoubted importance as one of the processes determining the structure of assemblages of species in this habitat. Firstly, space is a common resource for all intertidal organisms, either as a substratum on which to live, or over which to feed. Competitive interactions for space are known to be important and critical in many intertidal habitats, because space, as a two dimensional resource, is often in short supply. Secondly, the majority of the intertidal organisms have widespread dispersive stages of their life history. Since there is little opportunity for regulation of numbers in local populations, recruitment to the shore can be in unpredictably high densities, and situations in which numbers of organisms increase beyond carrying capacity of some local habitat can be widespread in organisms with dispersive propagules. Thus, competitive interactions have often been studied in such organisms in intertidal rocky shores. Thirdly, intertidal rocky shore organisms are very suitable for experimental manipulations, due to the high density and sessile characteristics (e.g. algae, barnacles) or relatively sedentary nature (e.g. limpets, chitons, starfish) of most organisms. Consequently, experimental manipulations can be done in relatively small areas and be easily controlled and replicated in space and time.

Competition is generally divided into exploitative competition, where individuals, by using resources, deprive others of benefits to be gained from those resources; and interference competition, where individuals harm one another to acquire the resources (e.g. by fighting, producing toxins) (Schoener, 1983).

Several forms of competitive interactions were also described with more detail by Schoener (1983). He considered that consumptive competition could occur when some quantity of resource (e.g. food, water, nutrient) is consumed by an individual, thereby depriving other individuals of it. Pre-emptive competition occurs when one organism already occupies space, making it unavailable for another individuals; it occurs primarily in sessile organisms. Overgrowth competition occurs when another individual or individuals grow over or upon a given individual, therefore depriving that individual of light (as in plants) or access to water-borne food (as in sessile, filter feeding animals) and possibly harming that individual by some consequence or physical contact. Chemical competition occurs when an individual produces some chemical (toxin) which diffuses into the medium or substrate and harms other individuals. Territorial competition occurs when an individual aggressively defends, or by its behaviour signals its intention to defend, a unit of space against other individuals; it occurs primarily in mobile organisms. Encounter competition occurs as the result of an interaction between mobile, non-spatially attached individuals, in which some harm comes to one or more; such harm can include energy losses, theft of food, injury, or death by predation, fighting or mere accident.

Early work on the role of competition in intertidal rocky shore communities focussed on sessile species (e.g. Connell, 1961; Dayton, 1971; Menge, 1976). Sessile organisms such as barnacles and mussels can compete for space when this is in short supply either by pre-emptive or overgrowth mechanisms. In many of these studies it has been suggested that importance of competitive interactions may very often be reduced due to factors like predation or disturbance that may reduce population densities of the competing species to such low levels that there are sufficient resources for all species (e.g. Paine, 1966, 1974; Dayton, 1971). The inferior competitors could have access to free space, and coexist with the potentially dominant species.

The recognition that competition among mobile animals on rocky shores may be fundamentally different from that among sessile organisms (Underwood, 1978a; Creese & Underwood, 1982) led to proliferation of studies on the importance of competition among mobile gastropods species (Marshall & Keough, 1994). Intertidal gastropods are often considered to be well suited to studies of competition (Underwood, 1984) and, experimental investigations in many parts of the world revealed that competition interactions are a prevalent characteristic of many species of grazing gastropods, particularly limpets (e.g. Branch, 1975a, b, 1976; Underwood, 1978a, 1979, 1984; Black, 1979; Creese, 1980; Creese and Underwood, 1982).

Both exploitative and interference competition can occur among intertidal gastropod species (Underwood, 1979; Branch, 1981). Territorial behaviour of gastropods that actively defend an unit of space over which they feed against the intrusion of other grazers were described for *Lottia gigantea* (Stimson, 1970) in North American coasts, and for several species of South African limpets such as *Pattela longicosta* and *Patella tabularis* (Branch 1975b, 1981). Inter- and intraspecific exploitative competition have also been experimentally demonstrated in a great number of studies (e.g. Underwood, 1978a, 1984; Creese and Underwood, 1982; Lasiak & White, 1993; Marshall & Keough, 1994). These investigations have shown that competition can have important consequences on the population dynamics and structure of marine assemblages. However, a multiplicity of processes can modify the outcome of competitive interactions (e.g. physical factors in the environment, disturbances, predators). Therefore, these studies need to be repeated at different spatial or temporal scales, and with a large number of species, so that any conclusion about the general effects of competition can be reached (Connell, 1983; Underwood, 1992).

Rationale and aims

The present work aims to analyse patterns of distribution of intertidal species on rocky shores and to investigate the role of grazing and competition in structuring communities. In Chapter 2, intertidal zonation patterns along the continental Portuguese coast are described and the quantitative comparison of distribution patterns in the mid-shore zone was made. So far, the intertidal rocky shore communities of the Portuguese coast have been studied in a scattered way by different authors and most of the information concerns a specific biological group or the communities of a portion of the coast. A study of this nature, covering the whole littoral coast, is particularly important if we consider that Portugal is a geographical limit for both boreal and subtropical and Mediterranean species. It may contribute for studies on the response of species distribution to global climatic change. There is also the necessity to provide baseline studies for future management and conservation programmes on intertidal rocky shores. Additionally, this study is fundamental as a reference for experimental work and may also provide an observational basis for testing hypotheses. Subsequently, the remaining chapters were devoted to experimental ecology studies on causes of distribution patterns, essentially focussed on the importance of grazing and competition by limpets in intertidal communities. The factors determining vertical distribution patterns on the shore, particularly the effects of grazing limpets on the upper limits of low shore algae, were investigated in Chapter 3. The hypothesis that grazing by limpets directly determines the upper limit of distribution of the red algal turf was tested. The work was undertaken in both Portugal and U.K. with a nested experimental design to assess whether the grazing effect is modified by different factors operating at various spatial scales. The analysis of competition interactions amongst the limpets *Patella depressa* Pennant and *Patella vulgata* L. on the northern coast of Portugal, was done in Chapter 4. Little is know about competition interactions among these species. Both species are abundant grazers that co-occur in mid-littoral zone of the northernmost shores of Portugal. However, *Patella vulgata* is a northern species, and its density decreases along the Portuguese coast, being occasional or rare in some shores further to the south. The proximity to the southern limit of distribution of *Patella vulgata*, makes it an attractive subject for testing hypotheses about interspecific competition. Inter- and intraspecific interactions were analysed simultaneously through an asymmetric experimental design to estimate their relative importance. A further analysis on intra- and inter-size-class competition in the limpet *Patella depressa* was conducted in the central coast of Portugal. This experiment is described in Chapter 5 and tested the effects of increased and decreased densities on parameters such as mortality, growth and weight of the limpets (among others) and the influence of different size classes in competitive interactions. The major results and conclusions obtained from the various chapters are integrated in Chapter 6.

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CHAPTER 2

Intertidal rocky shore communities of the continental Portuguese coast: analysis of distribution patterns

Boaventura, D.; P. Ré; L. Cancela da Fonseca; S.J. Hawkins. Intertidal rocky shore communities of the continental Portuguese coast: analysis of distribution patterns. Submitted to *Marine Ecology*.

CONTENTS

INTRODUCTION

The amount of literature concerning distribution patterns of rocky shore organisms is vast. Classical descriptive works include the universal scheme of zonation proposed by Stephenson & Stephenson (1949, 1972), the extensive study of zonation patterns on the British Isles by Lewis (1961, 1964) and, the similar approach for the Mediterranean by Pérès & Picard (1964). Simultaneously with the studies on zonation patterns (e.g. Lewis, 1964; Brättstrom, 1980; Norton, 1985; Russell, 1991) marine ecologists started to analyse the influence of physical and biological factors on marine intertidal communities (e.g. Southward, 1958; Ballantine, 1961; Connell, 1972; Underwood, 1981; McQuaid & Branch 1984; Hawkins & Hartnoll, 1985) and to perform experimental analyses to understand the functioning of rocky shore communities (e.g. Dayton 1971; Paine, 1974; Menge, 1976; Lubchenco & Menge, 1978; Benedetti-Cecchi et al., 1996). Manipulative studies of community dynamics encompassed physical disturbance and succession of intertidal communities (e.g. Dayton, 1971; Emerson & Zedler, 1978; Sousa, 1979, 1984; Dethier, 1984; Farrell, 1991; Benedetti-Cecchi & Cinelli, 1993; McCook & Chapman, 1997) or experimental investigations on the effects of competition (e.g. Connell, 1961; Branch, 1976; Underwood, 1978, 1984), grazing (e.g. Lubchenco, 1978, 1980; Hawkins, 1981; Hawkins & Hartnoll, 1983; Benedetti-Cecchi & Cinelli, 1992; Dye, 1993; Benedetti-Cecchi et al., 1996; Jenkins et al., 1999a, 1999b), predation (e.g. Paine, 1966; Menge 1978a,b, 1983; Menge & Lubchenco, 1981) and recruitment (e.g. Thorson, 1966; Denley & Underwood, 1979; Hawkins & Hartnoll, 1982; Petraitis, 1990; Menge, 1991; Jenkins et al., 1999c). An extensive literature has recently been synthesised by Paine (1994), Little & Kitching (1996) and Raffaelli & Hawkins (1996).

Much less attention has been given to rocky shores of the Portuguese coast. Early studies conducted in the beginning of the XX century were mainly devoted to the study of the biology of certain taxonomic groups (e.g. Cúmano, 1939; Nobre, 1940; Palminha, 1951). Until the present date most of the published information concerned a specific biological group or the study of communities of a restricted area of the coast (*e.g.* Almaça, 1960, 1990; Monteiro Marques et al., 1982; Santos & Melo, 1984; Guerra & Gaudêncio, 1986; Lopes, 1989; Marques *et al*, 1993, Sacarrão, 1994; Cruz, 1999), although Saldanha (1974) has made an important contribution for the study of littoral communities of the entire Arrábida coast and Múrias (1994) has studied in detail the intertidal communities of the northern Portuguese coast. Few broadscale studies on distribution patterns of several species include the work of Fischer-Piette (1957, 1958, 1963) and Ardré (1970). More recently, however, the recognition that the study of distribution patterns and the development of experimental ecology may play a crucial role on understanding the organization of rocky intertidal communities of the Portuguese coast, has seeded the implementation of several national and European research projects.

The present study aims to describe intertidal zonation patterns along the Portuguese coast and to compare quantitatively the patterns of distribution in the mid-shore zone. The qualitative descriptive study provide a useful framework of reference in terms of major zones, dominant organisms at different levels on the shore, geographical changes of fauna, and has never been done for the entire Portuguese coast. A study of such nature, covering the whole littoral coast, is particularly important if we consider that Portugal is a geographical limit for both boreal and subtropical and Mediterranean species (Ardré, 1970; Saldanha, 1974; Fischer-Piette, 1957, 1958, 1963). Hence, it may contribute for studies on the response of species distribution to global climatic change. There is also the necessity to provide baseline studies for future management and conservation programmes on intertidal rocky shores. Intertidal resources are heavily exploited and the effects of human influence increasing pollution on coastal areas, in particular the occurrence of oil spills, may have major impacts on the rocky shore ecosystem (see Southward & Southward, 1978). Additionally, this study is fundamental as a reference for experimental work already in progress and may also provide an observational basis for future experimental work. The quantitative comparison of distribution patterns on low and upper mid-shore zone along the Portuguese coast will give an insight on the structure of intertidal communities. Despite the profusion of studies in intertidal ecology, there are few quantitative studies analysing the spatial variation of distribution patterns. This has never been attempted for the whole Portuguese coast.

MATERIAL AND METHODS

Study sites

The present study was carried out on the Portuguese continental coast which extends for more than 800 Km. In order to test if there was any variation in species distribution and abundance along the intertidal rocky shores of Portuguese coast a total of 27 shores were sampled (Fig.1).

Santos (1994) has synthesised relevant aspects of the coastal oceanography of Continental Portugal, including seasonal variation in the sea surface temperature, coastal upwelling effects and circulation regimes. Two different oceanographic regimes can be considered during winter and summer periods, with frequent upwelling of cold water occurring in the latter. Sea surface temperature on the western Portuguese coast show marked seasonality varying between 13º and 15ºC during winter, and reaching values of 20º or higher during summer period. Temperatures on the south coast are in general slightly higher (a difference of approximately 1º/1,5ºC) due to the influence of warmer currents. Information available from wave data acquired with three directional wave stations installed along the Portuguese coast (Costa, 1995) showed that the mean conditions do not differ much along the west coast which is exposed to the prevailing Northwest oceanic swell. Seasonal variation is also clear in the sea state, with the higher swell occurring during winter and reaching values over 5m on the west coast and over 3m on the south coast. In the south coast the wave conditions are less severe, since it is not exposed to the wave components predominant on the west coast, particularly to the swell generated in the north Atlantic. The most frequent storms are from WNW in the west coast and from SW in the south coast (Costa, 1995). The tidal regime in the Portuguese coast is semidiurnal. The extreme tidal range of spring tides is approximately of 3.5 to 4 m along the Portuguese coast, and spring low tides occur in the morning and in the evenings.

The morphology of the Portuguese coast is marked by the presence of several capes along the coast particularly south of Nazaré, and several rivers of significant runoff on the north and central coast (Santos, 1994). Three main rocky shore zones (north, centre and south) separated by large extensions of soft sediment areas can be considered in the Portuguese coast. Rock types that form intertidal substrates in each of these zones vary (Carvalho, 1992). In the northern region rocky shores are in general formed by granite rocks: from Moledo do Minho until Aguda most of the studied rocky shores were formed by granite, except Vila Chã where rock platforms consisted of shales. The central zone is composed of limestone and sandy limestone with surfaces that vary from smooth to irregular. Shales compose most of the bedrock on the shores from the south west coast and part of the south coast, being replaced by sandy limestone towards the east of the south coast. The last rocky shore ledges on the south coast are located in Olhos d'Água. Sampling stations were chosen to represent important areas of open bedrock. Areas near to sandy beaches and boulder shores were avoided whenever possible.

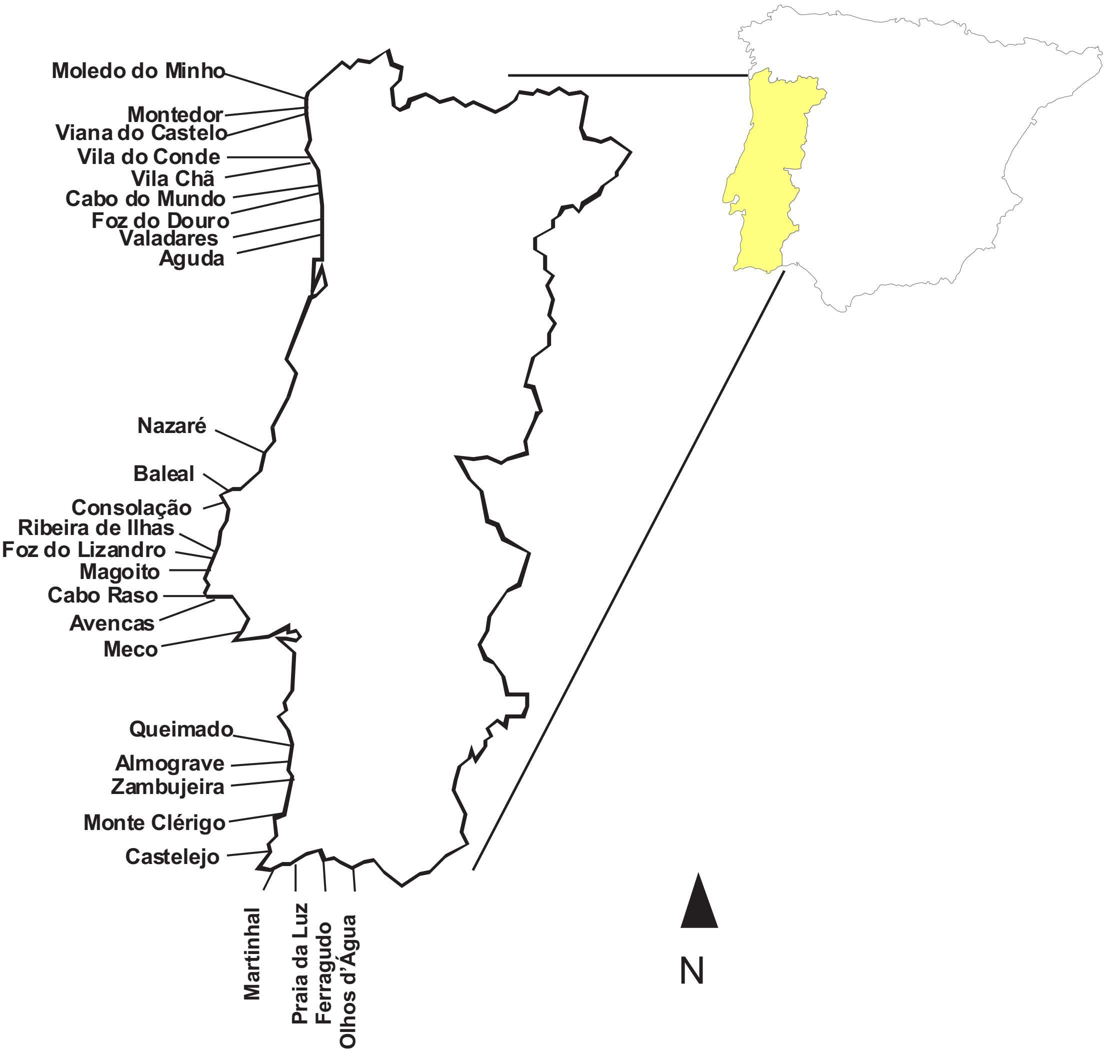

Figure 1- Study sites.

Experimental Design

Due to logistic constraints, each of the 27 shores was only visited once during the spring of 1997. The coast was divided in three main regions: north, centre and south. Nine shores were sampled in each of these main regions. Previous observations on the rock platform indicated that different organism assemblages were distributed at different levels on the shore. These could be broadly classified according to zonation schemes in a lower algal bed zone, an animal dominated eulittoral zone and a littoral fringe (after Lewis, 1964). The lower algal zone has a relatively high number of species with respect to the time available for sampling during low tide. Conversely, the diversity in the littoral fringe is considerably reduced when compared to that in lower levels on the shore. Therefore, it was decided to concentrate the quantitative sampling effort of this study on the mid-shore zone. Thus, the factor "level on the shore" included the lower mid-shore zone where mussels and encrusting algae occur, and the upper mid-shore zone mainly dominated by barnacles. Five replicate quadrats of 50 x 50 cm were sampled in each level.

Sampling Methods

Zonation patterns

To assess the major zonation patterns in each of the 27 locations the shore was levelled and qualitative sampling was done along each transect (Fig. 2). The main biotic assemblages and zones were identified, their extent was measured and the upper and lower limit of each zone were measured in relation to chart datum using a level (Fig. 2a). A simple levelling device based on water in a tube with both extremities tied to a ruler was used. The differences between the height of the water in the rulers correspond to the vertical difference in height of the ground. Measurements of height were taken along the shore transects, at successive intervals, from the water line at the time of low water. Positions in relation to chart datum were later calculated by addition of the height between low water and chart datum. Despite some limitations in accuracy this levelling method is very easy to operate on the shore. Providing the sea is not too rough, or the atmospheric pressure extremely high or low, the described levelling procedure is sufficiently accurate for most purposes, and to enable comparisons between sites and occasions (Hawkins & Jones, 1992).

Quantitative sampling

Non-destructive methods (point intersection) (see Hawkins & Jones, 1992) were used within the lower and upper mid-shore area in moderately exposed shores along the Portuguese coast. Five replicate plots were counted in each of the two mid-shore areas using a quadrat of 50 x 50cm with 49 intersection points (Fig. 2b). The percentage cover of algae and sessile animals was estimated and the total numbers of limpets and other mobile animal species were counted. The species present inside the plot, which did not match any intersection point were recorded. Since shores are a three-dimensional structure, whenever large algae were present sampling was stratified in different layers and canopy cover was distinguished from substrate cover. Photos of the quadrats were taken with a *Nikon* F70 (35-80 mm lens) and kept as a record. Sampling was stratified by considering only open freely draining rock.

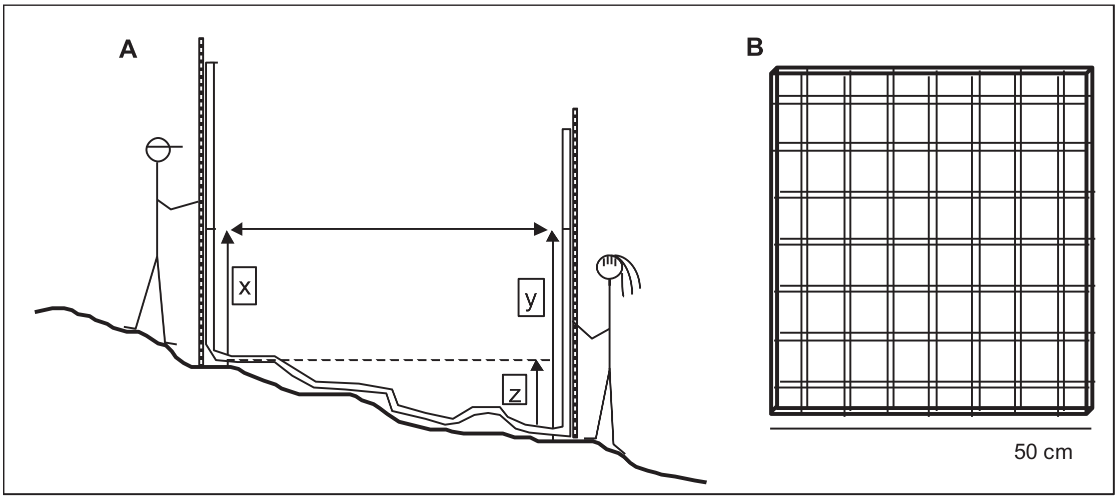

Figure 2- Level (A) and sampling quadrat (B).

Study organisms

The identification of organisms was done *in situ* whenever possible. In case of taxonomic uncertainty the specimen was collected and examined under the binocular microscope in the laboratory. Considering the high diversity of the intertidal communities sampling was focussed on conspicuous species either because they were common in terms of percentage cover or density, or because they were important species in a biogeographic context for the Portuguese coast. Note that the scale of observation and studied organisms was also conditioned by the use of non-destructive methods. Due to the adopted methodology it was decided to sample the species for which identification and quantification in quadrats was reliable. Very small organisms (e.g. amphipods) and/or species with high motility (e.g. crabs) were not quantified. Species which differentiation in the field was difficult, such as certain algal epiphytes (e.g. species belonging to the genus *Ceramium* or *Polysiphonia*), were identified and quantified only to the genus. The term “Lithothamnia” was used to designate calcareous crusts species which are difficult to differentiate in the field (see Hawkins & Jones, 1992).

Data Analyses

Zonation patterns were depicted by diagrams for each visited location. The height above chart datum was used as the vertical scale. This enable description of the main zonation patterns on a broad geographic scale.

Multidimensional analysis was used to analyse quantitative data on species abundance and distribution. Due to the high total number of quadrats for the entire Portuguese coast, the 5 replicate quadrats sampled in each shore level were averaged before the multidimensional analysis was done. A matrix of similarities between each pair of samples was calculated using the Bray and Curtis similarity coefficient. This coefficient was adopted since it is not affected by joint absences and is sufficiently robust for marine data (Field et al., 1982). Percentage cover values and abundances were used simultaneously in the same matrix. According to Anderson & Underwood (1997), there is no mathematical reason for not calculating similarities coefficient between samples of mixed data (i.e. data made up of abundances, percentage cover and presence/absence information for different variables), provided that the interpretation of the results takes into account the potential difference in contribution or weight of certain variables because of their scale (Anderson & Underwood, 1997). In this study, the fourth root transformation of data was used in order to preserve information concerning relative abundance or percentage cover of species across samples, but also to minimise differences in scale (and therefore relative weight) among variables (Clarke, 1993; Anderson & Underwood, 1997). Non-metric multidimensional scaling was used as an ordination technique for graphical representation of community relationships (Clarke, 1993). Although using a complex algorithm this method has several advantages. Some of its strengths are its dependence only on a biologically meaningful view of the data, since it works on the sample dissimilarity matrix and not on the original data array, and its distance preserving properties by construction of a configuration where distances between points have the same rank order as the correspondent dissimilarity between samples (Clarke, 1993). Hierarchical agglomerative clustering was performed on the same similarity matrix using group average linking to cross-check the results obtained with the MDS. This procedure is particularly advised for stress values close to 0.2 (Clarke, 1993). The ANOSIM permutation test was used to assess the significant differences between pre-defined groups of sample sites in the multidimensional analyses (Clarke, 1993). Two different null hypotheses were tested: i) there is no difference between the two studied shore levels, ii) there are no differences between regions. The second hypothesis was tested separately for the low and upper mid-shore. The Similarities Percentages procedure (SIMPER) (Clarke, 1993) of fourth-root transformed macrobenthonic abundances was used to determine the contributions from individual species to the Bray-Curtis dissimilarities between levels and regions. Graphical descriptors in the form of K-dominance curves were plotted for species abundance for each level and region.

Univariate analyses of community structure included the Shannon-Wiener (H’) diversity index and the distribution of limpet species. A two-factor analysis of variance was done to test the null hypothesis of no differences in species richness across regions and levels. Analyses of variance on density of limpets along the Portuguese coast were done using a three-way mixed model. Grazing limpet species were analysed in a particular way because they are important in a geographical comparison context but also because its effects on community structure are currently under study in several locations of the Portuguese coast. The design included three factors: factor “level on the shore” (orthogonal, fixed with two levels), factor “regions” (orthogonal, fixed with three levels), factor “shore” (nested in regions, random with 9 levels). The analysis tested the null hypotheses of no differences in *Patella* species density in the two levels and any of the considered spatial scale.

All multidimensional analyses and calculation of biodiversity indexes were done using the PRIMER for windows v5.0 computer program (Plymouth Marine Laboratory, UK). Analyses of variance, tests of homogeneity, and SNK (Student-Newman-Keuls*) a posteriori* comparison tests were done using GMAV5 for Windows Statistical Software (Institute of Marine Ecology, Sydney, Australia).

RESULTS

Zonation Patterns

Figure 3 shows the symbols of the more important species displayed in zonation diagrams. Diagrams of zonation patterns examined on the rocky shores of the north, centre and south of coast Portugal are represented in figures 4 to 6. In general, the organisms on the shore were distributed in three major zones. The lichen *Verrucaria maura* and the gastropod *Melaraphe neritoides* are the species that commonly occupy the uppermost zone of the shore, the littoral fringe. The extension and position of this assemblage in relation to chart datum varies with exposure to wave action, being broader and reaching higher levels (above EHWS) on more exposed shores (e.g. Moledo, Montedor, Cabo Raso). Despite the fairly constant specific composition of the littoral fringe some variations were seen to occur. The perennial algae *Pelvetia canaliculata* and the annual *Porphyra umbilicalis* were observed in the lower part of the littoral fringe on some shores from the northern region (e.g. Montedor, Viana do Castelo, Vila do Conde). Further to the south, and/or in less exposed shores (e.g. Avencas, Meco), *Verrucaria maura* may be absent. Under these circumstances, the grey upper zone of the shore is generally composed of cyanobacteria and *Melaraphe neritoides*. It may also happen that this zone is dominated by ephemeral green algae such as *Enteromorpha* sp. (e.g. Avencas, Monte Clérigo), particularly if it is close to freshwater runoff from the cliff, or if the shore topography is likely to retain water for a longer period. In this situation other gastropod species like the pulmonate *Siphonaria pectinata* can be observed at this level.

The eulittoral zone is dominated by a variety of animal and algal species. A high percentage of space is occupied by sessile filter feeders such as barnacles and mussels. The barnacle *Chthamalus* spp. (mainly *Chthamalus montagui*) dominates on the upper mid-shore zone starting immediately below the littoral fringe. The extension of the zone dominated by *Chthamalus* spp. varied from shore to shore and its limits were sometimes hard to define since the barnacles may be sparse on both upper and lower limit of distribution and also overlap with other organisms (e.g. mussels), forming mosaic patterns. A variety of species can also cover the barnacles forming bands or patches. Apart from the already mentioned algae that can be found in the lower littoral fringe and also upper eulittoral zone, the lichen *Lichina pygmaea* often covers the barnacles in the upper eulittoral zone above MHWN. Unlike *Pelvetia canaliculata* that was confined to the northern region, this lichen was found along the entire coast. A band of *Fucus spiralis* can also be observed covering the middle of the barnacle zone. Although present in the north and south this algae was notably abundant on some shores of the central region between MHWS and MTL. Small areas of rock within the barnacle zone can also be covered with encrusting algae species as *Ralfsia* sp., *Petrocelis* sp. and *Hildenbrandia rubra*.

Mussels occur in the lower mid-shore zone of more exposed shores. On the northern region *Mytilus galloprovincialis* can extend up to MHWN whilst in the central and southern regions intertidal mussels generally occur below MTL. *Corallina* spp., *Caulacanthus ustulatus*, *Mastocarpus stellatus*, among other algal species can occur together with mussels as well as some red algal crusts like *Lithophyllum lichenoides* or “Lithothamnia”. Throughout the eulittoral zone many gastropod species are present and several of these species are important in a biogeographic context. *Littorina saxatilis* occurs amongst the barnacles in the upper eulittoral zone. This species was most abundant on the northern shores and becomes occasional or rare further to the south. *Monodonta* spp. (*M. lineata* and *M. collubrina*) and *Gibbula* spp. (*G. umbilicalis* and *G. cineraria*) are common at mid-shore level whilst *Nucella lapillus* occurs lower on the shore amongst the mussel beds. The latter suffers a progressively decrease in abundance from north to south. Amongst grazing limpets all the four species *Patella vulgata*, *Patella rustica*, *Patella depressa* and *Patella ulyssiponensis* can be seen in the eulittoral zone along the Portuguese coast. *Patella ulyssiponensis* is more abundant in the sublittoral fringe but can also occur in the lower eulittoral zone together with the mussels and *Lithophyllum lichenoides* patches. *Patella rustica* is a southern species that was not found on any of the northern shores. In the central and southern regions it is more abundant in the upper barnacles zone. In contrast, *Patella vulgata* is a northern species that is more abundant in the north than in the centre and south. Finally, *Patella depressa* is widely distributed and abundant along the entire Portuguese coast. It occurs, like *Patella vulgata*, throughout the eulittoral zone. The pulmonate gastropod *Siphonaria pectinata* was observed to be more abundant towards the south of Portugal.

The bottom zone of the shore, the sublittoral fringe, is characterised by a profusion of macroalgae which are only occasionally not submerged. This zone can extend up to Mean Low Water of Neap Tides and corresponds to the zone of the shore with a higher number of species. The sublittoral fringe of northern rocky shores is considerably different from the centre and south regions. Most of the shores on the north are distinguished by the presence of large brown algae (e.g. *Laminaria* spp., *Saccorhiza polyschides*, *Himanthalia elongata*) which generally occur below MLWS level. The red algae *Mastocarpus stellatus* was also more abundant in the north. The sublittoral fringe of centre and south regions is in general dominated by a red algal turf composed of *Corallina* spp., *Plocamium cartilagineum*, *Caulacanthus ustulatus*, *Gelidium* spp., *Laurencia pinnatifida*, among others. On more exposed shores *Corallina* spp. dominates over the other algal species and together with red encrusting algae forms a pink band on the low-shore zone. On more sheltered shores non-calcareous turf forming algae appear in higher proportions. In some shores of the central zone (e.g. Nazaré, Ribeira de Ilhas) the algae *Bifurcaria bifurcata* can cover extensive areas of the shore in the upper sublittoral fringe. The lower eulittoral and sublittoral zone of Martinhal exhibited a different pattern, being dominated essentially by ephemeral green algae. Abundant animal species in the sublittoral fringe are, for example, *Patella ulyssiponensis*, *Paracentrotus lividus*, *Sabellaria alveota*. *Pollicipes pollicipes* occurs throughout the Portuguese coast particularly on exposed shores.

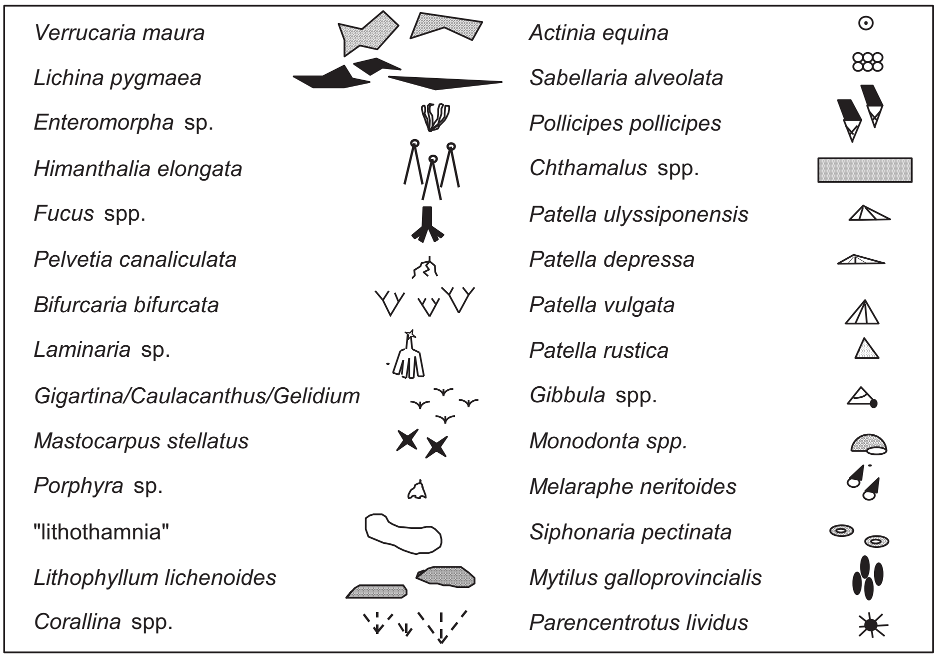

Figure 3- Symbols used for species in zonation diagrams.

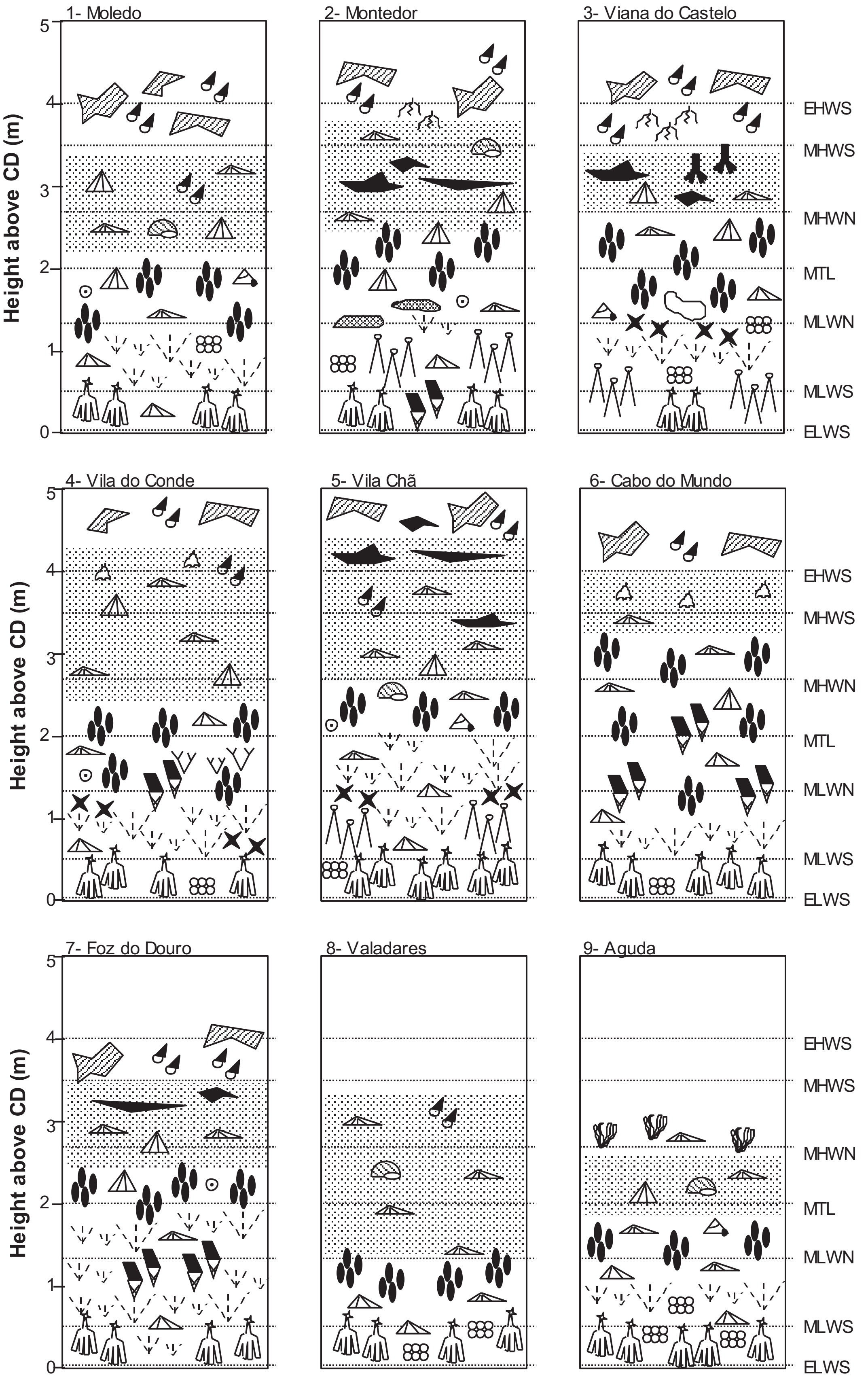

Figure 4- Zonation diagrams of the shores in northern region.

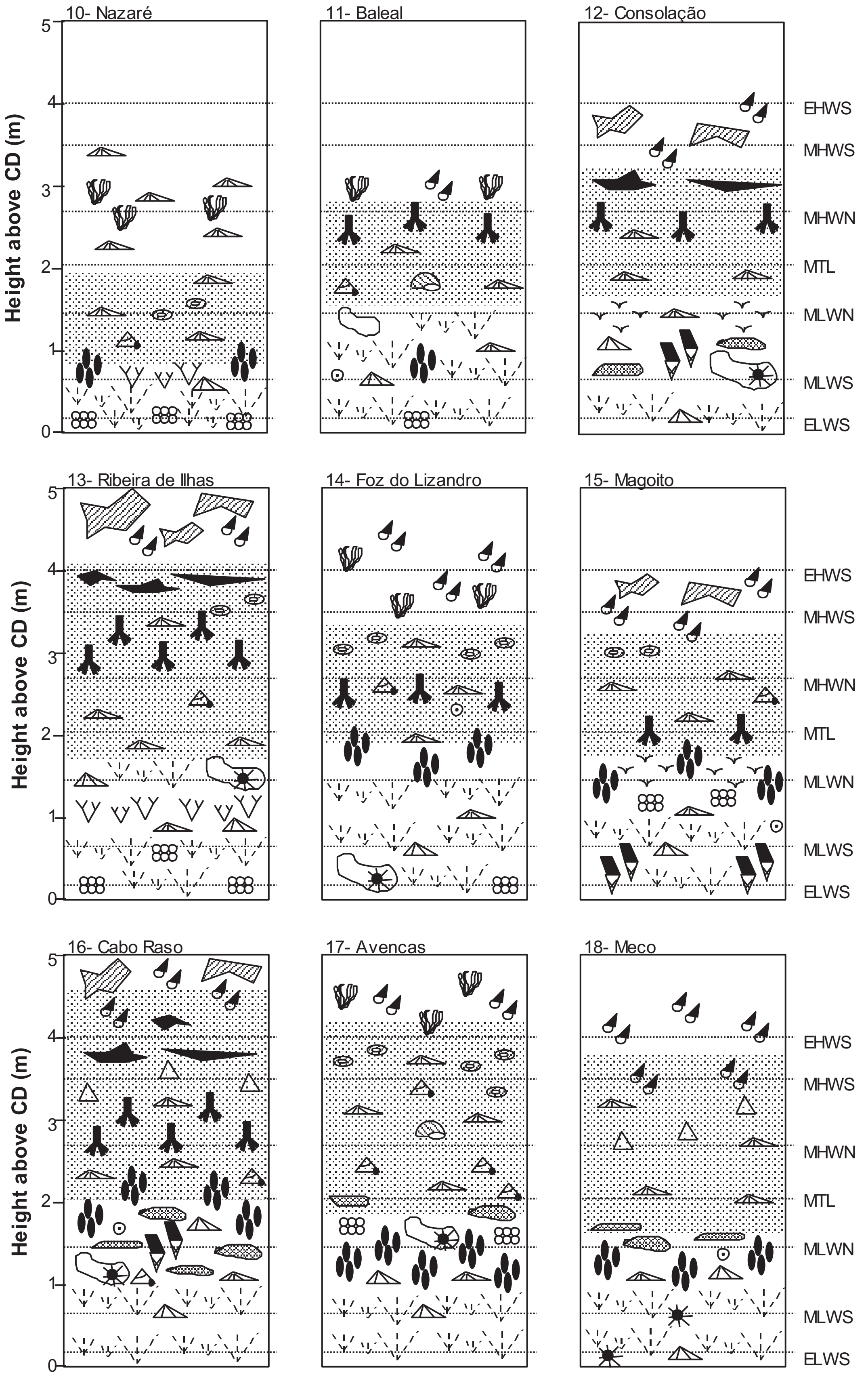

Figure 5- Zonation diagrams of the shores in central region.

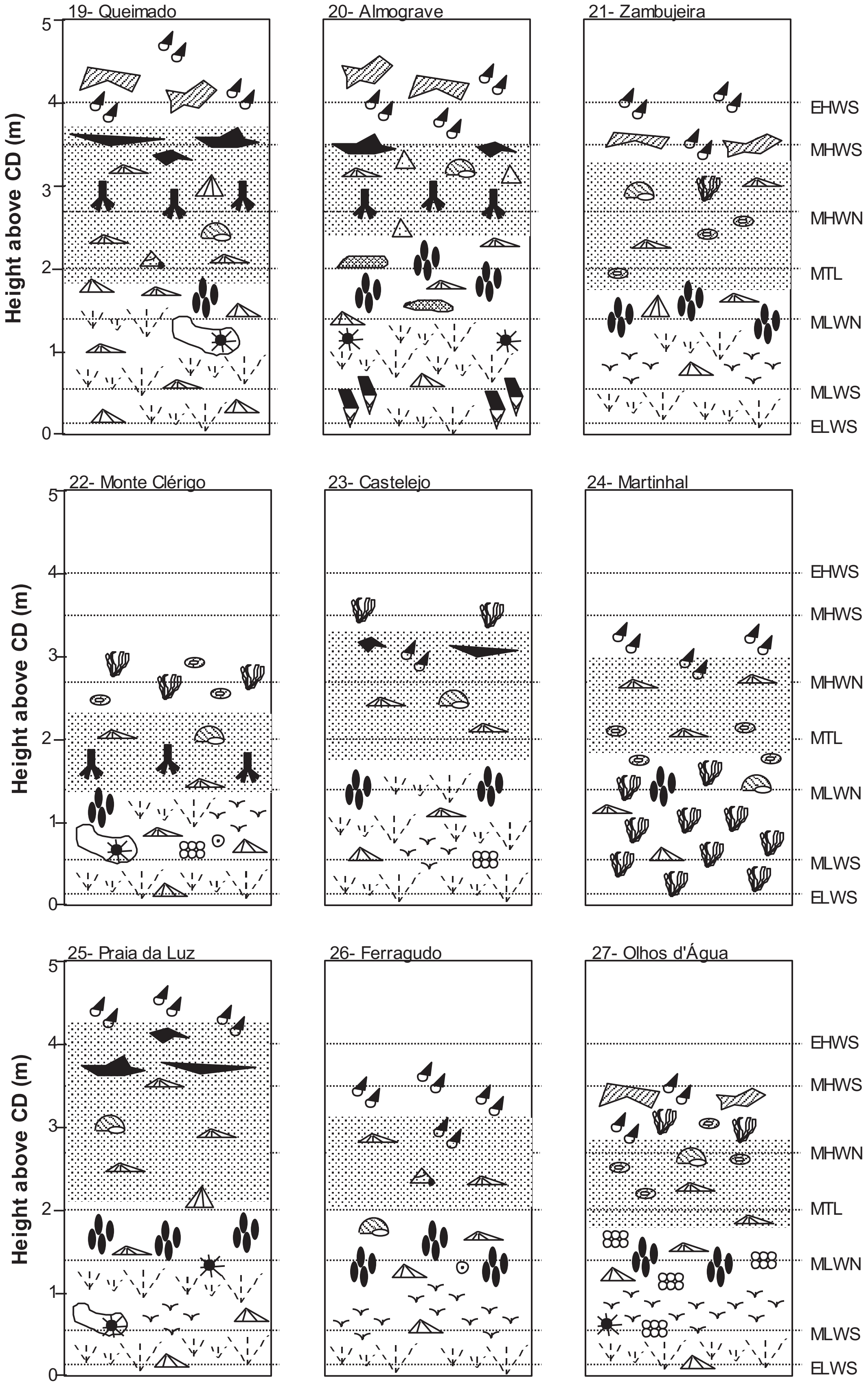

Figure 6- Zonation diagrams of the shores in southern region.

Comparative analyses of distribution patterns in low and upper mid-shore zone

The MDS configuration that resulted from the abundance matrix shows a separation of levels (Fig 7a) and a gradient referring to the regions (fig.7b). Samples that correspond to the average of replicate plots taken on the upper mid-shore are located in the left side of the figure whilst those taken in the lower mid-shore zone are positioned towards the right. Exceptions to this are the low mid-shore zone of Zambujeira and Baleal, which appear on the left side of the figure. Low mid-shore level of Martinhal, which appears on the top of the figure seems to be considerably different from all the other samples (Fig 7a). This was due to an extremely high abundance and dominance of ephemeral green algae at this level. Northern shores are located in the bottom of picture and relatively isolated from the centre and the south regions (Fig. 7b). No clear differences can be detected in the latter two regions. The distinction between levels was confirmed by the ANOSIM test. There was a significant difference, R = 0.53 (p = 0.1%), between the low mid-shore zone where mussels occur and the upper zone dominated by barnacles. ANOSIM test on factor regions, however, did not reveal any significant differences (R = 0.165, p = 0.1%).

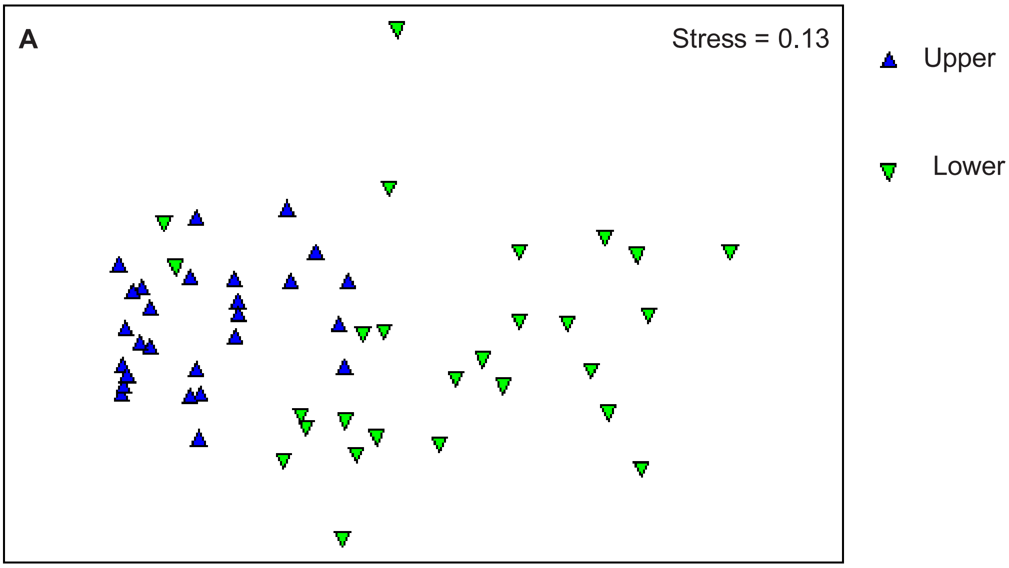

Figure 7a- MDS ordination of Bray-Curtis similarity matrix of √√ transformed species abundance data. A- Factor level.

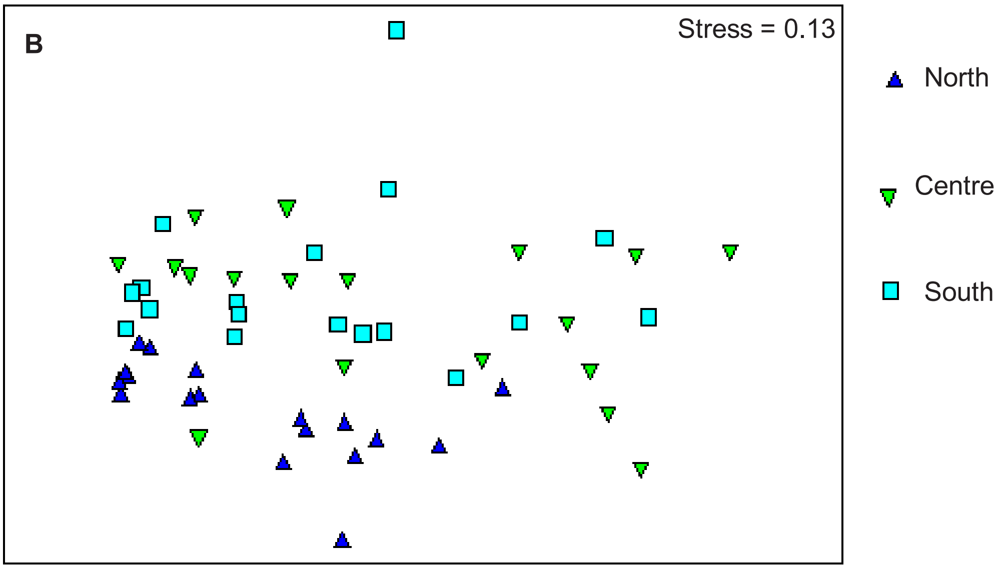

Figure 7b- MDS ordination of Bray-Curtis similarity matrix of √√ transformed species abundance data. B- Factor regions.

Although the lowest stress value of 0.13 still indicated a potentially useful 2-dimensional picture, these results were cross-checked by cluster analysis (Fig. 8). Hierarchical representation showed a clear separation of lower and upper mid-shore levels. The lower mid-sore samples that were more similar to the upper mid-shore zone were those from Baleal, Zambujeira, Praia da Luz e Almograve shores. These results confirm the trends shown in the MDS and, as indicated in the ANOSIM test, distinction between regions is not clear. The cluster also confirms the distinction of Martinhal lower level from all the other shores.

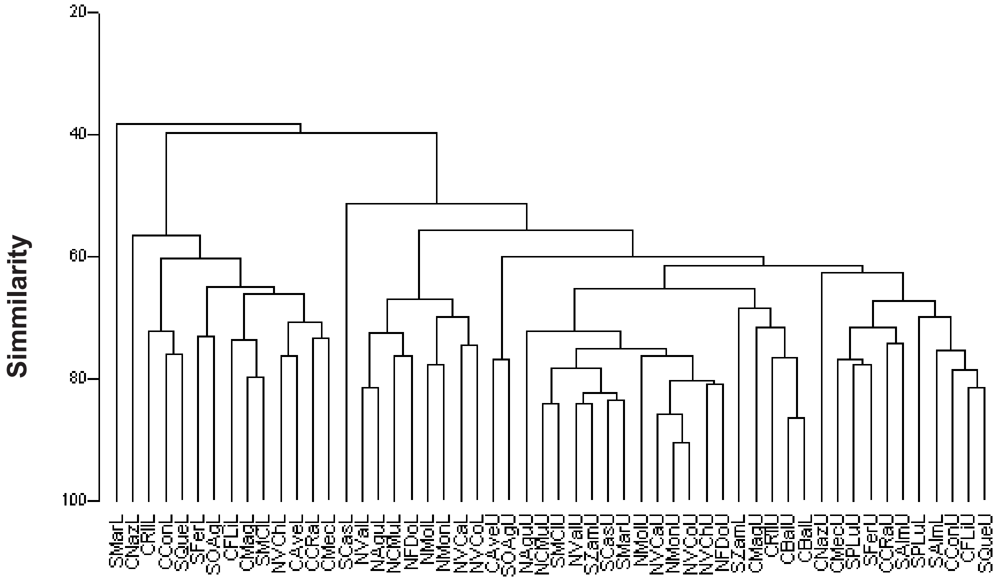

Figure 8- Dendogram from Bray-Curtis similarity matrix of √√ transformed species abundance data with group average linking (N____-North, C____- Centre, S____ - South; ____U- upper, ____L- Lower). Shore names are abbreviated (cf. Figs. 4 to 6).

Given the differences between levels and, since the MDS algorithm places most weight on the large distances, possible geographical variations in species communities were analysed separately for each level. Repeating the ordination within each level led to a more accurate display of the fine structure across regions.

The cluster obtained for the low mid-shore zone samples separated most of the northern shores from those located in the centre and south (Fig. 9). MDS configuration, with a stress value of 0.12, showed the same trends (Fig. 10). The MDS reflects also a higher similarity and less variability for the northern stations. ANOSIM analysis confirmed significant differences between the factor regions (R = 0.334, p = 0.1%). Pair-wise tests revealed significant differences between north and centre (R = 0.566, p = 0.2%), between north and south (R = 0.377, p = 0.2%) but no significant differences between centre and south regions (R = 0.108, p = 6.6%).

Geographic differences between regions for the upper mid-shore zone also separated the north from the centre and south in the cluster (Fig. 11) and in the MDS with a stress value of 0.18 (Fig. 12). ANOSIM test revealed significant differences for the region global test (R = 0.303, p = 0.1%). Results from pair-wise tests were consistent with those from the lower level and again revealed significant differences between north and centre (R = 0.61, p = 0.2%), north and south (R = 0.306, p = 0.2%) and no significant differences between centre and south (R = 0.025, p = 57.8%).

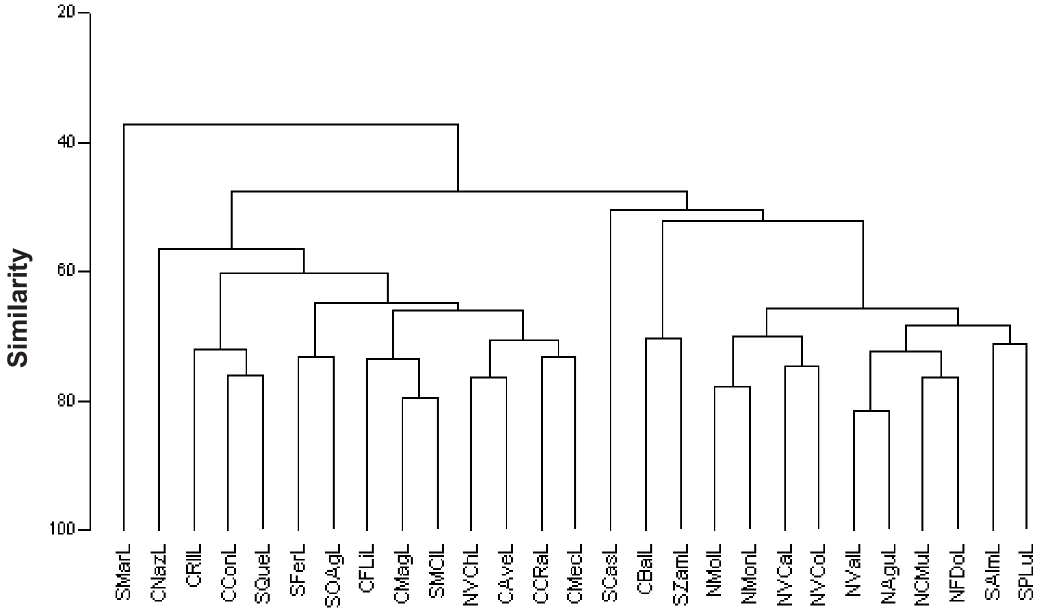

Figure 9- Dendogram from Bray-Curtis similarity matrix of √√ transformed species abundance data with group average linking for the lower mid-shore level (N____-North, C____- Centre, S____ - South; L- Lower). Shore names are abbreviated (cf. Figs. 4 to 6).

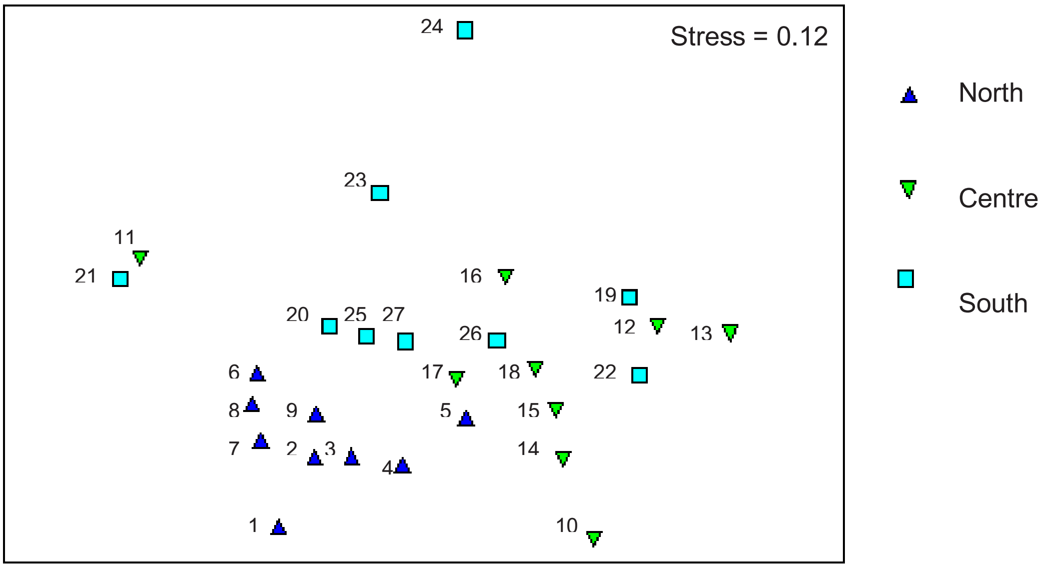

Figure 10- MDS ordination of Bray-Curtis similarity matrix of √√ transformed species abundance data for the lower mid-shore level. Different regions are represented by symbols and shore numbers are indicated (cf. Figs. 4 to 6).

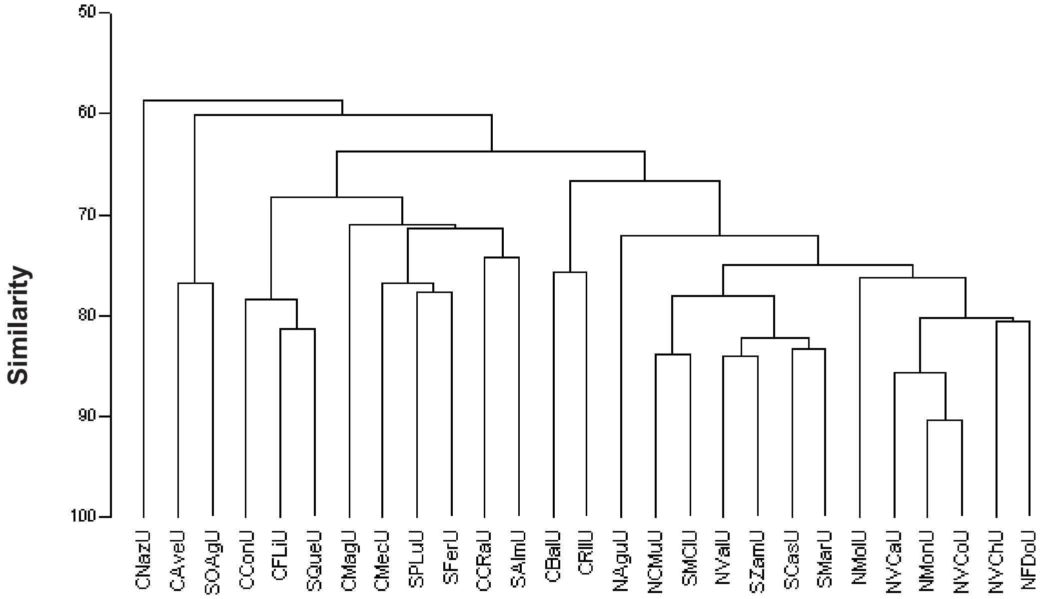

Figure 11- Dendogram from Bray-Curtis similarity matrix of √√ transformed species abundance data with group average linking for the upper mid-shore level (N____-North, C____- Centre, S____ - South; U- Upper). Shore names are abbreviated (cf. Figs. 4 to 6).

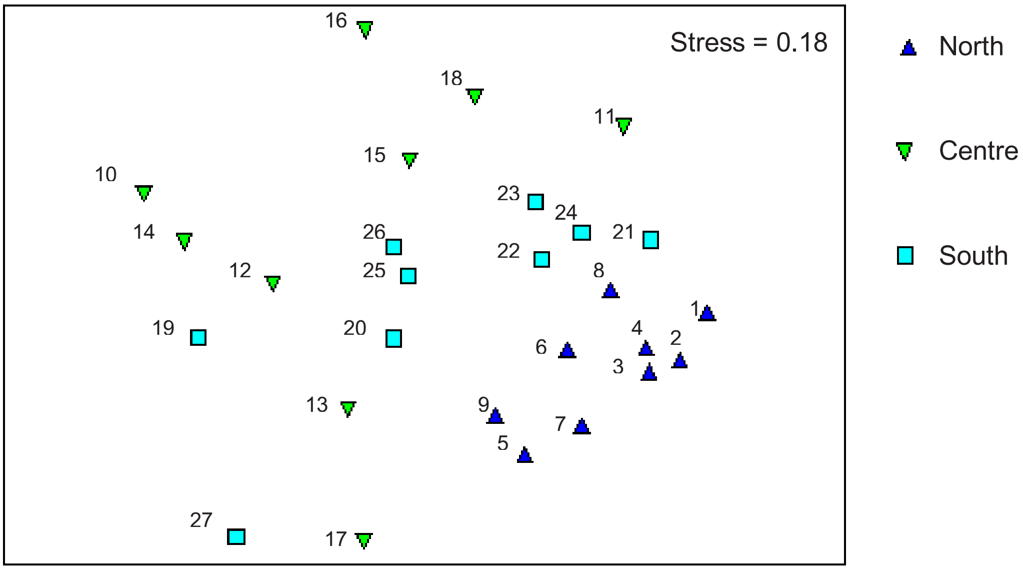

Figure 12- MDS ordination of Bray-Curtis similarity matrix of √√ transformed species abundance data for the upper mid-shore level. Different regions are represented by symbols and shore numbers are indicated (cf. Figs. 4 to 6).

SIMPER analyses of the transformed abundance data allow the examination of the species which contribute to the dissimilarity between levels and regions (Table 1 and 2). The upper mid-shore zone is separated from the lower mid-shore zone by a general reduction of red algae species (e.g. *Corallina* spp., "Lithothamnia", *Caulacanthus ustulatus* and *Gelidium* spp.) and the presence of relatively high numbers of a few species including *Chthamalus* spp., *Patella depressa*, *Siphonaria pectinata* and *Melaraphe neritoides*. Animal species important in characterising lower mid-shore communities include *Mytilus galloprovincialis, Patella ulyssiponensis* and *Sabellaria alveolata* (Table 1).

The northern region is separated from the centre and south regions by a higher average abundance of *Mytilus galloprovincialis*, *Patella vulgata* and *Littorina saxatilis*. Conversely in the centre and south regions there is a higher average abundance of *Corallina* spp., *Patella ulyssiponensis* and *Siphonaria pectinata* among other species (Table 2). Some species showed a gradient in abundance along the coast (Table 2) that supported the observations made for zonation patterns. Examples of this are *Mytilus galloprovincialis* and *Nucella lapillus*, which showed a progressive decrease in average abundance from north to south. The opposite trend, with higher average abundances decreasing from south to north also occurred, for example, with *Siphonaria pectinata*. Discontinuities in average abundance along the coast were also registered. *Patella ulyssiponensis* and *Corallina* spp. have considerable higher abundance in the centre than in either north or south region. In contrast, *Patella vulgata* is less abundant in the central region of the Portuguese coast than in the north and south.

Table 1- Summary of similarity terms (SIMPER) analysis. Differences (< and >) in average abundances or percentage cover per quadrat of species contributing to dissimilarities between upper and lower mid-shore level (after fourth root transformation). A cut off of a cumulative % dissimilarity of 80% was applied.

Species	Upper		Lower
Mytilus galloprovincialis	1.59	<	39.46
Chthamalus spp.	76.98	>	14.15
Patella ulyssiponensis	0.44	<	12.01
Gibbula spp.	5.50	<	10.37
Corallina spp.	0.04	<	11.13
Patella depressa	47.87	>	22.62
Ephemeral algae	0.23	<	5.36
Sabelaria alveolata	0.32	<	2.39
"lithothamnia"	0.20	<	4.00
Actinia sp.	0.13	<	2.95
Siphonaria pectinata	1.82	>	0.57
Patella vulgata	0.80	<	1.56
Melaraphe neritoides	0.67	>	0.21
Ralfsia sp.	0.79	<	0.99
Monodonta spp.	1.04	>	1.00
Littorina saxatilis	1.84	>	0.33
Caulacanthus ustulatus	0.03	<	1.62
Gelidium spp.	0.15	<	0.41
Lithophyllum lichenoides	0.10	<	1.56
Nucella lapillus	0.01	<	1.33

Table 2- Summary of similarity terms (SIMPER) analysis. Differences (< and >) in average abundances or percentage cover per quadrat of species contributing to dissimilarities between regions (after fourth root transformation). A cut off of a cumulative % dissimilarity of 80% was applied.

Species	North		Centre		South
Mytilus galloprovincialis	32.45	>	15.57	>	13.56
Patella vulgata	3.34	>	0.00	<	0.19
Gibbula spp.	10.0	>	9.29	>	4.51
Patella ulyssiponensis	2.69	<	11.71	>	4.27
Chthamalus spp.	47.28	>	42.14	<	47.27
Corallina spp.	0.38	<	11.50	>	4.88
Littorina saxatilis	3.07	>	0.04	<	0.14
"lithothamnia"	0.33	<	3.69	>	2.29
Patella depressa	36.48	<	39.51	>	29.76
Actinia sp.	1.19	<	2.63	>	0.80
Sabelaria alveolata	0.32	<	3.08	>	0.66
Monodonta spp.	1.20	>	0.67	<	1.19
Ralfsia sp.	0.43	<	1.04	<	1.19
Siphonaria pectinata	0.00	<	1.28	<	2.31
Melaraphe neritoides	0.54	>	0.52	>	0.25
Fucus spiralis	0.02	<	1.05	>	0.13
Ephemeral algae	0.17	<	0.66	<	7.54
Caulacanthus ustulatus	0.00	<	2.20	>	0.27
Nucella lapillus	1.42	>	0.58	>	0.01
Lithophyllum lichenoides	0.06	<	1.93	>	0.50
Gelidium spp.	0.05	<	0.25	<	0.54
Dictyota dichotoma			1.22	>	0.29

The K-dominance curves on the abundance of species for the two studied levels showed that the dominance was higher in the upper mid-shore level (Fig. 13a). This trend was confirmed by the result of analysis of variance done for the diversity index of Shannon-Wiener, which revealed a significant higher biodiversity in the lower mid-shore level (Table 3). Differences in cumulative dominance among regions were not so strong (Fig. 13b), and this was also reflected in the ANOVA on biodiversity (Table 3). Diversity index values were as expected inversely related to dominance, with highest mean value for the centre followed by the south and north regions. Despite the described rank order results, the SNK test for the factor regions were non-conclusive.

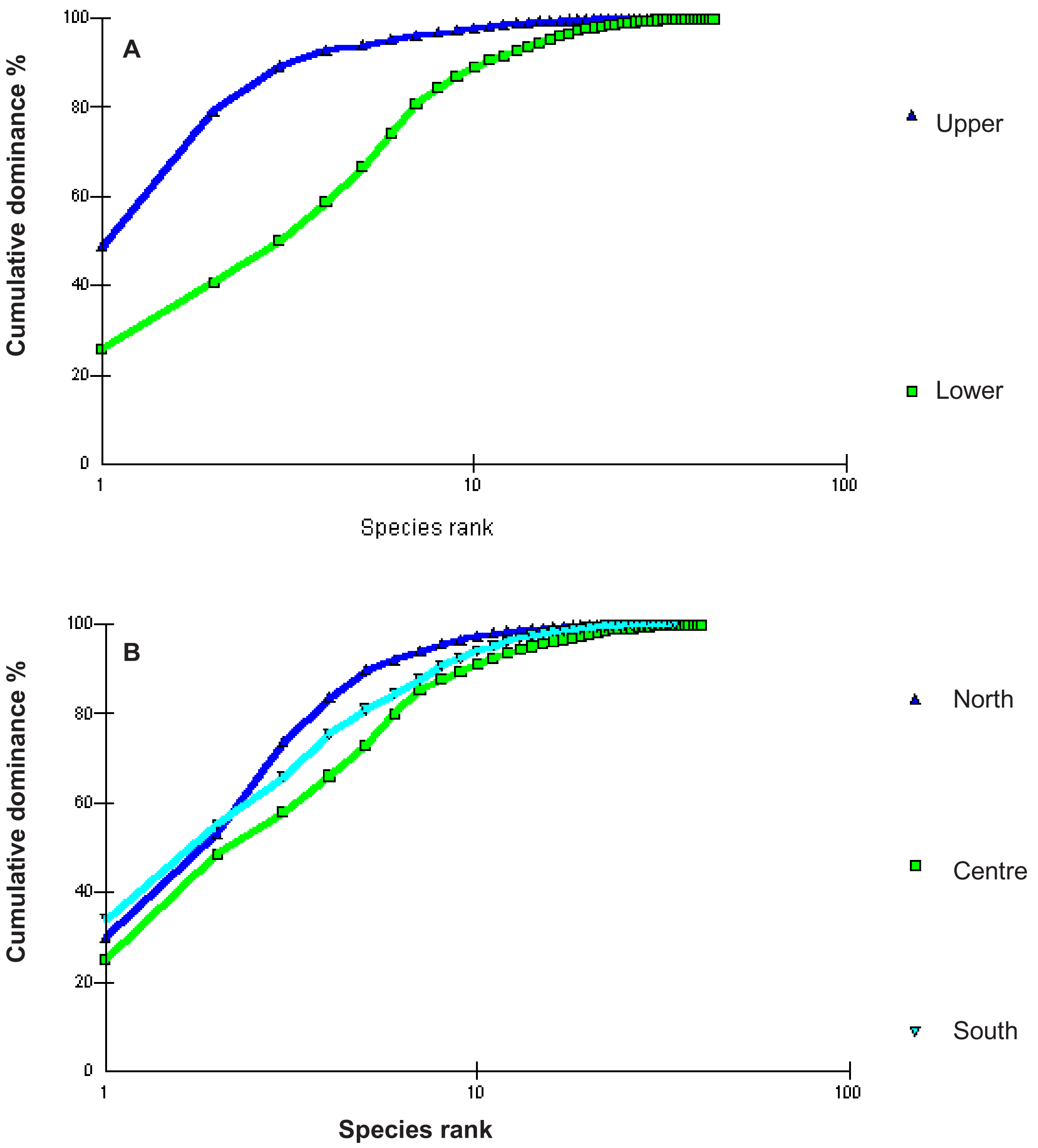

Figure 13- Cumulative dominance for levels (A) and regions (B).

Table 3- Anova on the biodiversity index of Shannon-Wiener. ns = not significant, *p<0.05, **p<0.01,***p<0.001

Source of variation	df	MS	*F*
Level = Le	1	3.40	44.87***
Region = Re	2	0.28	3.53 *
Le x Re	2	0.15	2.04 ns
Res	48	0.08	
Cochran's test		C = 0.37 ns	

Comparison of distribution and abundance of grazing limpets was done in particular for the species *Patella depressa* and *Patella vulgata*. These are the limpet species which are typical of the mid-shore. *Patella ulyssiponensis* and *Patella rustica* dominate the lower algal zone and the high shore levels respectively, and these species were not analysed formally.

Patella depressa is widely distributed and relatively abundant in the mid-shore throughout the entire Portuguese coast (Fig.14). However, a significant interaction between levels and shores was detected, indicating that the abundances of this limpet in the lower or upper mid-shore zone can vary depending on the shores (Table 4). No significant differences between levels were detected for the shores in the northern region, except for Cabo do Mundo where *Patella depressa* was more abundant in the lower than in the upper mid-shore zone (SNK test, SE = 6.91; Fig. 14). In contrast, this limpet was more abundant in the upper mid-shore zone for the majority of shores in the centre region. Significant differences in the abundance of *Patella depressa* between levels for the shores of the south region were not detected on three shores (Zambujeira, Martinhal and Olhos d'Água), it was higher in the lower zone only at Almograve, and higher in the upper zone for the remaining shores.

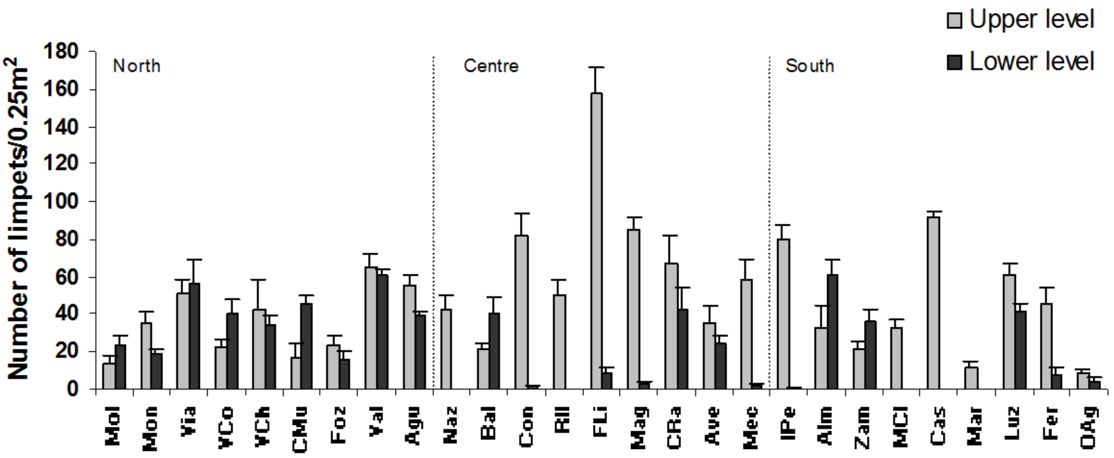

Figure 14- Mean number of limpets (±SE) of the species *P. depressa* in each shore. Shore names are abbreviated (cf. Figs. 4 to 6).

Table 4- Anova on the number of limpets from the species *Patella depressa*. ns = not significant, *p<0.05, **p<0.01,***p<0.001

Source of variation	df	MS	*F*
Level = Le	1	451632.20	13.08 **
Region = Re	2	2534.21	0.84 ns
Shores (Re)	24	3009.80	12.60 ***
Le x Re	2	16187.34	4.69 *
Le x Sh (Re)	24	3452.33	14.45 ***
Res	216	238.94	
Cochran's test		C = 0.10 ns	

Patella vulgata was clearly more abundant in the north than in the centre and south regions either for upper or lower mid-shore zone (Table 5, Fig 15). No significant differences between levels were obtained in the centre and south region (SNK test, SE = 0.44, p>0.05; Fig 15). On the northern region, however, where this species occurs with higher densities, *Patella vulgata* was more abundant in the lower mid-shore level (SNK test, SE = 0.44, p<0.01, Fig. 15). It should be noted that the variances were not homogeneous and, even transformation of the data did not solve this problem. The results presented correspond to the original (non-transformed data) and interpretation of significant results must be made with caution.

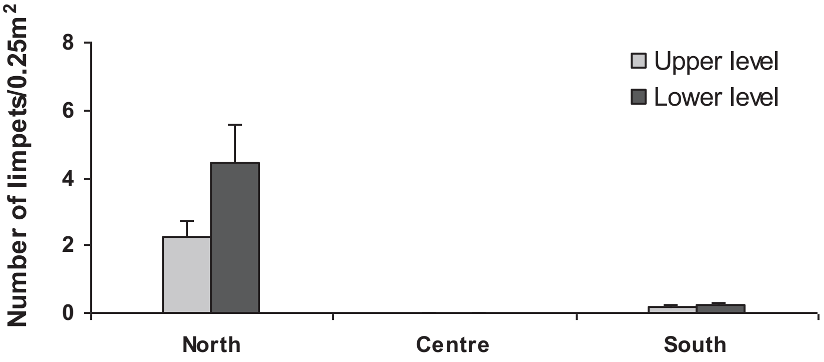

Figure 15- Mean number of limpets (±SE) of the species *P. vulgata* in each region.

Table 5- Anova on the number of limpets from the species *Patella vulgata*. ns = not significant, *p<0.05, **p<0.01,***p<0.001

Source of variation	df	MS	*F*
Level = Le	1	38.53	4.40 *
Region = Re	2	317.68	7.96 **
Shores (Re)	24	39.92	4.88 ***
Le x Re	2	35.23	4.02 *
Le x Sh (Re)	24	8.76	1.07 ns
Res	216	8.19	
Cochran's test		C = 0.75, p<0.01	

DISCUSSION

Vertical distribution patterns

The present study has provided qualitative and quantitative information on distribution patterns of intertidal marine organisms along the rocky shores of the continental Portuguese coast. A reference study of zonation patterns along the whole coast and a systematic comparison of abundances of organisms along a vertical and horizontal gradient has to date been missing in Portugal. Some constraints were found and there is much still to be done. For instance, the quantitative approach was only used for the upper and lower mid-shore zone and, it was not possible to analyse seasonal variation. Fortunately, these aspects will soon be complemented with the results from a national research project. None the less, the information obtained with the present study has clarified several questions related to the vertical and horizontal distribution of organisms on intertidal rocky shores.

The existence of a black littoral fringe characterised by the presence of encrusting lichens, small littorinid gastropods and cyanobacteria may be considered as a world-wide feature of the upper zone of intertidal rocky shores (Stephenson & Stephenson, 1972; Raffaelli & Hawkins, 1996). This pattern was also found on most of the shores along the Portuguese coast. Some variations, however, were seen to occur. These included the absence of the lichen *Verrucaria maura* and presence of cyanobacteria which conferred a grey colour to the rock, or the presence of ephemeral green algae. The abundance of *Melaraphe neritoides* was sometimes extremely reduced.

The eulittoral zone of Portuguese rocky shores is dominated by barnacles and sometimes mussels. Mussels occur in the lower mid-shore zone of more exposed shores. This pattern corresponds to that described for exposed north east Atlantic shores (Ballantine, 1961; Lewis, 1964; Raffaelli & Hawkins, 1996). Effectively, the whole coast of Portugal is exposed to the Atlantic swell. However, the prevalence of large seaweeds in the eulittoral zone with increased shelter, as described for cooler temperate regions (e.g. British Isles) is not common in Portugal. With some exceptions for a few northern shores, where *Pelvetia canaliculata*, *Fucus* spp. and *Ascophyllum nodosum* were observed, fucoid seaweeds do not occur or tend to be short turf forms. The only species observed on the centre and south region was *Fucus* sp. On sheltered shores mosaic distribution of organisms in eulittoral is reduced and barnacles appear to dominate mid-shore zone. It has been suggested (Hartnoll & Hawkins, 1985; Hawkins et al., 1992) that one of the major causes of the change from high fucoid cover on sheltered shores to dominance of filter-feeder animals on more exposed shores in the north east Atlantic, is the increase in grazing effectiveness along a gradient of increasing exposure. The lack of dense mid-shore seaweed beds in Portugal, however, is not only related to the exposure and its effects on modifying grazing efficiency, but mainly to the geographical distribution of some of these species, which distributional limit is located in the north of Portugal (e.g. *Ascophyllum nodosum*, *Himanthalia elongata*) (Ardré, 1970).

The distribution patterns observed on the sublittoral fringe showed a clear difference between northern shores where large brown algae are present and shores located in the central and southern regions, essentially dominated by red algal turf species. Hence, zonation patterns in Portugal may be seen as mixture of the patterns described for the north east Atlantic coasts (Lewis, 1964) and those described for the Mediterranean (Pérès & Picard, 1964). The results of this study also confirm the latitudinal variations in zonation patterns described by Hawkins et al. (1992). From north to southern Europe, animal dominated communities extend further into shelter at more southerly locations. Similarly, southwards, dominance by large brown algae declines low on the shore and red algal turves become more important (Hawkins et al. 1992).

The quantitative approach used in the present study not only confirmed the trends observed in descriptive work, but also enabled questions to be answered about possible differences in community structure between upper and lower mid-shore level and across north centre and south regions. Multidimensional analysis and the ANOSIM test have revealed clear differences in the structure of upper and lower mid-shore zone. The separation of two mid-shore zones may be an evidence of the over simplification of a zonation scheme based only on three major zones. The number of species found in the upper and lower level definitely contributed to the obtained differences. In general, the upper level exhibited a lower diversity and a higher dominance. The lower level of Baleal and Zambujeira was not separated in the general MDS analysis from the upper level stations also due to the lower average number of species recorded in these shores.

SIMPER analyses confirmed the species with the highest contribution to the dissimilarity between the two levels. *Chthamalus* spp., *Patella depressa*, *Siphonaria pectinata*, *Melaraphe neritoides*, *Monodonta* spp. and *Littorina saxatilis* had a higher abundance in the upper mid-shore level whilst *Mytilus galloprovincialis*, *Patella ulyssiponensis*, *Gibbula* spp., *Sabellaria alveolata*, *Actinia* sp., *Patella vulgata*, *Nucella lapillus* and a variety of algal species were more important to characterise the lower level. These results support the vertical distribution patterns described in this study and in the literature (e.g. Lewis, 1964; Stephenson & Stephenson, 1972; Saldanha, 1974).

Multidimensional analysis has separated the low shore zone of Martinhal from all the other shores. This was due to an extremely high abundance and dominance of ephemeral green algae at this level, probably related to the irregularity of the substratum. This shore had a different topography and the low shore zone consisted of large boulders.

Geographic variation

Portuguese rocky shores provide an excellent location for the study of biogeographical processes. There is a gradient along the Portuguese coast for many warm water sub-tropical and Mediterranean species (e.g. *Siphonaria pectinata*, *Oncidiella celtica*, *Patella rustica*, *Caulacanthus ustulatus*, *Lithophyllum lichenoides*) and boreal, cold-water species (e.g. *Ascophyllum nodosum*, *Himanthalia elongata*, *Pelvetia canaliculata*, *Patella vulgata, Nucella lapillus*) (c.f. Fischer-Piette, 1957, 1958, 1963). Some species show a decrease in abundance or have inclusive their geographic limits of distribution along the coast.

The present study included the comparison of the eulittoral community structure across different regions of the Portuguese coast. Despite the decrease in abundance of several species along the regional gradient (from both North to South and South to North) the differences in the community structure were not as clear as for the vertical gradient. A possible explanation for this is that the increase in complexity of the community from high to low shore is superimposed on the latitudinal changes. The latter do not affect community parameters like species richness, total number of individuals, biodiversity and eveness, with the same intensity as vertical distribution. Within each level, however, the northern region was considerably different from the south and central regions. SIMPER analysis revealed the species which contributed to the geographical separation of the northern region in relation to the centre and south. It has also given important information on the geographical decline in abundance of species such as, for example, *Mytilus galloprovincialis*, *Nucella lapillus* and *Siphonaria pectinata*. Although present along the entire coast, the mussel *Mytilus galloprovincialis* suffered a progressive decline in abundance from north to south. It is possible that this variation follows a general decrease in exposure. It is also important to notice that this data refer to intertidal mussels since dense subtidal populations can be found as described for Arrábida coast by Saldanha (1974). The abundance of the gastropod *Nucella lapillus* decreases from north to south and its southern limit of distribution seem to be located in the southern coast (Praia da Luz) as described by Nobre (1940). The occurrence of this gastropod in Portugal is closely related to the existence of mussel beds on which they feed. Mussel populations also provide shelter for *Nucella lapillus*. In contrast, the pulmonate limpet *Siphonaria pectinata* showed a decrease in abundance from south to north. Several species were more abundant in the centre than in the other regions. These included *Patella ulyssiponensis*, *Corallina* spp., *Fucus spiralis*, *Bifurcaria bifurcata* and *Lithophyllum lichenoides* among others.

Limpet distribution along the Portuguese coast was analysed in particular because *Patella* species are important in a geographical comparison context (as shown by SIMPER analyses) but also because its effects on community structure are currently under study in several locations of the Portuguese coast. *Patella ulyssiponensis* occurs throughout the Portuguese coast in the lower eulittoral and sublittoral fringe. Its abundance was higher in the central region. *Patella rustica* occurs at higher levels on the shore, being sometimes abundant in vertical surfaces. This species is more abundant in the centre and south. Hypotheses on the distribution of limpets along the vertical and horizontal gradient were tested specifically for *Patella depressa* and *Patella vulgata*, since these are the limpet species which are typical of the studied mid-shore zone. *Patella depressa* is widely distributed and abundant in all mid-shore area of the entire Portuguese coast. The relative abundance of this limpet in the lower or upper mid-shore zone varied, depending on the shores. *Patella vulgata* was more abundant in the north than in the centre and south regions either for upper or lower mid-shore zone. In the northern region, however, where *Patella vulgata* occurred with higher densities, it was more abundant in the lower mid-shore level.

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CHAPTER 3

The effects of grazing on the distribution and composition of low shore algal communities on the central coast of Portugal and on the southern coast of Britain

Boaventura, D.; M. Alexander; P. Della Santina; N.D. Smith; L. Cancela da Fonseca & S. J. Hawkins. The effects of grazing on the distribution and composition of low shore algal communities on the central coast of Portugal and on the southern coast of Britain. Submitted to *Journal of Experimental Marine Biology and Ecology*.

CONTENTS

INTRODUCTION

Considerable attention has been devoted to the study of vertical distribution of some species on the shore. Physical factors have long been thought to be responsible for the upper limits of distribution of most intertidal species (e.g. Baker, 1909; Connell, 1972). Experimental work has shown the importance of aerial exposure and desiccation in controlling the upper limits of distribution of high- and mid-shore fucoid algae (Schonbeck & Norton, 1978). Lower on the shore evidence was provided that physical factors determined the upper limit of some red algae (Lubchenco, 1980; Carter & Anderson, 1991). In contrast, lower limits of distribution have usually been associated with biological factors like competition, grazing or predation (Schonbeck & Norton, 1980; Lubchenco, 1980; Hawkins & Hartnoll, 1985). Experimental investigations of the factors affecting algal zonation in New England rocky shores by Lubchenco (1980) led to the conclusion that competition is the primary determinant of *Fucus* sp. lower limits (affecting presence or absence) and herbivory is of secondary importance (affecting abundance). Interspecific algal competition has also been shown to set lower limits of fucoid algae (*Pelvetia canaliculata* (L.) Decaisne & Thuret and *Fucus* spp.) in the U.K., in several experiments involving both field transplants, exclusion areas and laboratory cultures (Schonbeck & Norton, 1980) and canopy removal (Hawkins & Hartnoll, 1985).

More recently, the importance of biological factors such as grazing and competition have been shown to set upper distribution limits of some species (Underwood, 1980, 1985; Sousa et al., 1981; Underwood & Jernakoff, 1981, 1984; Hawkins & Hartnoll, 1985). Underwood (1980) demonstrated that upper limit of foliose macroalgae in Australian shores was primarily set by herbivorous molluscs. Thus, the upper limits of these lower algal beds would depend on the grazing of algal propagules by gastropods and only in the absence of grazers physical factors would become important in determining the upper limit of macroalgae (Jernakoff, 1983). After the Torrey Canyon oil spill, large-scale kills of limpets due to excessive dispersant application resulted in upward extension of some low shore species (Southward & Southward, 1978). Some canopy forming algae have also been induced to extend upwards after the removal of competitor algal species (Hawkins & Hartnoll, 1985).

A red algal assemblage with a distinct upper limit of distribution dominates the lower tidal levels of some sheltered and moderately exposed shores of central Portugal and south of Britain. This pattern also occurs elsewhere throughout the Northeast Atlantic region from the

British Isles (Lewis, 1964) southwards especially on steep shores (Saldanha, 1974). Such pattern can also be seen in the Mediterranean (Pérès & Picard, 1964) and Azores (Hawkins et al., 1990). Immediately above this boundary, limpets, encrusting algae and barnacles mainly occupy the lower mid-shore areas where the red turf and articulated calcareous coralline algae are rarely observed.

The overall aim of this work was to understand what factors determine vertical distribution patterns on the shore, particularly the effects of grazing limpets on the upper limits of low shore algae. The hypothesis that grazing by limpets directly determines the upper limit of distribution of the red algal turf was tested. The work was undertaken in both Portugal and U.K. with a nested experimental design to enable spatial scale comparisons.

According to Farrell (1988), following a temporary reduction in consumer abundance, prey species are likely to 1) quickly decrease to pre-removal levels, 2) gradually decrease to pre-removal levels over a period of time that corresponds with the maximum life span of the prey species or, 3) to remain above pre-removal densities. We were also interested to see whether limpets could graze back the algae established in ungrazed areas and we monitored their rate of decrease after removing the fences. On the other hand, previous experiments in New South Wales (Underwood & Jernakoff, 1981) demonstrated that direct interaction between algae and grazers could also determine the lower limit of grazer distribution on the shore. Therefore, we additionally investigated if limpets can invade experimental clearings in the turf zone and their ability to keep these areas cleared.

METHODS

Study sites and organisms

This study was carried out on the central coast of Portugal and southern coast of Britain. Two shores were chosen in each location: Cabo Raso (38º 42'N, 9º 29'W) and Estoril (38º 42'N, 9º 23'W) in Portugal; Heybrook Bay (50º 22'N, 4º 11'W) and Swanage (50º 37'N, 1º 57'W) in Britain. The sites were selected as they showed a red algal zone with a sharp upper limit of distribution. The ledges with these characteristics had a slope of more than 25º.

Portuguese locations have mean tidal range during spring tides of 2.84 m. The substratum is limestone bedrock that faces the open Atlantic Ocean. Strong surf action is frequent in winter but storms are intersperse with periods of sufficient calm to allow site visits. Mean tidal range of spring tides at Heybrook Bay and Swanage is 4.70 m and 1.50m respectively. Both are typical moderately exposed English Channel shores.

Although the Portuguese shores were more exposed than those in the U.K., a similar clearly visible boundary existed between the limpet/barnacle zone and a red algal turf (see Plate 1). In Portugal this kind of pattern frequently occurs in moderately exposed to more sheltered locations (Saldanha, 1974).

The experimental area comprised the upper part of the red algal turf and the lower mid-shore area composed of bare rock, limpets, encrusting algae and few barnacles, between mean low water of neap and mean low water of spring tides. The algal turf was essentially composed of articulated coralline and corticated macrophyte algae although some different species were found in Portugal and in the U.K. *Gelidium* spp. and *Caulacanthus ustulatus* (Mertens) Kützing were more abundant in Portugal while *Mastocarpus stellatus* (Stackhouse) Guiry was more frequent in Britain. Canopy forming algae such as *Himanthalia elongata* (L.) S.F. Gray and *Fucus serratus* L. only occurred in Britain and the encrusting alga *Lithophyllum lichenoides* Philippi was only found at the Portuguese location. Other macroalgae in both locations comprised a variety of filamentous red and foliose green algae, encrusting coralline algae and non-calcareous crusts. The most common herbivores were limpets although trochids were also present at Heybrook Bay and in Portugal. Limpet species on the Portuguese shores included *Patella depressa* Pennant and *Patella ulyssiponensis* Gmelin (*Patella aspera* Röding). On British shores *Patella vulgata* L., *P. depressa* and *P. ulyssiponensis* were all present in the experimental area. A detailed survey of the site at Swanage was made in the 1930s (Grubb, 1936). The shore has not changed much since the 1930s (Southward and Hawkins, pers. obs. 1950s-present day).

Experimental design

Limpet exclusion

In order to test the null hypothesis that there is no influence of grazing by limpets (*Patella* spp.) on the upper limits of distribution of the red algal turf, the limpets were excluded by fences with half-fenced and unfenced controls. In exclusion treatments (E), fences were put on the shore and macrograzers were removed. Half-fenced plots (HF) were used as controls with no manipulation of grazers to test if there was any artifact in the experiment due to the use of fences. The half-fences allowed potential limpet movements and tested whether algal settlement was enhanced or reduced by the fence structure either by direct or indirect (interactions with grazers behaviour) effects. Unfenced control plots (C) were marked with screws in each corner but with no fences and no manipulation of grazers. Two areas ("patches") were chosen in each of the shores and three replicates of each treatment were randomly assigned within each area ("patch"). Two additional sets of treatments were set up in the most exposed and visited site, Cabo Raso, to have spare replicates in case some were damaged by storms or visitors. Results from these additional patches (Patch 3 and 4) were not included in any statistical analysis but are graphically presented as extra information where appropriate.

Similar fixed plots of 1x0.5m were chosen in each patch and the treatment and controls were allocated randomly to them. These strips comprised the upper part of red algal belt (approximately 40 cm) and the lower part of mid-shore devoid of macroalgae (except for some encrusting species). This region of the shore was chosen to see if the red algal zone could extend its limits on the shore in the absence of limpets, either from propagules or vegetative growth. The plots were selected according to the following criteria: the presence of red algal turf with a sharp upper limit of distribution, rock slope greater than 25°, presence of limpets in the plots prior to any manipulation.

Fences made of a square mesh (13x13mm) welded plastic coated steel wire were attached to the rock by screws fixed into rawl-plugs in holes drilled by a petrol driven drill (Ryobi ER160). On the first day of the experiment, fences were put on the shore, limpets and other grazers were removed from exclusion plots, the first sampling of the plots was carried out and the position of the upper boundary of the red algal turf was levelled in each replicate in relation to chart datum. Subsequent sampling was non-destructive. The percentage cover of algae and sessile animals was estimated with intersection point method using a quadrat of 50x50cm with 49 intersection points. To quantify algal abundance, substrate cover and canopy cover were always distinguished. Thus a quadrat with several layers of different algal species could have more than 100% of total algal cover. The remaining sessile species present inside the quadrat that did not match any intersection point were recorded and arbitrarily assigned 1% value. The total number of limpets and trochids was counted. Plots were sampled either directly in the field or in the laboratory from 35mm colour slides of the plots (with the sampling quadrat) analysed under a binocular stereoscopic microscope. Photographic estimates were only used when the weather and sea conditions did not allow time for observation in the field. This procedure was only applied to plots with a single algal layer and to sessile species. Thus British plots, which often had a canopy layer, were always assessed on the shore.

This experiment was started in the summer of 1996 in both countries. The patches were sampled monthly up to six months and then every two months until the end of the second year. Two quadrats were sampled in each replicate (top and bottom quadrat) since the plot area was 1x 0.5 m. However, only the data from the top quadrats were analysed in this study. During each visit to the shore fences were checked and repaired if necessary. Any invading limpets were also removed from exclusion plots. Herbivore exclusion seemed to be more effective in Britain than in Portugal. Small limpets persistently entered the exclusions in Portuguese shores. This fact is probably related to size and density of limpets in these areas. Additionally, fences in Portugal needed frequent repair during the winter due to wave action. Thus the "exclusion treatment" of this experiment should be regarded as a significant decrease but not total absence of herbivores.

Limpet re-encroachment

After two years (summer of 98) the fences were removed, therefore limpets were allowed to return to the exclusion plots. The main objective of this second set of observations was to see if limpets were able to reduce already established macroalgae and if so, the time required for return to the original state. Unfenced and previously fenced plots were sampled as before and monitored every 15 days (spring tides) during the first month and then monthly. This was only logistically possible for the shores in Portugal.

Algal removal

To see whether limpets can naturally invade areas of the shore with no macroalgae and keep them cleared, macroalgae and limpets were removed downwards from the upper limit of turf algae. Three replicated areas of 50x50cm were scraped using chisel and paint scrapers in each experimental area. The upper limit of these areas matched the upper limit of turf algae on the shore. Cleared and control plots were sampled in the same way as described for experiment (A) and monitored every 15 days (spring tides) during the first month and then every month. This experiment started in the summer of 98 at the same time as the re-encroachment monitoring. Similar clearings were not made in the U.K.

Functional groups

The susceptibility of an alga to a herbivorous mollusc depends, in part, upon the size and toughness of the plant relative to the feeding abilities of the mollusc (Steneck & Watling, 1982). Further, herbivore-induced disturbances have functionally similar impacts on most morphologically and anatomically similar algae regardless of their taxonomic or geographic affinities (Steneck & Dethier, 1994). The objective of this study was to analyse plant-herbivore interactions and due to the diversity of low-shore communities and especially of the algal bed a functional-form approach was also adopted for the presentation of results. Moreover, a functional group analysis can be applied more broadly in space for making biogeographical comparisons (Steneck & Dethier, 1994). Algae were grouped in functional form groups as described by Littler & Littler (1980, 1984) and Steneck & Watling (1982). However, functional groupings of algae are based on anatomical and morphological characteristics that often correspond to ecological characteristics (Steneck & Dethier, 1994) and, in our study, the following groups were designated: microalgae, ephemeral algae, turf forming algae, canopy, calcareous turf forming algae, crustose coralline algae, non-calcareous crusts.

Data analysis

Total algal cover, algal species richness, and algal cover of the different functional groups in experiment (A) were analysed using a 4-way mixed model ANOVA. The factors tested were “grazing treatments” (fixed, orthogonal, 3 levels), “locations” (random, orthogonal, two levels), “shores” (random, nested within location, two levels), “patches” (random, nested within shores and location, two levels). Both the limpet re-encroachment and algal removal observations were analysed using a 3-way ANOVA. Comparisons were made just with two treatments (control vs. fence removed areas; control vs. algal removal areas) and for Portuguese location alone. The factors tested were “treatments” (fixed, orthogonal, two levels), “shores” (random orthogonal, two levels), and “patches” (random, nested in shores, two levels) with three replicates of each treatment.

Cochran’s C-test was used to check homogeneity of variance. Where this assumption was violated, appropriate transformations were used (Underwood, 1997). If necessary, percentage cover of each functional algal group was arcsine-transformed prior to the analysis of variance. When variances remained heterogeneous after transformation significant results were still discussed but should be regarded with some caution. Non-significant results are perfectly acceptable since this problem can lead to excessive type I error (rejecting the null hypothesis when it is true) (Underwood, 1997).

For each functional group, data were analysed at appropriate dates. Only spatial differences were tested at each one of these dates. Time-related comparisons were not made due to non-independence of repeatedly sampled plots. Tests of homogeneity, ANOVA and SNK

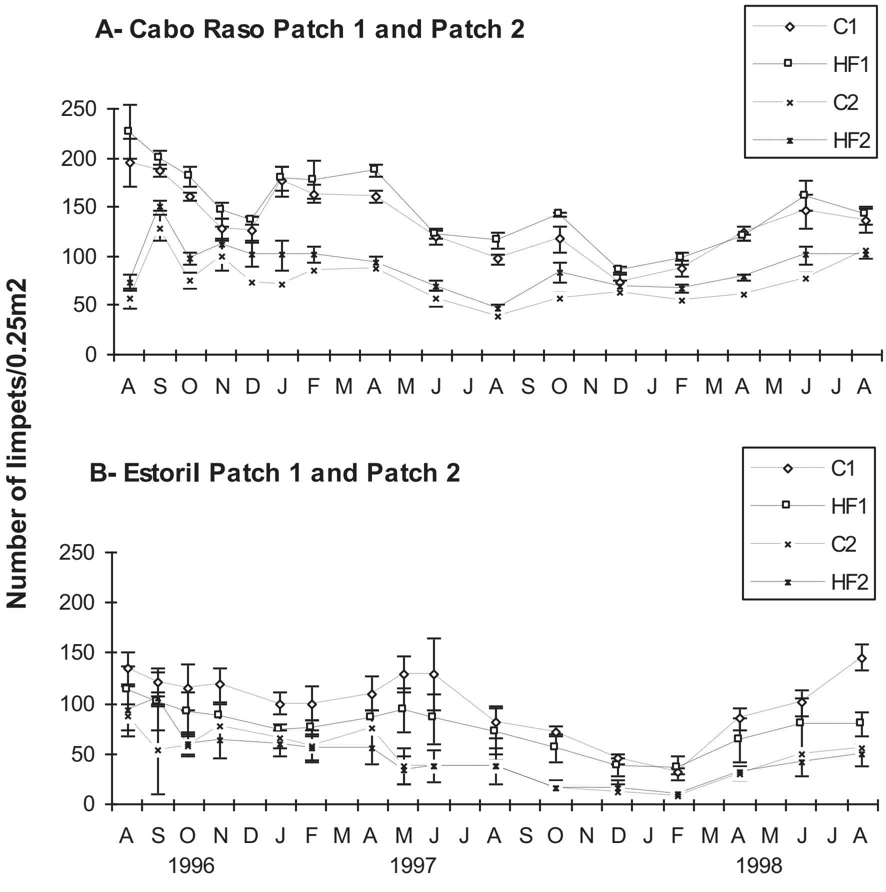
(Student-Newman-Keuls*) a posteriori* comparison tests were done using GMAV5 for Windows Statistical Software (Institute of Marine Ecology, Sydney, Australia).

RESULTS

Limpet exclusion

Limpet density

There were no differences in the abundance of limpets in control and half-fenced treatments (12mo $F_{1,1} = 3.26$, $P > 0.05$; 24 mo $F_{1,1} = 0.01$, $P > 0.98$), which indicates that the half-fence was an effective control for the use of fences. Grazer abundance fluctuated greatly during the two years but with the same trends in control and half-fenced plots (Fig. 1). There were significant differences in the number of limpets in different patches after both 12 ($F_{4,32}$= 11.63, $p<0.001$) and 24 mo ($F_{4,32}$= 13.08, $p<0.001$). The mean number of limpets was higher in patch 1 than patch 2 in Cabo Raso and Estoril and also in Heybrook on the last sampling date (Fig 1). Swanage consistently registered lower limpet density and less variation than the other shores.



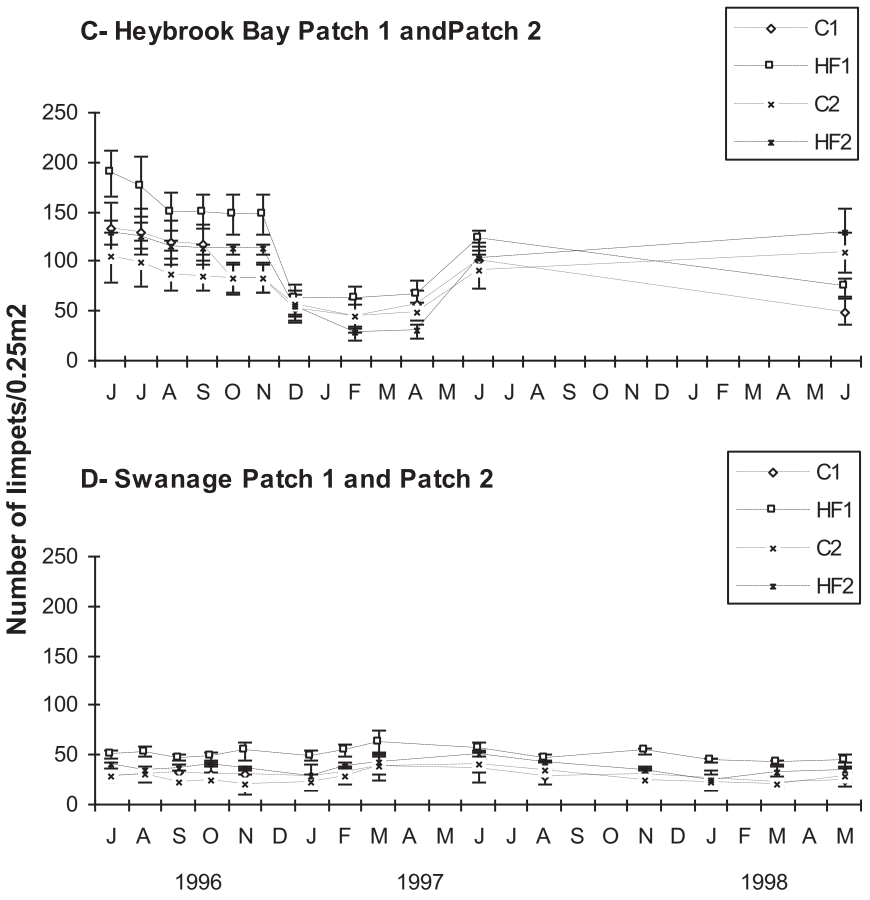


Figure 1- Mean number (±SE) of limpets in ungrazed treatments. C_- Control, HF_- Half-fence; _1- Patch 1, _2- Patch 2.

Total algal cover

Total algal cover is considered at first as this is the best response variable for biogeographical comparisons. Percentage cover of total macroalgae was far greater in exclusions than either in control or half-fenced treatments (Fig 2) throughout the experiment. On all shores except Heybrook Bay, treatment effects were apparent after one month (Fig. 2, Table 1). Two years after the starting date algal cover was significantly higher in exclusion plots than unfenced control and half-fenced control for all the sites (Table 1, SNK test).

Although there were clear differences between ungrazed and grazed areas, there were some differences in algal cover among sites (Table 1, Gr x Sh(Lo) significant at 1 and 24 months). Cabo Raso patch1 showed an initial increase of algal cover (89%) with a subsequent decline of 20% on the second month; then there was a more gentle recovery and after February (6 mo) percentage cover values remained above 95% until the end of the experiment (Fig 2 a). This pattern also occurred in the additional patches 3 and 4 at this shore although the increase on the second month was not as high as for P1 and with some greater fluctuations after

February (Fig. 2 c,d). After two years, the difference between mean algal cover in exclusion treatments and the other treatments was approximately 40% for both patch1 and 4; 70% in patch 3; and just 12% in patch 2. In fact, patch 2 showed similar consistent high values of algal cover in control and half-fenced treatments due to the presence of calcareous and non-calcareous crusts rather than erect algae (Fig. 2b), that contrasted with other patches (Fig. 2 a,c,d). At Estoril, variation in algal cover was greater, and only approached maximal levels from 12 months onwards (Fig. 2 e,f). Patch 2 in particular, exhibited the most irregular trends and it was observed that this patch was occasionally affected by sand deposition.

Rapid increase in cover had occurred by the end of the first month at Swanage (50-80% cover) (Fig. 2 i,,j); this was only apparent, however, by the fifth month at Heybrook (Fig. 2 g,h). Both sets of controls remained almost devoid of macroalgae in Swanage and in patch 2 at Heybrook (Fig. 2 h,i,,j). At Heybrook (patch 1), however, there was some algal colonisation of other plots (Fig. 2 g).

Table 1- ANOVA on the total percentage cover in response to limpet exclusion. ns = not significant, *p<0.05, **p<0.01, ***p<0.001

Total algal cover		1 mo		24 mo	
Source of variation	df	MS	*F*	MS	*F*
Grazing = Gr	2	4241.18	162.47 **	26690.90	40.71 *
Location = Lo	1	6701.65	3.14 ns	4118.54	0.39 ns
Shore (Lo) = Sh(Lo)	2	2130.89	9.96 *	10622.96	24.14 **
Patch (LoxSh) = Pa (LoxSh)	4	213.94	2.42 ns	440.06	2.23 ns
GrxLo	2	26.10	0.02 ns	655.58	0.15 ns
GrxSh(Lo)	4	1089.98	6.74 *	4245.69	27.54***
GrxPa(LoxSh)	8	161.84	1.83 ns	154.18	0.78 ns
Residual	48	88.46		197.62	
Cochran´s test		C = 0.30, p<0.01		C = 0.16 ns	
Transformation:		ArcSin (%)		None	
SNK tests		GrxSh(Lo), SE = 5.19 Cabo Raso, C=HF<E* Estoril, C=HF<E* Heybrook Bay, ns Swanage, C=HF<E**		GrxSh(Lo), SE = 5.07 Cabo Raso,C=HF<E** Estoril, C=HF<E** Heybrook, C=HF<E* Swanage, C=HF<E**	

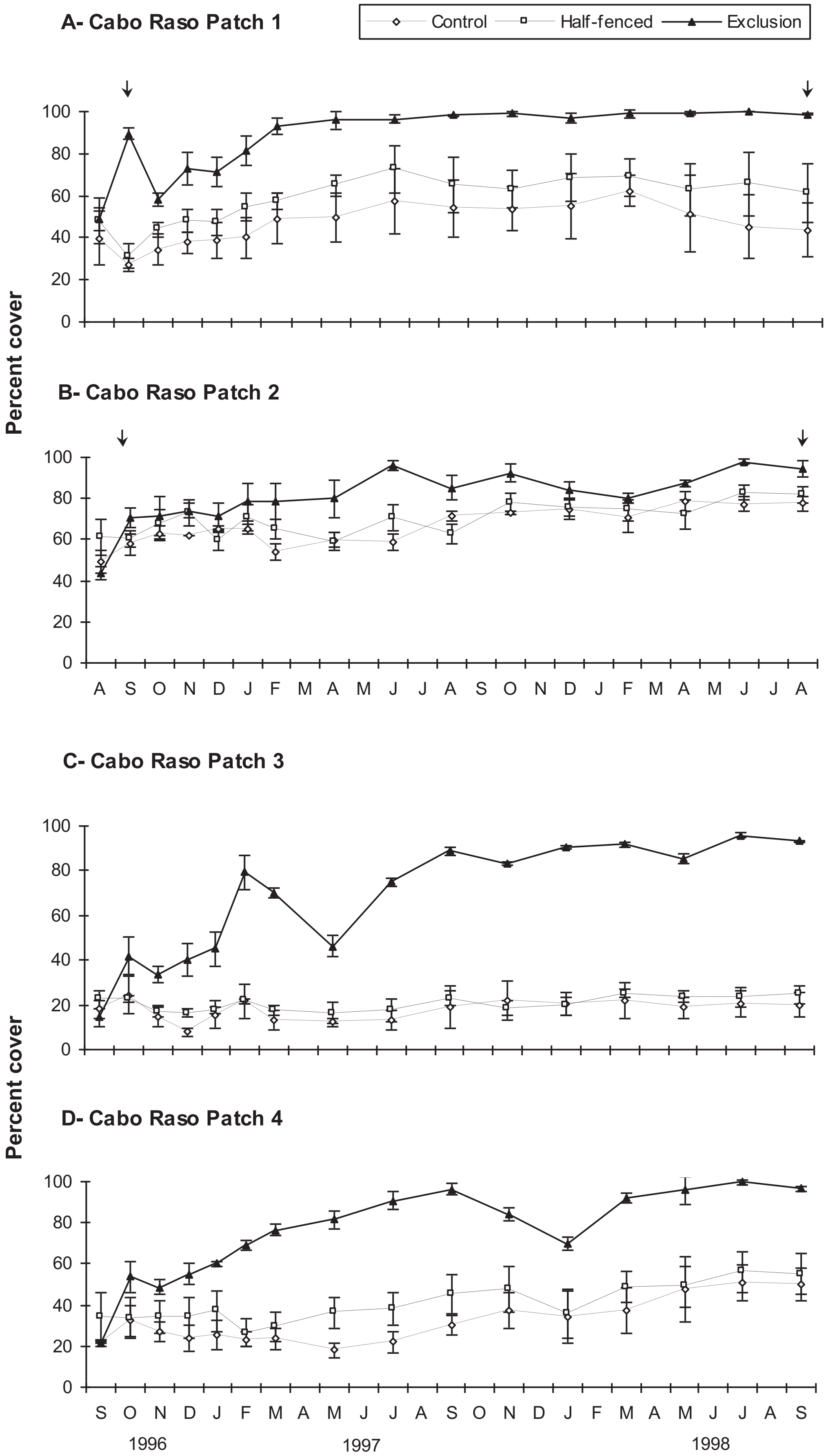
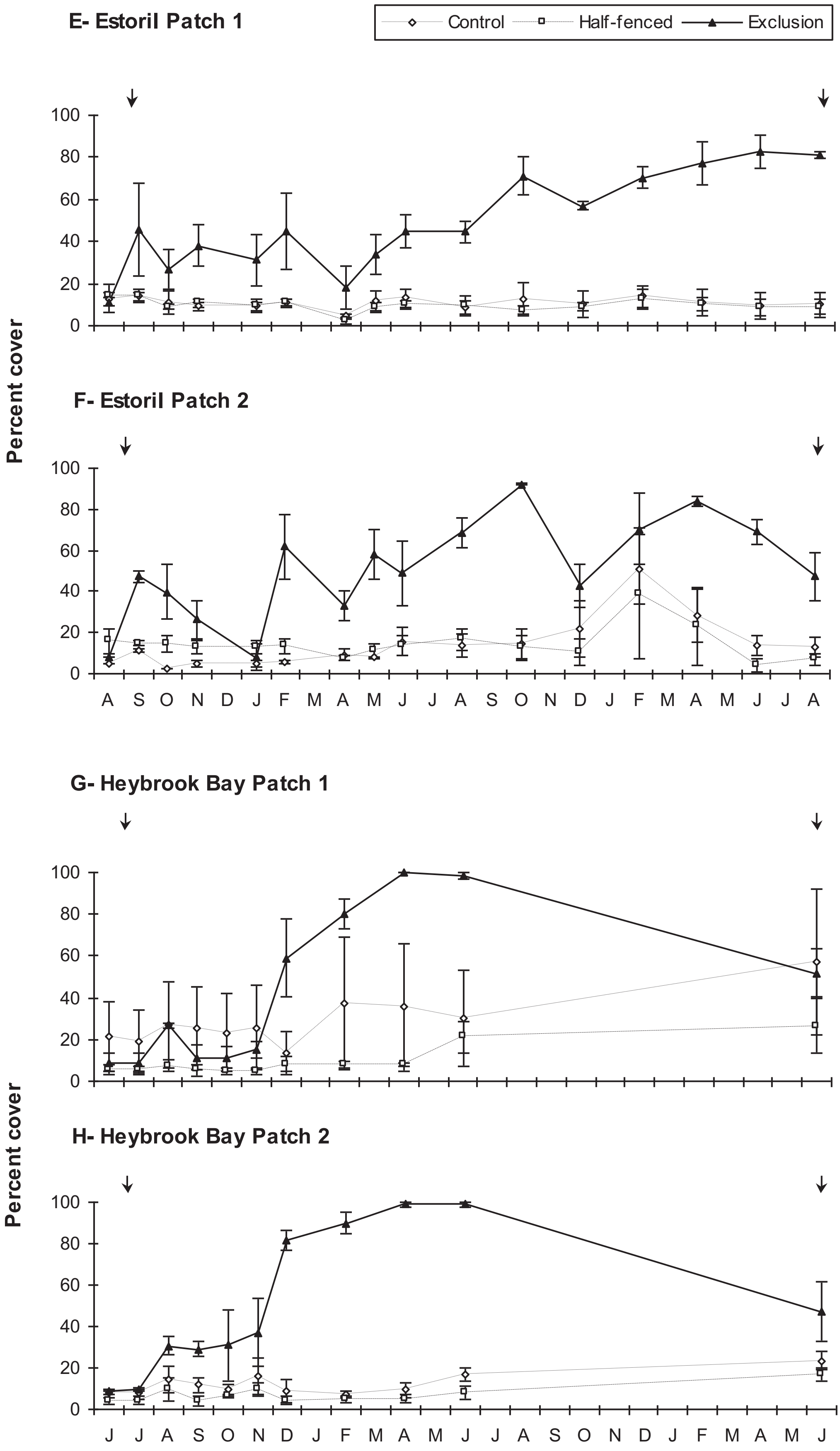


Figure 2- Effects of limpet exclusion on mean (±SE) % of total algal cover. Arrows indicate dates for which data were analysed (…).



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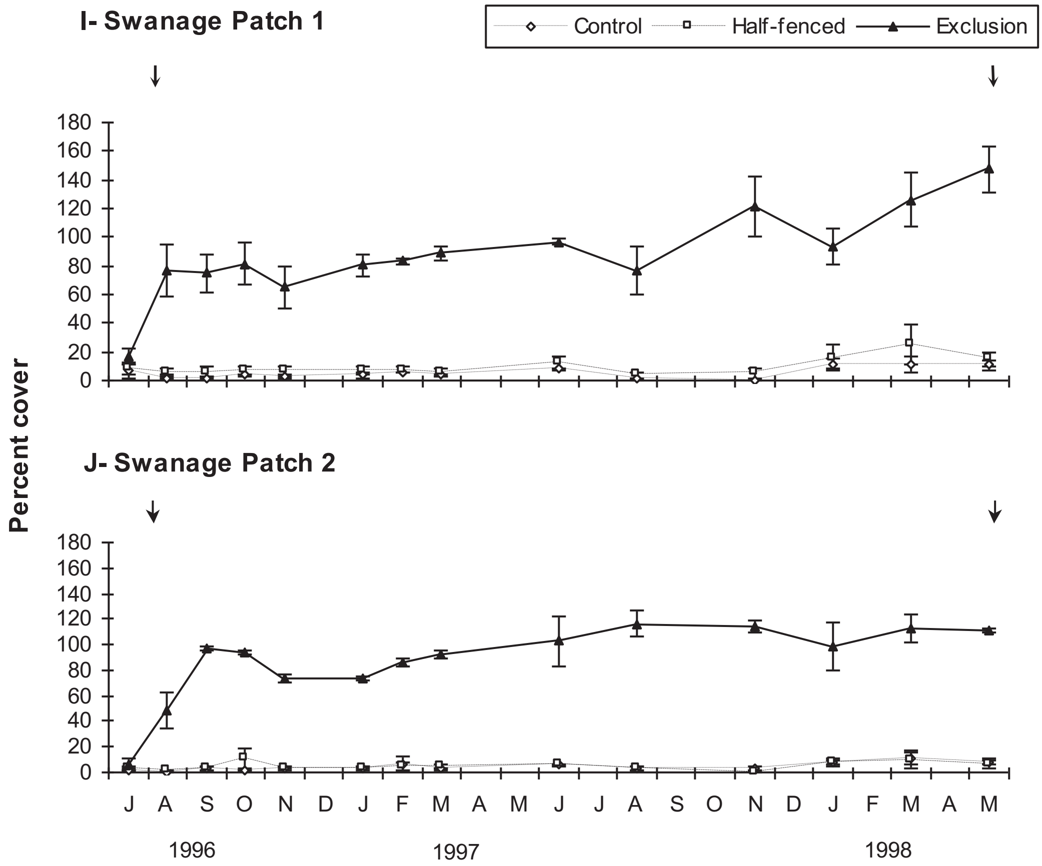


Figure 2- Effects of limpet exclusion on mean (±SE) % of total algal cover. Arrows indicate dates for which data were analysed.

Sequence of algal colonisation

To aid a statistical analysis a functional group approach has been used. Limpet exclusion experiments had different effects on the algal assemblage, depending upon the experimental sites and the functional group considered (see Fig. 3, Table 2).

There were no significant differences among treatments for any functional group at the start of the experiment (Table 2). Turf algae showed a significant difference between patches at Swanage at time zero (Table 2, SNK tests) but mean values were still very low (P1 = 3.5%, P2 = 0.2%) and had no influence in the outcome of the experiment.

Ephemeral algae significantly increased in exclusion plots on all shores except Heybrook Bay on the first month (Table 2, SNK tests). The effects of grazers on this functional group were, thus, more evident at the beginning of the experiment (Fig. 3 a,b,e,f, Plate 1 a). Variances were heterogeneous, so these significant differences should be regarded with some caution. From the first month onwards, differences between exclusions and controls were just found occasionally on a specific shore or patch (e.g. Swanage and patch 2 at Estoril). Figure 4 represents the most important species that colonised the ungrazed areas in the several patches. Only the exclusion plots are graphed as virtually no new algae colonised the controls, although encrusting forms persisted. Although some variability was evident, ephemeral algae (mainly *Ulva* sp. and *Enteromorpha* sp.) generally declined at all Portuguese sites after the second month. This pattern was shown clearly at patch 1 in Cabo Raso (Fig. 4a). At Estoril (patch2) the cover of ephemeral algae showed high fluctuations throughout the remainder of the experiment (Fig. 4d). At Swanage, cover remained relatively high during the first year (Fig. 4g,h). Interestingly, this ephemeral phase was missing at Heybrook. The lack of ephemeral algae at this site explains the absence of differences in total algal cover after one month reported above.

The effects of grazers on structurally more complex algae such as turfs became evident only after six months in Cabo Raso (Fig 3 c) and even later on the other shores. An interaction between grazing treatments and location was found after two years, indicating that the effect of limpets varied with the latitude. Percentage cover of turf algae was significantly higher in exclusion treatments in both Portugal and U.K. but this effect was greater in the south European location (mean value for Portugal 43,46% and 19.56 % for U.K.). In Portugal (Fig. 4 a,b,c,d, Plate 1 b), *Caulacanthus ustulatus* dominated the exclusion plots at the end of the experiment (values between 39% and 47% in the different patches), and also *Gelidium* sp. in patches 1 and 3 with 32% and 31% respectively. Non-calcareous crusts (*Ralfsia verrucosa* (Areschoug) J. Agardh and *Petrocelis* sp.) colonised some the additional patches (P3 and P4) during the period that mediated the decline in ephemeral and the increase of red algae.

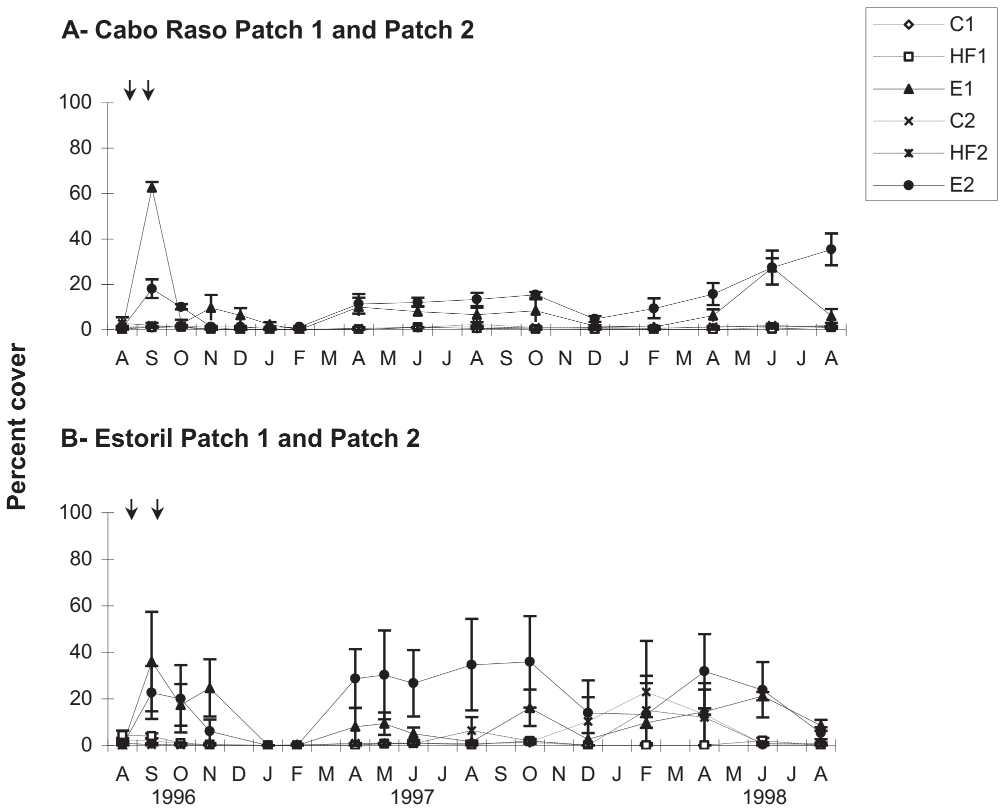
Very different colonisation patterns occurred in Britain (Plate 1 c,d,e). Despite the significant increase in red algae, the exclusions were dominated by canopy forming brown algae, which started to colonise the plots after the fifth month. Canopy cover became very dense and a significant higher cover in ungrazed areas was evident two years post limpet removal at Heybrook and Swanage (Fig. 3 g,h; Table 2, SNK tests). The interaction is due to differences among shores of the cover of canopy in exclusion treatments. The most abundant algal species differed in the two shores, however. After one year, *Himanthalia elongata* accounted for 69% and 77% cover in Heybrook Bay (patch 1 and 2) (Fig. 4 e,f). In contrast, *Fucus serratus* was more abundant in Swanage; at that time reaching percentage cover of 23% and 69% in patch 1 and 2, respectively (Fig. 4 g,h). The dense cover of *Fucus serratus* persisted until the end of the experiment in Swanage while a reduction of *Himanthalia elongata* was observed in the second year at Heybrook. On the other hand, in Swanage, *Fucus serratus* was more abundant in patch 2, whereas *Laurencia pinnatifida* (Hudson) Lamouroux showed higher values in patch 1. In Portugal, the exclusion of limpets did not lead to an increase in canopy cover during the study period. The only canopy forming algae included in this functional group in Portugal was *Codium tomentosum* Stackhouse, which never reached values greater than 10%.

The effects of limpets on other functional groups were not so evident. Microalgae showed an increase in February (6mo) on Portuguese shores ($F_{Gr \times Sh(Lo)\ 4,8} = 7.78$, $P<0.01$, SNK test< 0.05). A brown slick of diatoms occurred in February in patches 1 and 3 (10% and 28%) but seemed to be a seasonal event rather than part of a successional sequence since it occurred again in the second winter, although with reduced density. A peak of diatoms was also observed in both Estoril patches (27% and 48%) after the reduction in ephemeral algal cover (Fig. 4 c,d). Patch 2 showed a less dense cover of late colonisation stages and thus a relatively high cover of both ephemeral algae and diatoms in the second year. No significant differences were obtained for any other shores or dates. Calcareous turf forming algae showed no clear difference among treatments although an increase of 20% in the cover of corallines was observed in Cabo Raso (P1) and 10% in Estoril (P1). This occurred in exclusion plots and after 12mo but generally these algae died back in the summer. Crustose coralline algae showed no discernible changes through time; their abundances decreased and increased as the other algae covered them and disappeared. Non-calcareous crusts increased in response to limpet removal after 6 months, but only in Heybrook ($F_{Gr \times Sh(Lo)\ 4,8} = 5.83$, $P< 0.02$, SNK test< 0.01) and in the two additional patches of Cabo Raso (P3 and P4).

Table 2- ANOVA on the percentage cover of algal functional groups in response to limpet exclusion. ns = not significant, *p<0.05, **p<0.01, ***p<0.001

Ephemeral algae		0 mo		1 mo	
Source of variation	df	MS	*F*	MS	*F*
Gr	2	5.10	0.02 ns	6513.59	226.99 **
Lo	1	212.65	4.75 ns	253.81	0.59 ns
Sh(Lo)	2	44.78	2.50 ns	426.61	3.11 ns
Pa(LoxSh)	4	17.94	0.65 ns	137.21	1.77 ns
GrxLo	2	243.79	3.62 ns	28.70	0.03 ns
GrxSh(Lo)	4	67.32	3.29 ns	998.95	6.57 *
GrxPa(LoxSh)	8	20.46	0.75 ns	152.15	1.96 ns
Residual	48	27.40		77.71	
Cochran´s test		C = 0.2698, p<0.05		C = 0.4785, p<0.01	
Transformation:		ArcSin (%)		ArcSin (%)	
SNK tests				GrxSh(Lo), SE=5.04 Cabo Raso, C=HF<E** Estoril, C=HF<E** Heybrook Bay,C=HF=E ns Swanage, C=HF<E**	
Turf algae		0 mo		24 mo	
Source of variation	df	MS	*F*	MS	*F*
Gr	2	10.18	0.45 ns	4152.98	3.51 ns
Lo	1	2.69	0.02 ns	1067.58	1.94 ns
Sh(Lo)	2	115.19	1.20 ns	549.02	1.31 ns
Pa(LoxSh)	4	95.99	5.01 **	418.01	9.26 ***
GrxLo	2	22.70	2.02 ns	1184.87	129.25***
GrxSh(Lo)	4	11.24	0.76 ns	9.17	0.10 ns
GrxPa(LoxSh)	8	14.74	0.77 ns	89.71	1.99 ns
Residual	48	19.15		45.14	
Cochran´s test		C = 0.13 ns		C = 0.19 ns	
Transformation:		ArcSin (%)		ArcSin (%)	
SNK tests		Pa(LoxSh), SE = 1.46 Cabo Raso, P1=P2 ns Estoril, P1=P2 ns Heybrook Bay, P1=P2 ns Swanage, P1>P2**		GrxLo, SE = 0.87 Portugal, C=HF<E** U.K., C=HF<E**	
Canopy algae		0 mo		24 mo	
Source of variation	df	MS	*F*	MS	*F*
Gr	2	5.90	4.52 ns	4611.56	1.51 ns
Lo	1	0.01	0.00 ns	4137.75	11.02 ns
Sh(Lo)	2	9.20	2.08 ns	375.34	10.59 *
Pa(LoxSh)	4	4.42	0.81 ns	35.43	0.84 ns
GrxLo	2	1.30	1.40 ns	3061.97	3.74 ns
GrxSh(Lo)	4	0.93	0.16 ns	818.76	23.71***
GrxPa(LoxSh)	8	5.94	1.09 ns	34.53	0.82 ns
Residual	48	5.44		42.05	
Cochran´s test		C = 0.34, p<0.01		C = 0.37, p<0.01	
Transformation:		ArcSin (%)		ArcSin (%)	
SNK tests				GrxSh(Lo), SE = 2.40 Cabo Raso, C=HF=E ns Estoril, C=HF=E ns Heybrook Bay, C=HF<E** Swanage, C=HF<E**	

EPHEMERAL ALGAE



TURF ALGAE

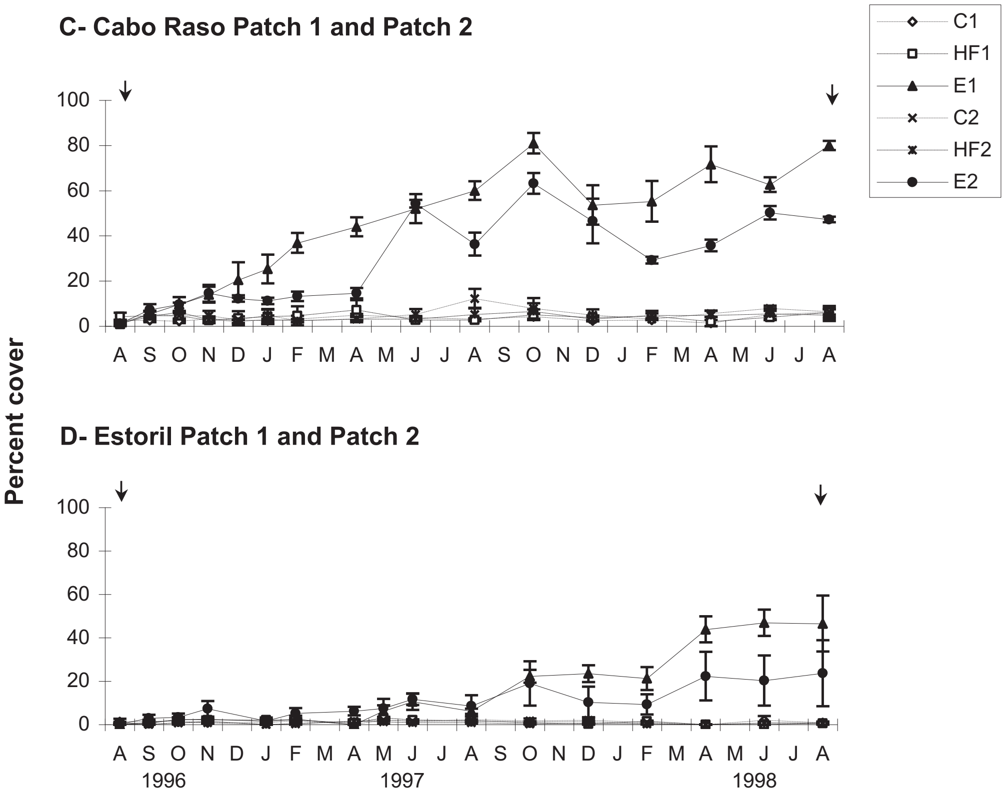
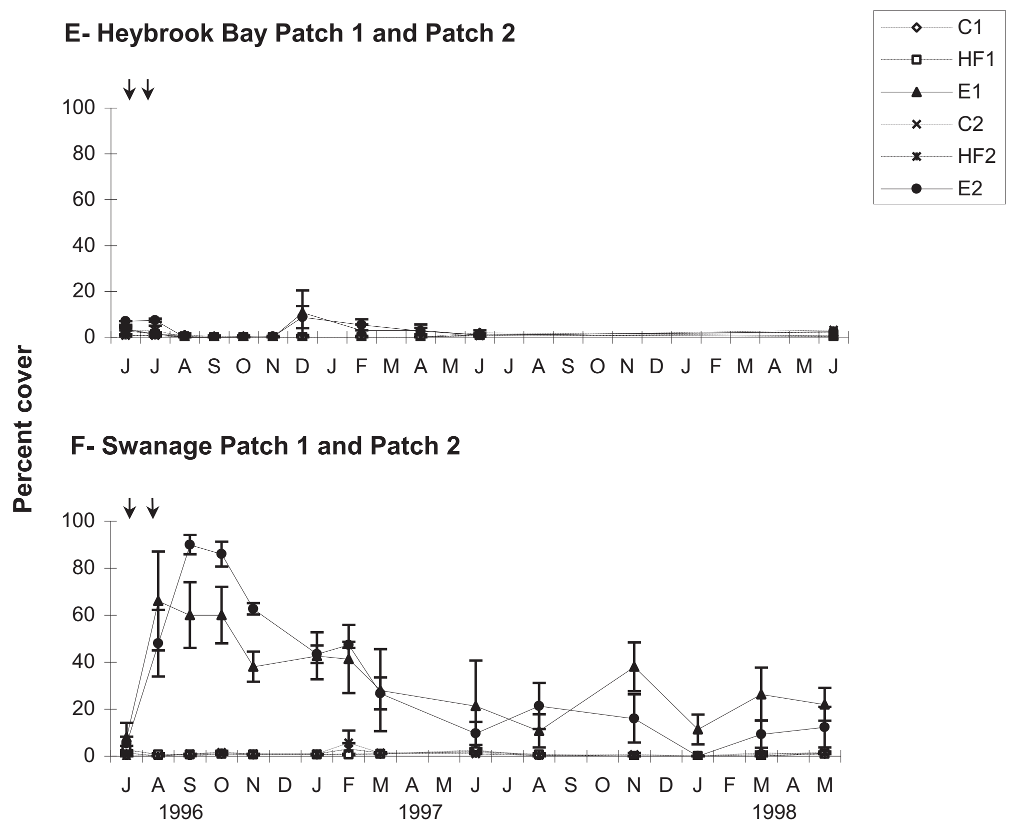


Figure 3- Effects of limpet exclusion on the mean % cover (±SE) of different functional groups in Portuguese (a, b, c, d) and British (e, f, g, h) locations. Arrows indicate dates for which data were analysed. C_- Control, HF_-Half fence, E_- Exclusion; _1- Patch 1, _2- Patch 2 (…).

EPHEMERAL ALGAE



CANOPY

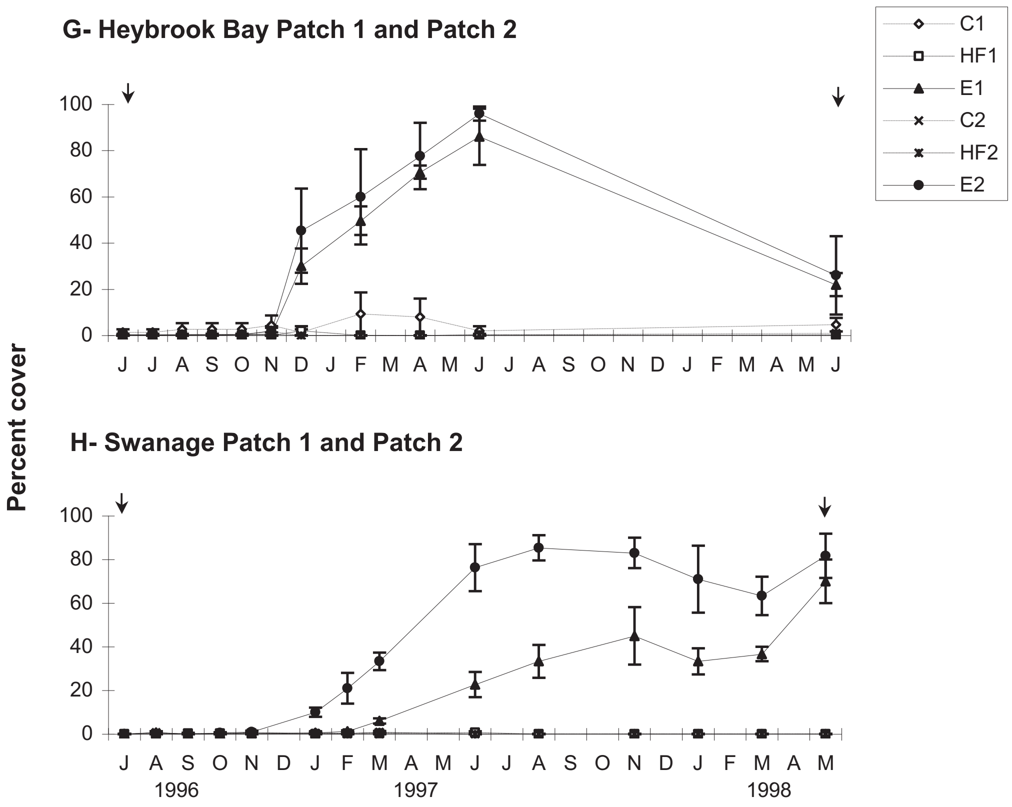


Figure 3- Effects of limpet exclusion on the mean % cover (±SE) of different functional groups in Portuguese (a, b, c, d) and British (e, f, g, h) locations. Arrows indicate dates for which data were analysed. C_- Control, HF_-Half fence, E_- Exclusion; _1- Patch 1, _2- Patch 2.

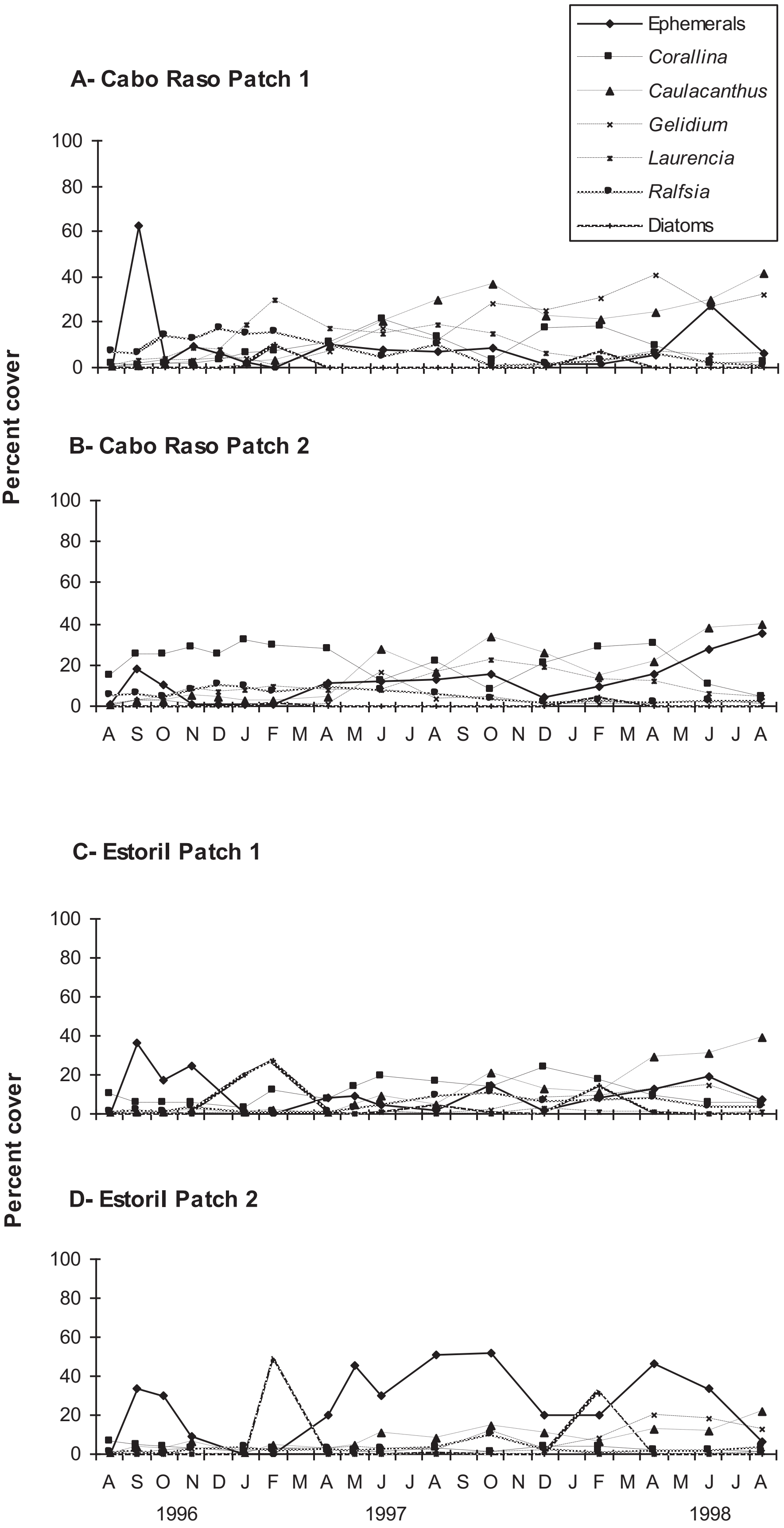


Figure 4- Effects of limpet exclusion on patterns of algal colonisation in ungrazed treatments. C_- Control, HF_-Half fence, E_- Exclusion; _1- Patch 1, _2- Patch 2 (…).

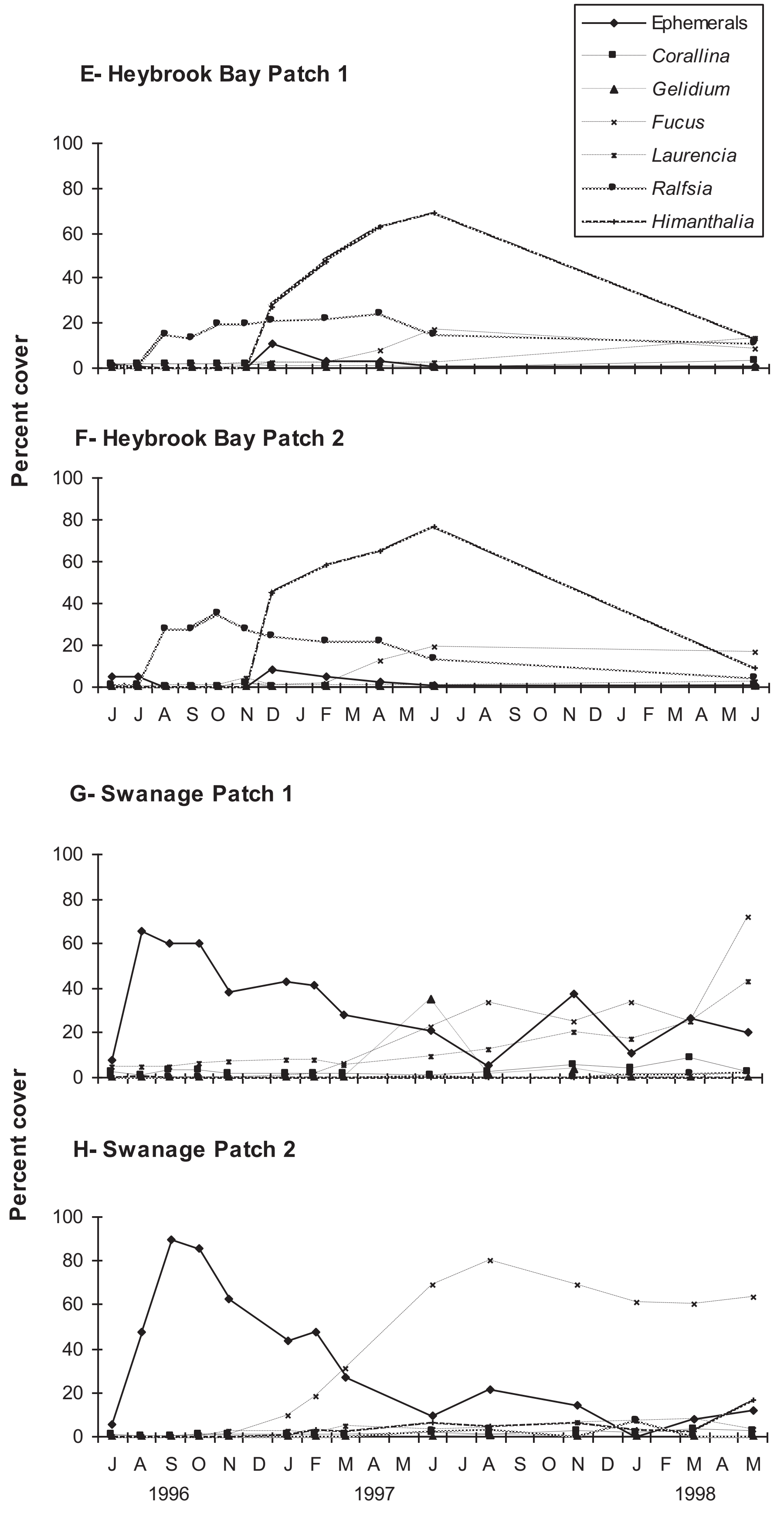


Figure 4- Effects of limpet exclusion on patterns of algal colonisation in ungrazed treatments. C_- Control, HF_-Half fence, E_- Exclusion; _1- Patch 1, _2- Patch 2.

Species richness

The number of algal species was greater in exclusion treatments at all of the experimental sites (Fig. 5, Table 3). The highest mean number of algal species was recorded in Portugal, particularly at Cabo Raso (Fig. 5). The algal species that occurred in ungrazed areas were essentially the same as those observed in grazed treatments, where they occurred only occasionally. However, as mentioned above, some different species occurred in north and south Europe at the two studied locations.

Table 3- ANOVA on the cumulative number of algal species in response to limpet exclusion. ns = not significant, *p<0.05, **p<0.01, ***p<0.001

Number of algal species		3 number of algal species in the 2 yr	
Source of variation	df	MS	*F*
Grazing = Gr	2	91.17	45.58*
Location = Lo	1	72.00	0.99 ns
Shore (Lo) = Sh(Lo)	2	72.47	13.38*
Patch (LoxSh) = Pa (LoxSh)	4	5.42	1.11 ns
GrxLo	2	2.00	0.61 ns
GrxSh(Lo)	4	3.30	1.89 ns
GrxPa(LoxSh)	8	1.75	0.36 ns
Residual	48	4.86	
Cochran´s test		C = 0.21 ns	
Transformation:		None	
SNK tests		Gr, SE = 0.29 C=HF<E*	

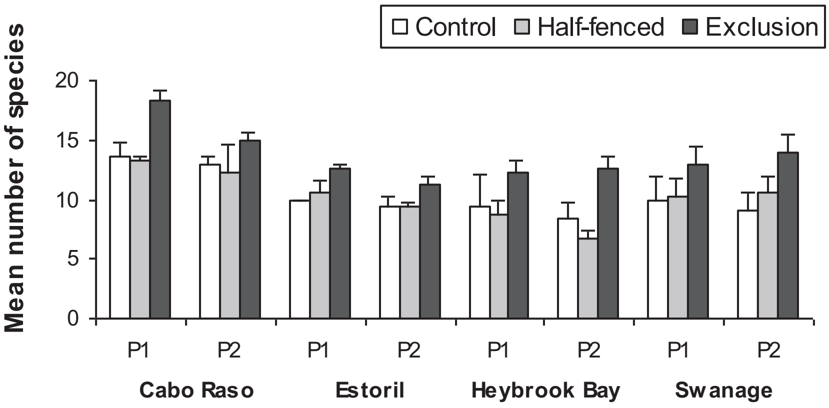


Figure 5- Effects of limpet exclusion on the mean number (±SE) of algal species. P1- Patch 1, P2- Patch 2.

Limpet re-encroachment

In all cases algal cover decreased upon removal of the fences. Cover of turf algae was very dense when the fences were removed (Plate 1 f, g), and it took 1-2 months before it started to decline at Cabo Raso (Fig. 6a). At Estoril, turf algae decreased in a more linear way in response to limpets re-encroachment (Fig. 6b). After six months no significant differences in the percent cover of turf were detected between the areas where the fences were removed and controls, for both patch 1 and 2 in Cabo Raso and Estoril (Table 4).

The decline in algal cover was correlated with the increase of grazers in the previous ungrazed areas. *P. ulyssiponensis* was observed to invade the areas in the first place followed by *P.depressa*. Generally the number of grazers increased slowly and after the six months it was still significantly higher in control plots (Fig 6 c,d; table 4), despite the obvious effects in algal cover.

In some patches a slightly higher percentage cover of *Mytilus* in the former exclusion plots was found after six months, suggesting that grazing by limpets could affect the attachment of mussels. However, these differences among treatments were not significant ($F_{1,1}$=0.62, p>0.05).

Table 4- ANOVA on the percentage cover of algae and number of limpets in response to fence removal. ns = not significant, *p<0.05, **p<0.01,***p<0.001

Limpets re-encroachment	6 mo	Turf algae (%)		Limpets density	
Source of variation	df	MS	*F*	MS	*F*
Gr	1	1.50	1.00 ns	1998.38	329.00 **
Sh	1	20.17	13.44 ns	782.04	0.15 ns
Pa(Sh)	2	1.50	0.45 ns	5361.38	12.47 ***
GrxSh	1	1.50	9.00 ns	0.38	0.00 ns
GrxPa(Sh)	2	0.17	0.05 ns	670.21	1.56 ns
Residual	16	3.33		430.04	
Cochran´s test		C = 0.45 ns		C = 0.32 ns	
Transformation:		None		None	
SNK tests				Gr, SE = 0.18 Control>Unfenced ** Pa, SE = 8.46 Cabo Raso, P1>P2 * Estoril, P1>P2 **	

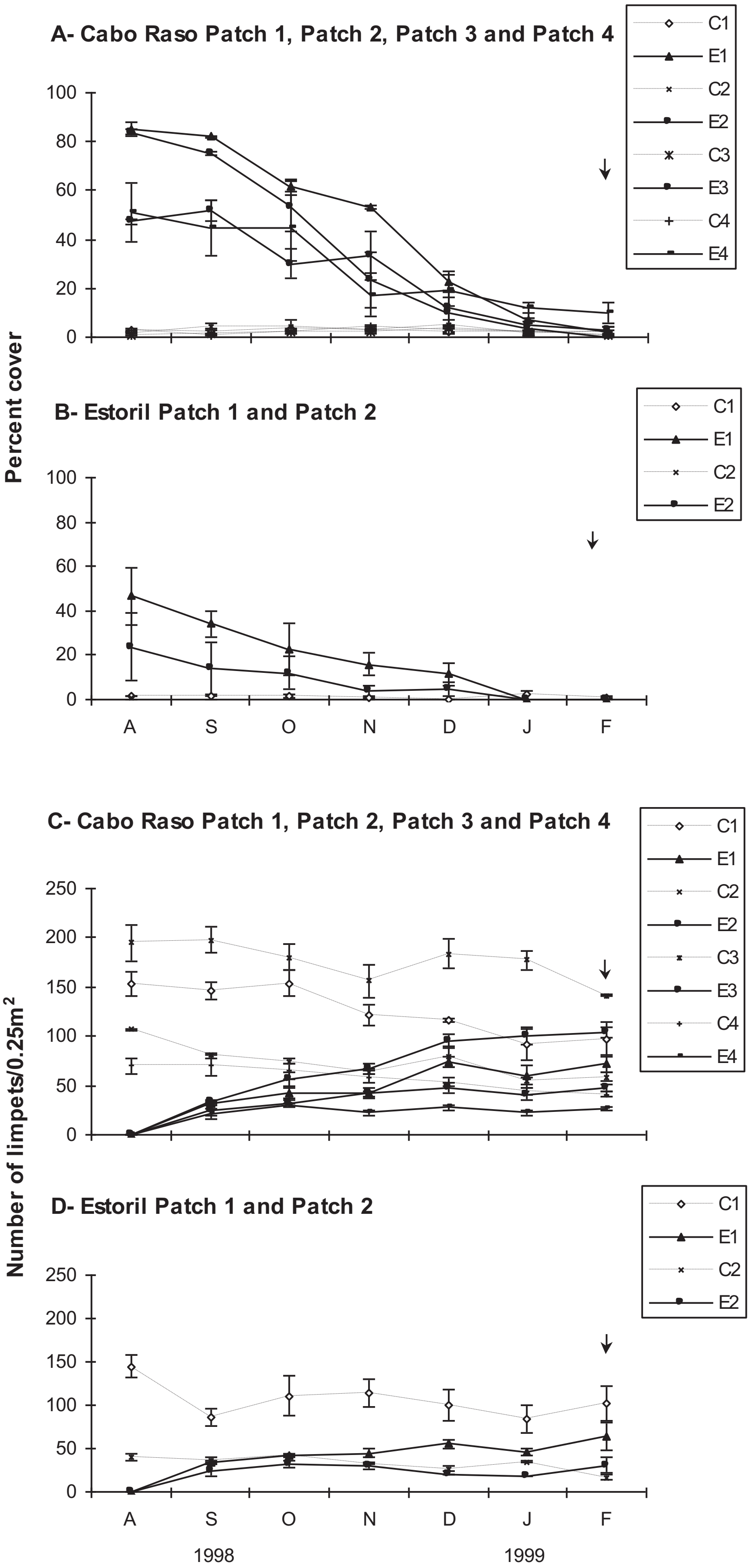


Figure 6- Changes in the mean % cover of turf algae (±SE) (a, b) and mean number of limpets (±SE) (c, d) following fence removal. Arrows indicate dates for which data were analysed. C_ - Control, E _- Previous exclusions; _1 – Patch 1, _2 – Patch 2, _3 – Patch 3, _4 – Patch 4.

Algal removal

Figure 7 shows the recovery of algae and invasion of limpets following clearance in Cabo Raso and Estoril. Calcareous turf algae recovered very fast and after six months no significant differences were found between removal areas and controls (Table 5). This was despite the fact that grazers also increased in cleared areas and, in contrast with re-encroachment, showed no significant differences between the two treatments after six months (Fig 7 c,d; Table 5). Thus, limpets naturally invaded the areas of the shore cleared of macroalgae but showed no ability to prevent subsequent re-colonisation by calcareous turf algae. Other turfs, however, were not observed in removal areas and ephemeral algae were just observed in the first months, when limpet density was low.

Table 5- ANOVA on the percentage cover of algae and number of limpets in response to algal removal. ns = not significant, *p<0.05, **p<0.01,***p<0.001

Algal removal	6 mo	Calcareous turf (%)		Limpets density	
Source of variation	df	MS	*F*	MS	*F*
Gr	1	20.17	0.04 ns	150.00	0.27 ns
Sh	1	468.17	0.50 ns	2400.00	1.23 ns
Pa(Sh)	2	943.50	2.58 ns	1950.00	9.76 **
GrxSh	1	541.50	1.58 ns	560.67	2.87 ns
GrxPa(Sh)	2	342.83	0.94 ns	195.33	0.98 ns
Residual	16	365.33		199.88	
Cochran´s test		C = 0.44 ns		C = 0.40 ns	
Transformation:		None		None	
SNK tests				Pa, SE =5.77 Cabo Raso P1=P2 ns Estoril P1>P2 **	

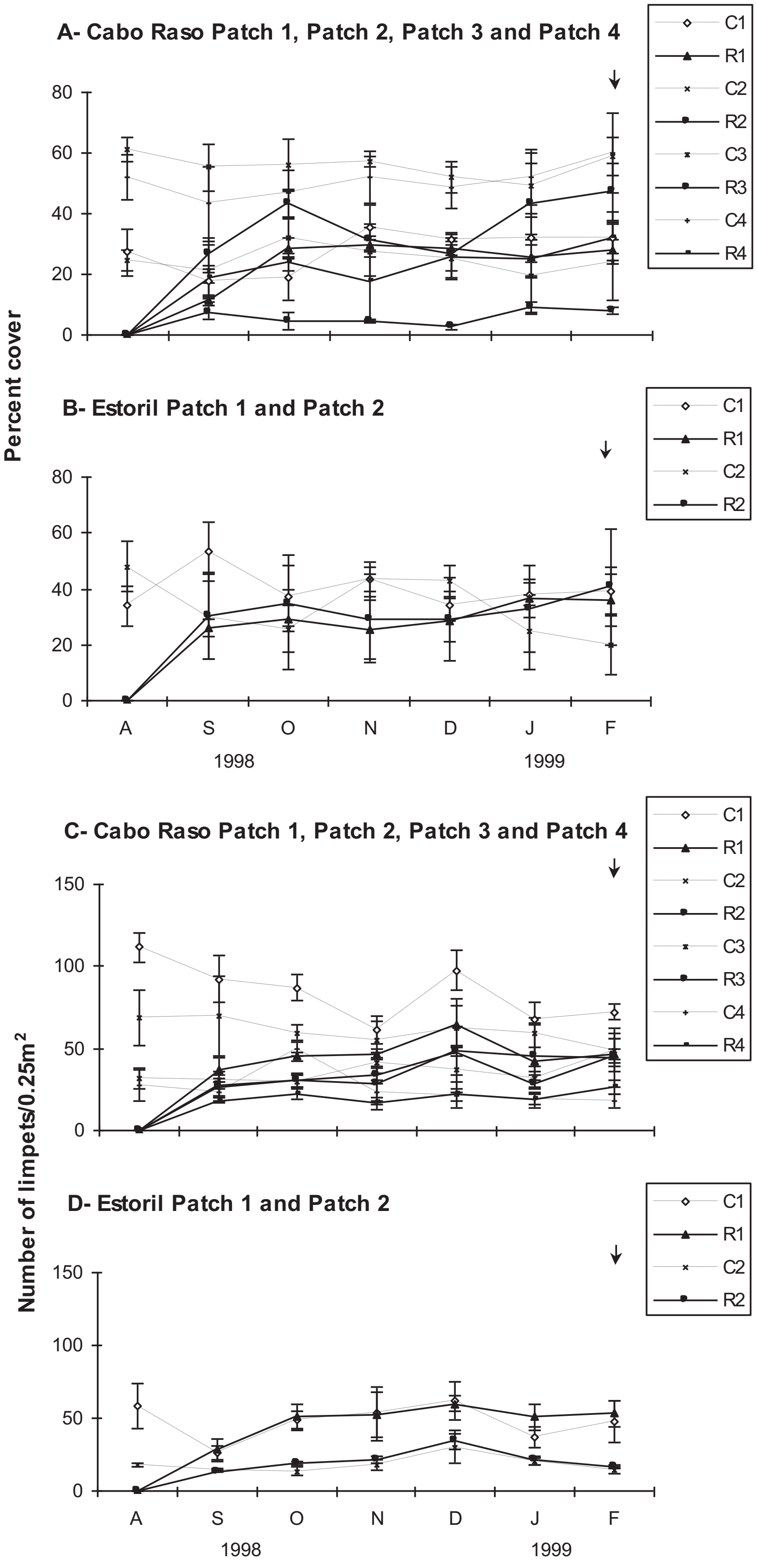


Figure 7- Effects of algal removal on the mean % cover of calcareous turf algae (±SE) (a, b) and mean number of limpets (±SE) (c, d). Arrows indicate dates for which data were analysed. C_ - Control, R_- Removal; _1- Patch 1, _2 – Patch 2, _3 – Patch 3, _4 – Patch 4.

DISCUSSION

Approach

The experimental design and methodology used in these experiments proved to be effective to test the initial hypotheses. No artifacts occurred and all the conclusions were based upon comparison with valid controls. The experimental design and methodology used in these experiments proved to be effective to test the initial hypotheses. Moreover, the design included several spatial scales (Locations, Shores, Patches) and it was possible to compare the effects of grazing across this range of spatial scales. Few studies have investigated the effects of grazing at more than one spatial scale (e.g. Sousa et al., 1981). The functional group approach was also adopted and proved to be useful for broad scale comparison of different communities.

Distribution patterns

The present study has shown that grazing by limpets has a significant influence on the upper limits of distribution of low shore turf forming macroalgae in the North East Atlantic coasts- both in Portugal and in the U.K. These experiments support the results obtained by Underwood (1980) on New South Wales coasts (Australia) that grazing, primarily by gastropods, is the major determinant of the upper limits of vertical distribution of many species of low shore foliose algae. However, some different results between the two studies are worth emphasising.

The experimental manipulations performed by Underwood (1980) at mid-tidal levels tested hypotheses about the effects of both grazing by molluscs and of physical factors in algal distribution patterns. Fences and cages were used to exclude grazers. Cages and roofs were also used to decrease the harshness of the environment during low tide whilst fences and the open areas had the normal environmental regime. An artefact occurred in his experiment as algae began to grow over the top of the cages. Most species of algae only grew to maturity inside cages, and remained as turf germ inside fences. Underwood (1980) then concluded that grazing prevents the establishment of foliose algae above their normal upper limit on the shore, but the effects of physical factors are an important influence on the growth, size, maturity, biomass and overall abundance of macroalgae. In our study physical factors were not tested (just indirectly considering the factor latitude) and only fences were used to exclude gastropods. Fences can be less effective in excluding limpets than cages but no artifact was seen to occur, and half-fenced treatments never differed significantly from control plots. In contrast with the results described above for Underwood's (1980) work, algae grew to maturity inside fences in our experiments. In fact, turfs reached approximately 10cm after two years and the length of the fronds of canopy forming algae exceeded 50cm. Another qualitative difference was the type of algae that colonise the exclusion in both studies; although a variety of algae colonised cages in New South Wales (e.g. *Ulva lactuca*, *Chaetomorpha* sp., C*ladophora* sp., C*olpomenia sinuosa, Corallina officinalis*, *Enteromorpha* intestinalis), very few algae prospered and perennial algae did not establish themselves inside fences. On the other hand, in both Portugal and Britain, perennial algae dominated exclusion plots at the end of the experiment.

Ideally, both physical and biological models should be tested at the same time (Underwood, 1985) but this was not possible in the present study. Physical factors may influence the size, abundance and biomass of foliose algae (Underwood, 1980, 1985; Underwood & Jernakoff, 1984) and indirectly affect algal distribution by modifying grazing rate and efficiency (Lubchenco, 1978). In Portuguese rocky shores it was observed that even in the presence of limpets, turf algae could extend their usual upper limits in damp conditions, like the runoff of sea water from a holding tank (see Plate 1 H). Nevertheless, results from this experiment indicated that grazers play a major role in directly setting its upper limits.

The difference in algal abundance between manipulated and unmanipulated plots lasted less than six months after the fences were removed. The community that developed while limpets were excluded was not a persistent alternative state. After re-encroachment of limpets macroalgae established in exclusions converged with the plots that were not perturbed. This result is consistent with the one obtained by Farrell (1988) after limpet re-introduction. Farrell (1988) connected this response to the size- or age-related escapes from predators. By contrast, Underwood (1980) noticed that, when cages were removed, mature cover of *Ulva* rapidly disappeared probably ripped off by waves, and that turf sporelings insides fences were removed by grazers once they were allowed into these areas. The mature perennial algae that developed in our experiments did not decline due to wave action. Macroalgae attained a size that might be expected to make them invulnerable to limpets grazing but they declined in less than six months (Lubchenco & Gaines, 1981; Hawkins & Hartnoll, 1983). One possible explanation would be that limpets preferentially graze on microalgal propagules but can alternatively consume adult turf. The role of a multi-species assemblage of *Patella* in this experiment may also be important for understanding how grazers reduced the cover of macroalgae turf. *Patella ulyssiponensis* was seen to invade the exclusions and to graze on established macroalgae in the first place, while *Patella depressa* appeared later when there were already some clearings between the turf. Differences in the radula morphology and feeding behaviour of the two species may account for the observed grazing pattern (Hawkins et al., 1989; Della Santina et al., 1993).

Algal removal resulted in a rapid colonisation of calcareous turf algae and in a quick invasion of adult limpets in the clearings. Initially the limpets were mainly *Patella ulyssiponensis* that occur naturally at this level on the shore, but eventually *Patella depressa* moved down-shore into the clearings. Underwood & Jernakoff (1981) tested the hypothesis that direct interaction between algae and grazers would determine the lower limit of grazer distribution on New South Wales shores. In their study, limpets were prevented from invading dense stands of foliose macroalgae and, when placed in clearings within the low-shore beds of algae, the limpets either moved away to higher, free space, or the clearings were invaded by rapidly growing algae and the limpets starved to death. These findings contrast with our results where limpets naturally invaded experimental clearings and remained in these areas despite algal colonisation. However, grazers showed no ability to prevent colonisation by calcareous turf algae at this level on the shore. This means that grazers are responsible for upper limits of distribution of macroalgae on the shore but below this limit, because algae colonise and growth more rapidly, they can not prevent algal growth.

Generally, our results corroborate Underwood (1985) suggestion of a dynamic balance between the activities of grazers at higher levels and the rapidity of colonisation and growth of the algae at lower levels, modified by physical factors which enhance algal growth or abundance and grazers efficiency. Interestingly, the experimental manipulations used in this study are not so "artificial" as they might be thought, since they can also be observed spontaneously in natural conditions. In Cabo Raso, a block of concrete that fell down from a holding tank ("*viveiro*") during a winter storm suffered almost the same process as the experiments described in this study (see Plate 1 H, I, and J). An initial phase without limpets led to the development of a algal turf almost identical to the exclusion experimental plots (Plate1 I, ≅ 8 months after the storm). This was followed by an invasion of limpets and reduction of the algal cover (Plate 1 J, ≅ 14 months after the storm) as happened in the fence removal experiments.

Sequence of algal colonisation and diversity

The effects of grazing molluscs on algal diversity have been considered in many of the studies regarding plant-animal interactions in intertidal communities (e.g. Lubchenco, 1978; Raffaelli, 1979; Lubchenco & Gaines, 1981; Jernakoff, 1983, 1985; Jara & Moreno, 1984;

Underwood & Jernakoff, 1984; Williams, 1993). The effect of herbivores on patterns of local species diversity is sometimes confusing because herbivores can increase plant diversity, decrease plant diversity, or both (Lubchenco, 1978; Jernakoff, 1983). Lubchenco (1978) stressed the importance of herbivore food preference and algal competitive abilities in understanding and interpreting different results obtained in these studies. Our results indicate that the mean cumulative number of species registered in each quadrat was always higher in ungrazed areas than in grazed areas (Table 3). This is similar to results obtained by Lubchenco (1978) for emergent substrata, and are consistent with the findings for low shore zones in other studies (e.g. Raffaelli, 1979; Williams, 1993). The turf is know to lessen mortality due to desiccation and grazing pressure (Hay, 1981; Steneck & Watling, 1982; Littler & Littler, 1984) and thus to facilitate the settlement of a variety of species, especially in the absence of grazers.

The earliest colonisers in the great majority of the ungrazed areas were ephemeral algae (*Ulva* sp. and *Enteromorpha* sp.), as found in many other studies (e.g. May et al., 1970; Sousa, 1979; Littler & Littler, 1980; Hawkins, 1981a, b; Jara & Moreno, 1984; Carter & Anderson, 1991; Dye, 1995). *Ulva* sp. and *Enteromorpha* sp. temporarily outcompeted perennials in grazer exclusion areas by growing faster but were eventually replaced by perennial species, which can recruit slowly and take over when the ephemerals die.

Our results did not, however, entirely conform to the typical sequence of algal colonisation found by many authors (Dayton, 1971, 1975; Underwood, 1980; Hawkins, 1981a, b; Underwood & Jernakoff, 1984; Jernakoff, 1985) as the arrival of diatoms, followed by opportunistic ephemeral algae and the later replacement by slower growing forms such as fucoids. In the first place, diatoms were never the initial colonisers, although they were present on some shores. A thick brown film of diatoms was only seen to occur in Portugal, during winter. Secondly, ephemeral algae were absent from one of the shores, Heybrook Bay. Absence of green algae has been observed in other summer initiated experiments (e.g. Hawkins, 1981a). Non-calcareous crusts mediated the transition from fast growing ephemeral algae to large perennial erect algae in some sites. Carter & Anderson (1991) also described a non-calcareous crust (*Ralfsia verrucosa*) in the sequence of algal colonisation after limpet exclusion in their work in South Africa. Finally, important spatial differences occurred in the colonisation patterns at the location level. In Britain, succession eventually led to dominance of large brown canopy forming algae, while in Portugal a rich turf of various red algae dominated ungrazed areas. The colonisation by large fucoids is a pattern well known in northern hemisphere temperate waters (Southward & Southward, 1978; Lubchenco, 1978; Hawkins, 1981a, b; Hawkins & Hartnoll, 1985; Kim & DeWreede, 1996; and many others).

Dominance by red algae after limpet exclusion is not so common but has been observed on some occasions (e.g. Jara & Moreno, 1984; Carter & Anderson, 1991) and especially after disturbance or canopy removal in low shore habitats (Sousa, 1979; Sousa et al., 1981; Benedetti-Cecchi & Cinelli, 1992).

In the British Isles, different species of brown algae colonised the two shores. *Fucus serratus* was more abundant at Swanage while in Heybrook Bay exclusions were dominated by *Himathalia elongata*. A slight increase in wave exposure may account for these differences. According to Ballantine (1961), *Fucus serratus* forms a distinct zone low on the shore from sheltered through moderately exposed sites. With increasing exposure, canopy cover declines and is replaced by *Himanthalia elongata* (Ballantine, 1961; Lewis, 1964). There was a marked decrease in the cover *of Himanthalia elongata* in Heybrook during the second year of the experiment. It is possible that this alga died back in the first summer. Bleaching of *Himathalia* “buttons” was previously observed in the Plymouth area by Hawkins & Hartnoll (1985) during an unusually hot summer. The variability described in patterns of algal colonisation reflects the large spatial scale analysed in this study.

Biogeographic comparisons

The present study revealed that ephemeral algae, turf algae and canopy were the functional groups mostly affected by limpet activities. Similar results were obtained by Duggins & Dethier (1985) in experiments of herbivory and competition in a low intertidal habitat. Benedetti-Cecchi et al. (1996), working in a Mediterranean low-shore community, also found an increase in turf algae after removal of *Patella* spp. In general, morphologically simple and highly productive algal groups responded quickly, while more complex forms, as large brown canopies and red corticated turf, appeared later.

Sousa et al. (1981) suggested that large brown algae do not form a persistent canopy in the low intertidal zone southern California in the absence of urchin grazing because of interactions with the red algal turf. They noted that removal of urchins significantly increased the recruitment of two long-lived species of large brown algae but the experimental plots were eventually dominated by perennial red algae. In contrast, in our study in South Britain we observed that canopy eventually dominated the turfs in ungrazed areas.

Grazers had no effect on the cover of calcareous turf and encrusting algae. Some variations occurred but significant differences were not discernible. In the Mediterranean (Benedetti-Cecchi et al., 1996), calcareous turf were seen to decline in abundance after limpets removal with a concomitant increase in coarsely branched algae. Benedetti-Cecchi et al. (1996) interpreted this fact as an indirect effect of limpets on calcareous turf, which would be competitively subordinate to the other groups of algae but more resistant to grazing. In Portugal, particularly in Estoril, calcareous turf increased in exclusion plots but this functional group did not resist summer stress and was observed to bleach and die-back. Encrusting coralline algae also bleached during summer in both exclusion and control plots and generally recovered during the following winter.

The usefulness of a functional group approach in helping to understand the mechanisms behind observed patterns in plant/herbivore interactions, namely between algae and molluscs, have been demonstrated in several studies (e.g. Littler & Littler, 1980, 1984; Steneck & Watling, 1982; Steneck & Dethier, 1994). Littler & Littler (1984) considered that this approach has important implications for biological monitoring in rocky intertidal and subtidal communities. Steneck & Dethier (1994) examined patterns of algal functional group abundance, diversity and dominance relative to extrinsic characteristics of the environment. They also created a model to predict algal community composition, or conversely, to gain insight about the environmental conditions in an area by examining the algae. This model was based on two environmental structuring parameters of disturbance and productivity potentials. The functional approach does have, however, some potential limitations. The functional group of any species of algae varies depending upon the part of the plant considered, stage of development or phase in the life cycle (Steneck & Watling, 1982). Alternate phases of heteromorphic algae are also usually assigned to different functional groups (Steneck & Watling, 1982), for example *Mastocarpus stellatus* and *Petrocelis*. Despite the limitations, the results obtained by considering functional groups corroborated and synthesised the general trends described for total algal cover and colonisation patterns. Additionally, a functional group analysis can be applied more broadly in space for making biogeographical comparisons Steneck & Dethier (1994). This has been useful for comparing results obtained in the present study between Portugal and Britain.

The particular hypothesis proposed in this study was to know if grazing by limpets determine the upper limit of distribution of the red algal turf and to see whether its effects were modified by different factors operating at various spatial scales. Limpet removal resulted in a significant increase in algal turf above its usual level on the shore on both locations (approximately 50cm above the limit). However, this effect was not homogeneous in the south and north of Europe. Percentage cover of turfs was much greater in Portugal. In England, canopy-forming algae eventually dominated exclusion, despite an initial increase in turf algae.

A general trend for large brown algae (e.g. Laminariales or Fucales) to predominate at higher latitudes while turf-forming red algae dominate the shore at lower latitudes is well documented in the north east Atlantic (see Hawkins et al., 1992). The importance of latitudinal variation in algal-herbivore interactions has been addressed in some studies (see review in Gaines & Lubchenco, 1982). Sousa et al. (1981) investigations indicated that biological interactions play a significant role in generating and maintaining latitudinal differences in the structure of temperate intertidal communities. They found that the response of algal assemblages to intensive grazing by sea urchins was similar at different latitudes, but unique patterns of interaction among algae in the southern location resulted in quite different patterns of succession and community structure in the absence of urchin grazing. Finally, they suggested that a north-south gradient in the abundance of vegetatively propagating species, in grazing intensity and in the frequency of space-clearing disturbances, might account for latitudinal variation in intertidal algal community structure along the pacific coast of North America. In the north east Atlantic, the canopy species that colonised ungrazed areas in Britain have their biogeographic limit of distribution in the North of Spain or Portugal and they do not naturally occur in centre of Portugal (our study site in this location). Thus, in our study, the physical environment seems to determine the latitudinal differences in both species composition and structure.

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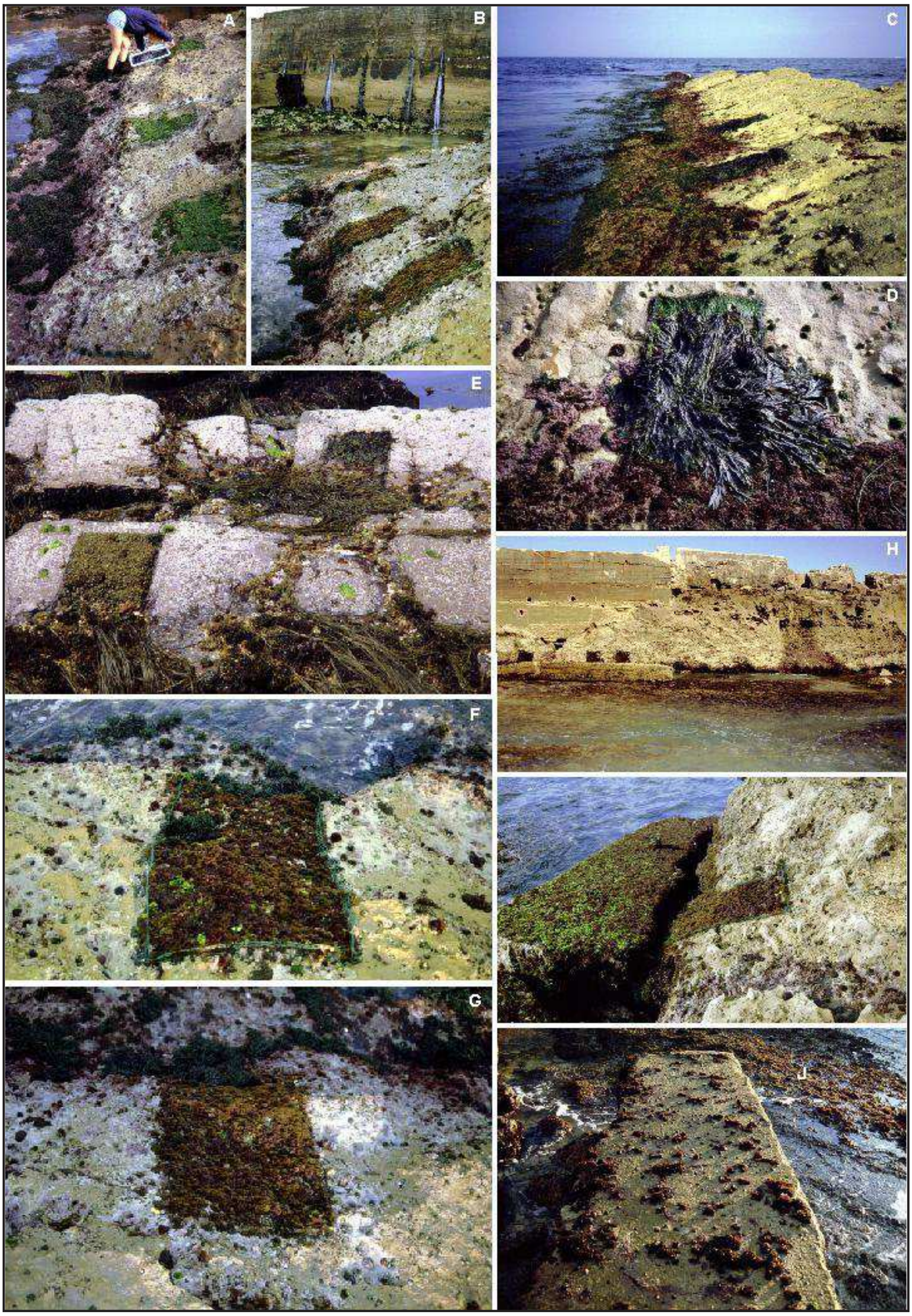

Plate 1- (A) Cabo Raso- Ephemeral algae 15 days after starting date, (B) Cabo Raso- Turf forming algae 2 years after starting date, (C) Swanage- general view of experimental plots, (D) Swanage- Canopy cover 2 years after starting date, (E) Heybrook Bay- *Himathalia elongata* and *Fucus serratus* 1 year after starting date, (F) Cabo Raso- experimental plot before fence removal, (G) Cabo Raso- experimental plot after fence removal (day 0), (H) Cabo Raso- general view of Patch 3, (I) Cabo Raso- detail of the block of concrete ≅8 months after a storm, (J) Cabo Raso- detail of the block of concrete ≅14 months after a storm (see text).

CHAPTER 4

Analysis of competitive interactions between the limpets *Patella depressa* Pennant and *Patella vulgata* L. in the northern coast of Portugal

Boaventura, D.; L. Cancela da Fonseca & S.J. Hawkins. Analysis of competitive interactions between the limpets *Patella depressa* Pennant and *Patella vulgata* L. in the northern coast of Portugal. Submitted to *Journal of Experimental Marine Biology and Ecology.*

CONTENTS

INTRODUCTION

Competition is generally viewed as the process where individuals of the same or different species are adversely affected by each other while trying to acquire the same common resource, which is in short supply (Birch, 1957; Tokeshi, 1999). Individuals of one species can suffer a reduction in fecundity, survivorship or growth as a result of resource exploitation or interference by individuals of another species (Begon et al., 1986). Competition is then likely to affect the population dynamics of the competing species, and consequently the species' distributions and evolution (Begon et al., 1986; Tokeshi, 1999). Competitive interactions between invertebrates have been much studied in rocky intertidal communities. These involved the study of competition for space between sessile invertebrates (e.g. Connell, 1961; Dayton, 1971; Menge, 1976) and for food among grazing gastropods (e.g. Haven, 1973; Underwood, 1978, 1984; Creese & Underwood, 1982; Lasiak & White, 1993). Competitive interactions among sessile organisms may be fundamentally different from that among motile animals (Underwood 1978). Competition for space among sessile invertebrates generally involves pre-emption or overgrowth mechanisms, whilst consumptive competition is more likely for mobile gastropods (Connell, 1983). Food resources can be renewed without the necessity of removing the dominant competitor and, because of motility, inferior competitive grazers can have access to some of the resources before dominant individuals consume them all. In contrast, competition for space is more absolute since space, as resource, is not often easily renewed, and the displacement of other animals or the prevention of new recruits from occupying space usually results in the death of one or more individuals (Underwood, 1978, 1984, 1992; Lasiak & White, 1993). Competition is then likely to occur in the rocky intertidal environment when space or food resources are in short supply or when recruitment from pelagic life stage occur in high densities (Underwood 1992).

The nature and extent of the interaction between inter- and intraspecific competition is particularly important to the coexistence and abundance of competitors (Marshall & Keough, 1994; Connell, 1983). Theoretically, the Lotka-Volterra model of interspecific competition is able to generate a range of possible outcomes: the exclusion of one species by another, exclusion dependent on initial densities and coexistence (Begon et al., 1986). If the effects of interspecific competition are stronger on a species than the effects of intraspecific competition, this may lead to exclusion. If however, intraspecific competition within the superior competitor is stronger than competition between species, coexistence can occur.

Coexistence is still possible even if one species is affected more strongly by interspecific competition than by intraspecific competition (Tokeshi, 1999).

Intraspecific competition is likely to be more intense than interspecific competition since individuals of the same species will usually tend to have a closer requirement for identical resources than is the case between individuals of different species (Underwood, 1992). In this case, intraspecific competition for food may cause a decrease in the density of the superior competitor, at a faster rate than the decreases in the inferior species, leading to the situation where the superior competitor cannot continue at sufficient densities to eliminate all members of the inferior species. This was experimentally demonstrated by Creese and Underwood (1982) and suggested as a possible mechanism promoting the coexistence of grazing gastropods. According to Underwood (1992), competitive exclusion of one species by another is extremely unlikely to occur for shallow coastal grazers. Nevertheless, where competitors coexist, it will be interesting to analyse the relative roles of inter- and intraspecific competition in determining the densities, growth and survivorship of both species.

Inter- and intraspecific competitive interactions have been studied simultaneously for several species of grazing gastropods in different regions, particularly in Australia (e.g. Underwood 1978, 1984; Creese & Underwood, 1982) South Africa (e.g. Lasiak & White, 1993) and Costa Rica (Ortega, 1985). In Europe *Patella vulgata* L. and *Patella depressa* Pennant coexist in the mid-shore from north Wales to the south of Portugal (Fretter & Graham, 1976). Little is known, however, about the importance of competitive interactions in the regulation of these species populations. Moreover, in order to reach any conclusion on the general effects and importance of competition, further experimentation on different species and with varied spatial and temporal scales is needed. The present study investigates inter- and intraspecific competitive interactions between *P. depressa* and *P. vulgata* on Moledo do Minho shore, in the northern coast of Portugal. Both species are abundant grazers that co-occur over most of the mid-littoral regions of this shore. However, Moledo do Minho is one of the few shores in the northern coast where *P. depressa* and *P. vulgata* are found in approximately equal proportions. *P.vulgata* is a northern species, which is close to its southern biogeographic limit on the Portuguese coast (Guerra & Gaudêncio, 1986). Its density decreases along the Portuguese coast, being occasional or rare on shores further to the south. Unless two competing organisms happen to occur in similar densities, then experiments to analyse the effects of intraspecific competition in relation to interspecific competition will be rather difficult (Underwood 1986, 1992). This fact, together with the proximity to the southern limit of distribution of *P. vulgata*, makes it an interesting subject for testing hypotheses about interspecific competition.

This study tested the effects of increased and decreased densities on mortality, length, weight and reproductive output of the grazing limpets *P. depressa* and *P. vulgata*. Inter- and intraspecific interactions were analysed simultaneously through an asymmetric experimental design to estimate their relative importance. Microalgal food resources were also assessed during the experiment.

MATERIAL AND METHODS

Study site and organisms

The present study on inter- and intraspecific competition amongst the grazing limpets *P. depressa* and *P. vulgata* was done at Moledo do Minho, on the northern coast of Portugal. This shore is a gently sloping granite bedrock beach facing the Atlantic Ocean. The experiments were carried out in mid-tidal in areas with an even substratum and almost devoid of macroalgae.

Limpet species at the studied site included *Patella ulyssiponensis* Gmelin (= *P. aspera* Röding), which dominated amongst low-shore algae; and the two studied species, *P. depressa* and *P. vulgata*, which were more abundant at mid-shore level. Previous estimates of the density and distribution of these limpet species along the Portuguese coast revealed that Moledo do Minho is one of the few shores where *P. depressa* and *P. vulgata* occur together at similar densities. This enabled analysis of inter- and intraspecific competitive interactions at mid tidal level, in the area of the shore where the distribution of both species of grazing limpets overlaps.

Experiments to determine the effects of inter- and intraspecific competition

Inter- and intraspecific competitive interactions were analysed through the experimental manipulation of adult animals (23-28mm) at different densities and different mixtures of the two species. Plastic coated wire fences, with a square mesh of 13x13 mm, were used to enclose the limpets inside plots of 25x25 cm. The fences were attached to the rock by screws inserted into rawl-plugs in holes drilled by a petrol driven drill (Ryobi ER160). Rubber tap washers were used to hold on the mesh to the substratum, and any gaps remaining between the base of the fence and the rock surface were filled with non-toxic silicone.

A density of 5 limpets per plot was adopted as control. This was the mean density of these species at the study site, which was assessed from previous sampling of the shore. The control density was then contrasted to increased and decreased densities of the same and the other species, in a total of twelve treatments (Table 1). This type of asymmetrical design was used in this experiment because inter- and intraspecific competitive interactions need to be investigated simultaneously (Underwood 1992), and such procedures have been described by Underwood (1978, 1984, 1986, 1992, 1997). Three replicates of each treatment were randomly allocated to the plots. The limpets were marked on the shell with nail varnish, using different colours for the two species. To test the effect of the fences on adult animals, which can have foraging excursions over a larger area than that enclosed by the experimental plot, unenclosed control animals were also used. These consisted of marking and monitoring the same number of animals (3 sets of 5 limpets from each species) in open areas of the shore.

The experiment ran for 21 weeks between May and October 1998. On every sampling occasion the fences were checked and repaired and the markings were re-touched. The limpets that died were replaced with new ones marked with a different colour. Mortality was recorded every 15 days and total shell length was registered at month intervals, *in situ*, without removing the animals. A calliper with extensions was used for this purpose, so that even the limpets that were close together or in small depressions could be measured. At the end of the experiment, after approximately five months, all the original limpets were collected. In the laboratory the length, width and height of the shell were measured. The sex of each individual was determined and the gonad stage evaluated according to previous studies on the breeding of *P. depressa* and *P. vulgata* (Orton et al., 1956; Orton & Southward, 1961) using the Orton's scale. Finally, the dry weight of each limpet was obtained.

Table 1- Experimental treatments and total number of limpets per fence.
D- *P. depressa*, V- *P. Vulgata*

2 (decreased)	**5 (control)**	10 (increased x2)	20 (increased x4)
1- 2D	3- 5D	5- 10D	9- 20D
2- 2V	4- 5V	6- 10V	10- 20V
		7- 5D5V	11- 5D15V
		8- 5V5D	12- 5V15D

Microalgal food assessment

To assess the influence of different densities of grazing limpets on the microalgal abundance, the chlorophyll concentration of the substratum was estimated. Rock chips were collected from the areas around the experimental plots during the experiment and, at the end of the experiment, rock chips were also taken within each enclosure. The extraction of chlorophyll from the rock chips was followed by spectrophotometric analysis using the method described by Thompson et al. (1999). The chlorophyll concentration ($\mu g.cm^{-2}$) was determined with the formula:

$[chlorophyll] = 13.0 \times Å665 \times v / d \times V$

where, 13.0 = constant for methanol, Å665 = net absorbance of solution at 665 nm, v = final volume of solution (ml), d = path length of cell (cm), V = surface area of sample (cm^2). The surface area of the rock chips was automatically calculated by computer after the use of image processing techniques.

Data analysis

Single factor analysis of variance were used to test the effect of the fences on the mortality, weight, length, chlorophyll concentration of both species between unfenced and fenced controls.

The effects of inter- and intraspecific competition on mortality, chlorophyll concentration, length and dry weight were analysed with an asymmetric analysis of variance. Absolute values of mortality and chlorophyll per replicate were used in the analysis. In the case of analysis on dry weight and length, however, each value corresponded to the average of all limpets in the replicate (this number varied between a minimum of 1 and maximum of 14 limpets). The factors *P. depressa vs. P. vulgata*, Density and Species were fixed. The partitioning of degrees of freedom and the sums of squares for the asymmetric analysis followed the methods described by Underwood (1986, 1997), and consisted in combining the sum of square values from separate analyses of variance. Where significant differences were found Student- Newman-Keuls (SNK) *a posteriori* multiple comparisons were used to compare the means. This comparison was made using the results of the individual analyses of variance (Table 2).

Table 2- Partitioning of degrees of freedom in the final asymmetrical analysis of variance and the origin of the calculated sum of squares.

Source of variation	df
Among all [a]	9
P. depressa vs. P. vulgata = P [b]	1
Among Exp. Treatments = T [b]	4
Control *vs.* others [c]	1
Among others [d]	3
Density = D [e1]	1
Species = S [e2]	1
Density x Species [e3]	1
P x T [b]	4
P x Control *vs*. others [f]	1
P x Among others [g]	3
P x D [e4]	1
P x S [e5]	1
P x D x S [e6]	1
Residual [a]	10 (n-1)
Total [a]	10n-1

[a] One-factor analysis of variance for all cells.
[b] Two-factor analysis of variance for "P" and "T".
[c] Sum of squares by subtraction between "Among Exp. Treatments" and "Among others".
[d] Sum of squares by addition of those in e1,e2,e3.
[e] Three-factor analysis of variance for "P", "D" and "S" omitting controls.
[f] Sum of squares by subtraction between "P x T" and "P x Among others"
[g] Sum of squares by addition of those in e4,e5,e6.

RESULTS

Effects of confinement

The species *P. vulgata* did not seem to be affected by the fence procedure as no significant differences were detected among fenced and unfenced controls in any of the studied parameters- proportional mortality, mean shell length, mean dry weight and chlorophyll concentration (Table 3B). The fence had no adverse effects on proportional mortality and mean shell length of *P. depressa* but mean dry weight was significantly higher in the unfenced than in the fenced control (Table 3A). No differences were detected for chlorophyll concentration between fenced and unfenced control areas for both species.

Table 3- *F* and P values of the one-way ANOVA between fenced and unfenced controls for the studied parameters, A- *P. depressa*, B- *P. vulgata*.

Fenced Control *vs.*	**A-** *P. depressa*		**B-** *P. vulgata*	
Unfenced control	$F_{1,4}$	P	$F_{1,4}$	P
Proportional mortality	0.21	P>0.05	1.27	P>0.05
Mean shell length	0.86	P>0.05	0.01	P>0.05
Mean dry weight	17.24	P<0.05	5.92	P>0.05
Chlorophyll concentration	0.21	P>0.05	1.27	P>0.05

Effects on mortality

Mean number of limpets alive in control and decreased density treatments showed a slight reduction during the experimental period, especially when compared to the decline observed for the increased density treatments. The decline of limpets during the experimental period showed that *P. depressa* was more susceptible to intraspecific competition and that the number of surviving limpets converged to a lower value. At the end of the experiment mortality was higher for *P. depressa* than for *P. vulgata*, independently of the density or species mixture (Fig. 1; Table 4). Mortality in controls was lower than in increased density treatments but there was no significant difference in the double and quadruple densities at the end of the experiment (Fig. 1; Table 4). The addition of limpets from the other species did not significantly affect the mortality of *P. depressa* or of *P. vulgata* (Table 4).

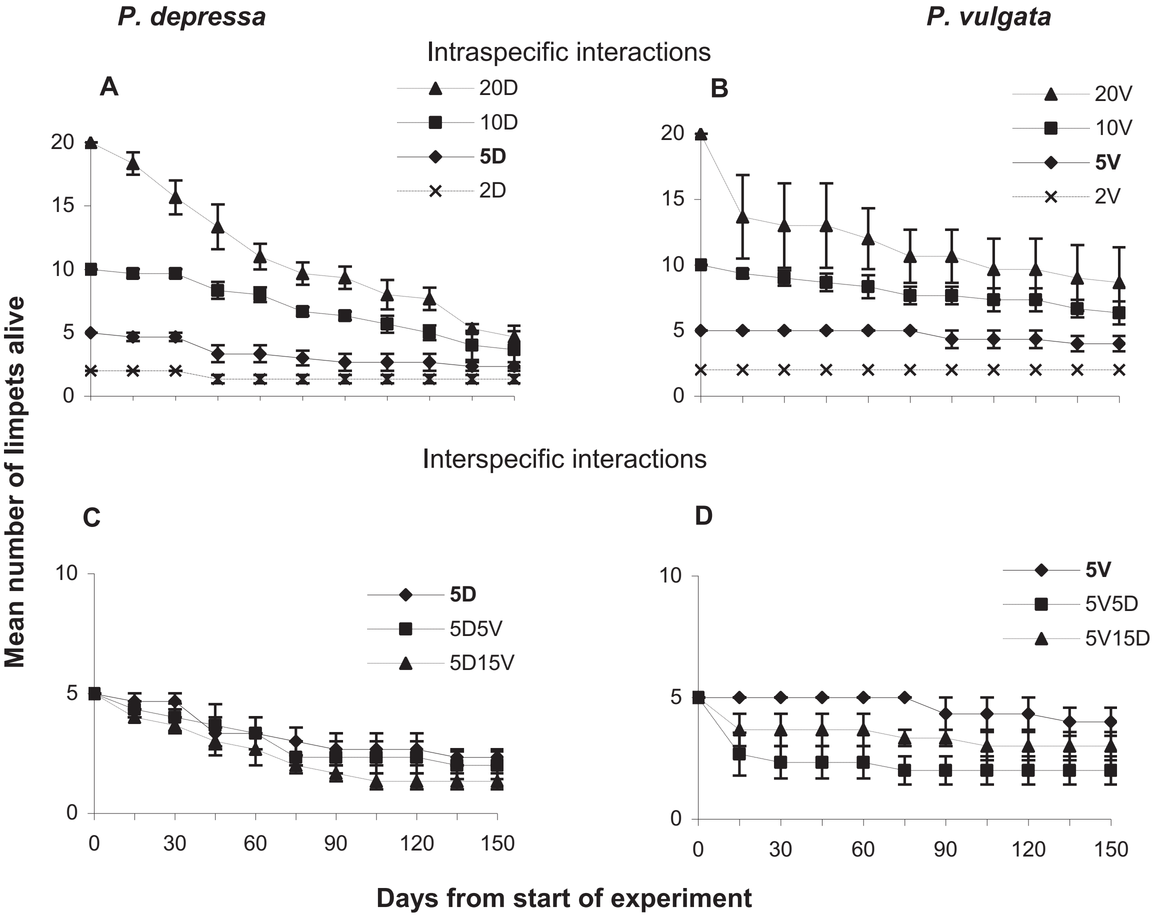

Figure 1- Limpet survivorship in the experimental treatments (cf. Table 1).

Table 4- ANOVA on the proportional mortality at the end of the experiment. ns = not significant, * p<0.05, ** p<0.01, *** p<0.001

Source of variation	df	MS	*F*
Among all	9	0.09	2.71 *
P. depressa vs. P. vulgata = P	1	0.39	11.59 **
Among Exp. Treatm. = T	4	0.08	2.35 ns
Control *vs.* others	1	0.23	6.78 *
Among others	3	0.03	0.87 ns
Density = D	1	0.03	0.80 ns
Species = S	1	0.00	0.00 ns
D x S	1	0.06	1.80 ns
P x T	4	0.03	0.86 ns
P x Control *vs.* others	1	0.02	0.64 ns
P x Among others	3	0.03	0.94 ns
P x D	1	0.03	0.80 ns
P x S	1	0.01	0.20 ns
P x D x S	1	0.06	1.80 ns
Residual	20	0.03	
Cochran's test		(Among all)	C = 0.19 ns

Effects on growth

Mean shell length did not increase markedly over the experimental period, since the animals had already reached an adult size from the beginning of the experiment (Fig. 2). Mean shell length in control and decreased density treatments remained, however, slightly higher than in increased densities. All the treatments with quadruple densities, except 5V15D, had lower total length values. These values exhibited some fluctuations during the experiment. Decreases in length were generally related to the death of larger animals. The treatment 5V15D was the only quadruple density treatment that was not lower than the double density, indicating that *P. depressa* had no effect on the length of *P. vulgata*.

At the end of the experiment, the mean length of *P. vulgata* was significantly higher than that of *P. depressa* (Table 5). The presence of the other species had no significant effect on mean shell length (Table 5). Nevertheless, intraspecific increases in density of *P. vulgata* resulted in lower lengths for this species and, thus, reduced the difference between total length of *P. depressa* and *P. vulgata* (Fig. 3). In contrast, where both species were present the difference remained higher. Length in the quadruple density treatments was lower than in the double density treatments (Fig. 3; Table 5). However, no significant differences were found among treatments (and between control and the treatments) and all the observed decreases displayed in Fig. 3 were only a few millimetres.

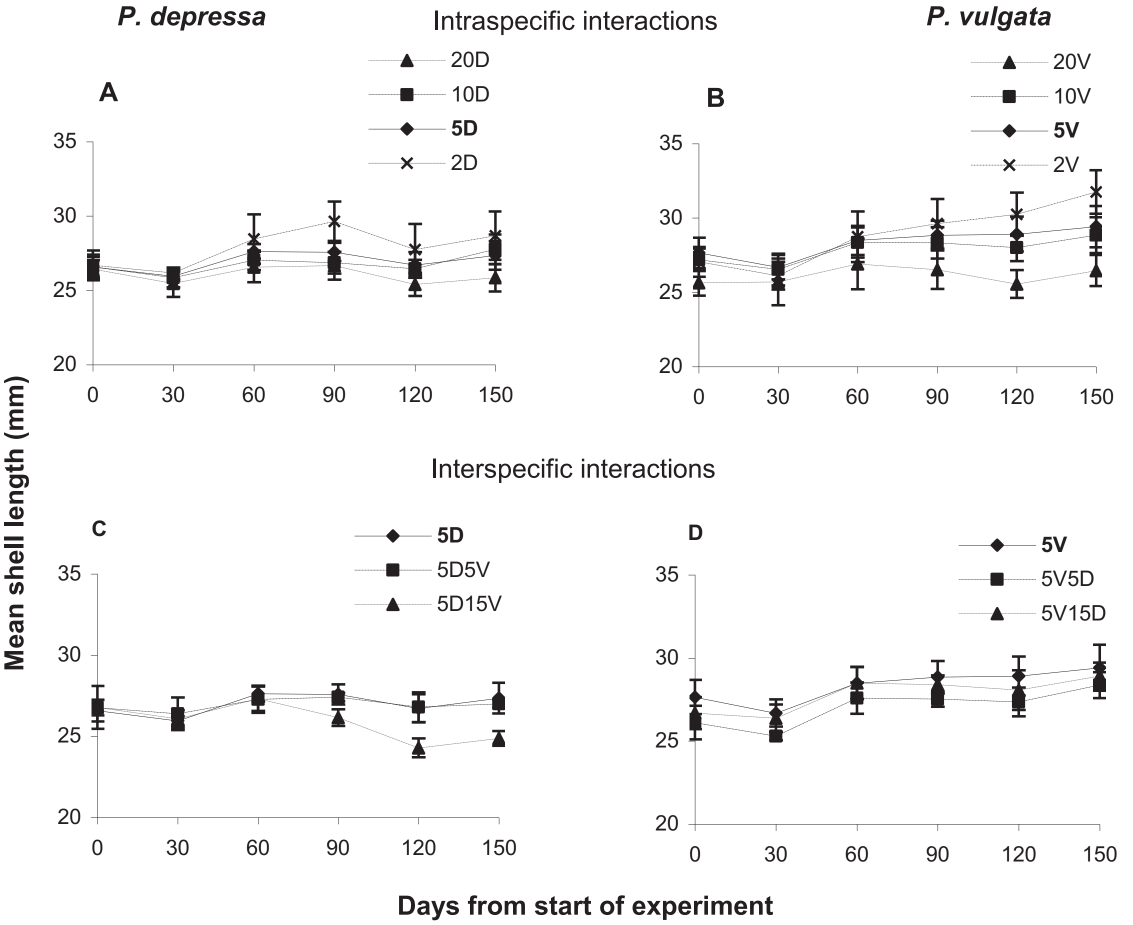

Figure 2- Mean shell length (±SE) during the experimental period (cf. Table 1).

Table 5- ANOVA on the mean shell length at the end of the experiment. ns = not significant, *p<0.05, **p<0.01, ***p<0.001

Source of variation	df	MS	*F*
Among all	9	6.43	2.44 *
P. depressa vs. P. vulgata = P	1	25.24	9.57 **
Among Exp. Treatm. = T	4	5.45	2.07 ns
Control *vs.* others	1	6.08	2.31 ns
Among others	3	5.24	1.99 ns
Density = D	1	12.98	4.92 *
Species = S	1	0.02	0.01 ns
D x S	1	2.73	1.04 ns
P x T	4	2.71	1.03 ns
P x Control *vs.* others	1	0.10	0.04 ns
P x Among others	3	3.58	1.36 ns
P x D	1	1.85	0.70 ns
P x S	1	5.17	1.96 ns
P x D x S	1	3.73	1.41 ns
Residual	20	2.64	
Cochran's test		(Among all)	C = 0.22 ns

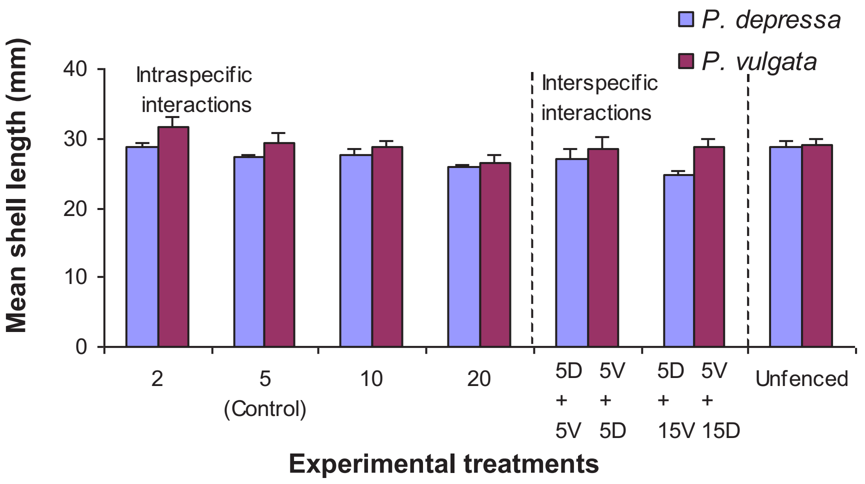

Figure 3- Mean shell length (± SE) at the end of the experiment (cf. Table 1).

Effects on weight

Mean dry weight was significantly higher for *P. vulgata* than for *P. depressa* in all experimental treatments in all densities and species combinations (Fig. 4; Table 6). Increasing densities significantly reduced the weight of the limpets in intraspecific treatments. In contrast, there was no significant difference between double and quadruple density for interspecific treatments (Fig. 4; Table 6, SNK tests). Adding the other species had no significant effect on the weight of the limpets at the double density but had a positive effect on weight at the quadruple density (Fig. 4; Table 6, SNK tests). Weight of the limpets at quadruple density was significantly higher in the treatments where both species were present, than in those where they were enclosed separately, probably due to the relief of pressure from intraspecific competition. Hence, the effects of competition on weight were more pronounced at the quadruple density and for intraspecific interactions.

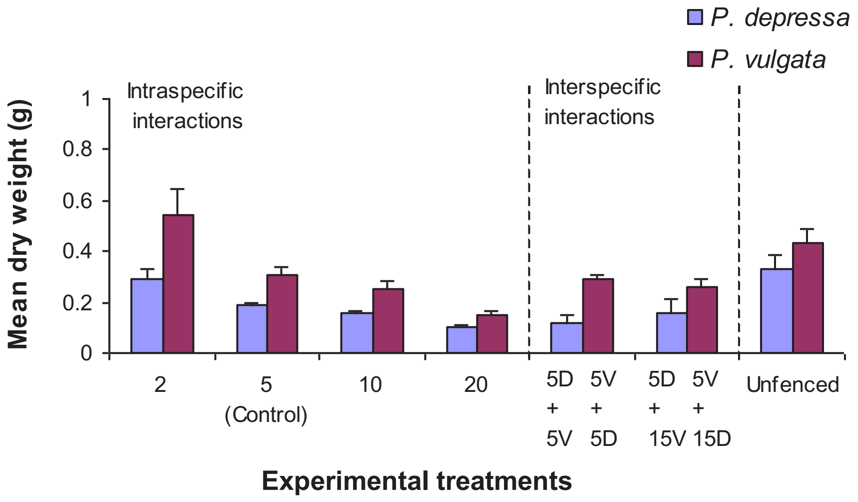

Figure 4- Mean dry weight (± SE) at the end of the experiment (cf. Table 1).

Table 6- ANOVA on mean dry weight at the end of the experiment. ns = not significant, * p<0.05, ** p<0.01, *** p<0.001

Source of variation	df	MS	*F*
Among all	9	0.02	6.55***
P. depressa vs. P. vulgata = P	1	0.09	35.76***
Among Exp. Treatm. = T	4	0.01	4.69 **
Control *vs.* others	1	0.02	7.07 *
Among others	3	0.01	3.89 *
Density = D	1	0.01	3.49 ns
Species = S	1	0.01	3.83 ns
D x S	**1**	**0.01**	**4.37** *
P x T	4	0.00	1.11 ns
P x Control *vs.* others	1	0.00	0.08 ns
P x Among others	3	0.00	1.46 ns
P x D	1	0.00	1.87 ns
P x S	1	0.01	2.37 ns
P x D x S	1	0.00	0.12 ns
Residual	20	0.00	
Cochran's test		(Among all)	C = 0.36 ns
SNK tests:		**Alone**	**Mixed**
D x S		10 20	10 20
SE = 0.02		0.21 > 0.13 *	0.20 = 0.21 ns
		10	**20**
		Alone Mixed	Alone Mixed
		0.21 = 0.20 ns	0.13 < 0.21 **

Effects on reproduction

The proportion of males from *P. depressa* was higher than the proportion of females in increased density treatments, except in the 5D15V treatment (Table 7). The proportion of males and females in control, unfenced control and decrease density was equivalent. For *P. vulgata*, the percentage of males was constantly higher for all treatments except the unfenced control. These results must be regarded with caution since the sex of the limpets was determined only at the end of the experiment and the initial proportions were not known. In addition, the number of animals alive was different in each experimental treatment by the end of the experiment. Thus, implications on sex changing due to competition need further study. Nevertheless, the occurrence of neuter individuals only in intraspecific increased densities is a good indication that competition suppresses onset of reproduction.

The analysis of the gonad stage at the end of the experiment also showed that the lower stages of development were most prevalent at increased densities (Fig. 5).

Table 7- Percentage of various sexes (and n value, for pooled replicates) at the end of the experiment for *P. depressa* and *P. vulgata* in the different treatments.

P. depressa	**2D** (n=4)	**Control 5D** (n=6)	**Unfenced 5D** (n=8)	**10D** (n=11)	**20D** (n=14)	**5D5V** (n=6)	**5D15V** (n=6)
Neuter	0%	0%	0%	9%	43%	0%	0%
Male	50%	50%	50%	55%	43%	67%	50%
Female	50%	50%	50%	36%	14%	33%	50%
P. vulgata	**2V** (n=6)	**Control 5V** (n=11)	**Unfenced 5V** (n=13)	**10V** (n=19)	**20V** (n=26)	**5V5D** (n=6)	**5V15D** (n=9)
Neuter	0%	0%	0%	0%	27%	0%	0%
Male	67%	82%	46%	74%	54%	83%	89%
Female	33%	18%	54%	26%	19%	17%	11%

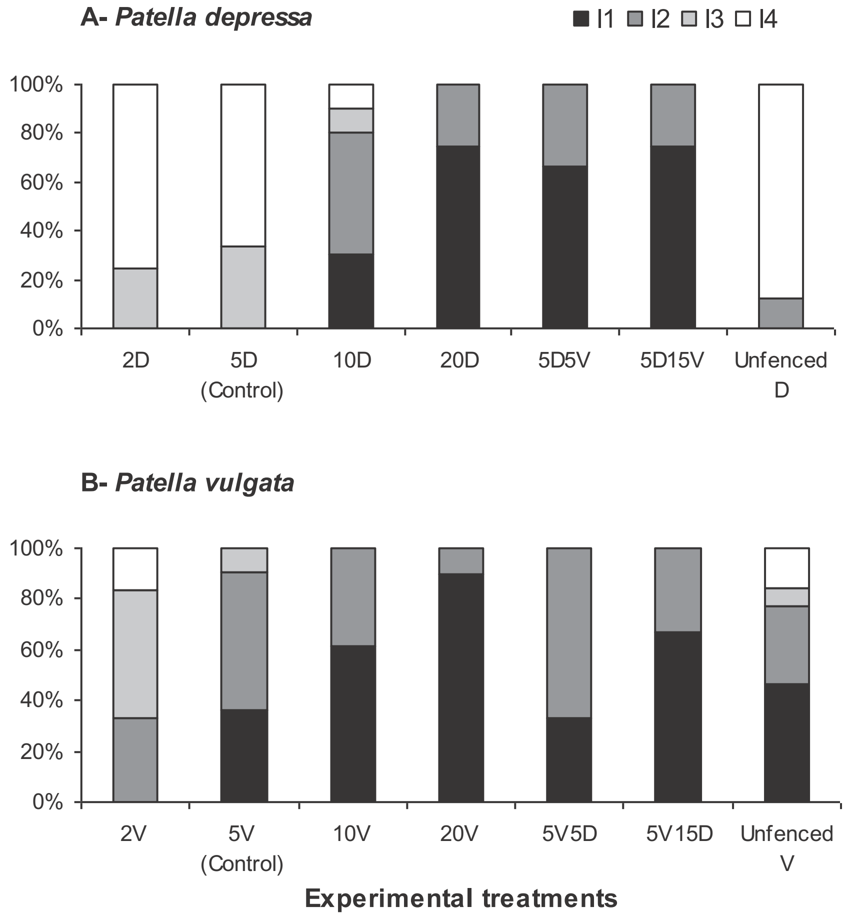

Figure 5- Gonad index (I1, I2, I3, I4- following Orton's (1956) scale) at the end of the experiment for *P. depressa* (A) and *P.vulgata* (B) (cf. Table 1).

Effects on microalgal food

No significant differences were detected in chlorophyll concentration in the different treatments (Fig. 6; Table 8). There was, thus, no obvious relationship between the standing stock of food available and the changes verified for mortality, length, weight or sex. There is some indication, however, of shortage of food resources because the values of chlorophyll concentration were in general very low.

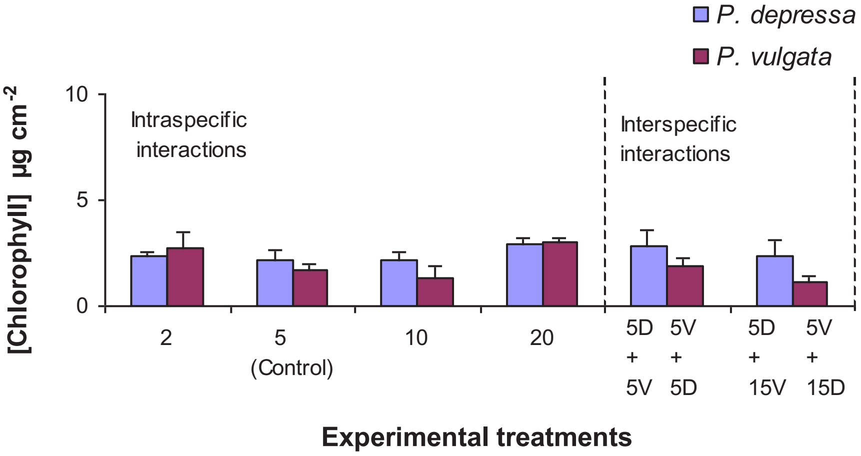

Figure 6- Mean chlorophyll concentration (±SE) at the end of the experiment (cf. Table 1).

Table 8- ANOVA on the chlorophyll concentration at the end of the experiment.ns = not significant, * p<0.05, ** p<0.01, *** p<0.001

Source of variation	df	MS	*F*
Among all	9	1.27	0.70 ns
P. depressa vs. P. vulgata = P	1	3.68	2.03 ns
Among Exp. Treatm. = T	4	1.56	0.86 ns
Control *vs.* others	1	0.43	0.24 ns
Among others	3	1.94	1.07 ns
Density = D	1	0.52	0.29 ns
Species = S	1	0.59	0.33 ns
D x S	1	4.70	2.59 ns
P x T	4	0.38	0.21 ns
P x Control *vs.* others	1	0.05	0.03 ns
P x Among others	3	0.49	0.27 ns
P x D	1	0.12	0.07 ns
P x S	1	0.76	0.42 ns
P x D x S	1	0.59	0.33 ns
Residual	20	1.82	
Cochran's test		(Among all)	C = 0.23 ns

DISCUSSION

Inter- and intraspecific competition amongst *P. depressa* and *P. vulgata*

In the majority of field experiments, the degree of resource competition or interference is experimentally manipulated by changing the population densities of the competitors (Connell, 1983). When competition occurs, it is necessary to detect differences in parameters such as mortality, growth, weight of individuals with and without the potential competitor (Connell, 1983; Underwood, 1992).

Inter- and intraspecific competitive interactions among *P. depressa* and *P. vulgata* have not been experimentally studied before. Competition between *P. aspera* and *P. vulgata* in Irish rocky shores has been deduced to occur because one species had reduced in numbers when the other was abundant. *P. aspera* occupies areas of strong wave action, but reduces in number as wave action declines and is progressively confined to the low-shore and replaced by *P. vulgata* (Thompson, 1979, 1980). This replacement may mean competitive displacement, but there is no proof of this (Branch, 1981).

The present experiments have revealed effects of inter- and intraspecific competition on the survivorship, length, weight and reproduction of these two species of limpets. Limpets in decreased densities showed the higher survivorship, length, weight and gonad index for both species. Conversely, increasing densities resulted in increased mortality, reduced length and weight, and reduced gonad development. The analysis of interspecific interactions by addition of individuals from the other species had no significant effect on mortality or growth. Although both species could negatively affect each other, the effect on mortality and growth of *P. depressa* by addition of *P. vulgata* did not differ from the effect on mortality and growth of *P. vulgata* when *P. depressa* was added. Thus, interspecific interactions were symmetrical. Results from tissue weight, however, indicated an asymmetry between the relative strengths of inter- and intraspecific interactions. Intraspecific increases in density resulted in a more accentuated reduction of weight than when both species were present. The occurrence of neuter individuals only in increased densities single species plots corroborated the evidence of a stronger intraspecific interaction.

At the end of the experiment the *P. depressa* had a lower survivorship and growth than *P. vulgata*. *P. depressa* has also greater negative density dependence. This seems to be a characteristic of the species instead of an effect from competition since it was constant in all the treatments, including controls and decreased densities. These results conform to work on population dynamics of both species, that indicate higher length and weight for *P. vulgata* (Guerra & Gaudêncio, 1986). The fact that inter- and intraspecific interactions did not reverse this situation may play an important role in the coexistence of the species.

The mechanism by which species compete in the present experiment was not clear. Vertical and seasonal patterns in exploitative competition between intertidal gastropods have been addressed in some studies. Underwood (1984) investigated inter- and intraspecific competition between intertidal gastropods at various heights on the shore and different periods of the year. Lasiak & White (1993) examined competitive interactions between two species of limpets during winter and summer period. Experimental results demonstrated that intensity of competition could vary on a spatial and temporal basis according to the densities and mixtures of grazer species and according to the availability of microalgal food. In the present study microalgal food availability was assessed through determination of chlorophyll concentration. However, the expected inverse relation between chlorophyll levels and density of limpets in the different treatments such as that found in previous works (e.g. Underwood, 1984; Lasiak & White, 1993; Marshal & Keough, 1994) was not obtained in this experiment. Thus, there was no evidence from this experiment to prove that exploitation of resources was the direct cause of reduced survivorship, growth, weight and fecundity with increasing densities. It is possible that even a small density of limpets was able to maintain microalgal food resources at the low observed values. Further experimentation with other methods of food assessment is needed.

Coexistence of the species and biogeographic limits of distribution

The effects of competition between species of intertidal gastropods have been investigated in several regions and occasions and have shown that inter- and intraspecific interactions can clearly lead to a reduction in density of each species (Underwood, 1978; 1984; Creese & Underwood, 1982; Ortega, 1985; Lasiak & White, 1993). In addition, many of these studies have revealed asymmetric interspecific competition with the existence of a superior competitor (Connel, 1983; Schoener, 1983). Under these circumstances, coexistence of species has been attributed to the intense or relatively higher intraspecific competition of the superior competitor. The present study differed from the previous ones in the sense that competitive interactions between *P. depressa* and *P. vulgata* were examined close to the biogegraphical limit of distribution of *P. vulgata*. Proportions of *P. depressa* and *P. vulgata* in Moledo do Minho are similar but, further to the south along the Portuguese coast, the densities of *P. vulgata* decline considerably, being occasional or rare in some places. In view of this pattern of distribution it could be expected to find superiority of *P. depressa* in competitive interactions. However, at the end of the experiment no significant differences were found in the effects of *P. depressa* on *P. vulgata* and vice versa. Moreover, the existence of a strong intraspecific competition indicated that both species are able to coexist. Hence, in the studied shore, where the two species density is similar, and despite the proximity to the biogeographic limit of distribution, *P. depressa* coexist with *P. vulgata*, and the latter does not appear to be an inferior competitor.

Notwithstanding the results obtained in this study and the necessity of further experimentation on different species and spatial and temporal scales, it is essential to be aware of limitations of the experimental approach in broad spatial-temporal contexts of species competition and coexistence. Tokeshi (1999) has referred to the problem of the scale and mode of competition. He considered that despite the general agreement by contemporary ecologists that experimental approaches are a powerful method for testing hypotheses, including the importance of competition on community organisation, the detection of a competitive effect is strongly dependent upon its relative magnitude against background noise. This would mean that only relatively strong competitive effects would be detected by experiments, which are typically of short duration. According to him this can lead to a gap in the understanding of the potential importance of relatively weak competition operating over a long period of time. A set of species might exhibit intense competition precisely because its effects are of short duration and do not significantly affect the state of coexistence in the long term. Tokeshi (1999) even suggested that in terms of species coexistence, the cases of intense competition might be relatively unimportant in the evolutionary context compared with weak, but long lasting, competition.

In addition, it is also necessary to consider how interspecific competition is influenced by and interacts with unpredictable environments (Begon et al., 1986). Fluctuations in recruitment, predation, human pressure on the shores, or global warming are some examples of factors that can affect the competitive interactions and any competition prediction. Because of this, the importance of competition has been frequently discussed. The detection of interspecific competition does not necessarily lead to its importance (Tokeshi, 1999). To assess the relative importance of competitive interactions it would be essential to study other ecological processes such as predation or disturbance in conjunction with competition (Underwood, 1992). Thus, further investigation is essential in order to clarify the competitive interactions observed among grazing gastropods, like limpets.

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CHAPTER 5

Intra- and inter-size-class competition in the limpet *Patella depressa* Pennant in the central coast of Portugal

Boaventura, D.; L. Cancela da Fonseca & S.J. Hawkins. Intra- and inter-size-class competition in the limpet *Patella depressa* Pennant in the central coast of Portugal. Submitted to *Journal of Animal Ecology*.

CONTENTS

INTRODUCTION

Competition results from the requirement by two or more individual organisms for a common resource, which is in short supply (Birch, 1957; Branch, 1975a). The effect of grazing gastropods in preventing the proliferation of macroalgae in intertidal rocky shores has been well documented (see Lubchenco & Gaines, 1981; Branch, 1981; Hawkins & Hartnoll, 1983; Hawkins et al., 1992 for reviews). In mid-shore areas grazers often subsist on microbial films, whose abundance is variable and can be limiting in summer as a result of high temperatures and higher grazer activities (Nicotri, 1977; Underwood, 1984a; Hill & Hawkins; 1991). Thus, where limpet numbers are high, resources can be limiting. This is potentially made worse by unpredictable recruitment events or continual input of juveniles. Therefore, on intertidal rocky shores, food resources are probably limiting much of the time either due to the high grazing pressure and/or to low supply of food (Underwood, 1978, 1992; Hawkins & Hartnoll, 1983), leading to the common occurrence of competitive interactions among marine invertebrate grazers (Underwood, 1978). Individuals of closely related species usually have a great overlap in the resources they require, and will presumably compete if they coexist (Branch, 1975a). Intraspecific competition is likely to be even more intense since individuals of the same species will probably have a closer requirement for identical resources (Branch, 1975a; Underwood, 1992).

The relative importance of inter- and intraspecific competition is particularly interesting for the outcome of the competition process and for the abundance and coexistence of competitors (Connell, 1983; Marshall & Keough, 1994). Partitioning of resources or range of the habitat occupied can also be related to competitive interactions. In theory, increasing intraspecific competition should expand a species niche whereas increased interspecific competition should reduce it (Branch, 1981; Connell, 1983).

The approach used in the study of inter- and intraspecific competition has undergone some changes throughout the years. Early investigations of competition amongst grazing herbivores involved the study, under natural conditions, of the influence of increased and decreased local densities of grazers on the mortality, growth rate, size or reproductive output (e.g. Branch, 1975a, 1976; Black, 1979; Creese, 1980). The recognition that the effects of competition on a species depend on the relative importance of inter- and intraspecific interactions, and that these interactions should be investigated simultaneously, led to the proliferation of studies with a more complex experimental design (e.g. Underwood 1978, 1984b). For an appropriate detection of competition, and to better understand the role of competition in structuring communities, experimental designs started to include a control density of one species, which was then contrasted to experimental plots with different densities of that species in combination with a second one (see Underwood, 1986, 1992). Furthermore, it was necessary to identify the common resource which is limiting for the species and to understand the mechanism by which the species compete (Underwood, 1978). Therefore, the supply of food started being measured while evaluating exploitative competition in some studies (e.g. Underwood, 1984b; Lasiak & White 1993).

Hence, inter- and intraspecific competitive interactions have often been experimentally demonstrated for intertidal grazing gastropods (see Branch 1981; Connell, 1983; Schoener, 1983 for reviews). However, most of the studies of competition amongst grazing gastropods have analysed interspecific competition for food between adult animals (e.g. Haven, 1973; Underwood, 1978, 1984b; Creese & Underwood, 1982; Ortega, 1985; Lasiak & White, 1993). Considerably less attention has been given to the effects of competition between different size- or age-classes for a given species although it might be important in the outcome of competitive abilities shown by the larger/adult individuals. The size of an animal is of crucial importance in determining its food requirements, feeding abilities, and interference abilities (Marshall & Keough, 1994). Effectively, body size has been suggested by several authors as being important in competitive superiority (Connell, 1983) leading to asymmetry in competitive interactions (Schoener, 1983). As pointed out by Marshall & Keough (1994), size-dependent competition might have particular importance in situations of variable recruitment. Under this circumstance, variation in the size structure of the population is likely to occur, and to dramatically affect the intensity of intraspecific competition, either in space or time. The only studies to date on competitive interactions on different size- or age-classes for marine gastropods were done in Australia. Underwood (1976) has studied competition between age-classes of the neritacean *Nerita atramentosa* and Marshall & Keough (1994) studied competition between size-classes in the limpet *Cellana tramoserica*. Little information is still available on the effects of such size- or age-class competitive interactions, and these have never been studied for the limpet *Patella depressa*.

On the rocky shores of central coast of Portugal *Patella depressa* is the most abundant grazing limpet at mid-tidal level. The other grazing limpet that inhabits this same shore level, *Patella vulgata*, is rare since it is close to its southern biogeographic limit of distribution (Fretter & Graham, 1976; Guerra & Gaudêncio, 1986). At Cabo Raso, *Patella depressa* clearly dominates throughout the eulittoral zone, occurring in high densities, which makes it an ideal subject for testing hypotheses about intraspecific competition.

The present study investigated the role of competitive interactions in different size-classes (small vs. large) of the limpet *Patella depressa* (in the areas where the distribution of the different size-classes overlap). Considering the observed distribution patterns it was predicted that intraspecific competition would be intense, and competitive abilities of the different size-classes for food resources were experimentally determined. Animals were fenced at different densities and mixtures of sizes to assess the relative importance of competition between and within size-classes. Concomitantly, microalgal food resources were also quantified.

In particular, this study tested the effects of various densities and different size-classes on parameters such as mortality, growth, weight and sexual development in the limpet *Patella depressa*.

MATERIAL AND METHODS

Study site and organisms

This investigation of the effects of increased and decreased densities on different size-classes of the limpet *Patella depressa* Pennant was conducted on the central coast of Portugal, at Cabo Raso (38º 42'N, 9º 29'W). The site is moderately exposed to the prevailing north-west winds and faces the Atlantic Ocean. The experiments were made in mid-littoral level above the red algal turf zone in areas not subjected to heavy wave action. At this level, the limestone bedrock formed an even substratum almost devoid of macroalgae and barnacles.

Limpet species in the central coast of Portugal included mainly *Patella rustica* L. (high-shore), *Patella depressa* (mid-shore) and *Patella ulyssiponensis* Gmelin (= *Patella aspera* Röding)(low-shore). Although a few individuals of *Patella vulgata* L. can sporadically occur in mid-tidal levels this habitat is dominated by *Patella depressa.* This allowed testing the effects of competition between and within size-classes of *P. depressa*, at mid tidal level, without the interference of interspecific interactions with other limpet species. Although small limpets were most abundant closer to mean low water, the mid-shore is where both small and large individuals occur.

Experiments to determine the effects of competition within and between size-classes

Twelve treatments were used with increased (x 2, x 3), decreased (x 1/2) and natural densities of limpets and different mixtures of the two size-classes (see Table 1). The control densities correspond to ten large or small limpets per enclosure. This control density was based on previous sample estimates of the abundance of these limpets in the mid-shore area using two different sample size quadrats (50 x 50 cm and 25 x 25cm). The other levels of experimental densities were also selected according to the range of densities found in nature. For instance, quadrupling of the natural densities was not used, as it would be far above the natural range. The treatments 10L, 20L, 30L, 10L+10S, 10L+20S were used to investigate the effects of intra- and inter-size-classes on large limpets, where as the treatments 10S, 20S, 30S, 10S+10L, 10S+20L were used to examine the same effects on small limpets. All treatments with large limpets and all treatments with small limpets were also compared in the general analysis. The treatments 10L+10S and 10S+10L had exactly the same densities and size mixtures but were used separately so that the effects on large and small limpets could be examined independently. This experimental design is analogous to the approach used (and advocated) for experiments on interspecific competition (see Underwood 1992 for details). In this experiment number of limpets rather than biomass were manipulated, because the prediction of competitive interactions was based upon the distribution patterns and abundance of grazing limpets on the shore. Manipulating biomass under the assumption of a linear relationship between biomass and resource requirements would increase the number of small limpets much higher than that observed under natural conditions. We also manipulated size-classes instead of species and included decreased density treatments. It is useful to have some density treatment below the range of natural densities because it is interesting to compare the performance (e.g. fecundity, growth rate, etc.) at higher densities not only with the control but also at the lowest treatment densities, where plenty of food resources are available. In the present work decreased density treatments were used as a reference and this information is graphically presented but is not included in the general statistical analysis. Three replicates of each treatment were randomly assigned to the experimental plots.

Large (24.5 mm, ± 0.10 S.E.) and small limpets (13.2 mm, ± 0.09 S.E.) were enclosed at different densities and size combinations in experimental fenced plots. These plastic coated wire fences made of a square mesh enclosed an area of 625 cm^2. The fences were attached to the rock by screws, passing through foam rubber strips, and inserted into rawl-plugs in holes drilled by a petrol driven drill (Ryobi ER160). The strips had the length of the fence and enabled the base of the fence to follow small irregularities of the substratum. The sponge was used to assure that small limpets would not cross the plot underneath the fence. Still, any gaps remaining between the base of the sponge and the substratum were filled with non-toxic silicone.

The experiment ran from the 29th of March to the 9th September of 1998, for a total of 165 days. The experimental animals were collected from adjacent areas of the shore and allocated to the treatments. Previous tests with marked limpets were done to check if large and small limpets of *P. depressa* could survive transplantation on the same shore level and among different levels on the shore. Although very few animals had died in these preliminary observations, the fences were checked daily for the first 4 days and, during this period, missing limpets were replaced. During the rest of the experiment, mortality of limpets was recorded at fortnight intervals and dead limpets were replaced by other individuals of the same size-class to maintain densities. The total length of each individual was registered monthly on the shore, without removing animals, using calipers with two extensions so that even animals in small depressions or that were close together could be measured more accurately. The limpets used in this work were marked with colour code using nail varnish. Original limpets were marked with white colour and all the limpets that were used to maintain densities were marked with red colour. This procedure enabled to check if any limpets escaped from the fences. Since the colour dots faded with time the limpets were re-marked whenever possible. The two size-classes of animals were easily distinguished. Individually marking was not possible and the measurements were always treated considering the averages. To assess the effects of confinement, ten large and small limpets from the same shore area were also marked using a different colour. This unfenced control allowed comparison of unfenced animals with those fenced at control density.

At the end of the experiment all of the original marked limpets inside and outside the fences were collected for morphometric analysis (length, width, height, volume of the shell) wet and dry weight, sex determination and gonad stage evaluation. The sex and gonad stage of each limpet was based on the Orton's scale (Orton et al., 1956). Mean growth rates were calculated with the formula $r = \ln (L_t/L_0)/t$, where, L_0 = length at start, L_t = length at the end and t = days of the experiment.

Table 1- Experimental treatments and total number of limpets per fence. L- large size-class, S- small size-class

5 (decreased)	**10 (control)**	20 (increased x2)	30 (increased x3)
1- 5L	3- 10L	5- 20L	9- 30L
2- 5S	4- 10S	6- 20S	10- 30S
		7- 10L10S	11- 10L20S
		8- 10S10L	12- 10S20L

Estimation of microalgal food resources

The availability of food was indirectly assessed by determination of chlorophyll concentration with spectrophotometric analysis of rock chips (Hill & Hawkins 1990; Thompson et al., 1999). Rock chips were removed by chisel from areas around the plots during the experiment and from both the experimental plots and surrounding areas at the end of the experiment. The concentration of chlorophyll present in three replicates of each treatment (one rock chip within each fence) was estimated using the formula [chlorophyll] = 13.0 x Å665 x v / d x V, (where 13.0 = a constant for methanol, Å665 = net absorbance of solution at 665 nm, v = final volume of solution (ml), d = path length of cell (cm), V = surface area of sample (cm^2)) and the methods described by Thompson et al. (1999). The area of the rock chips was obtained with image processing analysis.

Data analysis

Single-factor analysis of variance was used to test if there was any significant difference between unfenced and fenced controls.

Asymmetrical analyses of variance were used to test the effects of inter- and intra-size-class interactions for the two size-classes. This type of design has been described elsewhere by Underwood (1978, 1984b, 1986, 1992, 1993, 1997). Asymmetric designs can be used to detect competitive interactions to cover the situation where there might be a single control plot and a number of experimental densities of one or more species (Underwood, 1992). Another situation where this particular case of ANOVA has been used is for environmental studies such as beyond BACI (Before-After-Control-Impact), which involve a contrast between one disturbed location and the average of the multiple controls (Underwood, 1992; Glasby, 1997). Note that this situation is considerably different from other unbalanced designs. This latter term is reserved for the designs consisting of ‘unequal’ number of replicates within a group rather than unequal numbers of levels within treatment groups (Glasby, 1997).

The method of construction of the asymmetrical analysis used in this study follows that described in Underwood (1997) and consists in combining the sum of square values from separate analyses of variance. The partitioning of degrees of freedom and the sums of squares for the analysis are represented in Table 2. The factors Large *vs.* Small, Density and Size were fixed. When the null hypothesis (of no difference between densities, size, or their interaction) was rejected, then the comparisons among means were done using the results of the individual analyses of variance (Table 2) against the overall residual using the Student- Newman-Keuls (SNK) *a posteriori* multiple comparisons.

ANOVAs were used to test the effects of competitive interactions on the mean proportional mortality, chlorophyll concentration, total length, growth rate and weight at the end of the experiment. Whilst mortality, chlorophyll concentration and growth rate analyses were made with the absolute values per replicate, total length and weight analyses used the average of the measures taken for all the individuals in the replicate (Large limpets- 5 < n < 14; Small limpets- 3 < n < 23). Homogeneity of variances was checked with Cochran's C-test. This assumption was valid for all studied variables except weight, which was transformed using Log (X).

Table 2- Partitioning of degrees of freedom in the final asymmetrical analysis of variance and the origin of the calculated sum of squares.

Source of variation	df
Among all [a]	9
Large *vs.* Small = L [b]	1
Among Exp. Treatments = T [b]	4
Control *vs.* others [c]	1
Among others [d]	3
Density = D [e1]	1
Size = S [e2]	1
D x S [e3]	1
L x T [b]	4
L x Control *vs*. others [f]	1
L x Among others [g]	3
L x D [e4]	1
L x S [e5]	1
S x D x S [e6]	1
Residual [a]	10 (n-1)
Total [a]	10n-1

[a] One-factor analysis of variance for all cells.
[b] Two-factor analysis of variance for "L" and "T".
[c] Sum of squares by subtraction between "Among Exp. Treatments" and "Among others".
[d] Sum of squares by addition of those in e1,e2,e3.
[e] Three-factor analysis of variance for "L", "D" and "S" omitting controls.
[f] Sum of squares by subtraction between "L x T" and "L x Among others"
[g] Sum of squares by addition of those in e4,e5,e6.

RESULTS

Effects of confinement

No significant differences between fenced and unfenced controls were found for the large size-class of limpets at the end of the experiment, in any of the studied parameters: proportional mortality, mean shell length, growth rate, mean shell height, mean dry weight and chlorophyll concentration (Table 3A). This indicates that the large-sized individuals were not affected by the fencing procedure. For the small size-class of limpets significant differences were only obtained for mortality, which was significantly higher in the unfenced than the fenced control. Inability to find highly vagrant small marked limpets outside experimental plots could justify these differences; there are, however, other possible explanations for this fact (see discussion). No significant differences between the two types of control in the small size-class were revealed for any other parameter (Table 3B).

Table 3- *F* and P values of the one-way ANOVA between fenced and unfenced controls for the studied parameters. A- Large size-class, B- Small size-class.

Fenced Control *vs*. Unfenced	**A- Large size-class**		**B- Small size-class**	
control	$F_{1,4}$	P	$F_{1,4}$	P
Proportional mortality	1.32	P>0.05	36.57	P< 0.01
Mean shell length	1.29	P>0.05	2.80	P>0.05
Growth rate	1.50	P>0.05	1.73	P>0.05
Mean shell height	0.99	P>0.05	7.11	P>0.05
Mean dry weight	0.03	P>0.05	4.34	P>0.05
Chlorophyll concentration	0.02	P>0.05	0.00	P>0.05

Effects on mortality

Fenced controls and decreased density treatments showed only a very slight reduction, in the mean number of limpets alive during the experiment (Fig 1 a,b).

Mean number of large and small limpets alive in increased density treatments decreased during the experimental period (Fig. 1). Within the large size-class, mean number of limpets fenced at double and triple densities declined considerably during the experimental period, decreasing to control levels by the end of the experiment (Fig. 1a). Within the small size-class the effects were more apparent only for the density treatment 30S (Fig. 1b). Survivorship of limpets in increased density treatments between size-classes also suffered a decline during the experimental period (Fig. 1 c,d). Analysis of variance on the proportional mortality for the two size-classes of limpets, at the end of the experiment, revealed a significant effect of density (Table 4). The effect of density on mortality was independent of the size-class and mixture, being significantly higher in the triple than in the double density treatment (Table 4, SNK tests).

The addition of individuals from the other size-class had a significant effect on mortality but this effect was different for large and small limpets (Table 4, SNK tests). Large limpets alone had significant higher mortality then when fenced together with small limpets (Fig. 1 a,c; Table 4, SNK tests). In contrast, small limpets showed higher mortality when fenced with large limpets then when fenced alone (Fig. 1 b,d; Table 4, SNK tests). Thus, fencing large and small limpets separately resulted in a significant higher mortality for large limpets (Fig. 1 a,b; Table 4, SNK tests). Conversely, fencing both size-classes together caused a significantly higher mortality for the small size-class (Fig. 1 c,d; Table 4, SNK tests). This indicates that the effect of large on small limpets (Fig. 1d) was much stronger than the converse (Fig. 1c).

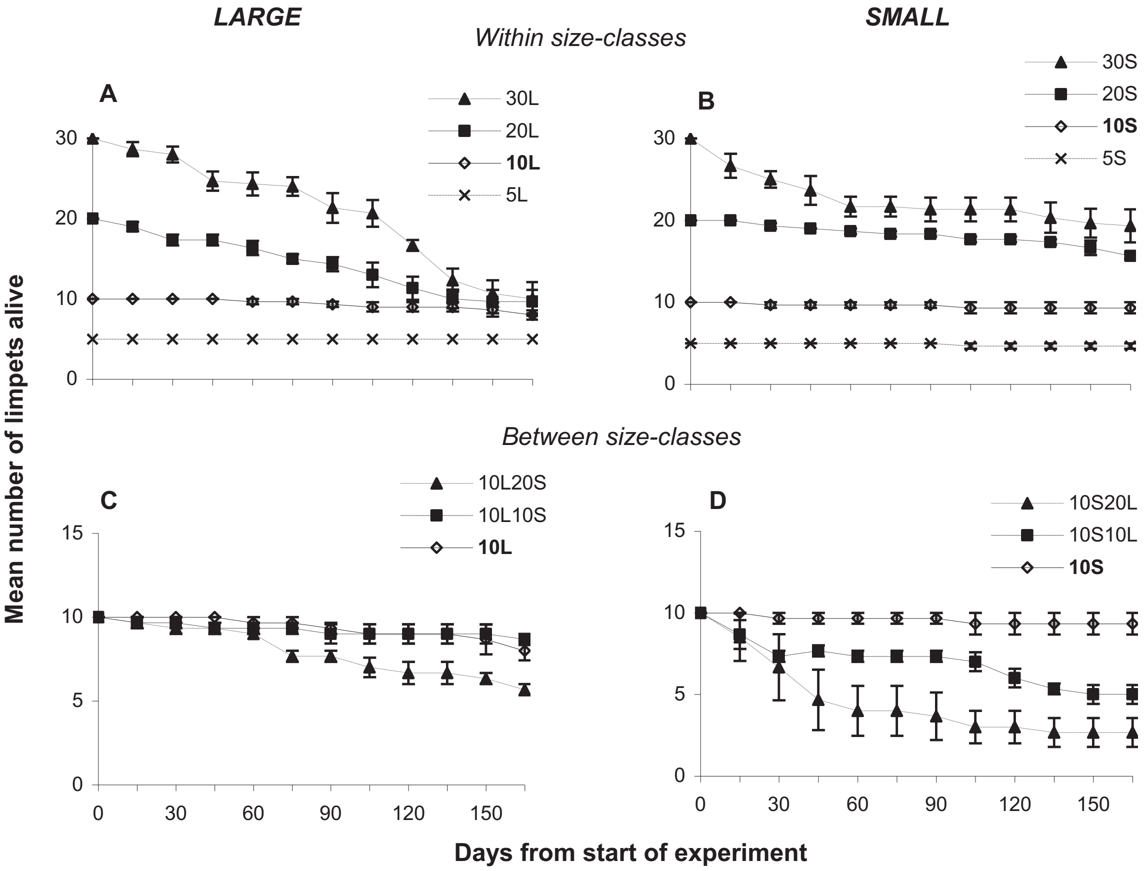

Figure 1- Limpet survivorship in the experimental treatments (cf. Table 1).

Table 4- ANOVA on proportional mortality at the end of the experiment. ns = not significant, *$p<0.05$, **$p<0.01$, ***$p<0.001$

Source of variation	df	MS	*F*
Among all	9	0.15	14.23 ***
Large *vs.* Small = L	1	0.00	0.17 ns
Among Exp. Treatm. = T	4	0.19	17.14 ***
Control *vs.* others	1	0.46	42.97 ***
Among others	3	0.09	8.53 ***
Density = D	**1**	**0.25**	**23.44** ***
Size = S	1	0.00	0.06 ns
D x S	1	0.02	2.07 ns
L x T	4	0.16	14.83 ***
L x Control *vs.* others	1	0.03	2.39 ns
L x Among others	3	0.21	18.98 ***
L x D	1	0.00	0.21 ns
L x S	**1**	**0.61**	**56.62** ***
L x D x S	1	0.00	0.11 ns
Residual	20	0.01	
Cochran's test		(Among all)	C = 0.22 ns
SNK tests			
L x S:		**Alone (S1)**	**Mixed (S2)**
SE = 0.04		Large Small	Large Small
		0.59 > 0.29 **	0.28 < 0.62**
		Large	**Small**
		L L+S	S S+L
		0.59 > 0.28	0.29 < 0.62**
Density:		**20**	**30**
SE = 0.03		0.34 <	0.54**

Effects on growth

Mean shell length and growth rate

Mean shell length of limpets increased during the experimental period, particularly in control and decreased density treatments (Fig. 2). The increase in the total length was more dramatic for small limpets (Fig. 2 b,d) which showed almost linear growth throughout the experiment. By inspection of the graphics (Fig. 2) it is possible to see that in treatments where the growth was higher there was an increase in the shell length from the beginning of the experiment. In contrast, large limpets in increased density treatments (Fig. 2 a,c), and small limpets in the treatments 10S10L and 10S20L (Fig. 2 d), had a slight increase of the shell length only after approximately 60 days that corresponded to the beginning of the summer season.

Small limpets had a greater growth rate than large limpets during the experimental period, as would be expected (Fig. 3). The growth rate was highest for decreased density and control treatments (Fig. 3) where small limpets reached almost the same mean shell length than large limpets by the end of the experiment (Fig. 4). At increased densities, however, mean shell length of small limpets was still significantly smaller than that of large animals (Fig. 4; Table 5, SNK tests), regardless of the size mixture. Double and triple densities did not differently affect mean shell length (Table 5) but resulted in different growth rates (Table 6). Growth rate of large and small limpets was significantly lower for triple than double densities (Table 6, SNK tests). The addition of small limpets did not affect the length and growth rate of large limpets. Mean shell length and growth rate of small limpets, however, was significantly reduced by the presence of large animals (Tables 5 and 6; SNK tests).

Mean shell length and growth rate of small limpets in controls was significantly higher than in the other treatments. No significant differences were detected among treatments for large limpets.

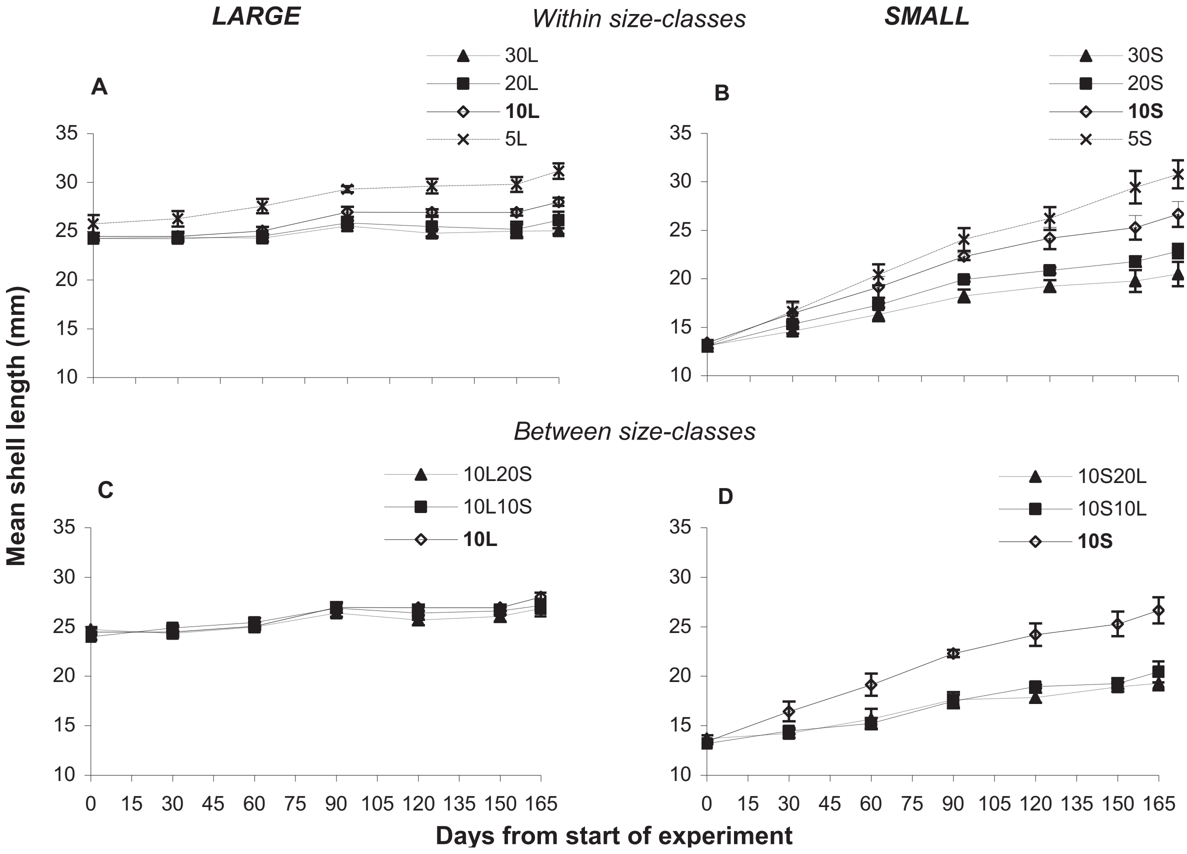

Figure 2- Mean shell length (± SE) during the experimental period (cf. Table 1).

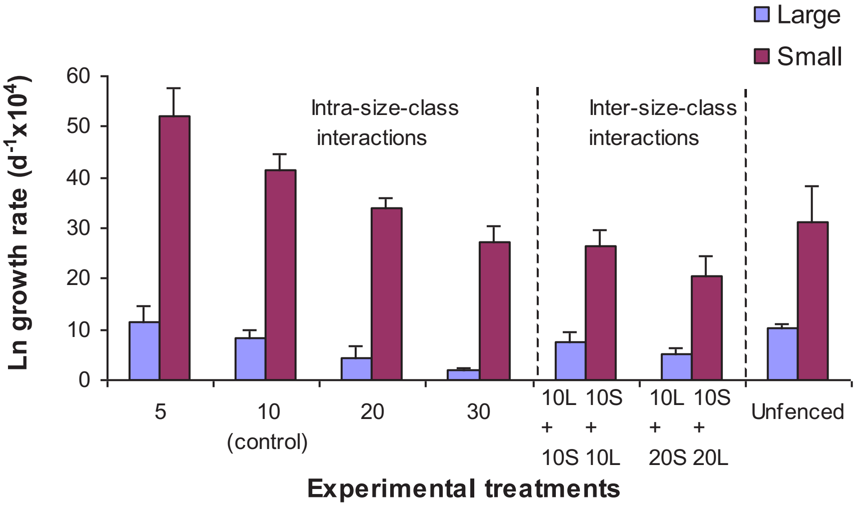

Figure 3- Mean growth rate of limpets (±SE) over the experimental period (cf. Table 1).

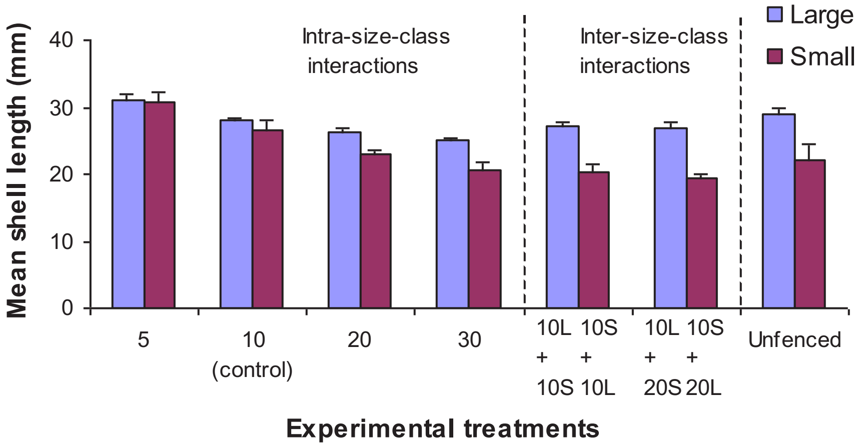

Figure 4- Mean shell length (± SE) at the end of the experiment (cf. Table 1).

Table 5- ANOVA on the mean shell length at the end of the experiment. ns = not significant, * $p<0.05$, ** $p<0.01$, *** $p<0.00$

Source of variation	df	MS	*F*
Among all	9	31.57	14.04 ***
Large *vs.* Small = L	1	165.00	73.39 ***
Among Exp. Treatm. = T	4	20.15	8.96 ***
Control *vs.* others	1	69.66	30.98 ***
Among others	3	3.65	1.62 ns
Density = D	1	9.23	4.11 ns
Size = S	1	0.23	0.10 ns
D x S	1	1.49	0.66 ns
L x T	4	9.63	4.28 *
L x Control *vs.* others	1	21.01	9.34 **
L x Among others	3	5.83	2.60 ns
L x D	1	1.64	0.73 ns
L x S	**1**	**15.80**	**7.03 ***
L x D x S	1	0.06	0.03 ns
Residual	20	2.25	
Cochran's test		(Among all)	C = 0.23 ns
SNK tests			
L x S:		**Alone (S1)**	**Mixed (S2)**
SE = 0.61		Large Small	Large Small
		25.57 > 21.66 **	26.99 > 19.84**
		Large	**Small**
		L L+S	S S+L
		25.57 26.99 ns	21.66 > 19.84*

Table 6- ANOVA on growth rate. ns = not significant, * $p<0.05$, ** $p<0.01$, *** $p<0.001$

Source of variation	df	MS	*F*
Among all	9	594.69	30.73 ***
Large *vs.* Small = L	1	4504.87	232.76 ***
Among Exp. Treatm. = T	4	132.32	6.84 **
Control *vs.* others	1	389.61	20.13 ***
Among others	3	46.56	2.41 ns
Density = D	**1**	**115.99**	**5.99 ***
Size = S	1	23.09	1.19 ns
D x S	1	0.60	0.03 ns
L x T	4	79.52	4.11 *
L x Control *vs.* others	1	146.57	7.57 *
L x Among others	3	57.17	2.95 ns
L x D	1	19.80	1.02 ns
L x S	**1**	**151.13**	**7.81 ***
L x D x S	1	0.58	0.03 ns
Residual	20	19.35	
Cochran's test		(Among all)	C = 0.22 ns
SNK tests			
L x S:		**Alone (S1)**	**Mixed (S2)**
SE = 1.80		Large Small	Large Small
		3.16 < 30.48 **	6.22 < 23.50**
		Large	**Small**
		L L+S	S S+L
		3.17 6.22 ns	30.48 > 23.50*
Density:		**20**	**30**
SE = 1.27		18.04 >	13.65*

Shell height in decreased density treatments

It was observed both during the experiment and at its termination that small limpets in decreased density treatments had a flatter shell than the large ones. This was despite the fact that they reached approximately the same total shell length as large limpets by the end of the experiment, which corresponded to a mean shell increment of 17mm. One-way ANOVA showed that shell height was significantly higher in decrease density treatment for the large than for the small size-class ($F_{1,4}$ = 13.48, $P<0.05$; SNK test< 0.05). The trend lines of the shell/height relationship (Fig. 5) also reflect the different shell shape between small and large limpets. The flatter shell in the small limpets is typical of a fast growing form.

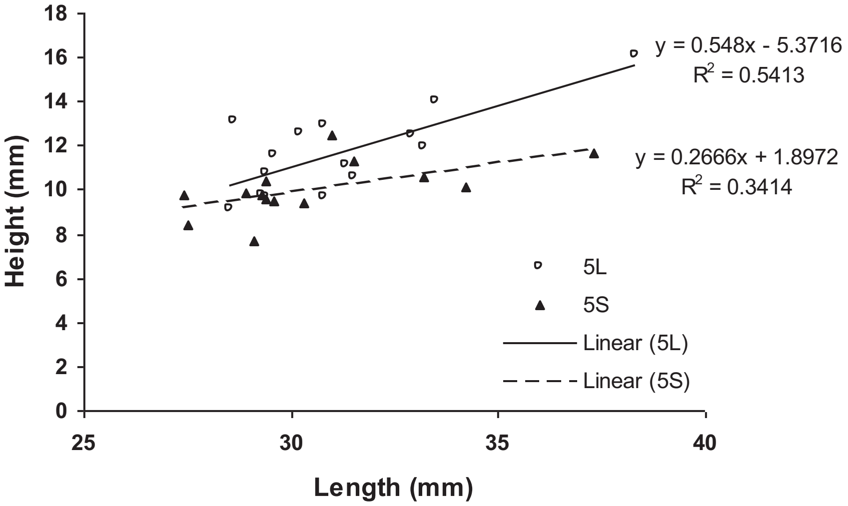

Figure 5- Relation between height and length in the decreased density treatments.

Effects on dry weight

Despite the similarities in the length of large and small limpets in control and decreased density treatments mentioned above, results from mean dry weight at the end of the experiment showed that small limpets still had a consistently lower tissue weight than large limpets (Fig. 6, Table 7). The weight of large and small limpets in controls was significantly higher than in the increased densities (Fig. 6, Table 7). Double and triple density did not differently affect the mean dry weight of limpets nor did the size mixture had any influence.

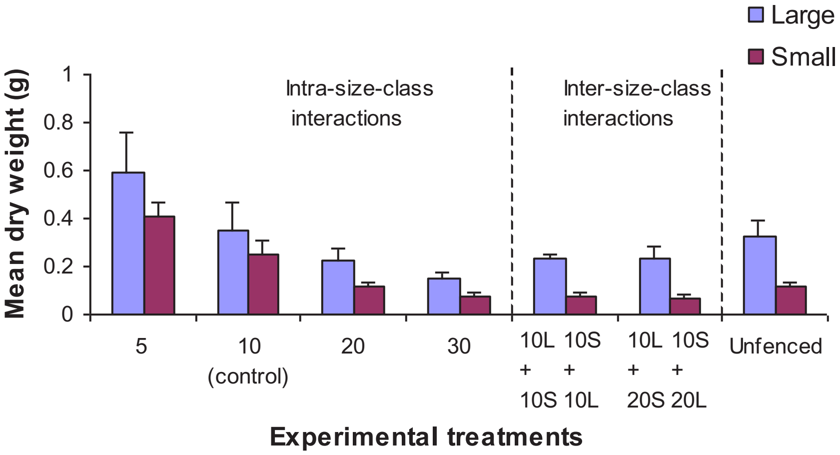

Figure 6- Mean dry weight (± SE) at the end of the experiment (cf. Table 1).

Table 7- ANOVA on mean dry weight at the end of the experiment. ns = not significant, * p<0.05, ** p<0.01, *** p<0.001

Source of variation	df	MS	*F*
Among all	9	1.00	7.53 ***
Large *vs.* Small = L	1	4.82	36.36 ***
Among Exp. Treatm. = T	4	0.83	6.29 **
Control *vs.* others	1	2.80	21.14 ***
Among others	3	0.18	1.34 ns
Density = D	1	0.29	2.21 ns
Size = S	1	0.00	0.03 ns
D x S	1	0.23	1.77 ns
L x T	4	0.21	1.56 ns
L x Control *vs.* others	1	0.46	3.46 ns
L x Among others	3	0.12	0.93 ns
L x D	1	0.00	0.00 ns
L x S	1	0.37	2.76 ns
L x D x S	1	0.00	0.02 ns
Residual	20	0.13	
Cochran's test	Transfomation = log (X)		C = 0.23 ns

Effects on reproduction

Sex

Results from sex determination at the end of the experiment showed that neuter individuals only occurred in the increased density treatments (Table 8). In the large size-class neuter animals occurred only when the density was increased to the triple while for the small size-class both double and triple densities had neuter limpets. A larger male percentage was also found in the increased density treatments suggesting that sex ratio can be influenced by the different experimental treatments. However, since the sex was determined only at the end of the experiment and there was no information about the sex proportion in the start of the experiment, these results should be interpreted with caution.

Table 8- Percentage of various sexes (and n value, for pooled replicates) at the end of the experiment for large and small size classes in the different treatments.

Large	**5L** (n=15)	**Control 10L** (n=24)	**Unfenced 10L** (n=19)	**20L** (n=29)	**30L** (n=30)	**10L10S** (n=26)	**10L20S** (n=17)
Neuter	0%	0%	0%	0%	10%	0%	6%
Male	60%	46%	58%	65%	63%	62%	70%
Female	40%	54%	42%	35%	27%	38%	24%
Small	**5S** (n=14)	**Control 10S** (n=28)	**Unfenced 10S** (n=12)	**20S** (n=47)	**30S** (n=58)	**10S10L** (n=15)	**10S20L** (n=9)
Neuter	0%	0%	0%	4%	12%	7%	22%
Male	50%	64%	58%	60%	53%	67%	33%
Female	50%	36%	42%	36%	35%	26%	45%

Gonad stage

In addition to the trends described above in relation to sex proportion, the stage of gonad development also seemed to vary according to the different experimental densities and size combinations (Fig. 7). Limpets with gonad index 4 were present only in decreased densities and controls. In increased density treatments the gonad development only reached at most stage 2 or 3. The effects of increased densities were more obvious for the triple density treatment in the large size-class whereas for small limpets a double density was enough to produce a response in the gonad stage.

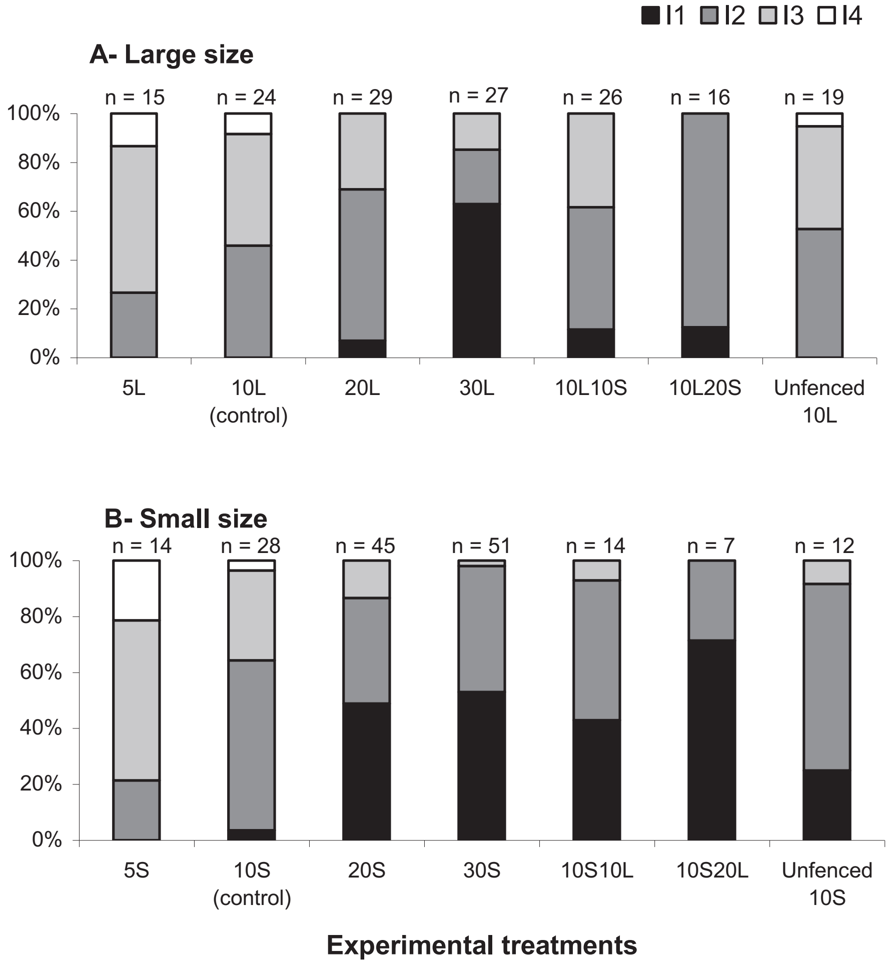

Figure 7- Gonad index (I1, I2, I3, I4- following Orton's (1956) scale) at the end of the experiment for large (A) and small (B) size classes (cf. Table 1).

Food assessment

In contrast with the effects of different densities and size combinations on mortality, biometry parameters and reproduction, results from chlorophyll concentration did not show any clear trends (Fig. 8). The chlorophyll concentration in the large size-class was significantly higher in the control than in the treatment 30L (Table 9A, SNK tests) but there were no significant differences among all the other treatments regardless of their density or size combination. Density and size had no significant effect on chlorophyll concentration in the small size-class, nor any significant difference between the large and small size-class was found (Table 9). The obtained results might be related to high variance and methodological procedures.

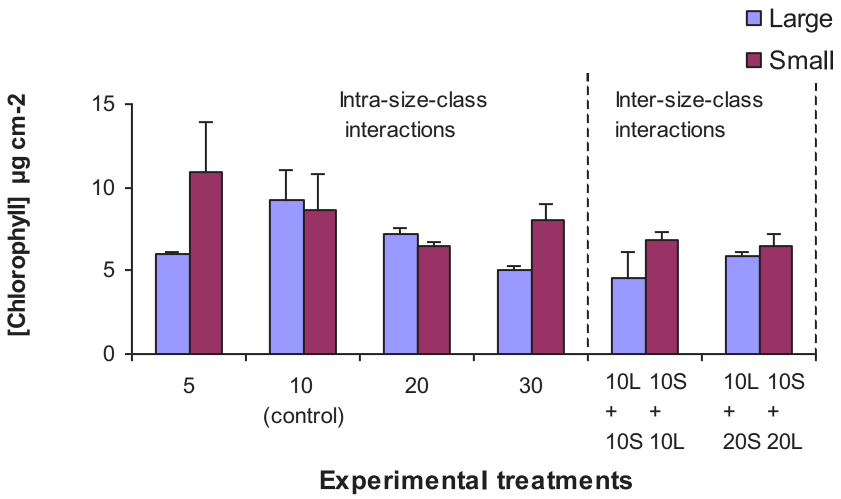

Figure 8- Mean chlorophyll concentration (±SE) at the end of the experiment (cf. Table 1).

Table 9- ANOVA on the chlorophyll concentration at the end of the experiment. ns = not significant, * p<0.05, ** p<0.01, *** p<0.001

Source of variation	df	MS	*F*
Among all	9	5.64	1.87 ns
Large *vs.* Small = L	1	3.95	1.31 ns
Among Exp. Treatm. = T	4	8.22	2.73 ns
Control *vs.* others	1	30.92	10.25 **
Among others	3	0.66	0.22 ns
Density = D	1	0.23	0.08 ns
Size = S	1	1.62	0.54 ns
D x S	1	0.11	0.04 ns
L x T	4	3.49	1.16 ns
L x Control *vs.* others	1	2.97	0.98 ns
L x Among others	3	3.66	1.21 ns
L x D	1	3.48	1.15 ns
L x S	1	0.08	0.03 ns
L x D x S	1	7.42	2.46 ns
Residual	20	3.02	
Cochran's test			C = 0.42 ns

DISCUSSION

Competitive interactions within and between size-classes

The results from the present experiments provided clear evidence of intraspecific competition in the limpet *Patella depressa*, within and between size-classes. Decreased density led to a better performance in growth, weight and gonad development of both large and small limpets, and to a reduction in mortality. Increases in density within and between size-classes significantly reduced the survivorship of both large and small limpets. The effects of size resulted in different responses for the large and small size-class. Large limpets suffered a higher mortality when fenced on their own than when fenced together with small limpets. Conversely, the mortality of small limpets was higher when the large competitors were present than when fenced on their own. These results reveal different strengths in the competitive interactions. Large limpets have a higher competition within the size-class and are also superior competitors to the small limpets.

Sub-lethal effects on length and growth were more pronounced in the small size-class. Small limpets had the highest growth rates during the experiment and reached almost the same size as large limpets in control and decreased density treatments but remained with a considerably lower size at increased densities. The addition of limpets from the other size-class, resulted once more in different responses in the large and small limpets. The addition of small limpets did not affect the growth and length of large limpets whilst the addition of large limpets significantly reduced growth and length of small limpets. Dry tissue weight remained higher for large than small limpets and higher in controls than in increased densities.

Size has been considered as being important in determining competitive superiority, with the larger individuals (either from different species, age- or size-class), being usually superior (Connell, 1983; Schoener, 1983). Our results match this general expectation. A higher requirement for food among large limpets and their size difference could lead to asymmetry in competition for food (through exploitation or interference competition). Competitive superiority has been frequently discussed for marine intertidal communities (e.g. Dayton, 1971; Underwood, 1978; Creese & Underwood, 1982; Schoener, 1983; Connell, 1983; Marshall & Keough, 1994). Other reasons determining competitive ability of grazing gastropods can in many occasions be related to the feeding biology of the species, such as, the feeding behaviour, extent of grazing excursions and, differences in structure of the radulae (Underwood, 1978; Creese & Underwood, 1982; Lasiak & White, 1993; Marshall & Keough, 1994).

The effect of density on intraspecific competition has often been demonstrated by an increase in mortality and/or a reduction in growth and weight of the animals (e.g. Branch, 1975a; Underwood, 1976). The effect of size- or age-classes has been more difficult to assess.

Asymmetry in intraspecific competition in the limpet *Cellana tramoserica* was, however, described by Marshall & Keough (1994) in south Australia. They found that competition between limpets was asymmetrical, with small limpets being superior to large ones in competitive ability. Large limpets were affected by competition with both large and small size-classes, whilst small limpets were only affected by other individuals of similar size. The asymmetry in size-class competition was attributed to the fact that microalgae were not equally accessible to large and small limpets. Smaller radulae allowed small limpets to utilise additional food reserves, for example within small pits, for which they did not compete with large limpets. The changes in microalgae abundance supported their results and indicated that exploitative competition was occurring. Thus, the results of the present study contrast markedly with the findings of Marshall & Keough (1994). Our experiments were established on a very smooth rocky surface where large and small limpets had apparently equal access to microalgal food, so these results do not necessarily go against the explanatory model proposed by Marshall & Keough (1994). It shows, however, that competition might be variable in intensity or occurrence form time to time and place to place and that, is therefore important to analyse competitive interactions in different systems before any general conclusion is taken. Different competitive mechanisms and/or methodological approaches in the experiment can be responsible for the observed differences. The effects of competition within and between size-classes in *Cellana tramoserica* were investigated by manipulating biomass. In our experiments on competition in *Patella depressa* densities were manipulated instead. It is possible that manipulation of biomass under the assumption of a linear relationship between biomass and resource requirements, which would increase the number of small limpets in the different treatments, could have a higher effect on large limpets. Under these circumstances, however, the proportion of small and large limpets in the experimental plots would be, in our case, very different from that observed in natural conditions. By manipulating densities we assured that the number of limpets in the several treatments matched the range of densities observed on the shore, so that any inferred conclusion in this study applies to natural conditions.

Unfenced controls plots were used in this experiment to test if there was any artefact due to the use of fences. The use of fences may interfere with the behaviour and foraging activity of the limpets since their movements were limited to the fenced area and were thus unable to move as far as in natural conditions. It may also indirectly affect the quantity of microalgae due to changes in the natural environment. Large limpets did not seem to be affected by the use of fences since there were no significant differences between fenced and unfenced control for any of the studied parameters. No significant differences were detected on the tissue weight, growth rate, mean shell length and height of small limpets between the two controls. However, mortality of small limpets was greater in the unfenced control than in the fenced control. Several explanations can be offered for this fact. Firstly, this might be due to inability to relocate marked limpets in the unfenced controls during the experiment. Secondly, predation could cause preferential reduction of the limpets in the unfenced areas. Finally, competition with large limpets in the unfenced controls could lead to increased mortality.

Although not impossible, the loss of marked animals is unlikely. The paint marks were retouched in every visit to the shore and, even though limpets could move over wider areas in the unfenced control, all the area was checked carefully to find the tagged animals.

Predation of limpets is also unlikely to justify the differences on mortality between unfenced and fenced areas. Fenced plots had no roof so predators could have had access to both areas equally. It is also possible that the fences could modify the behaviour of the predators. Possible predators in this area would be birds and crabs. Birds were never observed to eat limpets. There is some indication that crabs may eventually eat limpets as they were seen to eat dead limpets on this shore (Flores pers. com.). Predation does not seem to play a major role in decreasing the severity of competitive interactions in this community, such as described in the literature for North American shores (Connell, 1961, 1970; Dayton, 1971; Paine, 1974; Menge, 1976). Nevertheless, this subject needs to be investigated in future studies.

Competition with large limpets could justify the higher mortality in unfenced plots. Density of small limpets was the same in both controls yet inside fenced areas they were protected from encounters with large limpets. On the contrary, limpets in unfenced controls were allowed to forage over an unlimited area and, encounters with large may have had some influence in the densities observed at the end of experiment. Under these circumstances, however, comparisons between inside and outside fences can be confounded by the different and uncontrolled densities and mixtures of sizes outside the fences (Quinn & Keough, 1993).

The effect of competitive interactions on output of gametes may be important in the sense that this has a direct influence on recruitment, and hence in the future abundance of the species (Branch, 1975a). Results of sex and gonad development followed the patterns described for mortality. Neuter individuals and the animals with the lower gonad index occurred at higher proportions in increased densities indicating that this factor is likely also to affect the reproductive output. The effect on the output of gametes may be direct reducing the relative size of the gonad or, it may be indirect by simply reducing the mean size of the sexual individuals (Branch, 1975a).

Competition for food resources: exploitative or interference competition?

There was some evidence that food resource was in short supply. Grazers at natural and increased densities were suppressing entirely the growth of macroalgae, and were thus eating all the available food. In contrast, green ephemeral algae immediately colonised decreased density treatments. However, no significant differences in chlorophyll concentration were found among the several treatments at the end of the experiment. Several explanations can be offered for the lack of clear trends in chlorophyll concentration as those seen for the other studied parameters. First, it is possible that problems with the methodological procedure used in the experiment were involved. It was very difficult to remove thin rock chips from the limestone bedrock and the height of the rock chips probably added variability to the data. Hence, differences in chlorophyll concentration would only be detected if a very strong effect occurred. Secondly, it was observed that some of the rock chips had endolithic blue-green algae. It would have probably been better to do the estimate of chlorophyll concentration but to also use scanning electron microscopy (SEM). Using both methods simultaneously it would be possible to check for quantitative and differences in the microfilm and also to check whether the composition of the film differed among treatments. Finally, interference competition between large and small size-classes cannot be ruled out. Effectively, and despite some evidences of competition for food, this experiment did not differentiate completely between exploitative and interference competition between large and small limpets. Active defence of territories, as those described for *Lottia gigantia* (Stimson; 1970, 1973) and *Patella longicosta* (Branch, 1975b, 1976), is unlikely to occur in the limpet *Patella depressa*. Territoriality has never been described for this species, nor any territorial behaviour was observed in many hours of observation on the shore. However, interference interactions could result from i) direct encounters between large and small limpets; ii) crowding of large limpets around small limpets, therefore restraining their movements; or iii) an indirect effect due to space occupied by large animals, with high densities of large individuals simply limiting the space over which small limpets can forage. Some of these mechanisms have been proposed by Lasiak and White (1993) to justify the lack of significant differences in chlorophyll levels among treatments whilst a reduction in tissue weight was observed. In fact, the interference explanation could account for most of the observed trends on mortality and sub-lethal effects in the present study.

Outcome of competitive interactions: effects on coexistence and distribution patterns

It has been demonstrated in a wide number of studies that density dependent processes can regulate the abundance of limpet populations (see Branch, 1981; Hawkins & Hartnoll, 1983; Underwood, 1992 for a review). In *Patella depressa* population at Cabo Raso small limpets were clearly affected by competition with larger individuals. It was also observed that, within the wide range of habitat occupied by this grazer in the mid-shore region, the small limpets are more abundant on the lower zone. This distribution pattern of juveniles closer to the water has been described for several gastropod species (Underwood, 1979; Branch, 1981) and is generally regarded a form to reduce mortality due to desiccation (Lewis & Bowman, 1975). Starvation is also less likely to occur on the lower shore since the microalgal food resources are generally more abundant at low levels (Castenholz, 1963; Nicotri, 1977; Underwood, 1984a,b). In view of the dramatic impact large limpets can have on small size-class it could be postulated that the absence of small limpets from areas on the shore, where large limpets occur in high densities, could be a result of competitive interactions. In fact, niche partitioning, migration and dispersion behaviours can be considered as a mechanism for reducing competitive interactions (Branch, 1975b; Branch, 1981). However, results from the present study revealed that other factors, like the competition within the size-classes, might play a more important role in the coexistence of the size-classes than niche partitioning. It was experimentally demonstrated by Creese and Underwood (1982) that competitive exclusion in interspecific competition is extremely unlikely to occur among shallow coastal grazers. Due to the shortage of food the densities of the superior competitor will be reduced by intraspecific competition to a level below that necessary to keep producing a deleterious effects on the inferior competitor. An analogous regulatory mechanism may enable coexistence between size-classes in the present study. Hence, the major factor allowing coexistence between size-classes, is probably the effect of a very high competition within the large size-class, which reduces density below levels at which they can completely eliminate small limpets. Niche partitioning and high rates of recruitment of juveniles can also influence the structure and stability of the population.

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CHAPTER 6

General discussion and conclusions

CONTENTS

GENERAL DISCUSSION AND CONCLUSIONS

The causes of distribution patterns on rocky shores and the role of grazing and competition as structuring agents of intertidal communities were studied in the present work.

Intertidal rocky shore communities of the continental Portuguese coast were analysed using a qualitative and quantitative approach. A reference study of zonation patterns along the whole coast and a systematic comparison of abundances of organisms along a vertical and horizontal gradient have undoubtedly been missing in Portugal until now.

Local and broader scale patterns

A littoral fringe characterised by the presence of encrusting lichens, small littorinid gastropods and cyanobacteria was found on most of the shores along the Portuguese coast. This may be considered as a world-wide feature of the upper zone of intertidal rocky shores (Stephenson & Stephenson, 1972; Raffaelli & Hawkins, 1996).The eulittoral zone of Portuguese rocky shores is essentially dominated by barnacles and sometimes mussels. This pattern corresponds to that described for exposed north east Atlantic shores (Ballantine, 1961; Lewis, 1964; Raffaelli & Hawkins, 1996). The distribution patterns observed on the sublittoral fringe showed a clear difference between northern shores where large brown algae are present and shores located in the central and southern regions, essentially dominated by red algal turf species. Hence, zonation patterns in Portugal may be seen as mixture of the patterns described for the north east Atlantic coasts (Lewis, 1964) and those described for the Mediterranean (Pérès & Picard, 1964). The results of this study also confirm the latitudinal variations in zonation patterns described by Hawkins et al. (1992). From north to southern Europe, animal dominated communities extend further into shelter at more southerly locations. Similarly, southwards, dominance by large brown algae declines low on the shore and red algae turf become more important (Hawkins et al. 1992).

The quantitative approach used in the present study not only confirmed the trends observed in descriptive work, but also enabled questions to be answered about possible differences in community structure between upper and lower mid-shore level and across north centre and south regions. Multidimensional analysis and the ANOSIM test have revealed clear differences in the structure of upper and lower mid shore zone. The number of species found in the upper and lower level definitely contributed to the obtained differences. In general, the upper level exhibited a lower diversity and a higher dominance. SIMPER analyses confirmed the species with the highest contribution to the dissimilarity between the two levels.

Chthamalus spp., *Patella depressa*, *Siphonaria pectinata*, *Melaraphe neritoides*, *Monodonta* spp. and *Littorina saxatilis* had a higher abundance in the upper mid-shore level whilst *Mytilus galloprovincialis*, *Patella ulyssiponensis*, *Gibbula* spp., *Sabellaria alveolata*, *Actinia* sp., *Patella vulgata*, *Nucella lapillus* and a variety algal species were more important to characterise the lower level. These results support the vertical distribution patterns described in this study and in the literature (e.g. Lewis, 1964; Stephenson & Stephenson, 1972; Saldanha, 1974).

Portuguese rocky shores provide an excellent location for the study of biogeographical patterns and processes. Despite the decrease in abundance of several species along the regional gradient the differences in the community structure were not as clear as for the vertical gradient. A possible explanation for this is that the increase in complexity of the community from high to low shore is superimposed on the latitudinal changes. The latter do not affect community parameters like species richness, total number of individuals, biodiversity and eveness, with the same intensity as vertical distribution. Within each level, however, the northern region was considerably different from the south and central regions. SIMPER analysis revealed the species which contributed to the geographical separation of the northern region in relation to the centre and south. It has also given important information on the geographical decline in abundance of species such as, for example, *Mytilus galloprovincialis*, *Nucella lapillus*, *Siphonaria pectinata* and *Patella vulgata*. Hypotheses on the distribution of limpets along the vertical and horizontal gradient were tested specifically for *Patella depressa* and *Patella vulgata*, since these are the limpet species which are typical of the mid-shore zone studied. *Patella depressa* is widely distributed and abundant in all mid-shore area of the entire Portuguese coast. The relative abundance of this limpet in the lower or upper mid-shore zone varied, depending on the shores. *Patella vulgata* was more abundant in the north than in the centre and southern regions either for upper or lower mid-shore zone. In the northern region, however, where *P. vulgata* occurred with higher densities, it was more abundant in the lower mid-shore level.

Despite the effort and amount of information gathered in this study, there is much still to be done regarding the distribution patterns of organisms along the Portuguese coast. For instance, the quantitative approach was only used for the upper and lower mid-shore zone and, seasonal variation was not analysed. Fortunately, these aspects will soon be complemented with the results from a national research project. None the less, the information obtained with the present study has clarified several questions related to the vertical and horizontal distribution of organisms on intertidal rocky shores of the continental Portuguese coast.

Experimental ecology

The importance of experimental ecology as one of the most profitable methods of determining the factors affecting the distribution and abundances of species has been recognised world-wide. Intertidal organisms have proved to be suitable to experimental manipulation because of the ease access to the shore, and because of the relatively sessile nature of the organisms (Underwood, 1979). A great part of the work in this thesis involved the experimental study of distribution patterns of organisms on the shore, in particular the effects of grazing and competition in intertidal communities.

Causes of distribution patterns

The effect of grazing on the distribution and composition of low shore algal communities was studied on the central coast of Portugal and on the southern coast of Britain. A red algal turf is often found just below the barnacle/limpet zone of many European shores, especially on steep shores of moderate exposure. The hypothesis that grazing by limpets determines the upper limit of distribution of the red algal turf was tested in moderately exposed shores in both countries. We also aimed to assess whether the grazing effect is modified by different factors operating at various spatial scales. Grazers were excluded by fences, and there were half-fenced and unfenced controls. The experimental design and methodology used in these experiments proved to be effective to test the initial hypotheses. No artifacts occurred and all the conclusions were based upon comparison with valid controls. Moreover, the design included several spatial scales (Locations, Shores, Patches) and it was possible to compare the effects of grazing across this range of spatial scales. Few studies have investigated the effects of grazing at more than one spatial scale (e.g. Sousa et al., 1981). A morphological group approach was also adopted and proved to be useful for broad scale comparison of different communities.

The present study has shown that grazing by limpets has a significant influence on the upper limits of distribution of low shore turf forming macroalgae in the North East Atlantic coasts- both in Portugal and in the U.K. These experiments support the results obtained by Underwood (1980) on New South Wales coasts (Australia) that grazing, primarily by gastropods, is the major determinant of the upper limits of vertical distribution of many species of low shore foliose algae.

Exclusion plots were rapidly colonised by green ephemeral algae in the months immediately after the beginning of the experiment (summer); these algae were later replaced by perennial algae. The percentage cover of turf-forming macroalgae showed a significant increase at both locations. Their upper limit of distribution extended more than 50 cm in most of the shore areas. In contrast, control and half-fenced plots remained devoid of algae. After two years, ungrazed areas were mainly colonised by red algal turf (e.g. *Caulacanthus ustulatus, Gelidium* spp.*, Laurencia pinnatifida*) in Portugal, while canopy cover (*Fucus serratus* and *Himanthalia elongata*) dominated in Britain. The establishment of opportunistic species of algae, and/or an increase in abundance of fucoids is usually found in experiments where grazers are removed from areas of the shore (Dayton, 1971; Underwood, 1980; Lubchenco, 1980, 1982; Lubchenco & Gaines, 1981; Hawkins, 1981a,b; Hawkins & Hartnoll, 1983; Jernakoff, 1983, 1985; Underwood & Jernakoff, 1984; Raffaelli & Hawkins, 1996). The establishment of turf algae in grazer exclusion plots is not so common (but see Jara & Moreno, 1984; Carter & Anderson, 1991). By the end of this experiment mature perennial algae dominated exclusion plots in both Portugal and Britain.

After two years of this experiment, the fences were removed and the fate of established macroalgae was monitored at the Portuguese location. After re-encroachment of limpets macroalgae established in exclusions converged with the plots that were not perturbed and the difference in algal abundance between manipulated and unmanipulated plots lasted less than six months. The community that developed while limpets were excluded was not a persistent alternative state. This result is consistent with the one obtained by Farrell (1988) after limpet re-introduction. The mature perennial algae that developed in our experiments did not decline due to wave action and macroalgae reached a size that might be expected to make them invulnerable to limpets grazing (Lubchenco & Gaines, 1981; Hawkins & Hartnoll, 1983), but still they declined in less than six months. One possible explanation would be that limpets preferentially graze on microalgal propagules but can alternatively consume adult turf. The role of a multi-species assemblage of *Patella* in this experiment may also be important for understanding how grazers reduced the cover of macroalgae turf. *Patella ulyssiponensis* was seen to invade the exclusions and to graze on established macroalgae in the first place, while *Patella depressa* appeared later when there were already some clearings between the turf. Differences in the radula morphology and feeding behaviour of the two species may account for the observed grazing pattern (Hawkins et al., 1989; Della Santina et al., 1993).

Additional experiments on algal removal resulted in a rapid colonisation of calcareous turf algae and in a quick invasion of adult limpets in the clearings. Initially the limpets were mainly *Patella ulyssiponensis* that occur naturally at this level on the shore, but eventually

Patella depressa moved down-shore into the clearings. However, grazers showed no ability to prevent colonisation by calcareous turf algae at this level on the shore. This means that grazers are responsible for upper limits of distribution of macroalgae on the shore but below this limit, because algae colonise and growth more rapidly, they can not prevent algal growth.

In conclusion, although physical factors probably have an important influence on the size and abundance of sublittoral fringe macroalgae, grazers play a major role in directly setting its upper limits. Turf algae extended their upper limits of distribution in ungrazed areas at both studied locations. Furthermore, turf forming algae exclusively dominated ungrazed areas in southern Europe, while canopy rapidly became the dominant morphological algal group in northern Europe. Physical factors acting at both local and geographical scales are likely to explain these differences. Grazing by limpets was probably responsible for the decrease in algal cover after fences removal but limpets showed no ability to prevent or decrease algal colonisation in experimental clearings below the turf upper limit. Hence, the upper limit of algal turf seems to be in permanent dynamic balance between the activities of grazers at higher levels on the shore and the rapidity of colonisation and growth of the algae at lower levels, being modified by physical factors which favour algal growth or grazing efficiency.

The effect of season on the sequence of algal colonisation was not included in the present study. This was not logistically possible since it would involve at least the duplication of starting dates within each season. However, this work has provided new information for testing future hypotheses. For instance, the addition of the factor time would be interesting to test one hypothesis derived from the present work, that season would affect mainly the early colonists and the later succession stages would be essentially the same perennial species observed during this study.

Competitive interactions between the limpets *Patella depressa* and *Patella vulgata* were analysed on the northern coast of Portugal, where both species co-occur in similar proportions. Increased, decreased and normal densities of limpets were used to test the effects of competition on the growth and mortality of the limpets, and the influence of different species in competitive interactions. Inter- and intraspecific competitive interactions among *P. depressa* and *P. vulgata* have not been experimentally studied before. Competition between *P. aspera* and *P. vulgata* in Irish rocky shores has been deduced to occur because one species had reduced in numbers when the other was abundant. *P. aspera* occupies areas of strong wave action, but reduces in number as wave action declines and is progressively confined to the low-shore and replaced by *P. vulgata* (Thompson, 1979, 1980). This replacement may mean competitive displacement, but there was no experimental proof of this (Branch, 1981).

When competition occurs, it is necessary to detect differences in parameters such as mortality, growth, weight of individuals with and without the potential competitor (Connell, 1983; Underwood, 1992). The present experiments have revealed effects of inter- and intraspecific competition on the survivorship, length, weight and reproduction of these two species of limpets. Both species of grazing molluscs showed increased mortality and reduced growth and weight in increased density treatments. Limpets in decreased density treatments showed lower mortality and higher growth rate. Although both species could affect negatively the other, there were no significant differences between the effect of *P. vulgata* on *P. depressa* and the effect of *P. depressa* on *P. vulgata* on mortality and growth. Results from tissue weight, however, indicated an asymmetry between the relative strengths of inter and intraspecific interactions. Intraspecific increases in density resulted in a more accentuated reduction of weight than when both species were present.

The present study differed from the previous works in the sense that competitive interactions between *P. depressa* and *P. vulgata* were examined close to the southern biogegraphical limit of distribution of *P. vulgata*. Proportions of *P. depressa* and *P. vulgata* in Moledo do Minho (north of Portugal) are similar but, further to the south along the Portuguese coast, the densities of *P. vulgata* decline considerably, being occasional or rare in some places. In view of this pattern of distribution it could be expected to find superiority of *P. depressa* in competitive interactions. However, at the end of the experiment no significant differences were found on the effects of *P. depressa* on *P. vulgata* and vice versa. Moreover, the existence of a strong intraspecific competition indicated that both species are able to coexist. Hence, in the studied shore, where the two species density is still similar, and despite the proximity to the biogeographic limit of distribution, *P. depressa* coexist with *P. vulgata*, and the latter does not appear to be an inferior competitor.

Another experiment testing intra- and inter-size-class competition in the limpet *Patella depressa* was done in the central coast of Portugal. In this location *Patella depressa* is the dominant species at mid-shore level. Twelve treatments with different combination of densities and size-classes were assigned to experimental plots. Decreased densities led to a better performance in growth, weight and gonad development of both large and small limpets, and to a reduction in mortality. In contrast, both size-classes of limpets showed increased mortality and reduced growth in increased density treatments. The effects of size resulted in different responses for the large and small size-class. Large limpets suffered a higher mortality when fenced on their own than when fenced together with small limpets. Conversely, the mortality of small limpets was higher when the large competitors were present than when fenced on their own. Sub-lethal effects on length and growth were more pronounced in the small size-class. Small limpets had the highest growth rates during the experiment and reached almost the same size as large limpets in control and decreased density treatments but remained with a considerably lower size at increased densities. The addition of limpets from the other size-class, resulted once more in different responses in the large and small limpets. The addition of small limpets did not affect the growth and length of large limpets whilst the addition of large limpets significantly reduced growth and length of small limpets. In general, these results revealed different strengths in the competitive interactions. Large limpets have a higher within size-class competition and are also superior competitors to the small limpets. In view of the dramatic impact large limpets can have on the small size-class it could be postulated that the absence of small limpets from areas on the shore, where large limpets occur in high densities, could be a result of competitive interactions. However, results from the present study revealed that, other factors, like the competition within the size-classes, might play a more important role in the coexistence of the size-classes. It was experimentally demonstrated by Creese and Underwood (1982) that competitive exclusion in interspecific competition is extremely unlikely to occur among shallow coastal grazers. Due to the shortage of food the densities of the superior competitor will be reduced by intraspecific competition to a level below that necessary to keep producing a deleterious effects on the inferior competitor. An analogous regulatory mechanism may enable coexistence between size-classes in the present study. Hence, the major factor allowing coexistence between size-classes, is probably the effect of a very high competition within the large size-class, which reduces density below levels at which they can completely eliminate small limpets. Niche partitioning and high rates of recruitment of juveniles can also influence the structure and stability of the population.

The availability of food was indirectly assessed in both competition experiments by determination of chlorophyll concentration with spectrophotometric analysis of rock chips. The expected inverse relation between chlorophyll levels and density of limpets in the different treatments such as that found in previous works (e.g. Underwood, 1984; Lasiak & White, 1993; Marshal & Keough, 1994) was not confirmed in these experiments. Thus, there was no evidence from this study to prove that exploitation of resources was the direct cause of reduced survivorship, growth, weight and fecundity with increasing densities. Several explanations can be offered for the lack of clear trends in chlorophyll concentration as those seen for the other studied parameters. Different processes could have also been occurring in the experiments in the north and in the centre of Portugal.

In the experiment of inter- and intra-size-class interaction in the centre of Portugal there was some evidence that food resource was in short supply. Grazers at natural and increased densities were suppressing entirely the growth of macroalgae, and were thus eating all the available food. In contrast, green ephemeral algae immediately colonised decreased density treatments. The cover of algae in decrease density treatments declined towards the end of the experiment as the animals increased their size. The obtained results showed a high variability in chlorophyll concentration probably due to the presence of endolithic blue-green algae in the limestone rock chips. Hence, differences in chlorophyll concentration would only be detected if a very strong effect occurred. The variability in chlorophyll concentration may also be related to patchy distribution of resources. Escape to grazing pressure in decrease densities may lead to this patchy distribution and high variability. The reduction of variability in chlorophyll concentration with increasing densities supported this idea.

Interference competition between large and small size-classes of *Patella depressa* cannot be ruled out. Interference interactions could result from: i) direct encounters between large and small limpets; ii) crowding of large limpets around small limpets, therefore restraining their movements; or iii) an indirect effect due to space occupied by large animals, with high densities of large individuals simply limiting the space over which small limpets can forage. Some of these mechanisms have been proposed by Lasiak and White (1993) to justify the lack of significant differences in chlorophyll levels among treatments whilst a reduction in tissue weight was observed. In fact, the interference explanation could account for most of the observed trends on mortality and sub-lethal effects in the present study and for the competitive superiority of large limpets.

In the experiment on inter and intraspecific competition between *Patella depressa* and *Patella vulgata* run in the north of Portugal there was no such a great variability in chlorophyll concentration data. This may be partially associated to a different granite rocky substrate, not so favourable to the presence of endolithic blue-green algae. Mean values of chlorophyll were also relative low. This may indicate the shortage of food resources and it is possible that even a small density of limpets was able to maintain microalgal food resources at the low observed values. The rate of renewal of resources and the rate of consumption by limpets could then play an important role in the availability of food on the shore. Further experimentation with other methods of food assessment would be interesting.

The importance of competition has been frequently discussed (e.g. Underwood, 1992; Tokeshi, 1999). The detection of interspecific competition does not necessarily lead to its importance (Tokeshi, 1999). A wide variety of processes can affect the intensity or the outcome of competitive interactions (including physical factors in the environment, disturbances, predators, etc.). According to Underwood (1992) it is not possible to predict accurately the outcome of a competitive interaction unless the processes affecting the supply of the resources and the non-competitive processes affecting the abundances of the competitors are investigated. The present work has revealed significant consequences of competitive interactions. Competition is likely to be strong even at natural densities since individuals in decrease density treatments, when relived from this pressure had a better performance in terms survivorship, growth, weight and reproduction.

The present work has revealed that both grazing and competition are major biological factors determining the structure of intertidal rocky communities. This work has also contributed to refute old ideas on the causes of distribution patterns. Notwithstanding the obtained results on grazing and competition these factors cannot be regarded in isolation from other aspects of the ecology of the participants. This leads to the necessity of further experimentation on processes such as predation and the effects of physical harshness and disturbances on the studied rocky shores.

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