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INTERTIDAL ECOLOGY OF NORTHERN PORTUGUESE ROCKY SHORES

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ABSTRACT

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INTERTIDAL ECOLOGY OF NORTHERN PORTUGUESE ROCKY SHORES

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Abundance and zonation of species were described for northern Portuguese rocky shores. All shores displayed exposed or moderately exposed zonation patterns, with mussels and barnacles dominating the eulittoral zone. Biogeographic trends were analysed through non–metric multidimensional scaling, using also data from southern Portuguese sites. Differences between the northern and southern coast were mainly observed at the lower shore level. Several southern limits of cold–water species of brown macroalgae were observed in this region. Northern shores formed a distinct group within the Portuguese coast and were similar to those found on the northern coast of Spain, French Brittany and southwest coast of the United Kingdom.

The dynamics of midshore mussel assemblages was investigated at several spatial and temporal scales. A model was put forward, using wave action as the main factor driving the variation of mussel occupancy through time. Percentage cover of mussels, barnacles and free space were highly variable through time. Mussels did not display any seasonal patterns at the shore or site scales. Conversely, the percentage cover of barnacles decreased significantly during the winter, whilst free space increased after it. The proposed model was rejected, and a new model was developed based on the evidence gathered. The new model predicted that gains and losses in area would be similar within each season but higher during the winter. Moreover, losses in the winter would be compensated by growth of mussels on top of barnacles. These predictions were partially supported by the analyses of gains and losses in area at the individual patch scale.

Species interactions were investigated through field experiments. The exclusion of limpets enhanced the development of macroalgae. Both ephemeral and perennial species appeared after limpet exclusion, but the results were not consistent among shores or years. Barnacles were shown to enhance mussel secondary settlement, thus supporting the predictions of the new model. Overall, the results suggest that the patch dynamics of the mussel/barnacle mosaics should be highly dependent on barnacle population dynamics.

The effects of an oil spill on mussel percentage cover and limpet density were assessed through the use of 'beyond BACI' analyses. No effects were detected, either on mussels or limpets, most probably because the variability caused by the oil spill was within the natural range of variability of these populations.

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Contents

Chapter 1

General Introduction

Coastal zones face a variety of pressures as a consequence of high levels of human activity. The northern Portuguese coast is not an exception, and rocky shores, in particular, are heavily exploited. During the year, many animals are collected for food, either for personal use or for trading in local markets. Harvesting of seaweed is still practised on some regions, not only as a source of fertilizer for traditional farming, but also for the manufacture of carrageenans. During the summer months, the shore is also used for leisure activities, and the human population in the littoral increases several fold. Yet, the impact of all those activities over intertidal organisms is not fully understood (Raffaelli and Hawkins, 1996).

Two other factors can affect the coastal zone: erosion and pollution. Although it is a natural phenomenon, erosion is of major concern. Building over non–consolidated sand dunes or on the top of chalk cliffs, ignoring the risks of winter storms and the strength of the sea, is a widespread practice all over the Portuguese coast. Uncontrolled development of coastal defences, whether to protect single houses or entire villages, interferes with the dynamics of coastal sediments, with the obvious consequences. Chronic pollution is usually associated with industrial and domestic effluents. Discharging raw sewage directly into the sea is commonplace in Portugal. Since in most cases industrial effluents are mixed with domestic wastes, elevated levels of heavy metals and other persistent contaminants are usually observed in sea water. However, one of the most problematic sources of pollution on the northern coast of Portugal is oil spills.

The north of Portugal is served by a large commercial harbour (Leixões, Oporto), which also includes an onloading terminal of one of the biggest oil refineries in the country, a few kilometres north (Cabo do Mundo). The entrance to the harbour is usually difficult for large vessels, mainly due to the harshness of the sea, especially during winter months. Several accidents occur throughout the year, not only with oil–tankers but also with trawlers and other small ships. During the last ten years, at least four major oil spills occurred.

The source of the oil spills is not always attributable to accidents with oil–tankers: at least three of the observed oil spills originated inland, two of them due to a malfunctioning of a pipeline valve, and the third because of an illegal discharge of two tons of crude oil directly into a sewer. An underwater pipeline, built in 1998, solved most of the problems related to harbour approaches and entrance, thus increasing the rate of oil transfer during the year. Nevertheless, it has also increased the rate of small scale oil-spills, with origins probably related to illegal cleaning of vessel tanks or negligent usage of the offshore buoy. Since in most cases the released crude is of light type, it does not sink immediately, and is carried by the prevalent inshore swells to the coast. The midshore is usually the worst affected zone, and the tidal movements often contribute to the dispersion and deposition of the crude on sandy and rocky shores.

In recent years, environmental concern has drastically increased, and local authorities, as well as governmental institutions, have paid more attention to the issue. Sewage treatment, planning regulation, ecosystem restoration, all have been widely discussed but seldom implemented. As public opinion becomes better informed, there is an increasing pressure from governmental and regulatory authorities over the scientific community to identify the consequences of human activities on the environment, as well as to develop adequate measures to mitigate their impacts.

Unfortunately, the whole coast of Portugal – and particularly the northern rocky shores – has been neglected by marine ecologists in the last decades, with little work done since Nobre (1931, 1938a,b, 1940) and Ardré (1970, 1971). The absence of baseline data makes it impossible to evaluate the putative effects of such impacts, thus opening a door to a sterile discussion, where the lack of strong and scientific arguments prevail.

The main purpose of my thesis is to contribute to a deeper knowledge of the major structuring forces on the intertidal shores of northern Portugal, so as to provide consistent data for the analysis of human impacts on these ecosystems. After some initial description of pattern, emphasis will be put in the most recent advances and interpretations of community organization. Oil-spills, like any other impacts of human activity over the coastline, can be seen as a source of disturbance. Unlike the traditional approach to the understanding of community structure, recent ideas explicitly consider disturbance as a major structuring agent of biological communities contributing to their patchy nature (Wu and Loucks, 1995). Therefore, in the first Chapter, a detailed review of patch–dynamics will be made in the context of intertidal ecology.

1.1 Patterns and processes on rocky shores

Rocky shores have long been investigated in several parts of the world (Stephenson and Stephenson, 1972). Since they are virtually two–dimensional systems they are far less complex than their terrestrial counterparts. Moreover, the ease with which manipulative experiments can be carried out on them, and the relative small scale at which strong environmental gradients can be observed, makes them attractive for experimental ecologists (see Raffaelli and Hawkins, 1996, for a review). One of the most striking features of intertidal rocky shores is the conspicuous distribution of organisms in well defined belts, called 'zones'. This particular pattern is in some way related to the vertical gradient of physical conditions, from fully marine to terrestrial, which is amplified by the tides (Lewis, 1964). The stress gradient is mainly unidirectional (Lewis, 1964; Raffaelli and Hawkins, 1996): in the upper parts of the shore the organisms will be exposed to the air during much longer periods than those that live in the lower zones, and since almost all forms of life inhabiting intertidal shores are marine species, this means that they will have less time to feed and will be more exposed to the harshness of terrestrial life (larger daily temperature variations, sunlight, heat, cold). As biologists failed to find any straightforward correspondence between the boundaries of organisms distribution and tidal levels, a descriptive framework based on biological characteristics (Stephenson and Stephenson, 1949, 1972) was developed (but see Ricketts *et al.*, 1968; Foster *et al.*, 1988).

1.1.1 Describing the patterns

Zonation patterns have been described by several authors in the 19th century (e.g., Audouin and Milne-Edwards, 1832; Vaillant, 1891) and early 20th century (e.g., Baker, 1909; Walton, 1915; Colman, 1933) but it was the work of Stephenson and Stephenson (1949) that showed, for the first time, the consistency of such patterns on a world-wide scale. Several schemes of zonation have been proposed since then, differing in their terminology, the number of zones considered and even in the way of delimiting them (Pérès and Picard, 1958, 1964; Lewis, 1964; Ricketts *et al.*, 1968). Numerous descriptions of zonation patterns on intertidal rocky shores can be found everywhere in the world (see Raffaelli and Hawkins, 1996, for review). These works showed how variable zonation patterns could be. Two main factors contributed to this variability: wave action and biogeography.

The effects of wave action on the zonation of intertidal organisms are evident. On sheltered shores in the north-east Atlantic, the midshore is usually blanketed by large brown fucoid algae. As exposure to wave action increases, the algae are replaced by other species, such as barnacles, limpets and mussels. In very exposed environments, seaweed are restricted to the lower zone (Lewis, 1964). Biogeographic differences also account for the variability of observed zonation patterns. Although there are some cosmopolitan species, most organisms are endemic to certain regions or oceans. Sometimes these species belong to the same genera or to the same functional group. But even at smaller scales there are striking differences in species occurrence. In the north-west Atlantic, a replacement of brown by red seaweed occurs towards the south (Hoek and Donze, 1967; Hoek, 1975, 1982; Hawkins *et al.*, 1992). Northern or southern limits of distribution of several species can be found along the European coasts (e.g., Southward and Crisp, 1954; Fischer-Piétte, 1957; Crisp and Southward, 1958; Fischer-Piétte, 1963; Lewis, 1964; Ardré, 1971; Southward *et al.*, 1995; Raffaelli and Hawkins, 1996), and these boundaries are not even stable, as observed by Fischer-Piétte (1957, 1963) on the Iberian and French Atlantic coasts.

1.1.2 Exploring the processes: causes of distribution patterns

With the accumulated evidence about patterns of zonation along the vertical gradient, ecologists became interested in the mechanisms that determine those boundaries. Since an obvious gradient of physical conditions exists, it is not surprising that the first attempts to explain zonation patterns were focused on the direct effects of physical stress on marine organisms. Colman (1933) suggested that there were critical levels beyond which organisms could not survive. He tried to correlate tolerance limits to temperature and humidity with the gradient found on the shore. This approach was later criticized and refuted by Underwood (1978), and Hartnoll and Hawkins (1982) found little support for the existence of such regions of change by examining some real tide gauge readings. Many studies were carried out in the laboratory to determine the tolerance limits to temperature and humidity of several species (e.g., Baker, 1909; Broekhuysen, 1941; Biebl, 1952; Southward, 1959; Wolcott, 1973), but in most cases they have shown that species could stand conditions that were not found on their natural environments.

1.1.2.1 Physical factors

Transplantation of species to upshore levels was adopted as an experimental protocol to access the effects of physical harshness on organisms. Several organisms were showed to die more quickly when moved above their natural boundaries, such as barnacles (Hatton, 1938) and brown algae (Schonbeck and Norton, 1978, 1979a,b,c; Norton, 1985), suggesting that at least the upper limits of species distribution were determined by physical constraints. Field observations of dying organisms due to extreme temperatures (e.g., Lewin, 1954; Foster, 1971; Hawkins and Hartnoll, 1985) reinforced this idea, and some species were demonstrated to be more susceptible to sudden changes in temperature than others (Southward, 1959; Lüning, 1980). But the transplantation protocol has some weaknesses since subtle lethal factors can operate cumulatively towards the upper limits and the precise mechanism is possibly much more complex than expected (Underwood and Denley, 1984).

The hydrodynamic forces (drag, lift, and the acceleration force) exerted over the sessile and mobile organisms can have several effects: dislodgement is the most drastic one, but other subtle effects occur, such as inability of propagules to attach (Vadas *et al.*, 1990), and reduction of foraging activity (Della-Santina *et al.*, 1993). Gaylord *et al.* (1994) suggested that mechanical factors (in particular the acceleration force) may be important in limiting the size of intertidal macroalgae, and this was demonstrated later by experimental manipulation of wave–exposed and wave–protected forms of *Fucus gardneri* (Blanchette, 1997).

1.1.2.2 Interactions among species

Despite the logical problems and limitations of the approaches used to couple physical constraints and zonation, there is no doubt that the former play an important role in determining the latter. By the early 1960s manipulative experiments became popular and research was shifted towards the understanding of the effects of biological interactions. Connell (1961b,a) has demonstrated unequivocally that both competition and predation can set the lower limits of barnacles. Subsequent studies revealed that the lower boundaries of many intertidal species were also set by direct competition (Lubchenco, 1980; Schonbeck and Norton, 1980; Hawkins and Hartnoll, 1985; Chapman, 1990; Santelices, 1990) or predation (Connell, 1961b, 1970; Paine, 1971, 1974).

Grazing by macro–herbivores was shown to set both upper and lower limits of several algal species (Hawkins and Hartnoll, 1983b; Raffaelli and Hawkins, 1996, for review). After the pioneering experiments of Lodge (1948) and Burrows *et al.* (1954) a whole series of experiments focusing on the importance of grazing were carried out almost all over the world (see Lubchenco and Gaines, 1981; Gaines and Lubchenco, 1982; Hawkins and Hartnoll, 1983b, for reviews). The effect of grazers was most pronounced in the case of the lower limits of ephemeral algal species (Southward and Southward, 1978; Menge, 1976; Lubchenco, 1978; Lubchenco and Menge, 1978; Hawkins, 1981a,b), but perennial species were also affected (Menge, 1976; Lubchenco, 1978, 1980; Lubchenco and Menge, 1978). On the other hand, Southward and Southward (1978) observed a raising of low–shore red and brown algae after a massive killing of grazers following the Torrey Canyon oil spill, which was demonstrated later by means of experimental manipulation (Underwood, 1979, 1980; Underwood and Jernakoff, 1981).

Thus, evidence suggests that physical factors set the upper limits of most high–shore species, while biological interactions (such as competition, grazing, and predation) are responsible for setting the upper limits of mid and low–shore ones (Hawkins and Jones, 1992; Raffaelli and Hawkins, 1996). In the absence of such constraints, upshore extensions are ultimately restricted by the physical conditions. With few exceptions (e.g., Schonbeck and Norton, 1980), lower limits have so far only been shown to be set by biological interactions (Raffaelli and Hawkins, 1996; but see Underwood, 1986).

1.2 Community structure and dynamics

The research on the causes of species distribution has revealed the complexity of intertidal communities. Both physical factors and biological interactions seemed to act in concert to set distribution patterns. Physical factors acted in an ultimate manner setting the broad range of conditions over which a species survives and reproduces. Biological interactions acted most directly being the proximate cause of many observed distribution patterns (Barnes and Hughes, 1982). The understanding of intertidal community structure and dynamics was the next logical step. Paine's experiments (Paine, 1966, 1969, 1974; Paine *et al.*, 1985) definitely brought to light the role of species interactions in community organization.

1.2.1 The keystone species concept

In Mukkaw Bay, on the exposed coast of Washington State, the continuous removal of a top–predator (*Pisaster ochraceus*), led to a dramatic shift in the community structure: after three years, 25 species had disappeared (including eight common space–occupiers), and mussels virtually dominated all the space (Paine, 1974). This experiment was also carried out in New Zealand and Chilean shores with similar, although not so striking, results (Paine *et al.*, 1985). Paine concluded that *Mytilus californianus* was a *competitively dominant* species and it could easily exclude almost all other organisms by overgrowing. The action of *Pisaster* prevented mussels from space monopolization and thus enabled other *inferior–competitors* to thrive in this community. Its effect on the community structure was so obvious that he coined them with the term 'keystone predators' (Paine, 1969).

Although originally introduced to refer to a predatory species, the term 'keystone' was loosely applied to all organisms that have disproportionately large effects on their communities. The idea that communities and ecosystems were dominated by the actions of a few species embedded in a web of species having little or no effect on each other has become a central point of debate in ecology. The discussion about 'trophic cascades', and 'top–down' versus 'bottom–up' regulation of communities still continues (see Menge, 1992; Power, 1992; Strong, 1992). Trophic cascades, that is, the drastic effects experienced by lower–level species in a food chain, as a consequence of the activity of top–level species (predators or keystone species), are thought to be unusual. Well established examples of trophic cascades in marine ecosystems, such as the sea–urchin/kelp forests (Dayton, 1985; Elner and Vadas, 1990) have been questioned (see Strong, 1992). There are several documented cases of ecosystems where keystone species seem to be absent (Keough and Butler, 1979; Menge *et al.*, 1986; Underwood and Denley, 1984, for review).

Some authors argue that the keystone concept is itself vague and useless: apparently, in similar ecosystems, the effects of a keystone species can be very different (Strong, 1992). In fact, another important aspect was the demonstration that keystone predators could reduce, instead of increase, community diversity: the mussel matrix provides shelter for a number of species and every mechanism that reduces mussel abundance will greatly affect the existence of such species (e.g., Suchanek, 1985; Tokeshi and Romero, 1995). In an attempt to resolve this paradox, emphasis was put on the variation of the strength of interactions (Menge *et al.*, 1994; Navarrete and Menge, 1996), but with no clear conclusions.

1.2.2 Complex interactions among species

As the number of experimental manipulative studies increased, biologists became aware of the complexity of species interactions in intertidal and subtidal ecosystems (Dayton, 1971; Underwood *et al.*, 1983). Creese and Underwood (1982) observed that competition between mobile species of grazers is usually asymmetrical. Most of the previous work emphasized direct effects, such as competition and predation, where changes in abundance of a species resulted from its interaction with another species. But there is another potential source of variation in community structure: indirect effects. Species can, through their direct interactions with another species, indirectly alter the abundance of other species with which they do not interact directly. Indirect effects are a well established empirical fact (Paine, 1966; Dayton, 1971; Menge, 1976; Lubchenco and Menge, 1978) and several studies addressed this topic, either theoretically or by means of experimental manipulation (Menge, 1978b,a; Paine, 1980; Underwood *et al.*, 1983; Bender *et al.*, 1984; Hartnoll and Hawkins, 1985; Menge *et al.*, 1986; Abrams, 1992; Abrams and Matsuda, 1996; Wootton, 1992, 1993) but the role of this kind of interactions is far from being clear.

Indirect effects can confound the experiments carried out in the field, especially those that run for long periods (Bender *et al.*, 1984; Navarrete, 1996), and they can take much more time to become 'apparent' to the researcher (Menge, 1996). Moreover, they can cancel each other, and they can even be larger than direct effects (Abrams, 1992). Menge (1996) used 23 experimentally based studies from intertidal habitats and analysed the correspondent food webs, finding that there were 83 subtypes of indirect interactions (7 of which were already known, such as keystone predation or apparent competition). Most of these types of indirect interactions were, however, rare or their effect on the community structure was negligible. Nevertheless, he found that indirect effects could account for 40% of variation in community structure. This amount of variability was independent of species richness (and thus food web complexity) and indicates that strongly direct and indirect interactions produce roughly the same level of alteration of community structure.

Care must be taken when interpreting the results of an experiment and a good knowledge of the natural history of the species involved is fundamental so that indirect effects can be separated from their direct counterparts. Nevertheless, in his review, Menge (1996) found that almost all investigators were able to identify and first manipulate those species responsible for most indirect effects, and suggests that indirect effects may be more predictable than expected on the basis of theory.

1.3 Disturbance and the provision of space

Space is probably the most important resource for intertidal organisms, especially for those that have a sessile stage in their life cycle (Connell, 1961b; Dayton, 1971; Paine and Levin, 1981; Sousa, 1984c; Raffaelli and Hawkins, 1996). Therefore, the processes involved in the creation of free space are of vital importance to the persistence of many species (e.g., Connell, 1961b; Paine, 1966, 1974; Sousa, 1979a,b; Dayton, 1971; Blanchette, 1996). Both physical and biological processes act as agents of disturbance. The former are the kind most often associated with the term 'disturbance' and their role in natural communities has been the primary focus in several studies (see Sousa, 1984c, for a review). Agents of biological disturbance encompass everything, from predation or grazing to non–predatory behaviour that inadvertently kills or dislodges other organisms, thus providing new bare space for other colonizers.

1.3.1 Types of disturbance

In intertidal communities the major agent of disturbance is undoubtedly water motion. During severe storms the impact of waves on both sessile and mobile organisms can lead to their dislodgement and subsequent death (Paine and Levin, 1981). Besides direct action upon organisms, water motion can have an indirect effect by means of throwing objects against the substrate (Dayton, 1971; Shanks and Wright, 1986). In less stable environments, like boulder shores, wave action may turn the boulders frequently, thus providing new space for colonizers (Sousa, 1979a). Other types of indirect effects of water motion include the abrasion by sand or gravel (Sousa, 1984c) and scouring by cobbles in rock–pools (van Tamelen, 1996).

Another common cause of disturbance is that resulting from human activity. Trampling can severely damage some intertidal organisms, particularly seaweed (Brosnan and Crumrine, 1994; Addessi, 1994; Povey and Keough, 1991). More drastic anthropogenic disturbances include the direct and indirect effects of oil spills: after the *Torrey Canyon* oil spill in Cornwall, a massive kill of the grazers due to the use of dispersants, resulted in an impressive shift of the limpet–barnacle dominated communities to an algal dominated community. The shores were blanketed mainly by *Fucus* and it took several years to attain their initial state (Southward and Southward, 1978; Hawkins and Southward, 1992).

Extreme temperatures can also act as disturbance agents. In São Paulo (Brazil), the mussels are prevented from outcompeting other species by extreme high temperatures during the summer (Petersen *et al.*, 1986). Lower temperatures can have similar effects as demonstrated by Carrol and Highsmith (1996). Large scale disturbances like hurricanes (Moring, 1996), storms (Reusch and Chapman, 1995) or ice scouring (McCook and Chapman, 1991, 1997), although less frequent, have enormous consequences on the structure of intertidal communities. Although the main consequence of physical disturbance is the provision of space, it can affect organisms, and thus community structure, in several other ways. For example, wave action and temperature can drastically reduce the foraging activity of mobile predators due to an increased risk of dislodgement or thermal stress, respectively, thus increasing the chances of survival of sessile organisms until they have escaped predation by reaching larger sizes (e.g., Crothers, 1985; Dungan, 1996).

Grazing and predation are the two main agents of biological disturbance. Predation, unlike physical disturbance, is considered a *selective agent* since predators feed preferentially on one or few types of prey. In intertidal systems the main predators are usually starfish (Paine, 1966), whelks (Connell, 1961b) and probably crustaceans and fish (Edwards *et al.*, 1982). Paine (1966, 1969, 1974) has demonstrated that the removal of the main predator could lead to the complete domination of space by the mussels, accompanied by the disappearance of 10 out of 18 conspicuous space–occupiers. By contrast, grazing is usually less selective affecting mainly algae (Hawkins and Hartnoll, 1983b; Raffaelli and Hawkins, 1996), although herbivores can bulldoze or accidentally consume sessile invertebrates (Dayton, 1971; Hawkins, 1983). In the north–east Atlantic, grazing by limpets can prevent fucoids from attaching to the shore, leaving the space for other colonizers such as barnacles (Hawkins and Hartnoll, 1983a,b). Limpets do not feed much directly on adult seaweed but their grazing activity probably takes every micro-organism indiscriminately, including algae germlings. However, once these algae reach a critical size they escape from grazing and can modify the environment by providing shelter, moisture, and shade to other species. Adult seaweed can also affect grazers negatively: it has been shown that low shore algae can settle and grow faster than molluscs can graze, thus preventing the downshore extension of intertidal grazers (Dayton, 1975; Paine, 1980; Underwood and Jernakoff, 1981; Hawkins and Hartnoll, 1983b).

Grazing activity can also indirectly enhance or inhibit other animal species. Dayton (1971) showed that in the absence of predatory dog–whelks, acmaeid limpets could increase the survival of the barnacle *Chthamalus fissus* by reducing the survival of the superior competitors *Balanus spp*. Once again, the acmaeid limpets did not selectively bulldoze on *Balanus* but the smaller size and flat morphology of *Chthamalus* after metamorphosis made them less likely to be bulldozed once they have settled in small crevices. Contrasting with limpets, littorinids, trochids and sea–urchins can feed on adult plants. Sea–urchins are responsible for the clearance of kelps from large areas, and can remain on these areas by catching drifting algal debris, thus keeping them free from subsequent recolonization by kelps (Dayton, 1984; Dayton *et al.*, 1992). Furthermore, littorinids were shown to be selective grazers which feed primarily on ephemeral green algae (Lubchenco, 1978; Petraitis, 1983).

More subtle interactions can also be seen as types of biological disturbance. For example, Santelices (1990) showed that sweeping or whiplash by large kelp fronds could prevent smaller algae from settling and growing in the 'bare rock' at lower intertidal in Chilean shores. Similarly, Hawkins (1983) observed that in the shores of the Isle of Man, sweeping by *Fucus* canopy could dislodge up to 80% of the newly settled barnacles (*Semibalanus balanoides*). Epiphytic or epizoic overgrowth can also affect the resistance of an organism to water motion. Drag can significantly increase when the surface of animals and plants is covered by other organisms, thus increasing the probability of dislodgement due to water movement (Sousa, 1984c). As shown by Dittman and Robles (1991) epiphyte algae can substantially reduce mussel growth and reproductive rates.

1.3.2 Succession after disturbance

Once the space is made available it is soon exploited by colonists and regenerating survivors, and a successional sequence of species replacements usually ensues (Sousa, 1984c). Several factors will constrain the possible pathways of these sequences, thus leading to patches that differ in species assemblages, or even population size–structure, genetic composition, and life history characteristics. The interactions of factors such as success of recruitment (that depends on patch creation time), propagule availability, patch size, shape and position within the community, patterns of subsequent disturbance, and finally the species–specific abilities to deal with competitors or predators, will strongly influence the outcome of succession, and ultimately are responsible for the overall patchiness of the community (Sousa, 1984b; Farrell, 1991).

Much effort has been put in understanding the mechanisms that govern species replacements whenever free space is available. If early colonists weakly interact with later successional species the appearance of a species will depend on when its propagules arrive in a disturbed area. Therefore, succession will be simply a function of the life histories of the species in a community. Alternatively, if species interact strongly, the establishment of a given species will be influenced by the earlier colonists. Connell and Slatyer (1977) defined three models of species succession, by considering the effect of earlier successional species on the establishment of later successional ones. In the *facilitation* model early colonists enhance the establishment of later successional species; in the *tolerance* model the earlier colonists have little or no effect on the establishment of later successional species; in the *inhibition* model, early colonists slow or prevent the establishment of later successional species.

Facilitation was once thought to be the dominant model of succession (Farrell, 1991; Berlow, 1997; Benedetti-Cecchi, 2000). Hacker and Gaines (1997) suggested that direct positive interactions appeared to be the most common in environments with relatively high physical disturbance, stress, or predation, where associated species could increase the growth and survival of other species unable to survive in isolation. Indeed, Stephens and Bertness (1991) showed that at high tidal heights on thermally stressful cobble beaches, infaunal mussels (*Mytilus edulis*) may buffer barnacles (*Semibalanus balanoides*) from thermal stress and increase barnacle survivorship, although in wave-splashed shores, mussels outcompete barnacles for space on hard substrata. Mussel recruitment is also enhanced by the presence of filamentous algae, as shown by Dayton (1971) and Sousa (1984b). Facilitation of algal colonization by barnacles has been demonstrated in several independent studies (Hawkins, 1981a,b; Hartnoll and Hawkins, 1985; Farrell, 1991; Benedetti-Cecchi, 2000): a thick cover of barnacles greatly reduces limpet grazing efficiency. Kim (1997) found that in the rocky intertidal shores of British Columbia (Canada) the facilitation mechanism was slightly different: the barnacles did not enhance *Fucus* recruitment, but instead, limpets facilitated the recolonization of these algae by grazing on the ephemeral green algae that, otherwise, would preempt the space. Although barnacles enhance recruitment of fucoid algae by reducing either herbivore pressure or desiccation stress, plants recruiting onto barnacles suffer higher mortality compared to those that settle directly onto the rock surface. Therefore, despite the initial positive effects of barnacles on fucoid recruitment, germlings growing on barnacles have a high probability of dislodgement before reaching reproductive age (Hartnoll and Hawkins, 1985; van Tamelen and Stekoll, 1997).

According to Raffaelli and Hawkins (1996) the tolerance model has not yet been unequivocally demonstrated, although some authors argue that the interactions between barnacle species (early colonizers) are an example of tolerance (Farrell, 1991; Berlow, 1997). Inhibition appears to occur more frequently than tolerance or facilitation (Connell and Slatyer, 1977). Ephemeral algae often cause inhibition in rocky intertidal communities (e.g., Sousa, 1979b; Robles and Cubit, 1981; Lubchenco, 1983; Sousa and Connell, 1992; Kim, 1997). For example Sousa (1979b) demonstrated that in boulder shores, earlier colonists like *Ulva* could inhibit the recruitment of perennial algae, as did some mid-successional red algal species (*Gelidium sp.* and *Rhodoglossum sp.*). But in the absence of physical disturbance, the inhibition of *Ulva* was prevented by selective grazing of this species by the crabs. In the end of the succession *Gigartina canaliculata* outcompeted the mid-successional species and dominated the community holding 60–90% of the cover after a period of 2–3 years. In the absence of disturbance, this monoculture would persist through vegetative reproduction, resisting invasion by all other species. Kim (1997) also showed that in the intertidal rocky shores of British Columbia (Canada) algal succession followed an inhibition model, in which the early colonist (ephemeral algae), inhibited the settlement of the latter species (*Fucus gardneri* and *Pelvetiopsis limitata*) for the first two years. However, this inhibition occurred only in the absence of limpets, because whenever present, they grazed a substantial amount of ephemeral algae, and consequently fucoids occupied space in the early stage of succession.

In both of the above cases consumers played an important role in breaking inhibitory processes. Several studies of succession have involved manipulation of consumers (see Lubchenco and Gaines, 1981; Hawkins and Hartnoll, 1983b; Sousa and Connell, 1992, for reviews) and they indicate that they can have a strong influence over the course of succession, accelerating it (Lubchenco and Menge, 1978; Sousa, 1979b; Robles and Cubit, 1981; Lubchenco, 1983) or slowing it (Dayton, 1975; Sousa *et al.*, 1981; Hawkins and Hartnoll, 1983b; Farrell, 1991).

According to Berlow (1997), historical and site–specific detail required to explain variation in patch composition depends on whether successional paths dampen, track or magnify extrinsic variations in initial conditions. He outlined three ways in which successional paths depend on historical events: *canalized succession*, *externally driven succession* and *contingent succession*. If early species have strong and consistent influence on later species, then the community may follow deterministic (repeatable) patterns of change over time (e.g., Connell and Slatyer, 1977; Lubchenco, 1983; Farrell, 1991). Succession can also be highly predictable if recruitment patterns are consistent over time. In both cases, succession is said to be canalized, and much of the current variation in community structure can be explained by the length of time since the last disturbance, provided that the mechanics of succession and recruitment are already known.

If extrinsic events override the effects of deterministic species interactions, variation in successional pathways may be driven externally by stochastic variation in environmental conditions, propagule availability, recruitment, disturbance and other events (Sousa, 1979a,b; Hawkins, 1981a; Paine and Levin, 1981; Gaines and Roughgarden, 1985). Current variation in community may be better explained by site characteristics, both current (e.g., proximity of propagule sources) and historical (e.g., initial conditions), and by models of external driving variables, such as those that are independent of a detailed knowledge of the mechanisms of species interactions. If the sign and magnitude of species interactions depend strongly on the context in which they occur, the interaction between stochastic and deterministic processes may result in highly contingent, rarely repeatable patterns of succession. In the case of externally driven succession, current variation of community structure can only be explained by a detailed knowledge of species interactions and the way they vary in the timing, sequence and intensity of externally driven events.

Some studies show that succession after disturbance is essentially contingent, thus making it difficult to generalize the observed patterns (e.g., Benedetti-Cecchi and Cinelli, 1993, 1994). Berlow (1997) investigated the patterns and importance of historical effects in a successional marine rocky intertidal community, in a series of experiments carried out on the central coast of Oregon, during three years. Succession in mid–intertidal patches in the mussel bed displayed very complex patterns of historical effects, which varied among species and between different stages of succession. However, embedded in this complexity were some consistent and repeatable successional trends. Some potentially important canalizing ('noise-dampening') forces in this system included physiological and/or life history trade-offs between dispersal ability and competitive ability. Strong direct biotic interactions buffered environmental variability. By contrast, 'noise-amplifying' forces included variable indirect effects of predators (the classical case of the facilitation of *Chthamalus* growth by whelks, which consumed preferentially *Balanus*), prey size escapes, and predator saturation (whelks consistently have a negative effect over all barnacle species but in the first year of the experiment the densities of *B. glandula* were so high that the overall effect of predation upon this species was weak). These results show how biotic interactions have the potential to simplify or complicate community responses to disturbance. Moreover, although physiological constraints and trade–offs can canalize some successional trends, questions remain about the general patterns of these trade–offs among different systems and about the conditions that regulate their relative importance (Petraitis *et al.*, 1989).

1.3.3 Factors that affect successional pathways

The time at which a patch is created is often of major importance for the subsequent recolonization of space (Sousa, 1984c), and it is usually linked to the availability of colonizers. Since most species have very different settlement periods, their persistence on the shore will depend on the time of patch birth. Usually early colonists are outcompeted by other late–successional species (see Sousa, 1979b, 1984b) but sometimes the former can hold the space indefinitely until other disturbance events break their dominance. For example Kim and Dewreede (1996) observed that in the high–shore of British Columbia (Canada), new substrata created a short time before the peak of fucoid recruitment in unmanipulated plots received a greater number of fucoid propagules, and this initial recruitment secured fucoid persistence in the later successional period (see also Hawkins, 1981b). Other algae that usually dominate the space were preempted from this zone until the patches of *Fucus* had disappeared due to ageing and wave action.

When late successional species are able to invade the open patch, dominance will be quickly attained. Therefore, small patches surrounded by this kind of organisms should be dominated more quickly than larger and isolated ones. In the mussel beds of the north–west coast of North America percentage cover of several algal species is highly correlated with the cover of epizoic conspecific adults within 1 m of the edge of the patches, which suggests that these species may disperse their propagules over relatively small distances (Sousa, 1984b; Williamson and Creese, 1996). Recruitment processes can also contribute to the maintenance of a high diversity mosaic at wave–exposed sites, but seem to be of minor importance at wave–sheltered sites (Menge *et al.*, 1993).

Robles (1997) investigated the consequences of extreme spatial and temporal variation in the recruitment of a prey species subjected to keystone and diffuse predation. Prior experiments on rocky shores of Santa Catalina Island (California) demonstrated that predation by spiny lobsters (*Panulirus interruptus*) maintained a distinctive red algal turf by killing juvenile mussels (*Mytilus californianus* and *M. galloprovincialis*) that otherwise would overgrow and replace the algae. However, long–term surveys revealed that high recruitment of the predominant mussel, *M. californianus* occurred only on the most wave–exposed sites in certain years. Mussel recruitment was small on relatively protected sites in most years. A predator exclusion experiment consisting of several fenced areas placed along the gradient of wave exposure demonstrated that the effects of predation depended upon the spatial differences in recruitment rates. Lobsters on wave–exposed sites functioned as keystone predators. On sheltered sites, however, little or no predation, whether by lobsters, fishes or whelks, was necessary to maintain the algal assemblage. Therefore, similar species assemblages could be maintained by different ecological processes.

The size, shape and the position of a cleared patch within the community can indirectly influence its re–population in several ways. Organisms surrounding the cleared area can, in some way, modify the patterns of water flow and thereby affect the availability of food and the density of settling propagules. Moreover, the undisturbed community around the patch can provide shelter and refuge for animals that forage in the gap (Suchanek, 1978; Sousa, 1984b). The vegetative in–growth of clonal organisms, or the encroachment of attached but semi–mobile organisms, will make a proportionately greater contribution than dispersed propagules to the recolonization of small patches if they occur along patch edges. The influence of patch size and shape is thought to be largely indirect, resulting from the interaction between patch size and grazing intensity (Sousa, 1984b). Small patches support higher densities of grazers, especially limpets, than larger ones. As a consequence, the assemblages of algae that develop within small and large patches differ markedly. In smaller patches, grazer–resistant algae appear. These species are thought to be inferior competitors because in larger patches, where the effects of grazing are small, they are outcompeted by grazer–vulnerable species (Sousa, 1984b; Farrell, 1989; Dye, 1993; but see Kim and Dewreede, 1996 and Menge *et al.*, 1993).

Apart from less frequent catastrophic events (e.g., Southward and Southward, 1978; Southgate *et al.*, 1984; McCook and Chapman, 1991; Reusch and Chapman, 1995; Carrol and Highsmith, 1996; Moring, 1996; McCook and Chapman, 1997; Dayton, 1984; Dayton *et al.*, 1992), disturbance is often viewed as a seasonal phenomenon (Dayton, 1971; Sousa, 1979a; Paine and Levin, 1981; Sousa, 1984b,c). The frequency of disturbances at smaller temporal scales (e.g., within a year) might be necessary for the persistence of many competitively inferior species. The regime of disturbance may greatly influence the outcome of a succession if the colonization process depends on free swimming larvae or widely dispersed algal propagules. However, if species propagate vegetatively, the effect of time or the frequency of disturbance is much less marked, and the patchiness will be the result of the life history of colonists (Menge *et al.*, 1993).

1.4 Patchiness in intertidal communities

Two features can characterize natural communities: they are dynamic systems and spatially heterogeneous (Sousa, 1984c). The abundance and age–structure of populations change with time and local extinctions are commonplace. The so called 'climax state' of a given community may only exist as an average condition over relatively large temporal and spatial scales (Connell and Sousa, 1983). Heterogeneity is then the result of a whole range of changing forces operating at different spatial and temporal scales. Therefore, natural communities are often seen as a mosaic of patches of free space interspersed with aggregates of one or more species. These aggregates may be very different from each other, thus contributing to the overall heterogeneity, and their specific composition will be determined by a combination of several variables, such as the creation time of the patch, the potential colonizers at that time and their ability to outcompete the other species.

Processes (e.g., disturbance, dispersal, growth, succession, species interactions) determine the patterns (patchiness), but patterns can also facilitate or constrain ecological processes (Wu and Loucks, 1995). Recognition of the causes and mechanisms of patchiness in ecological systems, as well as their spatiotemporal domains, is needed to understand their ubiquitousness and complexity. Moreover, patchiness is an important feature of many, if not all, ecological communities (Wu and Loucks, 1995), and the understanding of its dynamics (e.g., patch birth, growth and extinction rates), coupled with the knowledge about individual life-histories, is crucial if the structure of the communities is to be predicted.

1.4.1 Patchiness as a consequence of disturbance

In situations where hierarchical competitive interactions or differential longevity will probably lead to the monopolization of space, disturbance can maintain within–patch or community diversity by one of two mechanisms: *compensatory mortality* or *intermediate disturbance* (Sousa, 1984c; Petraitis *et al.*, 1989). The first term refers to cases where the dominant species suffers disproportionate mortality as compared to other species that it might, otherwise, exclude from patches. Selective predation of the starfish *Pisaster* over mussels is a classical example (Paine, 1974). Likewise, physical disturbance associated with wave action can have the same effects (Dayton, 1971; Paine and Levin, 1981).

Dayton (1971) has demonstrated the combined action of both physical and biological selective agents of disturbance. In the Washington State Islands, several species occurred in the eulittoral zone: the mussel *Mytilus californianus* was the principal space–occupier in wave–beaten shores. He found that log damage and wave exposure had complementary effects in providing free space in the mussel bed for other colonizers, as wave shock enlarged the areas created by log damage by wrenching the mussels from the substratum at the periphery of the bare patch. Competition for primary space resulted in a clear dominance hierarchy, with the barnacles (*Chthamalus dalli*, *Balanus glandula* and *B. cariosus*) dominating the algae (*Fucus distichus* and *Gigartina papillata*). Among the barnacles, *B. cariosus* dominated *B. glandula* and *C. dalli*. Mussels required secondary space (algae, barnacles or byssus threads) to recolonize the gaps, but they were able to grow over all other sessile species, being the competitive dominant of space in this community. Biological interactions were also important in determining the structure of the community. For example, several whelks of the genus *Nucella* fed indiscriminately on all species of barnacles and mussels (Connell, 1970). Mussels and *B. cariosus* could easily escape *Nucella* predation by growing larger but they were not able to monopolize space due to the combined action of the starfish *Pisaster ochraceus* and log damage .

Physical disturbance that does not cause compensatory mortality may nonetheless maintain within–patch diversity (Sousa, 1984c). To do so, the disturbance must renew resources (such as space) at a rate that allows continued recruitment and persistence of species that would otherwise be driven extinct. Under these circumstances, competitive exclusion of species is delayed or never occurs because some part of the ecosystem is routinely set back by catastrophes. In a set of field experiments carried out in intertidal boulder fields in southern California, Sousa (1979a) tested the effects of disturbance intensity on community diversity. In this habitat, the major source of disturbance occurs when waves, generated by winter storms, overturn the boulders, opening space and interrupting natural succession, thus determining subsequent levels of diversity and community structure. Because smaller boulders are more frequently overturned than larger ones, the plants and sessile animals of these shores are distributed in a patchwork of successional stages. Small boulders, with shorter disturbance intervals, supported only sparse early successional communities of the green algae *Ulva* and some barnacles. In contrast, large, infrequently disturbed boulders were dominated by the late successional red algae (*Gigartina canaliculata*). Boulders that were subjected to intermediate levels of disturbance supported more diverse species assemblages, with barnacles, *Ulva*, several mid successional species and *G. canaliculata*.

Petraitis *et al.* (1989) suggested that the maintenance of higher species diversity at intermediate levels of disturbance could only be explained by assuming that there were trade–offs in species–specific abilities that imposed constraints on immigration to, and extinction in patches. Changes in immigration and extinction, the processes that govern patch dynamics, depend on species–specific abilities to fend off competitors or to endure disturbance. Members of a species can resist competitors or disturbance, but they cannot resist both. They showed that, if these trade–offs did not exist, then the higher levels of diversity would not occur at the intermediate levels of disturbance. Moreover, if this assumption was slightly relaxed, unexpected results would arise.

1.4.2 Coupling patterns with processes

In contrast with the great amount of information about the role of species interactions on the structure and dynamics of communities gathered by marine ecologists, particularly in intertidal systems, few attempts have been made to incorporate these results into broader models, capable of predicting or explaining future variations. Coupling spatial and temporal scales is usually a cumbersome task (Wu and Loucks, 1995), and the lack of a mathematical framework to do so, has forced ecologists to study patchiness at spatial and temporal scales separately. Svane and Ompi (1993) examined the distribution of shell length, dry weight, and shell weight of mussels (*Mytilus edulis*) occurring in natural beds of two intertidal populations in Danish Fjords. Effects of station, patch size, and position within the bed were tested and the results showed large differences in mean size and weight between stations and that mussels sampled along an edge were significantly larger than elsewhere within a patch irrespective of station. The mussels in isolated small patches (< 30 cm diameter) were even larger. Patch dynamics on a spatial scale was found to be a function of recruitment, growth and mortality, and these factors were density dependent and predictable.

Nevertheless, there have been some attempts to link natural disturbance processes and community dynamics in broader models, dealing explicitly with patch variability (in space and time) and species composition. Levin and Paine (1974) developed a mathematical model that related community structure to levels of disturbance in systems where the effects of disturbing agents were localized in space and time. The proposed model, based on a set of non–linear equations, was able to predict the frequency distribution of renewed areas (patches) with regard to size and age (colonization stage). In a later work, Paine and Levin (1981) compared the predictions of the model with real data, using estimates of the frequency of patch birth, growth, death and shrinkage rates from 1975 to 1978. The age of older patches (created previously to the study) was estimated using *Balanus cariosus* size–structure. Two mechanisms of patch disappearance were identified: recolonization by lateral movement of border mussels (for smaller and medium–sized patches) and direct recruitment (for larger patches). Turnover time (rotation period) was estimated in 8.1–34.7 years (depending on location) using winter birth rates of patches. The minimum value estimated by the model was in close agreement with both the observed and calculated minimal recovery times. Patch birth was found to be a seasonal phenomena (but see Hunt and Scheibling, 1995). The model could also predict accurately the total area of bare rock in the year of 1978 based on the data of previous years (1975-1977), but if detailed size–structure of the patches was to be known, the model seemed to fail, mainly due to stochastic small–scale events. Paine and Levin (1981) recognized that much of the ability to predict successfully the age–size distribution was because it was a 'forced' model, that is, they have treated disturbance *as given*, rather than trying to predict and modelling it in the basis of past patterns.

A conceptual model was refined by Hawkins and Hartnoll (1983b) and Hartnoll and Hawkins (1985) to explain the patchiness of moderately sheltered limestone ledges on the Isle of Man (Irish Sea). The model itself had been proposed earlier by Lodge (1948), Burrows and Lodge (1950) and Southward and Southward (1978), among others. In this case, the mid–tide region was best described as a patchy network of fucoid clumps interspersed by areas of dense barnacle cover or bare rock with limpets. Grazing by limpets was an important structuring agent in this system. Dense barnacle covers affected limpets foraging, and thus grazing efficiency. This enhanced fucoid recruitment locally and, once they reached an 'escape–size' they became unaffected by limpet grazing activity. Under the new established *Fucus* canopy many dog–whelks and juvenile limpets aggregated. Dog–whelk predation reduced barnacle abundance, which allowed the return of adult limpets searching for shelter. The fucoids density was reduced by loss due to insecurely attached *Fucus* or ageing, and as a result a bare space with few barnacles and limpets was created. Finally, *Nucella* densities decreased due to lack of shelter, and limpets dispersed leaving behind a gap of bare rock suitable for new barnacle recruits. A dense barnacle cover, in turn, would be suitable for *Fucus* recolonization. A patch of *Fucus* could last for about three to four years, and the community functioned as a series of cycling patches, generally out of phase with each other. The complex interactions between species could shift the succession in these patches, thus contributing to the overall heterogeneity. Species recruitment also played an important role, adding another stochastic element to the system: a poor limpet recruitment coupled with high *Fucus* recruitment would increase the likelihood of the formation of fucoid patches. This likelihood would be further enhanced if high barnacle settlement had occurred. The model was recently tested by spatial statistical analysis (Johnson *et al.*, 1997) and modelled using cellular automata (Burrows and Hawkins, 1998) and individual based approaches (Johnson *et al.*, 1998), with very satisfactory results.

Dye (1992, 1993) also developed a model that accounted for the interactions between grazers and algae and gap size in the low intertidal on rocky shores in the Transkei region of southern Africa. Grazer density (*Patella longicosta*, *P. oculus* and *Oxystele tabularis*) was highest in small gaps and there was a direct relationship between the number of grazers and the ratio of bare rock to algae. This model was then discussed in terms of human exploitation of patellid limpets and the implications of this for low-shore community structure. The studied shores were subject to intense shellfish exploitation by coastal people. Large–scale removal of sessile species, such as the mussel *Perna perna*, created areas of bare rock, providing space for colonization. Rates of recolonization of experimentally-cleared areas in both protected and exploited sites were found to be variable. There was as much as a two-year delay before sessile macro-organisms reappeared, and the course of subsequent succession depended on the nature of the initial colonists. Large spatial and temporal variations in species diversity and richness were observed; it also appeared that emergent communities were less stable than adjacent controls. After eight to nine years, few of the cleared areas had developed communities similar to the original or to controls. These results were compared with those of a controlled exploitation experiment conducted in a nature reserve. Similar results were obtained despite the fact that exploitation was more selective for target species and did not involve total clearance. The long-term effects of human exploitation involved shifts in community structure towards earlier successional stages which persisted for long periods of time. Consequently, management options such as rotational cropping may be inappropriate in such a system.

1.5 Rationale, objectives and structure of the present study

Intertidal shores are, probably, the most affected ecosystems whenever an oil spill occurs, and they will be the main subject of the present study. Like any other biological communities, they are complex entities which vary in space and time. The structure of these communities is driven by the particular characteristics of each constituent species and their interactions, but also by external and usually chance events. Oil spills (and other human induced impacts) are not the only sources of disturbance acting upon intertidal shores. As shown in the previous section, many natural phenomena, such as storms (Dayton, 1971; Paine, 1974; Paine and Levin, 1981; Sousa, 1984c,b), extreme temperatures (Petersen *et al.*, 1986; Davison *et al.*, 1989), and sand or ice scouring (McCook and Chapman, 1991, 1997), can interfere with successional pathways, playing an important role at the community level (Raffaelli and Hawkins, 1996). Therefore, de–coupling intrinsic and extrinsic sources of variability is crucial for the assessment of the impact of human activities over the intertidal communities.

Unfortunately, there is little information about intertidal rocky shores in continental Portugal. Available information is scarce and consists mainly of qualitative descriptions, as it comes from old – and usually outdated – works (e.g., Nobre, 1903, 1931; Cúmano, 1939; da Cunha, 1940; Nobre, 1938a,b) or unpublished academic theses (Lopes, 1993; Marques, 1989). Basic processes, such as reproduction and recruitment of the principal intertidal species, have seldom been the subject of modern analysis (but see Gaudencio and Guerra, 1986; Guerra and Gaudencio, 1986). Moreover, marine communities were not studied as a whole until recently (Saldanha, 1974). Several works were developed since then (e.g., Castro and Viegas, 1980; Marques *et al.*, 1982, 1993), but they were carried out mainly in the central and southern coast of Portugal. Since the southern shores often resemble those from the Mediterranean (Picard, 1957), Portuguese shores were almost always classified as Mediterranean or nearly–Mediterranean (see Hawkins *et al.*, 1992). Therefore, a general description of the northern Portuguese shores will be made in Chapter 2. The study of vertical (zonation) and horizontal (biogeographic) patterns was necessary to set up the context for subsequent analyses and discussion. The main hypothesis being tested here is that northern shores differ significantly from their better known southern counterparts, thus deserving a more detailed attention by Portuguese marine ecologists. Their relationship to shores further north in Europe will also be explored.

Chapter 3 is dedicated to the study of the population dynamics of the principal intertidal species in the north of Portugal. The goal is to gather information about population variability over large temporal and spatial scales, and to identify any natural sources of disturbance. Space availability and disturbance regimes will be analysed. The hypothesis that winter storms reduce the density of the dominant space occupiers (Paine and Levin, 1981) will be tested. Special attention will be given to processes that may influence patch dynamics, such as species recruitment, particularly of limpets and barnacles.

Chapter 4 quantifies the dynamics of single patches in the mussel zone. Turn–over rates, growth, and dislodgement will be studied and compared with the previous results. Succession after removal of species will also be covered in this section. In Chapter 5 species interactions are investigated. Grazing is considered a major structuring force, as it can strongly influence the course of succession. The effect of grazers in the structure of the mussel bed will be studied by means of experimental manipulation. Other interactions, such as facilitation of mussel attachment by barnacles, will also be addressed in this study.

In Chapter 6 the impact of an oil spill will be analysed in the context of the spatial and temporal variation described above. The occurrence of an oil spill in the summer of 1998, affecting one of the studied sites, permits the analysis of the impact using modern analytical techniques (beyond BACI, Underwood, 1993). The results will then be interpreted on the basis of the accumulated information about the patch dynamics of the assemblage.

The importance of patchiness is well documented in intertidal systems. Even though much has been done to understand the mechanics of patch creation (Dayton, 1971; Sousa, 1979a; Hawkins, 1981a,b; Paine and Levin, 1981; Hawkins and Hartnoll, 1983b; Hartnoll and Hawkins, 1985; Dye, 1992, 1993; Svane and Ompi, 1993; Machado *et al.*, 1992), and succession after disturbance (Dayton, 1971; Sousa, 1979b; Lubchenco, 1983; Farrell, 1991; Berlow, 1997, e.g.,), there is still much to do to incorporate these results into broader models. Despite the stochastic nature of many agents of disturbance and other ‘extrinsic’ phenomena the patch dynamics of some intertidal systems have been successfully described (Levin and Paine, 1974; Paine and Levin, 1981; Hawkins and Hartnoll, 1983b; Hartnoll and Hawkins, 1985; Dye, 1992) and modelled (Johnson *et al.*, 1997; Burrows and Hawkins, 1998; Johnson *et al.*, 1998). In Chapter 7, all data will be integrated, and a conceptual model will be developed to explain the patch dynamics of intertidal mussel assemblages on northern Portuguese shores.

Chapter 2

Rocky Shores in Northern Portugal

2.1 Introduction

Extensive and qualitative surveys are usually the first step to establish patterns of similarities between regions, providing a framework for more intensive and particular studies (Stephenson and Stephenson, 1972; Lewis, 1980; Raffaelli and Hawkins, 1996). Despite the robustness of biogeographic evidence for the European coasts, some stretches of coastline are still poorly known, making it impossible to establish the exact boundaries of species distributions. The Portuguese shoreline falls into this category and, apart from a few extensive studies (Nobre, 1940; Ardré, 1970), most of the information is not readily available as it came from unpublished academic theses (e.g., Lopes, 1993; Marques, 1989) or earlier and outdated literature (Nobre, 1903, 1931, 1938b).

The first attempt to establish biogeographic boundaries along the Portuguese continental coast was made by Cúmano (1945) on the basis of echinoderm species distribution. He was able to divide the coastline into three main zones, with an increase of species diversity towards the south. Differences in species composition along this latitudinal gradient have been studied since then, and several authors reported northern or southern limits of distribution of several species within this area (Fischer-Piétte, 1957, 1958, 1963; Cúmano, 1945; Fischer-Piétte, 1963; Kensler, 1965; Ardré, 1970; Almaça, 1985; Bellan-Santini and Marques, 1984; Marques and Bellan-Santini, 1985). Nonetheless, and despite the accumulation of such evidence, differences in species composition along the Portuguese coast have not been tested formally and globally. Regions of change vary according to each author because most of the studies addressed only restricted groups of animals (e.g., Kensler, 1965; Lopes, 1993; Marques, 1989), or plants (Ardré, 1970). Furthermore, the observed boundaries are not static as species distribution have been shown to change significantly over short time scales (Fischer-Piétte, 1956, 1957).

The absence of a modern and systematic study was finally overcome with the pioneering work of Saldanha (1974) on the coast of Arrábida. Mainly based on the French methodology (Pérès and Picard, 1958, 1964; Bellan-Santini, 1969), he described the zonation patterns in the intertidal and subtidal rocky surfaces, providing an invaluable framework for future investigation. Further descriptions of zonation patterns were made in rocky and sandy shores near Lisbon (Castro and Viegas, 1980; Marques *et al.*, 1982; Reis *et al.*, 1982), revealing some similarities between the fauna and flora of this region and those from the North Africa and the Mediterranean. This idea, which has been stressed earlier by Picard (1957), was reinforced by the work of Fischer-Piétte (1938, 1957, 1958, 1963) who also found a Mediterranean character on the Asturian shores (NW Spain) and the Gulf of Gascony (SW France).

The northern Portuguese shores were not investigated for several decades after Nobre (1940) or Ardré (1971). Nevertheless, in the last 20 years a large volume of data was gathered for the Galician and Asturian coasts (Niell, 1980; Anadón and Niell, 1981; Fernández and Niell, 1981, 1982; Anadón, 1981, 1983; Fernández *et al.*, 1983, 1987; Arrontes and Anadón, 1990; Arrontes and Anadón, 1990; Arrontes, 1991), suggesting that the Atlantic shores of the Iberian Peninsula could not always be assigned to the 'southern type'. Based on this information, I undertook an extensive survey on the northern intertidal rocky shores and found remarkable differences between these sites and the well known southern coast (Santos, 1994). However, I was unable to perform a robust statistical test to demonstrate such differences due to a lack of suitable quantitative information and replicates for the southern shores.

In this study, a detailed description of northern Portuguese rocky shores will be made, not only to identify target species, or assemblages, which are relevant for the purposes of this thesis, but also to place the rest of this study within the Portuguese and European context. Three main questions will be addressed: a) *how variable are intertidal rocky shores in northern Portugal*? b) *what are the dominant species in the eulittoral zone*? and c) *are there any significant differences between northern and southern intertidal rocky shores*? As shown before, the answer to each of these questions can be given, at least partially. The available information about the Portuguese coast is fragmentary, but still useful if inspected carefully. Therefore, by coupling the data from Santos (1994) with a new set of samples taken from several sites, a much broader analysis of geographic patterns will be performed with the help of modern statistical techniques.

2.2 Materials and methods

2.2.1 Study area

The selection of the sites was based on the need to cover the longest practicable stretch of the coastline and to include shores of various rock types, aspect and exposure to wave action. Almost all the locations visited by Santos (1994) were revisited in this study, and seven new sites were added. The study area ranged from the northernmost rocky shore, near the Spanish border, to the Cape Raso, 400 Km south (figure 2.1). Rocky shorelines occur throughout this area interspersed at irregular intervals with sandy beaches and small inlets to lagoons and estuaries. It is basically an open coast and is subjected to swells from north-west of five metres maximum height. Tidal range does not vary considerably among sites and reaches about four metres at extreme spring tides.

Only fully marine stations were chosen, the brackish ones being avoided. The 35 selected shores (figure 2.1) differed slightly in their geological nature, topography and orientation. Almost all shores were faced westwards, with the exception of Baleal which was faced northwards. The northernmost stations were characterized by a gently sloping and highly broken bedrock, mainly granite or gneiss, in some cases associated with large patches of sand. From Buarcos to the south, the rock type is mainly calcareous and the coast is steep with high cliffs.

2.2.2 Terminology

The most recent ecological studies in intertidal and subtidal ecosystems on the Portuguese coast (e.g., Saldanha, 1974; Marques *et al.*, 1982) were exclusively based on the French descriptive framework (Pérès and Picard, 1958, 1964; Bellan-Santini, 1969), which was derived from the earlier work of Stephenson and Stephenson (1949). According to this scheme the shores were divided in three main zones: a supralittoral zone, dominated by the black lichen *Verrucaria maura*, a mediolittoral zone limited in its lower part by the encrusting algae *Lithophyllum lichenoides*, and an infralittoral zone extending below Extreme Low Water Spring level (ELWS) and usually dominated by red algae and laminarians.

Lewis (1964) pointed out the weaknesses of such framework, and its failure to apply to many situations due to the rigid definition of some of the upper and lower limits. He proposed a different scheme with two main zones: a sublittoral zone, characterized by the presence of laminarians (but not limited by ELWS level), and a

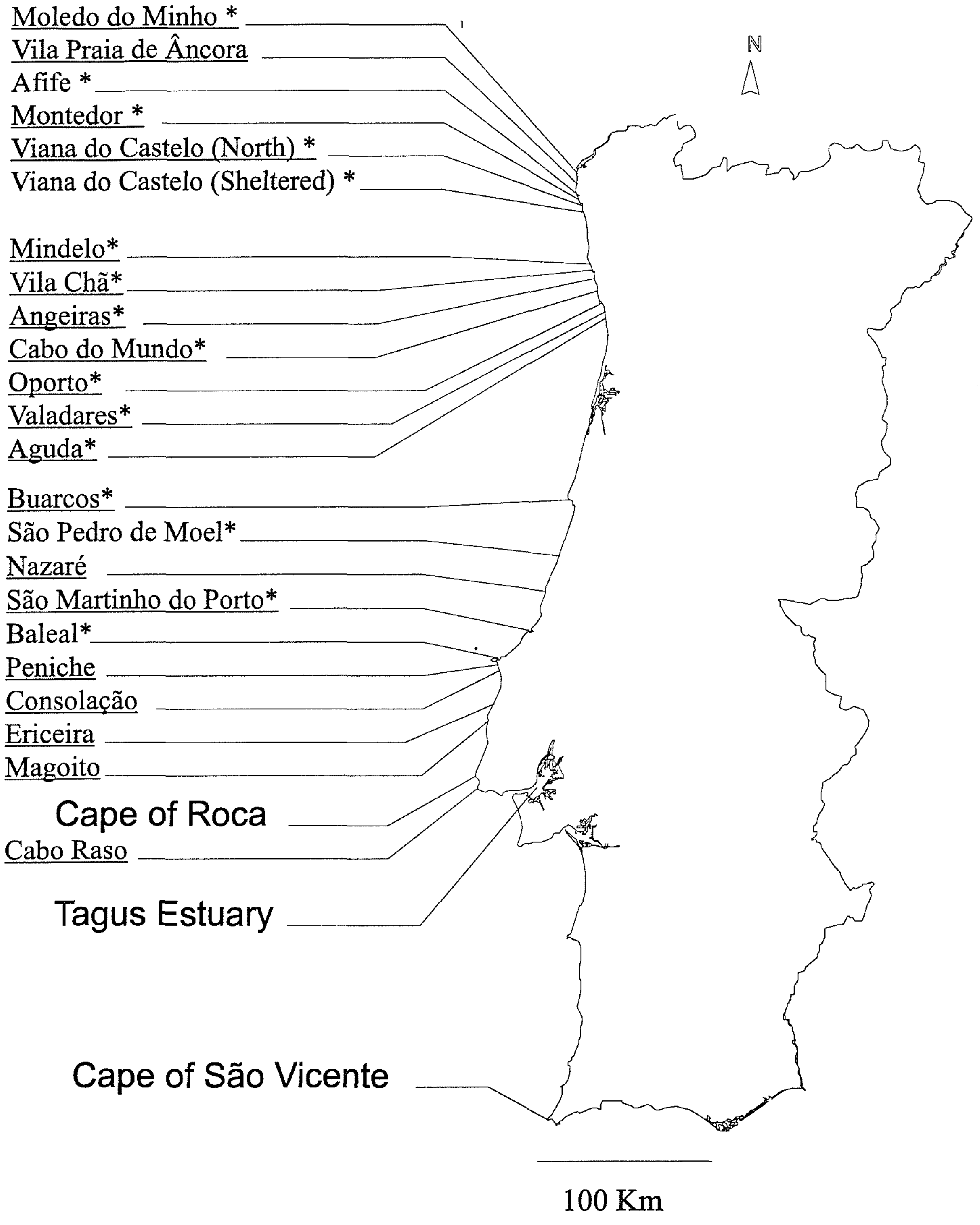


Figure 2.1: Study area. Shores marked with * were visited by Santos (1994), and shores underlined were sampled during the present study.

littoral zone, encompassing the rest of the shore subjected to the action of the tides. The littoral zone was then subdivided in two other zones: the eulittoral zone, and a littoral fringe, the latter comparable with the supralittoral zone of the previous scheme. This widely accepted framework (see Raffaelli and Hawkins, 1996) was adopted in this work, with the minor modifications proposed by Hawkins and Jones (1992). Nomenclature follows Lewis (1964).

2.2.3 Sampling techniques

The intertidal survey was undertaken during spring tides from April 1997 to July 1999, on stretches of natural coastline unprotected by man-made structures. Non-destructive methods were used according to Hawkins and Jones (1992). Animals and plants were recorded along up to four transect lines from the low water mark to the uppermost part of the shore. Zones were defined arbitrarily by the dominant species and their upper and lower limits were recorded relative to the chart datum. In each zone, density or percentage cover of conspicuous species was measured using 5–10 quadrats (50×50 cm subdivided in 10 cm subdivisions).

Whenever possible, animals and plants were identified *in situ*. Doubtful material was carried to the laboratory, fixed in 5% formalin with sea water, and identified under a binocular microscope. Species classification used in the present study follows Bárbara and Cremades (1993) for the algae, and Hayward and Ryland (1995) for the animals. Saldanha (1996) was used for the southern animal species not considered in the latter reference.

2.2.4 Data analysis

2.2.4.1 Zonation schemes

Zonation schemes were plotted for several shores in an attempt to reveal the main patterns occurring on the northern coast of Portugal. These schemes were based on those depicted in Lewis (1964), Hawkins and Jones (1992), and Raffaelli and Hawkins (1996). Only dominant species were plotted to keep the diagrams simple. More complete schemes for the northern region of Portugal can be found in Santos (1994).

2.2.4.2 Multivariate analysis

Community data are, by definition, multivariate. Therefore, the application of multivariate statistical analysis to community ecology is natural, routine, and fruitful

(Gauch, 1982). There is a vast array of algorithms available (Gauch, 1982; Digby and Kempton, 1987), which have been successfully applied to marine communities (Castric-Fey *et al.*, 1973; Castric-Fey, 1988; George and Fincham, 1989; Palmer, 1993; Castric-Fey and Chassé, 1991). The advantages and disadvantages of several multivariate methods have been discussed in detail (Chardy *et al.*, 1976; Fasham, 1977; Digby and Kempton, 1987; Warwick and Clarke, 1991), and among these methods, non–metric multidimensional scaling (MDS) was considered one of the most robust (Fasham, 1977; Digby and Kempton, 1987). Although based on a complex numerical algorithm, MDS is conceptually simple, making few assumptions about the form of the data or the inter–relationships of the samples (Clarke and Warwick, 1994).

The MDS was adopted and refined by Clarke (1993) for the analysis of changes in the structure of marine communities. Besides being a powerful descriptive tool, where the link between final results and the original data is relatively transparent and easy to explain, Clarke (1993) devised a suite of companion methods which are helpful in the interpretation and further testing of the data. Among these methods, the Analysis of Similarity (ANOSIM) is particularly useful, because it permits to statistically test hypotheses about the ordination of the data (Clarke and Warwick, 1994).

The statistical analysis was carried out using the software package PRIMER (Clarke, 1993). To build the initial matrix of species×sites, mean densities and percentage cover in each zone were transformed into abundance scores according to Crisp and Southward (1958) and Hawkins and Jones (1992). The highest value for each species in each site was then used. With this transformation, it was possible to include directly the data from Santos (1994) in the analysis. A similarity matrix was computed using the Bray–Curtis similarity coefficient. Since rankable scores were used instead of densities or percentage cover, no transformation or standardization of the data was necessary. The similarity matrix was then used to perform a standard MDS.

In my previous analysis (Santos, 1994), I found evidence for a north–to–south gradient in species occurrence and abundance, and identified three groups of shores according to their zonation patterns and dominant species. On the northernmost shores, especially from Moledo do Minho to Viana do Castelo, I observed a very consistent zonation pattern, similar to those found in Galicia (Niell, 1977; Bárbara and Cremades, 1993), Brittany (Fischer-Piétte, 1956) and southwest of England (Crisp and Southward, 1958; Lewis, 1964). The southernmost studied site, Baleal, was completely different from all other shores, mainly due to the dominance of typically southern species (e.g., *Asparagopsis armata*, *Patella rustica* and *Cystoseira tamariscifolia*). Although no other sites were sampled to the south of Baleal, it was concluded that it was a good representative of the southern type of shores, based on the available information for that region (e.g., Almaça, 1960; Saldanha, 1974; Marques *et al.*, 1982). Between Angeiras and Baleal, the shores were characterized by a mixture of both northern and southern species, and were grouped into a transition zone.

The hypothesis that there were consistent differences between the northern and the southern shores along the Portuguese coast was tested in the present work. The 35 sampling sites were divided into three groups according to the results of Santos (1994): a northern region, from Moledo do Minho to Cabo do Mundo (17 sites), a central region, from Oporto to São Martinho do Porto (12 sites), and a southern region, from Baleal to Cabo Raso (6 sites). Hereafter these groups will be treated as *northern*, *central* and *southern* regions, respectively. Differences between these regions were tested using ANOSIM (10000 permutations), followed by a dissimilarity breakdown analysis (SIMPER) to estimate the contribution of each species to the average dissimilarity between them.

2.3 Results

During the present survey, 19 shores were visited, at least twice, in a total of 118 transects, and 97 species were recorded (Appendix A). These included 53 species of macroalgae and the rest were animals. When compared with the results from Santos (1994), 13 new species were recorded. From these, six were only observed on the northern shores and the rest in the southern sites which were not sampled in that work.

2.3.1 Zonation patterns

All sites, but one, showed typical exposed or very–exposed zonation patterns (*sensu* Ballantine, 1961; Lewis, 1964), with the eulittoral zone dominated by mussels and/or barnacles, and an absence of fucoids (figure 2.2). In Viana do Castelo, however, there was an exceptional sheltered site blanketed by *Pelvetia canaliculata*, *Fucus spiralis*, *F. vesiculosus* and *Ascophyllum nodosum*. This type of zonation is unique to the Portuguese coast because *A. nodosum* does not occur further south, as observed earlier by Ardré (1970). Moreover, both *P. canaliculata* and *Fucus* were also dominant species on this shore, contrasting with their lower densities or total absence at the other sites to the south.

On the exposed shores, the littoral fringe – if present – was dominated by the prosobranch gastropod *Melaraphe neritoides* and by the black lichen *Verrucaria maura.* This belt extended from Extremely High Water Spring level (EHWS) up and could reach one or two metres high, depending on the degree of exposure to wave action (Lewis, 1964). This zone was the most consistent between sites. On some shores, its lower limit was hard to establish, mainly because *M. neritoides* could also be found among barnacles, down in the eulittoral zone, and *Chthamalus montagui* often reached the *Verrucaria* belt.

The eulittoral zone was much more variable. Nevertheless, it could be roughly divided into three subzones: upper, mid and lower eulittoral. On all shores, the upper eulittoral was dominated by the barnacle *Chthamalus montagui.* On some sites, the black lichen *Lichina pygmaea* was found within the barnacle zone. Because this lichen can cover a substantial portion of the rock surface, forming a very distinct belt, some authors have named the upper eulittoral as the *Chthamalus/Lichina* zone. However, this was seldom observed on the shores visited, and the upper eulittoral was only called the 'barnacle zone'.

Littorinids graze in the barnacle zone. Three species have been identified: *Littorina saxatilis*, *L. nigrolineata*, and *L. neglecta*, although there is considerable doubt about the latter (Graham, 1988; Johannesson and Johannesson, 1990; Reid, 1990). In this work they were treated as a species complex (*L. saxatilis* group), since in most cases it was very difficult to tell them apart in the field. Since these species have been identified as varieties of *L. saxatilis* in earlier literature (Nobre, 1940), and were arbitrarily treated as a species group by Santos (1994), this approach was used in the present work to provide comparable results. The two former species were common and extended from the barnacle zone to the mid eulittoral, sheltering in crevices or under mussels. *L. neglecta* was confined to the upper shore, and was usually found inside dead barnacle shells.

Limpets were the dominant grazers in the midshore, with *Patella depressa* being by far the most abundant species. *Patella vulgata* was restricted mainly to protected microhabitats, such as crevices or overhangs, and was rare in the southernmost sites. Here, another limpet species occurred (*Patella rustica*), but was confined to vertical rock walls in exposed places, usually above the populations of *P. depressa*. *Siphonaria pectinata* was also very abundant in the south of Portugal, living mainly among barnacles, in the mid and upper eulittoral zones. It became rare from Baleal

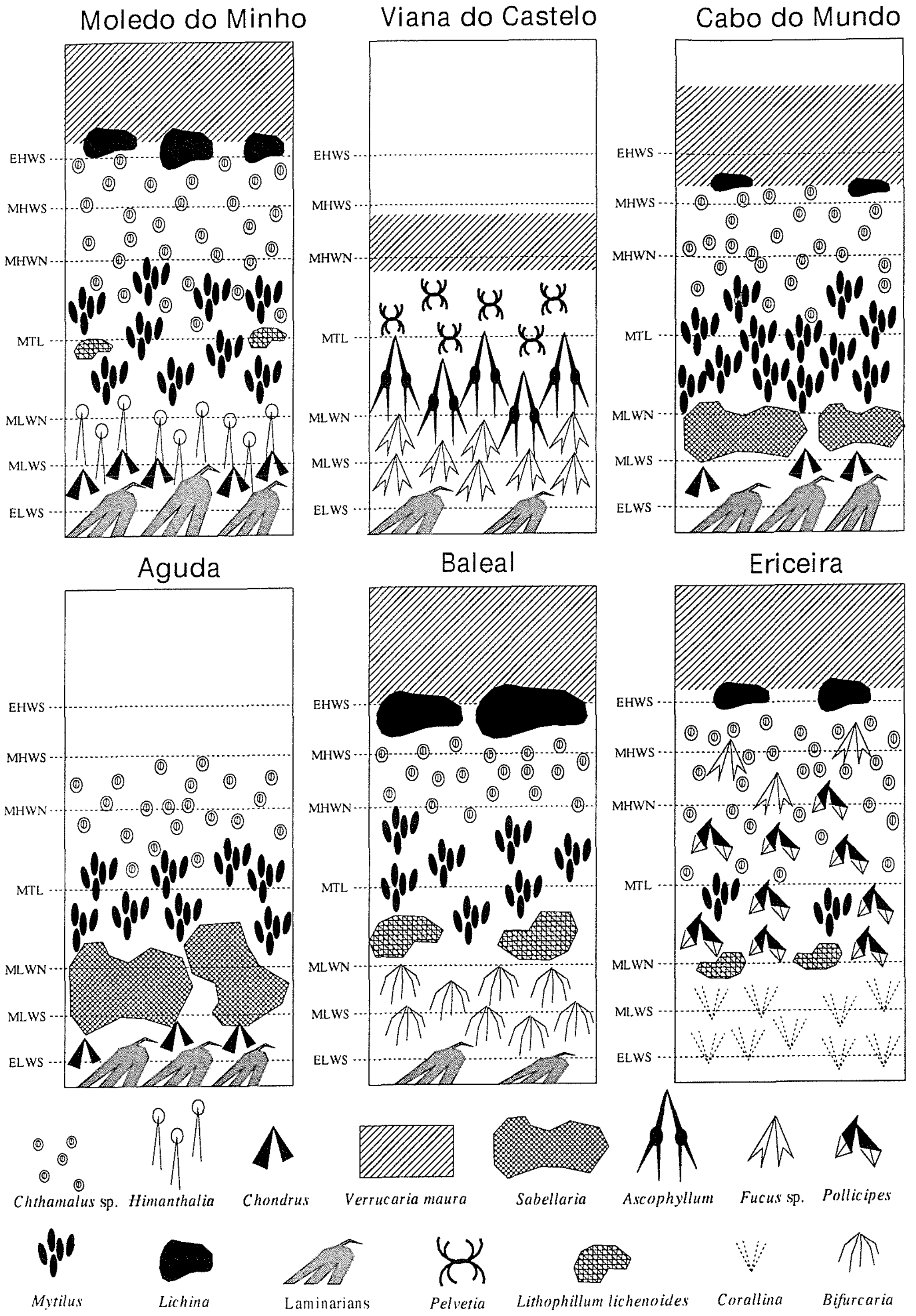


Figure 2.2: Main zonation patterns for different rocky shores in northern and central Portugal. All sites display exposed or moderately exposed zonation patterns, except Viana do Castelo, which is one of the only full marine sheltered sites in the northern coast of Portugal.

to the north, where only a few individuals were found, mainly in small rock–pools or among mussels.

From Moledo do Minho to Buarcos, the mid eulittoral was dominated by the mussel *Mytilus galloprovincialis*, and the barnacles *C. montagui* and *C. stellatus*. *C. stellatus* was less abundant than *C. montagui*, but since it grows larger than the latter, it often occupied a significant percentage of the rocky surface. Further south, mussel density decreased, and mussels were replaced by *Pollicipes pollicipes* in the more exposed shores (São Pedro de Moel, Peniche, Ericeira, Magoito), or by a monoculture of *C. montagui*.

Apart from ephemeral species (such as *Ulva* and *Porphyra*), only three algal species were seen in the midshore: *Mastocarpus stellatus*, *Laurencia pinnatifida*, and *Fucus spiralis*. *Mastocarpus* was more abundant in the northern shores and, together with its prostrate phase (formerly known as *Petrocelis cruenta*), could form a narrow but conspicuous belt between the mussels and the red algal turf. *Laurencia* was usually found among the red algal turf in the lower eulittoral, but in some shores it formed medium–sized patches within the mid eulittoral, especially when mussels were rare or absent (like in São Martinho do Porto). From Baleal to Cabo Raso, some *Fucus spiralis* were spotted in the barnacle and mussel zones. However, these were mostly isolated individuals, which have probably escaped limpet grazing, and never reached the size or the abundance of their conspecifics in more sheltered situations (like in Viana do Castelo).

Among the mussel patches, taking advantage of moisture and shelter provided by this species, several other animals were found. The predator *Nucella lapillus*, which feeds mainly on mussels, reached high densities on some shores (e.g., Cabo do Mundo). Trochids also occurred among mussels and barnacles, and two species were common at all the sites studied: *Gibbula umbilicalis* and *Monodonta lineata*.

The lower eulittoral was the most diverse zone. On the northern shores, it was characterized by a well developed algal turf, the understorey dominated by *Chondrus crispus* and the canopy by *Himanthalia elongata*. Several algal species were found within this zone, namely *Laurencia pinnatifida*, *Gigartina acicularis*, *G. pistillata*, *Pterosiphonia complanata*, *Gymnogongrus norvegicus*, *Calliblepharis jubata*, *Calliblepharis ciliata*, and *Corallina elongata*. In some shores, such as Vila Chã, Aguda, and Valadares, well developed sabellarian reefs (*Sabellaria alveolata*) usually excluded most – if not all – of the seaweed from this zone.

From Peniche to the south, the algal turf zone became narrower and dominated by *Corallina elongata* or *Gigartina acicularis*. This difference was more pronounced due to the absence of *Himanthalia elongata*, which reaches its southern limit in Vila Chã, and to a significant decrease in density of *Chondrus*. On the northern shores *Bifurcaria bifurcata* was confined to rock–pools, or to the sublittoral fringe, but from Buarcos southwards it was found on the exposed rocky surface. This trend reached its maximum significance in Baleal, where *B. bifurcata*, along with *Cystoseira tamariscifolia*, was the dominant species, thus forming an unique pattern among the Portuguese shores.

The algal turf also provides shelter for numerous animals. *Patella ulyssiponensis* (formerly known as *P. aspera*) was common in all sites and, although it is a typical lower shore species, it was also found among mussels or in rock–pools in the barnacle zone. Other species, like *Gibbula pennanti* and *Ocinebrina edwardsii* were also common within this zone. *Lithophyllum lichenoides* was found in the lower limit of the eulittoral zone in most of the southern shores. However, in the north, this species occurred in the mid eulittoral, usually above or among the mussel zone.

The sublittoral fringe was usually dominated by large kelps (*Saccorhiza polyschides*, *Laminaria hyperborea*, and *L. ochroleuca*). On some shores (Baleal, S. Pedro de Moel, Consolação) kelps were absent, and this zone was characterized by the presence of sea–urchins and the encrusting algae *Lithophyllum incrustans*. On the northern shores, kelps usually reached the Mean Low Water Spring level (MLWS). By contrast, from Baleal southwards their density decreased, and they were confined below ELWS level. *L. ochroleuca* became the dominant species (although being not as common as in the north), whilst *L. hyperborea* was absent, since it reaches its southern limit in Buarcos.

2.3.2 Biogeographic patterns

The MDS ordination revealed a clear separation between three shores (Viana do Castelo, São Martinho do Porto and Baleal) and the rest of the sampling sites (figure 2.3). The reasons for such separation were probably linked with the presence of very particular species or with abnormal abundance of some species that deviate from the general trends observed in the study area.

As shown before, Viana do Castelo displayed a zonation pattern typical of sheltered shores further north (Lewis, 1964), being blanketed by fucoids. One of the dominant species, *Ascophyllum nodosum*, could not be found anywhere else on the Portuguese coast. *Fucus spiralis* (and, in a lesser extent, *F. vesiculosus*), despite being present in other sites, never reached the abundance levels observed in this shore.

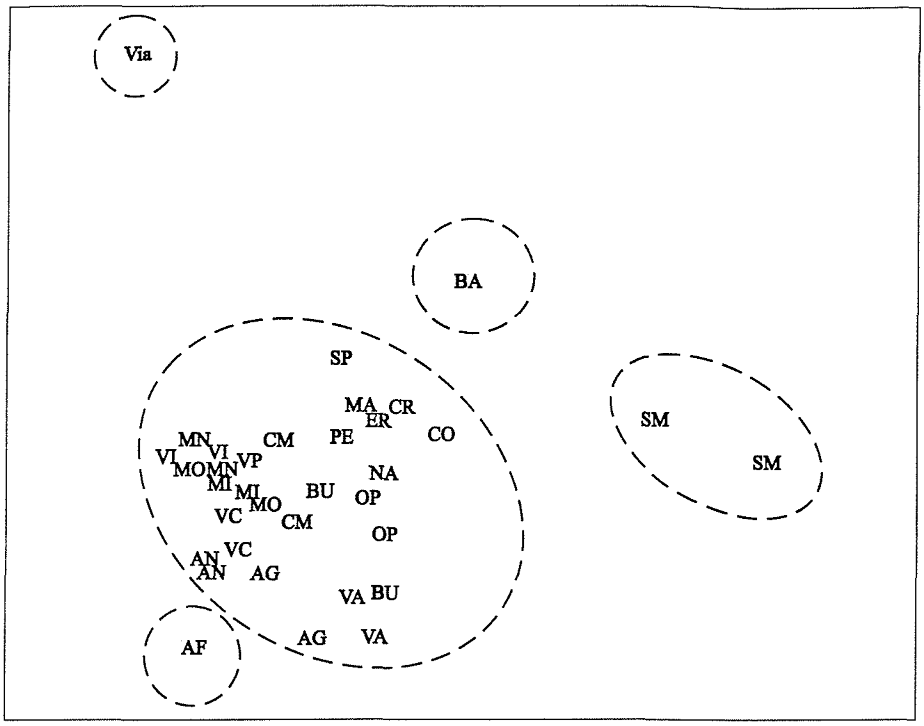


Figure 2.3: MDS ordination of sampling sites (*Stress*=0.15). MO = Moledo, VP = V. Praia de Âncora, AF = Afife, MN = Montedor, VI = Viana do Castelo (North), Via = Viana do Castelo (Sheltered), MI = Mindelo, VC = Vila Chã, AN = Angeiras, OP = Oporto, AG = Aguda, VA = Valadares, BU = Buarcos, SP = S. Pedro de Moel, SM = S. Martinho do Porto, NA = Nazaré, BA = Baleal, PE = Peniche, CO = Consolação, ER = Ericeira, MA = Magoito, CR = Cabo Raso. Note that some shores have replicates.

The littorinid *Littorina obtusata*, which is strongly associated with *Fucus*, was very abundant in this shore, contrasting with its absence at the other sites. Moreover, the absence of species like *Mytilus galloprovincialis*, as well as many of the common red seaweed from the algal turf, also contributed to the separation of this site.

Baleal is a northwards facing shore, and in some respects similar to other southern shores. The main difference was found in the sublittoral fringe, where both *Bifurcaria bifurcata* and *Cystoseira tamariscifolia* completely covered the rocky surface. Moreover, two species of red algae were also common within this zone: *Asparagopsis armata* and *Plocamium cartilagineum*. *Asparagopsis armata* is an alien species, and is very abundant in the upper sublittoral zone in the south of Portugal (Saldanha, 1974). However, this species was absent from this site northwards. *P. cartilagineum* was present in almost all sites but it was not as abundant as in Baleal. In São Martinho do Porto, the four species mentioned were also abundant in the lower

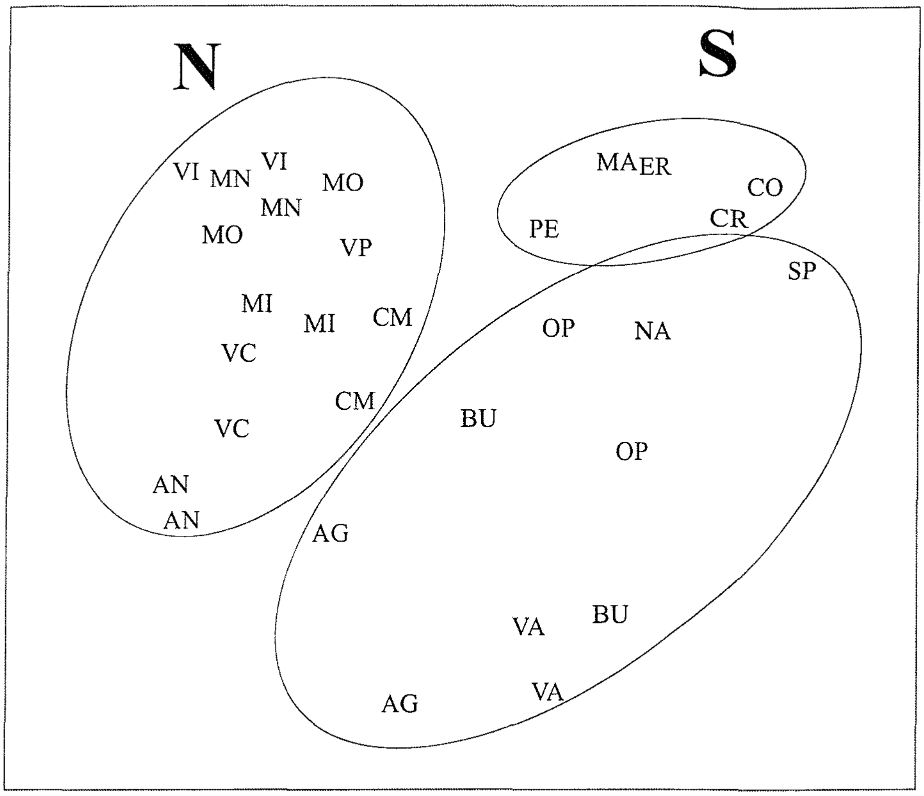


Figure 2.4: MDS ordination of sampling sites after exclusion of Afife, Viana do Castelo, São Martinho do Porto and Baleal. *Stress*=0.19

zone, but they did not form such a conspicuous belt as in Baleal. São Martinho do Porto seems to be the northern limit for *A. armata* and the limpet *Patella rustica* on the Portuguese coast. Apparently, mussels were absent from this site and even barnacles were only present at very low densities.

On the other hand, Afife was included in a previous analysis (Santos, 1994) because it was considered the southern limit of *Laminaria saccharina* on the European coast. This shore was plotted near to the main group of shores, but along with São Martinho do Porto, it was also very bare. At Afife, the bedrock never reaches more than two metres above MHWS level, and thus the absence of a littoral fringe and all associated species (like *Verrucaria maura* and *Melaraphe neritoides*), which might have contributed to the separation of this shore from the main group.

The four shores mentioned above (and their replicates) were excluded from the analysis, and a new MDS ordination was computed. This ordination (*stress*=0.19) showed a better scatter of all sites (figure 2.4), and even though a clear horseshoe effect was evident, with the northern and southernmost sites at each extremity, the diagram was still interpretable. The three regions considered were well separated,

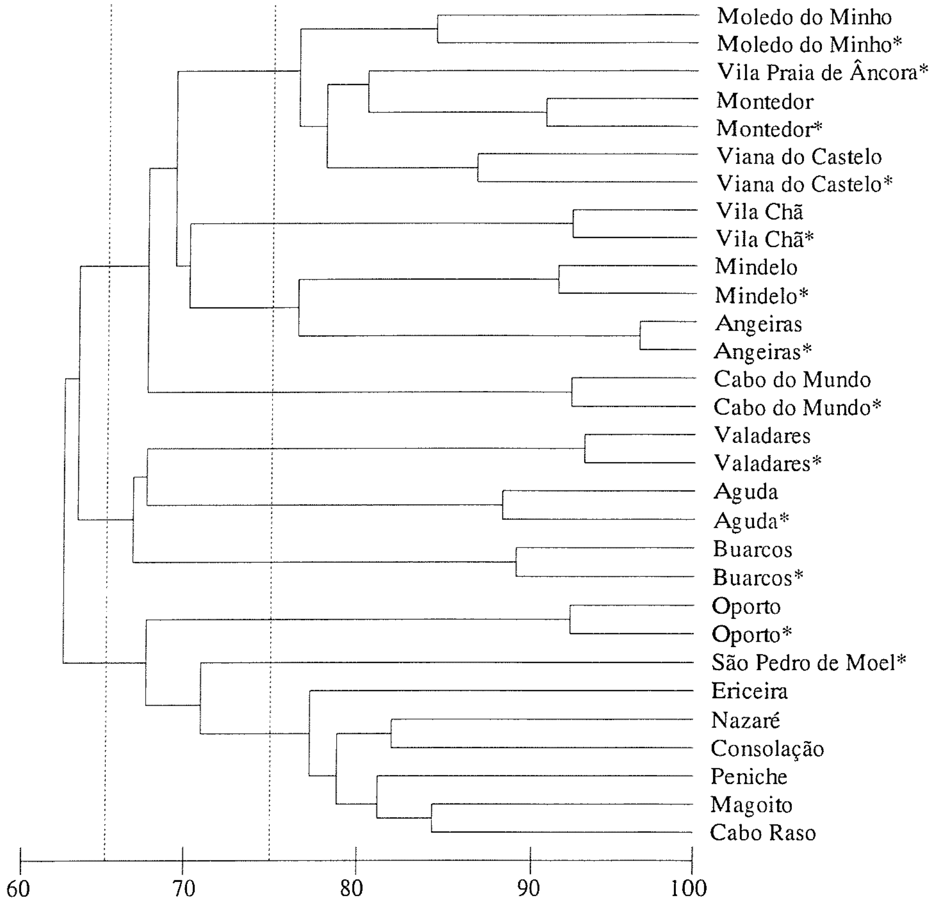


Figure 2.5: UPGMA clustering of all sites after exclusion of Afife, Viana do Castelo, São Martinho do Porto and Baleal, showing the 65% and 75% levels of similarity. Shores marked with * were sampled by Santos (1994).

with almost no overlap. The stress value of 0.19 implied a careful examination and interpretation of the results. According to Clarke and Warwick (1994), an ordination with a stress value between 0.1 and 0.2 still gives a useful 2–dimensional picture, although too much reliance should not be put on the detail of the plot. These authors suggest that the results should be cross-checked with those from an alternative multivariate method, namely by means of a superimposition of cluster–analysis groups. Therefore, an UPGMA cluster analysis was carried out using the reduced similarity matrix (30 shores).

The resulting dendrogram (figure 2.5) revealed a clear separation between northern and southern shores (64% similarity level), with no evidence for a transition (central) zone. Surprisingly, the station of Oporto was clustered within the southern group of shores. The superimposition of these results and the MDS ordination is depicted in figure 2.6. At the 75% similarity level, the cluster analysis revealed three

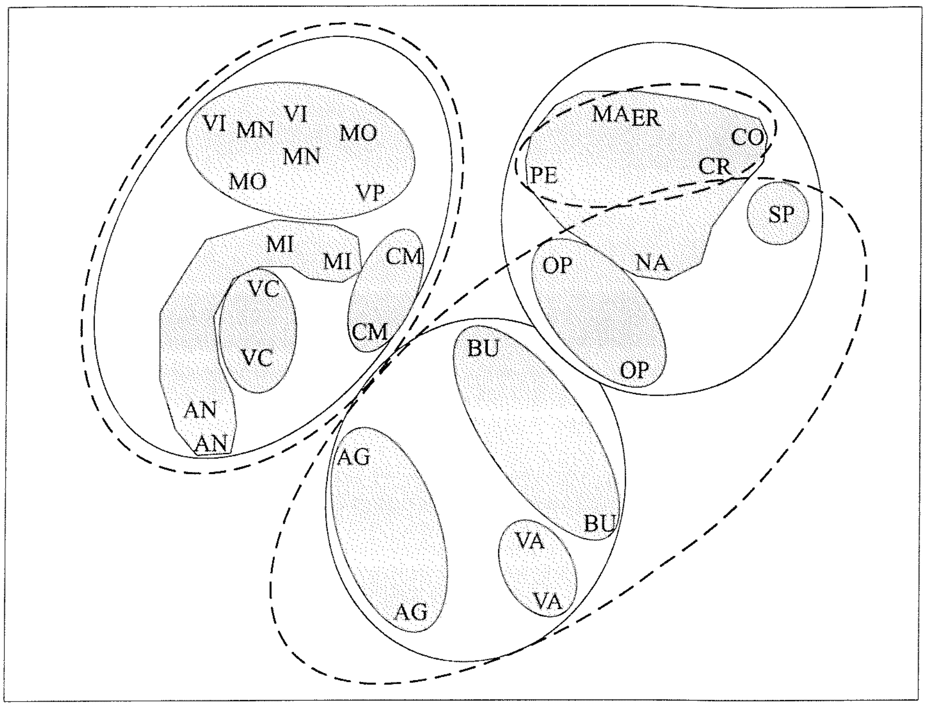


Figure 2.6: Superimposition of UPGMA cluster analysis and MDS ordination. The figure shows MDS groups (dashed lines), 65% (dark grey area) and 75% (light grey area) levels of similarity after UPGMA.

groups: the first one was coincident with the northern region, the second one only included shores from the central region, and the third one included shores from both the central and southern regions. Thus, the differences between the two ordinations were apparently due to the definitions of the limits of the central and southern regions.

The shores previously classified in the central region and clustered within the southern group are Oporto, Nazaré, and São Pedro de Moel. The clustering of Nazaré and São Pedro de Moel in this group could be easily explained by their geographic proximity to the southern region. The presence of Oporto within this group was not so straightforward. Among the northern shores, however, this one was the most affected by all kinds of human impacts: there are several sewage outfalls in the vicinity of this area, ship traffic is high due to the harbour of Leixões, and several oil–spills occurred in the near past. Some of the most typical northern species (e.g., *Himanthalia elongata*, *Pelvetia canaliculata*, *Laminaria hyperborea*, *Gymnogongrus* spp., *Calliblepharis* spp.) were absent from this site. Moreover, the sublittoral fringe, which is usually dominated by *Saccorhiza polyschides* on the northern shores, was almost bare here. This zone was covered by *Lithophyllum incrustans*, along with some individuals of *Laminaria ochroleuca*, which are the dominant kelps in the south.

Table 2.1: Pairwise tests after ANOSIM over the three groups of shores. N: northern region (Mindelo do Minho, Vila Praia de Âncora, Montedor, and Viana do Castelo, Mindelo, Vila Chã, Angeiras, and Cabo do Mundo); C: central region (Oporto, Valadares, Aguda, and Buarcos, São Pedro de Moel and Nazaré); S: southern region (Peniche, Consolação, Ericeira, Magoito, and Cabo Raso).

Groups used	Statistic value	Possible permutations	Permutations used	Significant statistics	Significance level
N vs C	0.660	3.2×10^6	10000	0	<0.001
N vs S	0.866	15504	10000	1	<0.001
C vs S	0.315	3003	3003	62	0.021

The ANOSIM analysis revealed a statistical difference between the three regions ($p < 0.05$), and a Global $R = 0.699$ indicates a good degree of discrimination between them (Table 2.1). The results of the SIMPER analysis are shown in Appendix B.

Similarity and dissimilarity between regions is depicted in Table 2.2. From the three regions considered, the most homogeneous was the southern one. Conversely, the most heterogeneous was the central region, which was included in this study as a transition zone. Dissimilarity values were not very different from each other, which means that the number of species shared between these regions was higher than the number of exclusive ones.

Table B.1 (Appendix B) lists the species which contribute the most to the dissimilarity between the northern and central regions. Species ratios were low, falling below 2.00. Nevertheless, three species could be considered as good discriminating species: *Himanthalia elongata*, *Gastroclonium ovatum*, and *Gigartina pistillata*. *Himanthalia elongata* was also the species that contributed the most to the average dissimilarity between northern and central regions, and among the listed taxa was one of the two exclusive species of the northern region. The other exclusive species was *Pelvetia canaliculata*, but its lower percentage contribution was probably a result of its discontinuous distribution and low abundance within the northern region.

All other species were common to both regions but they differed in their

Table 2.2: Average similarity between sites within regions (depicted in bold) and dissimilarity between the three regions considered, after ANOSIM.

Regions	Northern	Central	Southern
Northern	**71.45%**		
Central	38.42%	**66.42%**	
Southern	39.17%	35.98%	**78.16%**

average scores, suggesting that a gradient of abundance exists between them. A careful inspection of the averaged scores revealed that most of the listed species had a higher abundance in the northern region, meaning that this gradient was mainly unidirectional, from north to south. Only *Pollicipes pollicipes*, *Lithophyllum incrustans*, *Halichondria panicea* and *Anemonia viridis* were more abundant in the central region. *Pollicipes pollicipes* assumed a particular importance, because it was the dominant species in the mid eulittoral, were it replaces the mussels.

Two of the first 10 species listed were those which characterize the littoral fringe (*Verrucaria maura* and *Littorina neritoides*). This might have happened because in the central region the littoral fringe was sometimes absent (Valadares, Aguda), or almost non–existent (Buarcos), mainly because the bedrock did not extend above MHWS. On the other hand, seven species were typical of the sublittoral fringe (*Saccorhiza polyschides*, *Helcion pellucidum*, *Laminaria ochroleuca*, *L. hyperborea*, *Lithophyllum incrustans*, *Gelidium sesquipedale*, and *Marthasterias glacialis*). This can be interpreted in light of the previous results: from north to south the sublittoral fringe became less conspicuous, while *S. polyschides* and *L. hyperborea* were replaced by *L. ochroleuca* and *Lithophyllum incrustans*. The abundance of *H. pellucidum* was tightly associated with the kelp *S. polyschides*, and thus its high contribution to the overall dissimilarity.

Table B.2 lists the species that contributed the most to the dissimilarity between the northern and southern regions. *Himanthalia elongata* was once again the most important species (as it is absent in the south). Contrasting with the previous comparison, however, there were several good discriminating species. These could be subdivided into four main groups:

- Exclusive species of the northern region: *Himanthalia elongata*, *Gastroclonium ovatum*, *Laminaria hyperborea*, that were also responsible for the dissimilarities between northern and central regions. Once again, *Pelvetia canaliculata* had a small percentage contribution when compared with the other exclusive species of the northern region.

- Species whose abundance decreased southwards: *Chondrus crispus*, *Mastocarpus stellatus*, *Sabellaria alveolata*, *Saccorhiza polyschides*, *Helcion pellucidum*, *Mytilus galloprovincialis*, *Calliblepharis jubata*, *Pterosiphonia complanata*, *Lomentaria articulata*, and *Gigartina pistillata*.

- Species that were exclusive of the southern region: *Patella rustica*, *Codium adhaerens*, and *Asparagopsis armata*.

- Species whose abundance decreased northwards: *Fucus spiralis*, *Siphonaria pectinata*, and *Onchidella celtica*. *F. spiralis* was present in the exposed rocky surface of all southern shores, and was found on the northern shores as well. However, in this region it was always restricted to the sheltered (and thus unsampled) sites, explaining its lower abundance or absence in the northern region in the present study.

It should be noted that 18 of the 20 listed algae were characteristic of the lower eulittoral zone or the sublittoral fringe. From these, only four species were more abundant in the south than in the north, including two exclusive species. One of the dominant algal species in the southern lower eulittoral – *Corallina elongata* – did not appear in the 30 topmost species. Its abundance was not very different between northern and southern regions, which means that its dominance was probably due to the lack of other species rather than to an increase in percentage cover. These findings reinforce the previous observation that the sublittoral fringe and the lower eulittoral zone became less distinctive towards the south.

Dissimilarities between the central and southern regions are listed in Table B.3. *Patella rustica* was the best discriminating species, together with *Lithophyllum lichenoides*, *Codium adhaerens* and *Asparagopsis armata*. For the purpose of this comparison *P. rustica* and *C. adhaerens* were considered as exclusive species of the southern region. This is not strictly true, since both species exist in São Martinho do Porto, which was excluded from the present analysis, but was part of the central region. Therefore, these two species disappear northwards in the transition region.

Sabellaria alveolata, the second topmost species, was much more abundant in the central region. As stated earlier, this polychaete builds reefs that can reach considerable dimensions, often excluding many – if not all – of the major species in the lower eulittoral zone. The presence of well developed *Sabellaria* reefs seems to be one of the most striking characteristics of the transition zone.

2.4 Discussion

2.4.1 Zonation patterns

The observed zonation patterns illustrate the open nature of the northern Portuguese coastline, where large estuaries and inlets are almost absent and the only sheltered conditions are found inside harbours or in very particular situations. The lack of exposure scales for the Portuguese coast requires the use of those developed for the northern Spain (Niell, 1977; Bárbara and Cremades, 1993) or the United Kingdom (Ballantine, 1961; Lewis, 1964; Hawkins and Jones, 1992). However, there is no agreement in the range and number of degrees used in each of these scales. The observed geographic variation along large portions of coastline makes it impossible to apply any of them far from the sites where they were developed (Dalby, 1980). Nonetheless, all authors agree that the presence of large brown algae in the midshore indicates a low degree of exposure (see Raffaelli and Hawkins, 1996). On the other hand, the presence of a well developed littoral fringe, usually above EHWS, indicates strong wave action (Lewis, 1964; Saldanha, 1974).

The sites studied were mainly exposed or moderately exposed. This is particularly true for the northern shores, where a well developed mussel belt was found, and apart from the algal turf in the lower eulittoral, and *Mastocarpus stellatus*, no other seaweed were found in the midshore. Conversely, *Fucus spiralis* was often found in the upper eulittoral of the southern shores. This is the most tolerant species to wave action among the fucoids, and its presence in the midshore cannot be used as an indicator of a lesser degree of exposure (Lewis, 1964; Schonbeck and Norton, 1979c,b). Apart from that, the southern sites do not deviate much from the exposed patterns, the main differences being that mussels were usually replaced by *Chthamalus* or *Pollicipes*, the littoral fringe and the lower eulittoral zone were less conspicuous, and in the latter zone *Himanthalia elongata* was replaced by *Bifurcaria bifurcata*.

Northern shores displayed a pattern of zonation comparable to those described by Lewis (1964) for the southwest of the United Kingdom. Mussels, along with barnacles, were the dominant species in the eulittoral, whilst brown macroalgae such as *Himanthalia elongata* and a well developed red algal turf (mainly dominated by *Chondrus*) were observed in the lower eulittoral. The same pattern was also found in the exposed shores of Galicia, which suggests a certain homogeneity within the north–east Iberian Peninsula (Niell, 1977; Anadón, 1981; Anadón and Niell, 1981; Fernández and Niell, 1981; Anadón, 1983). Moreover, the typical zonation pattern of sheltered shores found in Viana do Castelo is also widespread throughout the Rias Baixas (Galicia, NE Spain).

Biogeographic variation should account for most of the differences found in the zonation patterns observed from north to south, as will be shown below. Nevertheless, it is worth noting the following: there was no apparent reason for the decrease in mussel density towards the south. *Mytilus galloprovincialis* is considered a southern species, and its distribution ranges from the Mediterranean and North Africa to the English Channel. This species is abundant in some of the southernmost shores, and since Portugal stands in the centre of its distribution area, it should not be subjected to the constraints associated with the limits of distribution.

2.4.2 Biogeographic patterns

The multivariate analysis revealed consistent differences among the three considered regions which can be attributable to two distinct phenomena:

- species that are present in one region and absent from the others, either because their distribution limits lie within the study area, or due to a gap in their geographical range.
- species that, although present in all or almost all the sites, display a clear gradient of abundance.

The existence of a gradient of species abundance along the Portuguese coast was formerly and independently described by several authors (Cúmano, 1945; Ardré, 1970; Lopes, 1993). These findings should be interpreted in the light of the biogeographic evidence for the European seas. The north–east Atlantic has been considered to comprise two main biogeographic regions: the Boreal and the Mediterranean–Atlantic (Ekman, 1967; Briggs, 1974). The first extends from the north of Scandinavia to the English Channel, encompassing the North Sea and the Baltic. The second comprises the rest of the coast, from the Channel to the north of Africa (Mauritania) and the Mediterranean Sea.

The Mediterranean–Atlantic region, in which the Portuguese coast is included, is a warm–water zone, and is much richer than the Boreal region, to the north. Far from being an homogeneous and distinct unit, it also includes several elements from the Boreal and Tropical regions, and has been subdivided in three sub–regions: the Lusitanian sub–region, from the English Channel to Gibraltar; the Mauritanian sub–region, from Gibraltar to the Cape Blanco; and the Mediterranean sub–region, encompassing the Mediterranean Sea (Ekman, 1967). When compared with the other sub–regions, the Mediterranean is richer, and possesses a considerable number of endemic species. Nevertheless, the Straits of Gibraltar do not represent an important biogeographic boundary (Ekman, 1967), and in fact several Mediterranean species reach the south of Portugal, while others extend as far as the English Channel. Likewise, some Boreal cold–water species reach the Lusitanian region, and go further south, reaching the north of Africa or penetrating into the Mediterranean.

The Portuguese coast is precisely in the middle of the Mediterranean–Atlantic region, thus being under the influence of these ‘northern’ and ‘southern’ elements.

The position is further confused by there being regions typified by upwelling or colder and wetter weather (north of Portugal and Spain) interspersed with warmer regions (southern Portugal and the Basque Country). Pockets of upwelling also occur further south in Portugal leading to advection of colder water onto the shore.

Several cold–water species were found to have their distribution boundaries within the study area: *Himanthalia elongata*, *Laminaria hyperborea*, *Pelvetia canaliculata*, *Delesseria sanguinea*, and *Halidrys siliquosa*. *Delesseria* and *Halidrys* are two rare species, often found isolated among other dominant seaweed. Although both species have been observed to the south of the limits described by Ardré (1970) in the 1960s, the same author stressed that their presence in the north of Portugal was sporadic and very variable, as proven by some records from Oporto, in the early 1900s (Ardré, 1971). The geographic boundaries of the first three species have changed significantly in the last three decades. *Himanthalia*, which was present in São Martinho do Porto (Ardré, 1970), is now limited to Angeiras, 200 Km north; *Pelvetia* reached the Berlenga Island (Rodrigues, 1963; Ardré, 1970), near Peniche, and is now limited to Cabo do Mundo (250 Km north); finally, *Laminaria hyperborea*, which was observed in Baleal (Ardré, 1970), is now limited to Buarcos (100 Km north).

For practical considerations, *Patella rustica*, *Codium adhaerens*, *Asparagopsis armata*, *Onchidella celtica*, and *Siphonaria pectinata* were considered to reach their northern limits within the study area. This was not strictly true, because all the species reappear on the Asturian coast (Fischer-Piétte, 1955; Niell, 1977; Fernández and Niell, 1981, 1982), which was found to have pronounced Mediterranean characteristics (Fischer-Piétte, 1955; Arrontes and Anadón, 1990) or even further north (*Onchidella* occurs in the southwest U.K., Hayward and Ryland, 1995). *P. rustica*, *C. adhaerens* and *Asparagopsis* do not extend further north from São Martinho do Porto. Therefore, their northern limit on the Portuguese coast is still the same after several decades (Ardré, 1970; Nobre, 1940). *Siphonaria* and *Onchidella* have gone through a considerable expansion since they were found by Nobre (1940) in the zone of Peniche. In the early 1990s Santos (1994) found them as far north as Angeiras and Valadares, respectively. During the present study, a density increase of *Siphonaria* was observed in all the northern sites where it was spotted by Santos (1994), and one individual was found in Viana do Castelo among the mussels, thus 40 Km north from the previous limit (Santos, 1994), and more than 150 km since the last observation of Nobre (1940). *Onchidella* was observed in Cabo do Mundo, 10 Km north from its previous limit (Santos, 1994), and more than 100 Km north from the earlier record of

Nobre (1940).

The regression and expansion of these species is not yet understood. The pioneering work of Fischer-Piétte (1956, 1957, 1958, 1963) in the north of the Iberian Peninsula has shown that intertidal species boundaries could change in a few decades. Climate change is a serious candidate to explain such variations (Southward *et al.*, 1995; Sagarin *et al.*, 1999), but human induced impacts cannot be disregarded. An increase of water or air temperature should favour the expansion of warm–water species. This is happening with *Siphonaria* and *Onchidella*, but not with other common southern species such as *Asparagopsis armata* and *Patella rustica*. It is noteworthy that *Siphonaria* is thought to be associated with ship traffic and harbours (which are common in the north of Portugal and Spain), and is observed sporadically in Galicia (Rolán, 1992), suggesting that its range can be limited by a specific inability to expand, rather than by any climatic constraints.

Nevertheless, the regression and expansion of species contributes either to increase the differences between northern and southern regions, this being more evident as it involves the disappearance of dominant species like *Himanthalia*, or to increase their similarities, due to the expansion of formerly exclusive but abundant species of the southern region, such as *Siphonaria*. Apparently, the rate of regression by northern species seems to be more pronounced than the rate of expansion of southern species, if the number of involved species is considered. This also applies to other taxa such isopods, amphipods, and pycnogonids (Santos, 1994).

Apart from the organisms that have geographic boundaries within the study area, several other species contributed to the dissimilarities found among the three regions considered by displaying a sharp gradient of abundance along the coastline. These included several seaweed from the lower eulittoral algal turf, and in particular *Chondrus crispus* and *Bifurcaria bifurcata*. *Chondrus* extends from the Arctic Ocean to the south of Portugal. It dominates the understorey in the lower eulittoral of the northern shores, but from Aguda to the south its density decreases sharply, and only very small individuals can be spotted in the lower shore, often in non–reproductive stages (Ardré, 1970).

Bifurcaria bifurcata is a southern species that extends from Morocco to Ireland, with several gaps within its range (Ardré, 1970). Although an inspection of the raw data reveals a density increase towards the south, this species is not uncommon on the northern shores, where it is confined mainly to rock–pools. *Bifurcaria* tends to replace *Himanthalia* on the shores where the latter is absent, becoming more common on open rock. This pattern was also observed by Lewis (1964) in the shores of the

United Kingdom, and by Fernández *et al.* (1983) on the northern Spanish coast. Fernández *et al.* (1983) attempted to divide the Atlantic coast of the Iberian Peninsula based on the presence or absence of *Himanthalia* and *Bifurcaria*. Not surprisingly, they have classified the Asturian and the Portuguese coasts as *Bifurcaria* dominated zones, whilst the Galician coast was classified as an *Himanthalia* dominated zone. The reasons for such failure are obviously linked with the lack of information concerning the Portuguese coast, although the work of Ardré (1970) should have provided enough information for an accurate analysis of this trend.

Finally, boundary regions must be considered along the Portuguese coast. Cúmano (1945) divided the coast of Portugal in three distinct regions, limited by the Capes of Roca and São Vicente. More recently Lopes (1993) found that the most significant differences in Porifera assemblages were observed at the level of Consolação and Magoito, but suggested that these findings supported the existence of a boundary located near the Cape of Roca. Ardré (1971) inspected exhaustively the northern and southern limits of seaweed and concluded that the Tagus Estuary, along with the Cape Carvoeiro (Peniche), were probably the most important boundaries within the Portuguese continental shelf. She found no northern limits of southern species above Cape Carvoeiro. On the other hand, most of the northern species did not extend beyond the Tagus Estuary. Ardré tried to correlate these observations with climatic and hydrographic data, but the absence of robust data made the interpretation of the results difficult.

Other authors were more cautious, and rather than searching for sharp boundaries responsible for the differences observed in species occurrence, chose to regard the Portuguese coast as a broad interface between two main biogeographic trends: a 'southern element', composed by warm–water species, mainly from the north of Africa, but also from the Mediterranean Sea, and a 'northern element', characterized by cold–water species, from the North Sea and the Arctic (Saldanha, 1974; Almaça, 1985; Marques, 1989). Given that the differences between the three regions considered in this study have the same order of magnitude (36–39%, see Table 2.2), the present results suggest the existence of a gradient of species abundance along the Portuguese coast, with some points of inflexion which vary between groups.

2.5 Conclusions

The following conclusions can be drawn from the previous results:

- Apart from a few exceptions, rocky shores in northern Portugal display zonation patterns typical of exposed sites and very similar to those found in Galicia (NE Spain), Brittany (France) and southwest coast of the United Kingdom.

- In the north of Portugal the midshore is invariably dominated by mussels, barnacles and limpets.
- On the northern shores, the main differences are observed at the lower eulittoral level, particularly in the red algal turf composition, and in the development of sabellarian reefs.
- Northern shores differ significantly from their southern counterparts in two ways:
  - species that are present in one region and absent from the others, either because their distribution limits lie within the study area, or due to a gap in their geographical range.
  - species that, although present in all or almost all the sites, display a clear gradient of abundance.

Chapter 3

Patch Dynamics of Mussel Mosaics

3.1 Introduction

Disturbance provides the space for new colonizers and the timing of initiation and the hierarchical nature of species interactions dictate the pathway of succession (Connell and Slatyer, 1977; Sousa, 1984c; Sousa and Connell, 1992; Wu and Loucks, 1995; Benedetti-Cecchi, 2000). Because disturbance events vary over space and time, communities are best described as areas or patches differing in their state of succession and, therefore, in their species composition. Each of these patches can, in turn, influence the adjacent patches by providing propagules for further colonization, buffering environmental variation, and thus increasing the complexity and stochastic nature of the system. Stability or equilibrium within a patch is seldom or ever reached because disturbance (either physical or biological) is always resetting the system to a previous state (see Sousa, 1984c, for a review).

Patchiness is a common phenomenon among marine benthic organisms (see Wu and Loucks, 1995; Raffaelli and Hawkins, 1996, for a review) and most easily observed in intertidal habitats (Sousa, 1984a). Mussel beds are one of the most conspicuous examples of patch formation occurring epibenthically on both hard and soft substrata (Paine and Levin, 1981; Paine, 1984; Svane and Ompi, 1993; Tokeshi and Romero, 1995). Mussels are thought to be competitive dominant species on wave–swept shores, and may exist as extensive monocultures (Dayton, 1971; Paine and Levin, 1981). More often mussel beds are an ever–changing mosaic of several species which inhabit newly–born gaps (Paine, 1974; Paine and Levin, 1981; Paine, 1984).

The patchy nature of mussel assemblages is believed to be tightly linked with disturbance events. Space is the primary limiting resource for sessile marine organisms (Sousa, 1984c), and since mussels tend to outcompete all other sessile species (Paine and Levin, 1981), there must be some external forces responsible for the continuous renewal of this important resource. Wave action is probably the principal disturbance event in temperate climates (Harger, 1970; Harger and Landenberger, 1971; Levin and Paine, 1974; Paine and Levin, 1981; Suchanek, 1985), although other factors, such as extreme temperatures, should also account for the renewal of space (Dayton, 1971; Povey and Keough, 1991; Petersen *et al.*, 1986). It is noteworthy that apart from North American sites, the dynamics of space use in mussel–dominated communities has not been studied intensively (but see Seed, 1969a,b). Therefore, a geographically biased basis of the knowledge is in contrast with the perceived importance and generality of some ecological paradigms derived from a number of studies on species interactions in the mussel beds in North American rocky shores (Tokeshi and Romero, 1995). Investigation on similar systems for different geographic regions is thus necessary for an integrative understanding of processes on different scales (Underwood and Denley, 1984; Underwood and Petraitis, 1993).

In very dynamic assemblages, like mussel beds, the knowledge of life–history of individual species, and particularly recruitment processes, assumes an overwhelming importance in the understanding of their structure and patchiness. Many marine organisms produce pelagic larvae that spend some time offshore in the plankton, and the input of new individuals into intertidal populations will be affected by chance events operating in the sea (the so called 'supply–side ecology', Underwood and Fairweather, 1989). Spatial and temporal variation in larval settlement have the potential to modify or even override more deterministic processes, thus increasing the complexity of community structure (Hartnoll and Hawkins, 1985; Robles, 1997) and usually contributing to the maintenance of a high diversity mosaic (Menge *et al.*, 1993).

On the northern Portuguese rocky shores the mid–eulittoral zone can be described as a mosaic made of two important space occupiers: mussels (*Mytilus galloprovincialis*) and barnacles (*Chthamalus montagui*). Mussels form more or less distinct patches interspersed with gaps that tend to be covered by *Chthamalus*, and only in very particular situations do they occupy all of the available space. Cleared areas with byssus threads, indicating recent dislodgement of *Mytilus*, can be observed throughout the year. Several putative sources of disturbance should be considered for this region: wave–action is the obvious candidate, and despite being a continuous phenomenon, it is likely to be stronger during the winter months, with a peak in

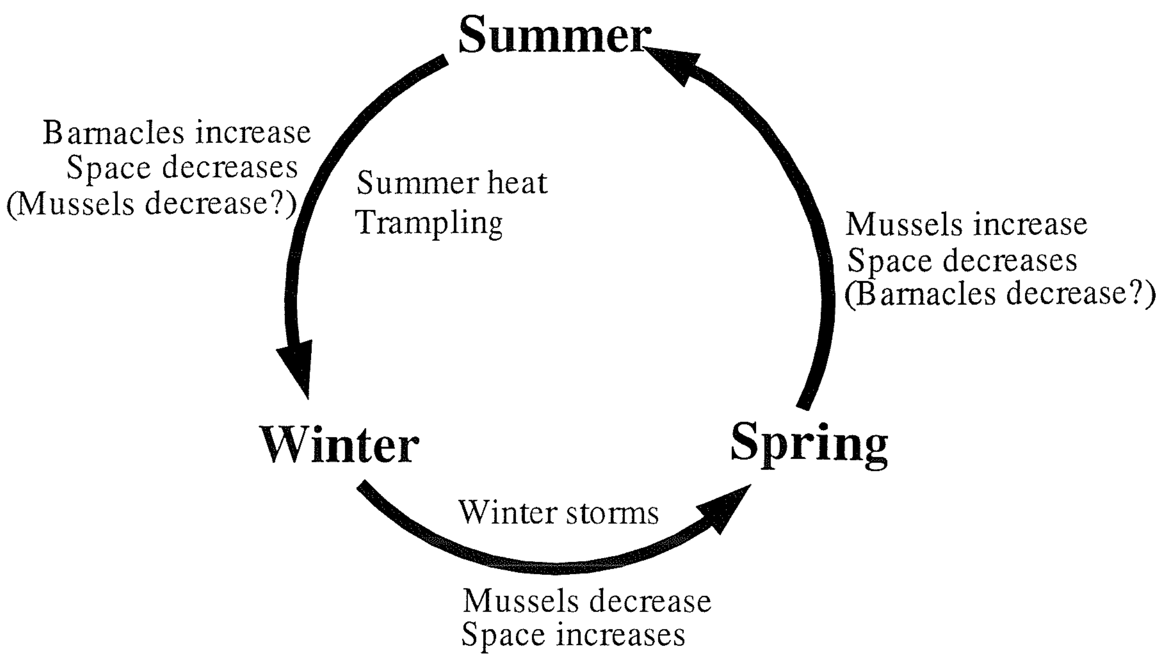


Figure 3.1: Proposed model for the variation of mussels, barnacles and bare rock in northern Portuguese rocky shores.

December–January, being weaker in the summer (Costa, 1987). On the other hand, the effects of heat and human trampling, both coincident with the summer months, should not be disregarded.

Heat is believed to play an important role in mussel dislodgement, especially in temperate and subtropical climates (Petersen *et al.*, 1986), but the assessment of its effects on mussels requires complex experiments (Helmuth, 1999). It is also important to stress that in the assemblage under study the main species – mussels, barnacles and limpets – have pelagic larvae. Once again, little is known about the reproductive and settlement periods of these species on the Portuguese coast. Sublittoral and eulittoral mussel populations (*M. galloprovincialis*) were the subject of an exhaustive study made by Saldanha (1974) in the southern coast of Portugal. The dynamics of limpet populations were analysed by Guerra and Gaudencio (1986) for the whole coast, although their study comprised only three sites. Finally, no published data exists about barnacle recruitment and population dynamics for the Portuguese shores, although some recent work was done in southern Portugal, as part of a European project (Cruz *et al.*, unpublished data).

Even with such scattered information, it is still possible to put forward a synthetic model that explains concisely the dynamics of this midshore system (figure 3.1). Since wave action is acknowledged to be the principal disturbance event on northern latitude shores (Harger and Landenberger, 1971; Paine and Levin, 1981), and on the northern Portuguese coast it is strongest during the winter months (Costa, 1987), the model predicts a significant decrease in mussel percentage cover after the winter season, and a corresponding increase in space availability. The average increase in air temperature and the heavy use of the shore by humans for recreational and subsistence purposes during the summer should also be regarded as a putative disturbance source (Petersen *et al.*, 1986; Brosnan and Crumrine, 1994; Tokeshi and Romero, 1995), and a decrease in mussel density should be expected towards the end of this season. Nevertheless, if wave action is in fact the main disturbance event controlling mussel density, the increase in space availability due to mussel dislodgement during the summer should be smaller than that of the winter. Furthermore, since local barnacles settle during late spring and throughout the summer (Lewis, 1986), there should be a simultaneous decrease in space availability towards the end of the latter season, thus cancelling out the gains due to mussel dislodgement. This uncertainty makes it impossible to guess the effect of the summer season on the availability of space. Finally, there should be a significant increase in mussel density during the spring to compensate for the losses during the winter (and possibly the summer). This increase can be made at the expense of barnacles or space, so a decrease in one or both variables should be expected.

The aim of the present study is to test whether the proposed model is valid for northern Portuguese intertidal mussel assemblages. The description and analysis of the variation of species density on a broad temporal and spatial scale will also be considered. Furthermore, an effort will be made to identify the main periods of settlement and recruitment of mussels, barnacles and limpets.

3.2 Material and methods

3.2.1 Study area and sampling sites

Six shores were selected on the northern coast of Portugal for the this study: Moledo do Minho, Montedor, Viana do Castelo, Cabo do Mundo, Foz do Douro and Aguda (figure 3.2). The first five shores were located in the northern region, defined in the previous Chapter, while the latter was located in the central region. As previously demonstrated, the main differences between these two regions are observed at the lower eulittoral level, the midshore being very similar. Because one of the overall aims of this work was to study the putative effects of oil spills on mussel

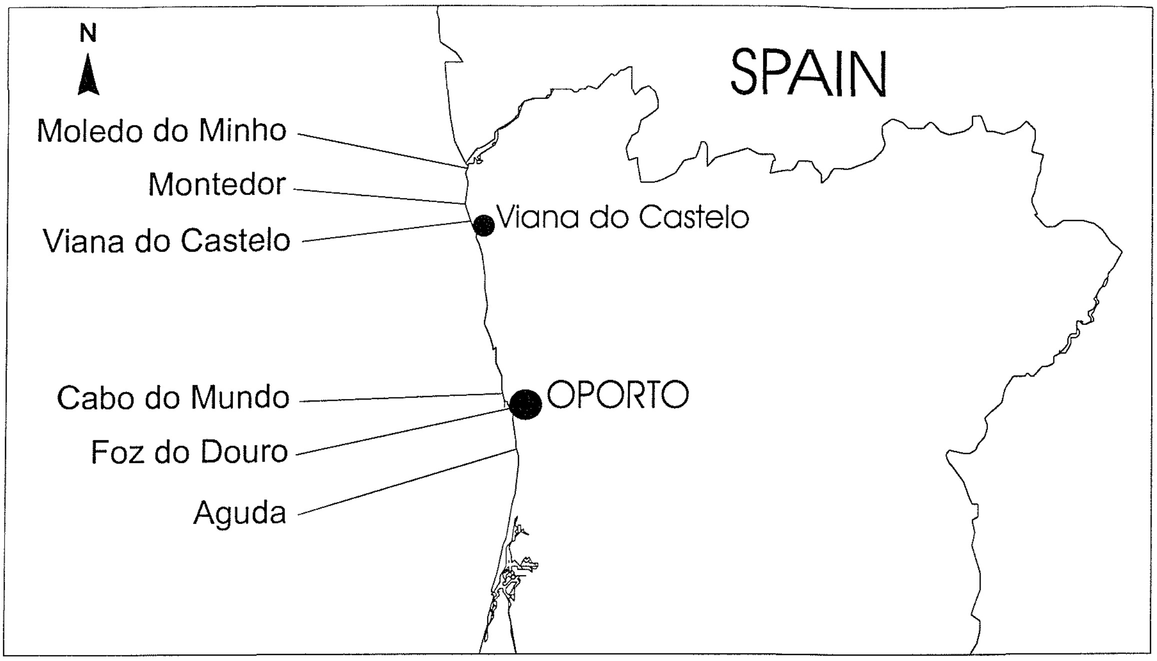


Figure 3.2: Detail of the northern Portuguese coast, where the work was carried out. Patch dynamics of the mussel/barnacle mosaic was studied at Moledo do Minho, Viana do Castelo, Cabo do Mundo and Aguda. Recruitment of limpets was studied in the four mentioned shores plus Foz do Douro. Montedor was used for other field experiments (see Chapter 5).

assemblages, the selection of the sites was conditioned by the need to have at least two shores near the harbour of Leixões, and thus more susceptible to be affected by such events, and at least two control sites, far from that source of pollution. The six shores faced westwards and differed slightly in their topography. Moledo and Aguda had large and gently–sloping ledges, whilst the other shores were more broken. Nevertheless, the selected shores were considered to be representative of moderately exposed northern Portuguese rocky shores.

3.2.2 Analysis of spatiotemporal variation

3.2.2.1 Data acquisition

Percentage cover of mussels and barnacles, and density of limpets were assessed on four shores: Moledo do Minho, Viana do Castelo, Cabo do Mundo and Aguda. Two species of limpets occur on the midshore: *Patella vulgata* and *P. depressa* (occasionally, some *P. ulyssiponensis* are also found, but always as isolated individuals). *P. vulgata* is less abundant than *P. depressa*, and adult individuals are particularly rare on gently–sloping surfaces. On the Portuguese shores, the two species cannot be easily identified by their shell morphology, thus needing a careful inspection of other characteristics, such as mantle tentacles and colour of the foot (Hawkins and Jones, 1992), or even the analysis of radular teeth under the binocular lenses (Fischer-Piétte and Gaillard, 1959). Since limpets usually reach densities of more than 200 individuals per square metre, it is often impracticable to try to assign each limpet to one of these species. This task becomes more complicated when smaller size–classes ($\leq$ 1 cm) are considered, given that most of the taxonomic features mentioned above cannot be used (Bowman, 1981). The two species seem to play a similar role in the structure of the midshore by grazing and bulldozing indiscriminately the rock surface, feeding on epilithic micro–algae and propagules (Hawkins and Hartnoll, 1983b). Therefore, there is no reason to separate them in the present study. Because previous data show that *P. depressa* is much more abundant than *P. vulgata*, hereafter the term 'limpet' will refer to the former species.

Two midshore algae were also considered in this study: *Porphyra* spp. and *Fucus spiralis*. The first is a complex of annual species (*P. umbilicalis* and *P. linearis*), which are common on all shores, and are often found covering both mussels and barnacles. According to Ardré (1970) *P. linearis* appears during winter months, and *P. umbilicalis* was observed throughout the year, but the small number of observations made by this author throws doubt on these periods of occurrence. *Fucus spiralis* was very rare or absent in exposed surfaces in northern Portuguese shores. However, at Cabo do Mundo there was a small area where some patches of *Fucus* could be seen among mussels and barnacles. The main reason for the inclusion of these species in the sampling was because midshore perennial algae are usually very sensitive to oil spills (Thomas, 1973). However, algae can also proliferate after the impact, especially if the mortality of grazers is large causing a significant decrease in grazing pressure (Southward and Southward, 1978), and thus it was important to have at least some data regarding their temporal variability.

Percentage cover of mussels, barnacles, *Porphyra* and *Fucus* was assessed by visual estimation, with the help of a 50 $\times$50 cm quadrat divided in 5 cm subdivisions (100 smaller quadrats, each representing 1% of the area). Visual estimation has proved to be better than point–intersection methods, especially if the number of intersections used is low or medium, and when a large number of replicates is needed (Meese and Tomich, 1992; Dethier *et al.*, 1993). The latter method can easily overestimate percentage cover if organisms are scattered through the sampled area (like barnacles), or underestimate it, if organisms are aggregated (like mussels).

Preliminary tests, comparing the values of mussel and barnacle percentage cover made by visual estimation (using the above quadrats) with those made by measuring the same area in digitized photos showed that the error was always below 5%, even when different observers were involved. Density of limpets was measured by direct counting, and was converted to individuals per square metre.

The shores were sampled at monthly intervals, from February 1997 to November 1999. In each shore, four different zones were selected based on their homogeneity in mussel/barnacle cover and on the need to find a suitable extension for repeated sampling. Ten randomly disposed quadrats were used to assess densities or percentage cover in each zone, in a total of 40 quadrats and an area of 10 m^2 per shore. This area represents less than 2.5% of the total area suitable for sampling on the smallest shore (Viana do Castelo), thus minimizing the probability of non–independence between samples (see Underwood, 1997).

3.2.2.2 Data analysis and hypotheses testing

Temporal variation of percentage cover of mussels, barnacles, *Fucus* and *Porphyra*, and density of limpets were averaged over the four areas in each shore and were plotted for each month. Standard deviation (S.D.) was used as a measure of dispersion (Sokal and Rohlf, 1981). Percentage cover of bare space was calculated as the remaining area after removal of mussel and barnacle percentages.

Test of hypotheses was carried out by means of multiway ANOVA. The three dependent variables under study were the percentage cover of the principal space occupiers – mussels and barnacles – and bare rock. The negative correlation between these variables (they must add up to 100%) has two important implications in the design of the ANOVAs: non–independence of data and model complexity. Non–independence of data can be a serious problem because it usually leads to an excessive type I error (Winer *et al.*, 1991; Underwood, 1981). Since percentage cover of mussels and barnacles was measured in the same quadrats (and bare rock was calculated as the remaining area), there was some degree of non–independence in the data sets. To overcome this problem, for each shore and in each sampling date, 10 out of the 40 available monthly estimates were randomly allocated to each of the three dependent variables.

To avoid a complex ANOVA model, a separate analysis was carried out for mussels, barnacles and bare rock. The inclusion of these three variables as a fixed factor in a single model would have been possible, and even desirable, because it would have increased the number of degrees of freedom for most of the tests, thus improving the overall power of the analysis (Underwood, 1997). Nevertheless, given the nature of such a factor (strong negative correlation between levels, because they add up to 100%), it would necessarily lead to a significant high order interaction with the other factors, which means that in the end the analysis would have to be carried out separately for each variable (Underwood, 1981, 1997).

The main goal of the analyses was to detect changes in species' occupancy and space availability that could be ascribed to external disturbance events. Since disturbance events considered in the context of the present study are typically seasonal, they were treated as 'seasons'. Three 'seasons' were considered in the model: 'winter' and 'summer', coincident with major disturbance events, and 'spring', included as a control level. The selection of appropriate sampling dates to detect changes within each season was not straightforward. The logic of the analysis required estimates of percentage cover at the beginning and the end of each season to detect such changes.

Given that three seasons were considered, a total of six estimates per year were necessary for the analysis. Percentage cover estimates were available from the three–year data series, but since the monthly estimates were not strictly regular throughout the three years, the selection of 'beginning' and 'ending' months for each season was, in some cases, slightly different for each shore.

Although there is no high quality quantitative information about wave action strength in northern Portugal, evidence suggests that it is stronger between December and March, and weaker between April and November (Costa, 1987). Thus, density estimates from late November or early December were selected for the 'beginning of winter' season, and from late February or early March for the 'ending of winter' season. In the case of summer, the warmest months are usually July and August, which also coincide with the highest use of the shores for recreational purposes. Hence, data from late June or early July was selected for the 'beginning of summer' season, and from late September or early October for the 'ending of summer' season. Finally, for the control season (spring), data from late March or April was selected for the 'beginning of spring' season, and from late May or June for the 'ending of spring' season.

Table 3.1 depicts the layout of the ANOVA, as well as the Mean Square estimates for each term in the analysis. Factor M, which stands for 'months', was used as a fixed factor with six levels: beginning and ending of winter, spring, and summer seasons, respectively. Factor S (shores), was used as a random factor to extrapolate the final results to a broader context, in this case the northern coast of Portugal. The

Table 3.1: Mean square estimates and degrees of freedom for the ANOVA model to test for the effects of shores, months and sampling dates, on space occupancy of mussels, barnacles and bare rock (Underwood, 1997, computed after). Planned orthogonal comparisons were included in the model, and are a repartition of the Months SS.

Factor	df	Mean square estimate
Months	5	$\sigma^2_e + 10\sigma^2_{D(M\times S)} + 30\sigma^2_{M\times S} + 120A^2_M$
Among winter months	*1*	
Among summer months	*1*	
Among spring months	*1*	
Among others	*2*	
Shores	3	$\sigma^2_e + 10\sigma^2_{D(M\times S)} + 180\sigma^2_S$
Months×Shores	15	$\sigma^2_e + 10\sigma^2_{D(M\times S)} + 30\sigma^2_{M\times S}$
Dates(Months×Shores)	48	$\sigma^2_e + 10\sigma^2_{D(M\times S)}$
Residual	648	σ^2_e

four levels of S were regarded as a small – but representative – subset of all possible exposed/moderately exposed rocky shores that could have been sampled in northern Portugal. Finally, factor D (sampling dates), which was not orthogonal to any of the other factors in the analysis (for the reasons stated earlier), was nested in the M×S combination. Since the main goal was to detect changes in space occupancy among selected periods (that is, within each 'season'), the number and the type of comparisons between months were stated *a priori*. Thus, from the 15 possible comparisons between the six levels of factor M, only three were meaningful in the context of the analysis: among winter months, among spring months and among summer months. These contrasts (or planned comparisons) are orthogonal and technically they are a repartition of the SS of factor M (Sokal and Rohlf, 1981; Underwood, 1997). However, they are not the only possible contrasts, as shown by their degrees of freedom, which do not add up to the degrees of freedom of factor M. The other possible orthogonal contrasts were pooled in a single term with two degrees of freedom, named 'Among others'. This term accounts for the remaining variation of factor M that is not explained by differences within the three 'seasons' considered, and it is not important in the final interpretation of the analysis.

Heterogeneity of variances was tested with Cochran's test (Underwood, 1997). To achieve homoscedasticity, and since observations were expressed as percentages, data were transformed with *arcsine* transformation (Sokal and Rohlf, 1981; Winer *et al.*, 1991; Underwood, 1997).

3.2.3 Species recruitment

Mytilus species usually have two distinct settlement phases (Bayne, 1964; Seed, 1969a). Pelagic larvae attach primarily to filamentous algae in the lower shore, where they grow up to 5 mm, and then move into the intertidal mussel beds, but some larvae are able to recruit directly into the mussel matrix (Suchanek, 1978, 1985). As primary settlement occurs mainly in the subtidal fringe it was not considered in the present work. Secondary settlement was monitored in a semi–quantitative way, by counting the presence or absence of small individuals ($\leq$5 mm) in the 50×50 cm quadrats used during the monthly sampling sessions.

Chthamalus montagui settles directly on any empty rocky surface (sometimes over mussels or other organisms) and their cyprids are easily identified with the help of a hand lens. In the first year roughened PVC plates were used as artificial substrata to monitor barnacle settlement. On each shore 20 plates were fastened to the rock surface by stainless steel screws. Plates were replaced weekly, and the number of cyprids was counted under binocular lenses. However, the use of PVC plates proved inadequate to monitor barnacle settlement due to the high rates of plate loss or damage, probably as a consequence of the harshness of the sea, and also to the patchy settlement of barnacles. Therefore, settlement of *C. montagui* was assessed by a semi–quantitative method during the subsequent monthly samplings. In each shore 40 randomly disposed 50×50 cm quadrats divided into 100 subdivisions (5×5 cm) were used. Only subdivisions encompassing any bare space were considered and the number of subdivisions where barnacle cyprids were present was counted. A percentage of bare space with cyprids was calculated, roughly indicating the settlement of *Chthamalus montagui.*

Settlement periods of *Patella* are hard to identify, mainly because it is difficult to detect and count settling spat due to their very small size (Bowman and Lewis, 1977). Moreover, after settlement, the small individuals may shelter for long periods in crevices or under the mussel matrix, taking advantage of the damper conditions of these microhabitats, and only recruiting to the open rock when they reach a considerable size (Lewis and Bowman, 1975). Therefore, the number of small individuals ($< 5mm$) was used as a measure of recruitment to open rock (Bowman and Lewis, 1977). Monthly sampling was carried out on five shores: Moledo do Minho, Viana do Castelo, Cabo do Mundo, Foz do Douro and Aguda, to establish growth rates and, especially, recruitment periods. Limpets enclosed in randomly disposed quadrats (50×50 cm) were measured to the nearest millimetre, both in the mussel and in the barnacle zones. Five to 10 quadrats were used in each zone so

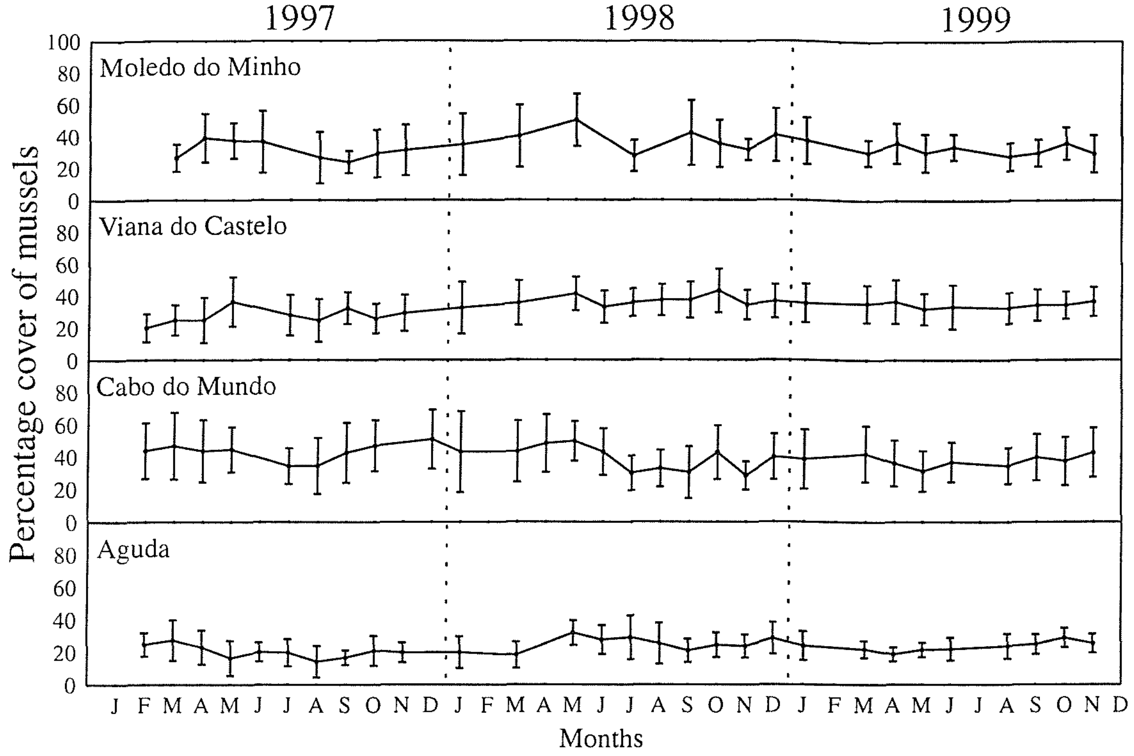


Figure 3.3: Variation in mean percentage cover of *Mytilus galloprovincialis* on the four shores studied. Dispersion is measured as $\bar{X} \pm S.D.$

as to have at least 200 individuals per zone. Size–frequency graphs were plotted for each month using 1 mm size–classes. The data was subjected to a Modal Progression Analysis using Bhattacharya's method in order to sort out normal components of length–frequency data, and to distinguish juvenile cohorts (King, 1995).

3.3 Results

3.3.1 Spatio–temporal variability

The temporal variation of percentage cover of *Mytilus galloprovincialis* on the four studied shores is depicted in figure 3.3. No apparent pattern could be identified from the graphs: percentage cover varied between 20–50% throughout the period considered. Cabo do Mundo had the largest cover of mussels, usually reaching 40–50%, whilst at Aguda the percentage cover of mussels was the smallest, never reaching more than 40%. Dispersion values (measured as SD) were high for all shores, being smaller at Aguda. The relation between dispersion and percentage

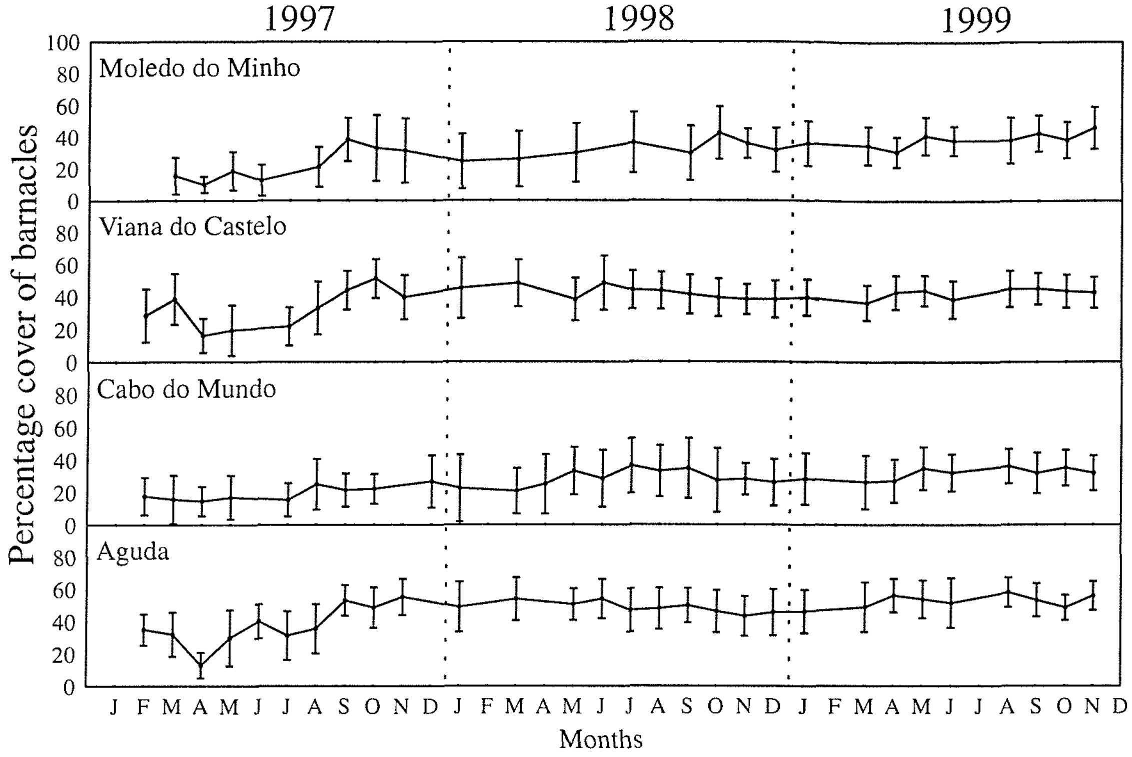


Figure 3.4: Variation in mean percentage cover of *Chthamalus montagui* on the four shores studied. Dispersion is measured as $\bar{X} \pm S.D.$

cover is straightforward: in places like Aguda, where the percentage cover is smaller, mussel patches are also smaller and are evenly interspersed on the shore; on the other hand, in places like Cabo do Mundo, where the average mussel density reaches 50%, mussel patches can reach much larger sizes, but the wider distribution of patch sizes increases the heterogeneity and, as a consequence, the variability within this zone.

Variation of percentage cover of barnacles is depicted in figure 3.4. Once again, there was no sharp seasonal pattern during the study period, although an increase in barnacle percentage cover could be seen in the first year in all shores (being less evident in Cabo do Mundo). This increase was coincident with an overall decrease in space availability (figure 3.5) observed in the first year. However, after this initial decrease, space availability also fluctuated smoothly around 20–40% cover. In 1998 there was a slight tendency towards a decrease in April–May, which was coincident with an exceptional secondary settlement of mussels observed on all shores.

Density variation of *Patella* is depicted in figure 3.6. As for the other species, there was no evident pattern of variation between years. Density of limpets was higher at Viana do Castelo and Moledo do Minho, and hundreds of small individuals

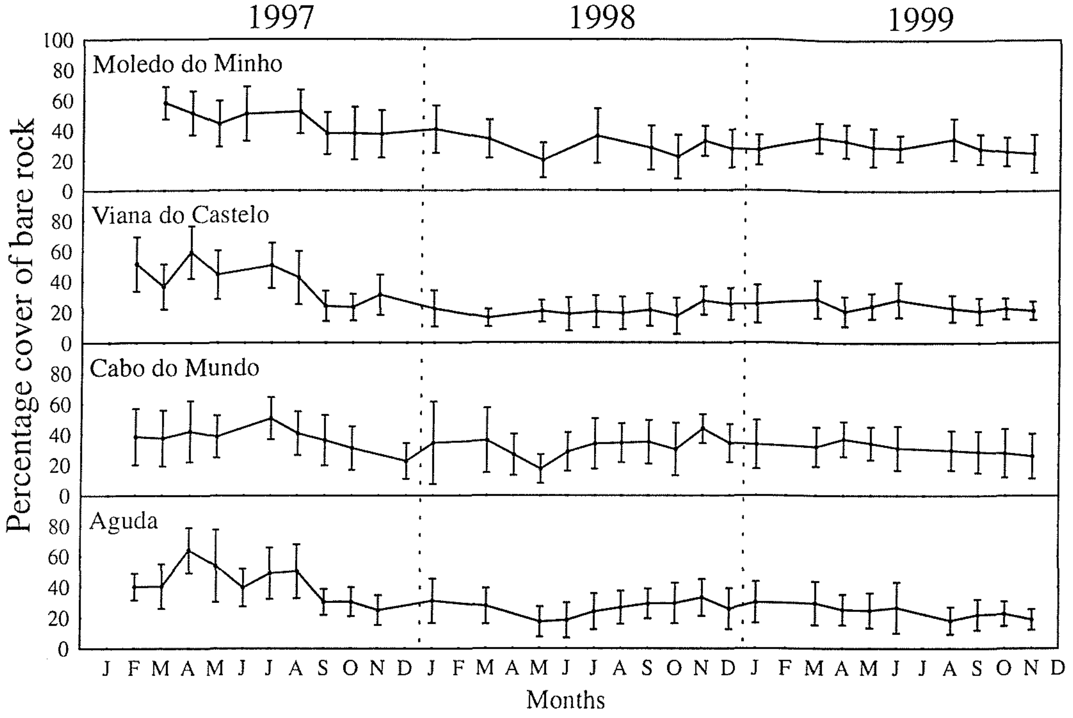


Figure 3.5: Variation in mean percentage cover of free space (bare rock) on the four shores studied. Dispersion is measured as $\bar{X} \pm S.D.$

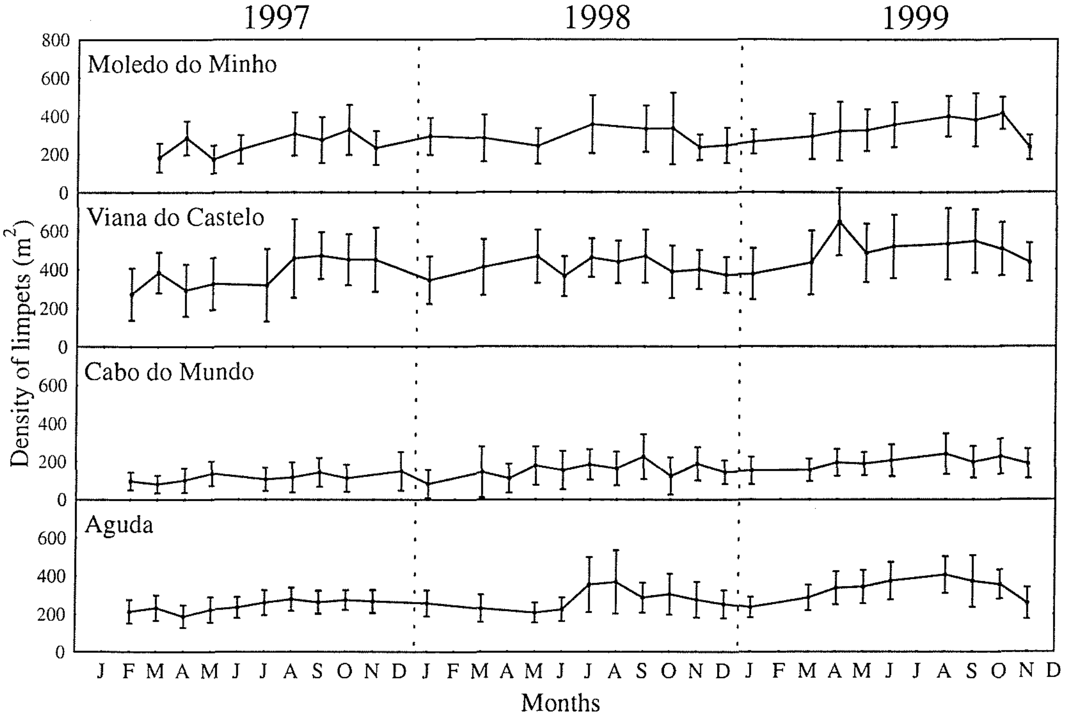


Figure 3.6: Variation in mean density of *Patella* spp. on the four shores studied. Dispersion is measured as $\bar{X} \pm S.D.$).

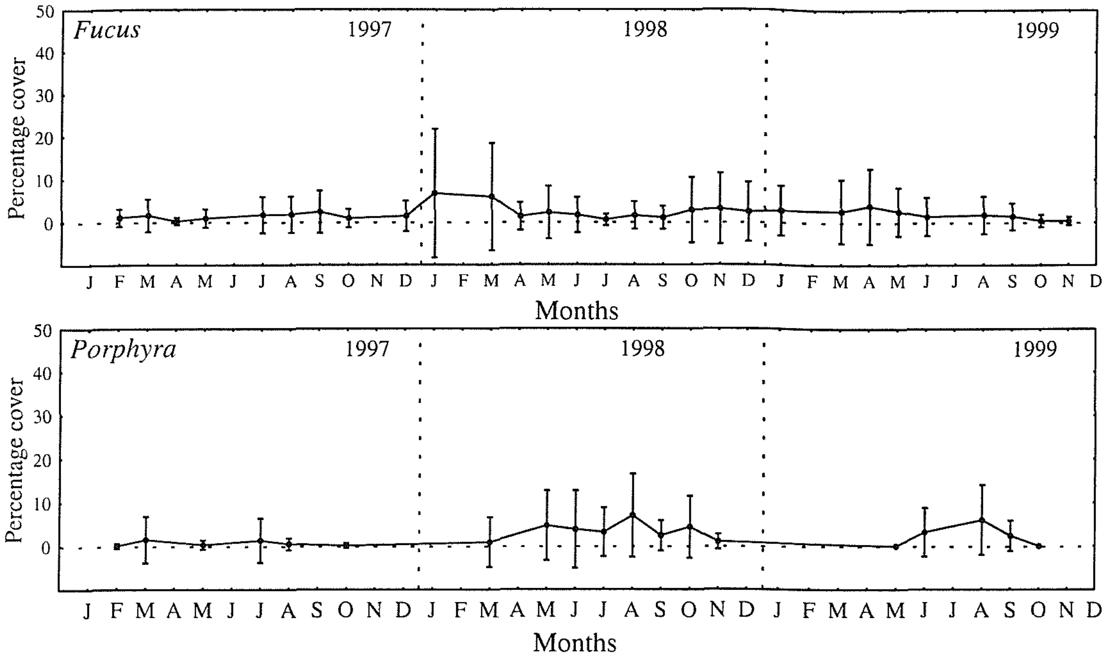


Figure 3.7: Variation in mean percentage cover of *Fucus spiralis* and *Porphyra* at Cabo do Mundo. Dispersion is measured as $\bar{X} \pm S.D.$.

(< 1.5 cm) were found among mussels on these shores. On Cabo do Mundo the density was smaller, probably due to the higher percentage cover of *Mytilus galloprovincialis*.

The percentage cover variation of the two macroalgae studied (*Fucus* and *Porphyra*) is depicted in figure 3.7. *Fucus spiralis* was more abundant in the winter and spring, but this was more evident in 1998 than in 1999. On the contrary, *Porphyra* was consistently more abundant in spring and summer, being absent in the winter months. Therefore, the observed species was most probably *Porphyra umbilicalis* and not *P. linearis* which is considered a winter species Ardré (1970).

3.3.2 Hypotheses testing

The results of ANOVA for the analyses of percentage cover of *Mytilus*, *Chthamalus* and space are depicted in table 3.2. Homoscedasticity was achieved for *Mytilus* (Cochran's C test=0.042, $P_{(v=9,k=72)} > 0.05$), barnacles (Cochran's C test=0.041, $P_{(v=9,k=72)} > 0.05$), and bare rock (Cochran's C test=0.038, $P_{(v=9,k=72)} > 0.05$) after *arcsine* transformation. Statistically significant differences among sampling dates ($P < 0.001$) were observed in the three analyses.

Table 3.2: Analysis of variance to test for the effects of months (M), shores (S) and sampling dates (D) on the percentage cover of mussels (*Mytilus galloprovincialis*), barnacles (*Chthamalus* spp.), and bare rock (statistically significant terms are depicted in bold).

A–*Mytilus galloprovincialis*

Source of Variation	SS	DF	MS	F	P	Against MS
M	457.74	5	91.55	0.78	0.589	M×S
Winter	28.98	1	28.98	0.25	0.627	M×S
Spring	94.95	1	94.95	0.81	0.384	M×S
Summer	121.67	1	121.67	1.03	0.326	M×S
Among others	214.14	2	106.07	0.90	0.358	M×S
S	9827.16	3	3275.72	24.73	**<0.001**	D(M×S)
M×S	1768.45	15	117.90	0.89	0.584	D(M×S)
D(M×S)	6357.51	48	132.45	3.94	**<0.001**	Residual
Residual	21764.80	648	33.59			
Total	40175.66	719				

B–*Chthamalus* spp.

Source of Variation	SS	DF	MS	F	P	Against MS
M	4083.15	5	816.63	6.49	**0.002**	M×S
Winter	1805.77	1	1805.77	14.36	**0.002**	M×S
Spring	510.18	1	510.18	4.06	0.062	M×S
Summer	732.48	1	732.48	5.83	**0.029**	M×S
Among others	1034.71	2	517.36	4.11	0.061	M×S
S	17495.08	3	5831.69	11.78	**<0.001**	D(M×S)
M×S	1886.05	15	125.74	0.25	0.997	D(M×S)
D(M×S)	23754.55	48	494.89	10.36	**<0.001**	Residual
Residual	30945.71	648	47.76			
Ttotal	78164.54	719				

C–Bare rock

Source of Variation	SS	DF	MS	F	P	Against MS
M	2186.31	5	437.26	3.54	**0.026**	M×S
Winter	897.22	1	897.22	7.27	**0.017**	M×S
Spring	128.07	1	128.07	1.04	0.324	M×S
Summer	963.84	1	963.84	7.81	**0.014**	M×S
Among others	197.17	2	98.59	0.80	0.385	M×S
S	3026.24	3	1008.75	1.93	0.127	D(M×S)
M×S	1850.22	15	123.35	0.24	0.998	D(M×S)
D(M×S)	25060.27	48	522.09	10.13	**<0.001**	Residual
Residual	33383.06	648	51.52			
Total	65506.10	719				

Since sampling dates nested in each month×shore combination came from three different years, the statistical significance of D(M×S) reflects a high level of inter–annual variability. The interaction M×S was not significant for the three analyses. This result is very important, meaning that any differences in percentage cover found within seasons were consistent among shores. Since factor S (shores) was treated as a random factor, the latter consideration can be extended to *all* moderately exposed intertidal rocky shores on northern Portugal, for which the selected shores are thought to be representative.

Differences between shores were found for both mussels and barnacles but not for bare rock. The first two differences were expected, since it was clear – from field observations – that at least mussel percentage cover was quite different between the surveyed shores. Barnacle percentage cover was expected to be negatively correlated with mussel density, but this correlation was not supposed to be high, since a third variable – bare rock – was also involved in the analysis.

That no differences were found in percentage cover of bare rock among shores suggests that available space is more or less constant across shores and does not depend on mussel or barnacle densities. It also means that the negative correlation between mussel and barnacle percentage cover was higher than expected.

For the main factor M (months), results were different for each of the three dependent variables. Mussel percentage cover was similar among periods ($P > 0.50$). On the other hand, differences were found for both barnacles and bare rock percentage cover ($P < 0.01$ and $P < 0.05$, respectively). A detailed analysis of contrasts showed that these differences could be observed among the winter and summer months. In both cases, there were no differences between other possible comparisons among months, as shown by the non–significance of the 'Among others' term. This latter result is quite important because, among other things, it means that there were no differences in percentage cover between consecutive months (the end of one season and the beginning of the other).

The averages of mussel, barnacle and bare rock percentage cover before and after each season are depicted in figure 3.8. In the case of barnacles, the observed differences can be ascribed to an increase in percentage cover during the summer and a decrease during the winter. On the other hand, space increases during the winter and decreases during the summer. The prediction that available space increases mainly during the winter still holds true, but this increase seems to result from barnacle loss rather than mussel dislodgement. Whatever the reasons for such results, the proposed model (as depicted in figure 3.1) was shown not to hold.

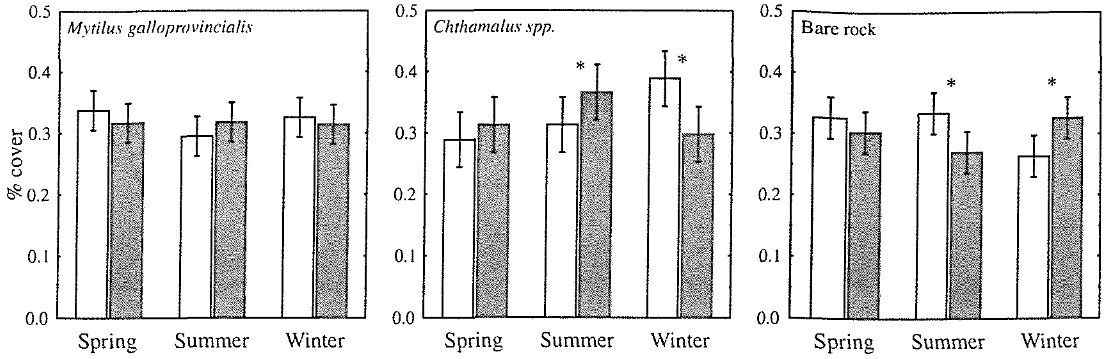


Figure 3.8: Average percentage cover for mussels, barnacles and bare rock at the beginning (white) and the end (grey) of each season. Statistically significant differences between periods are marked with *. Error bars measure $t_{(\alpha=0.05,\nu)} \times SE$.

3.3.3 Settlement and recruitment of *Mytilus*, *Chthamalus* and *Patella*

Mussel secondary settlement, as defined previously, was observed throughout the study period. Small mussels were spotted mainly near the margins of well established patches, and seldom formed new aggregates, but some individuals were observed to settle directly on empty barnacle shells. Since these small mussels were observed in all sampling dates and in almost all quadrats, the semi–quantitative assessment failed to produce any useful results. Despite this, it should be noticed that an exceptionally large settlement was observed in March and April 1998 (and to a lesser extent in 1999), especially in Aguda, and Moledo do Minho. Large numbers of small mussels ($<$ 1 cm) were found on the edges of older patches or clustered in newly born patches which reached considerable sizes ($>$ 100 cm^2, or about 5% of the occupied space).

Barnacle settlement displayed a very sharp pattern in all shores during the three years of observations (figure 3.9). Settlement started in late spring or early summer (usually in June), reaching its maximum intensity in September, decreasing abruptly in October and ending by November. The 'low' settlement rates found in the first year were most probably due to the method used (see Section 3.2.3), rather than to any failure in recruitment. In 1999 recruitment started earlier, in May (except for Aguda), and ended also earlier, in October. On the other hand, recruitment of *Patella depressa* was not evident from the data gathered in the first year (see Appendix C). Modal Progression Analysis failed to detect any cohorts in a consistent manner,

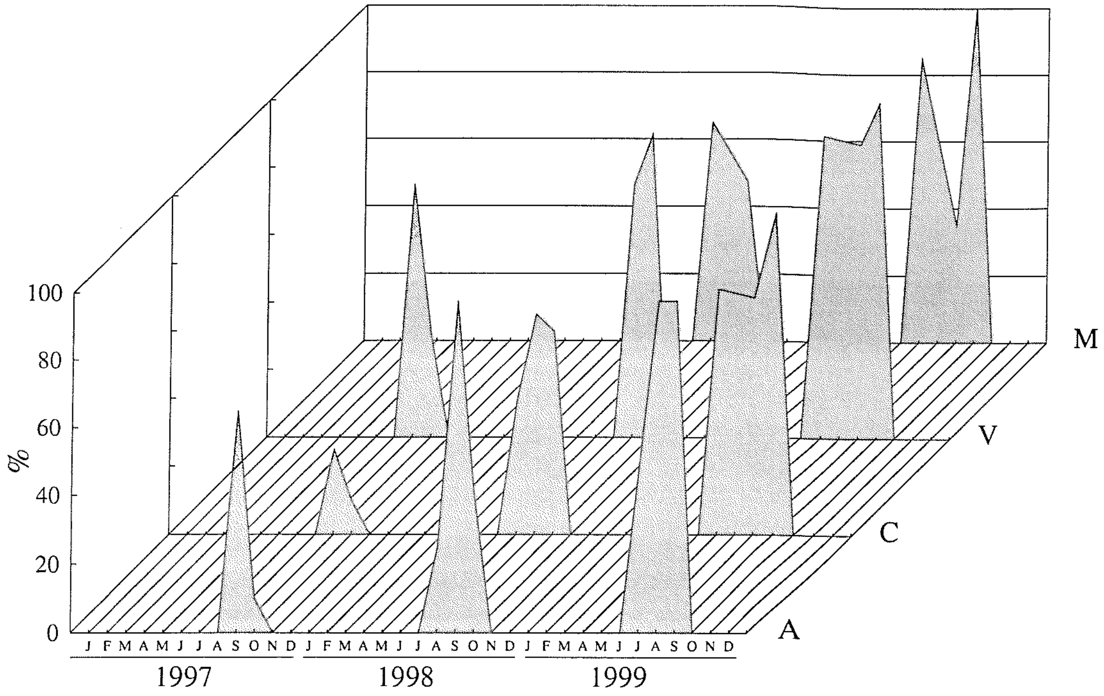


Figure 3.9: Settlement of *Chthamalus* spp. measured as percentage of 5×5 cm quadrats where cyprids were observed. A = Aguda; C = Cabo do Mundo; V = Viana do Castelo; M = Moledo do Minho.

suggesting that the input of new individuals to this habitat was continuous on the northern Portuguese shores, as would be expected in a multiple brooder (Burrows *et al.*, 1992).

3.4 Discussion

The lack of published data on the dynamics of space occupancy and colonization of *Mytilus galloprovincialis* littoral assemblages restricts the present discussion to comparisons with similar assemblages in North America (e.g., Paine, 1974; Levin and Paine, 1974; Paine and Levin, 1981; Petraitis, 1990, 1995, for *M. californianus* and *M. edulis* assemblages) and the United Kingdom (Seed, 1969a,b, for *M. edulis* assemblages). Variation in percentage cover or density of main species seems not to have followed any particular pattern during the 30 months of sampling.

The large values of dispersion (S.D.) found for almost all species on every shore suggest that the assemblage under study is characterized by a high degree of spatial heterogeneity, which agrees with the patchy nature of mussel beds around the world

(Suchanek, 1985). Clear seasonal patterns were only observed for the two algal species studied in Cabo do Mundo. *Porphyra* was more abundant during spring and summer months and, although no attempt was made to establish its true systematic status, the fact that this algae were absent in the winter rules out *P. linearis* and leaves *P. umbilicalis* as the most likely species (Ardré, 1970). The seasonality of *Fucus spiralis* was surprisingly coincident with the harshest months, and also agrees with the October to March growth period found by Ardré (1971). Nevertheless, both algae never covered more than 10–20% of the space (occasionally *Fucus* reached 40-50%, and *Porphyra* was only found over mussel patches) and any putative effect of these species in the dynamics of the mussel assemblage should be negligible (Farrell, 1991; Benedetti-Cecchi *et al.*, 1996).

Recruitment of limpets did not display any seasonal pattern either. A strong variation of seasonal patterns in the population dynamics of *Patella vulgata* were found by Lewis and Bowman (1975), presumably resulting from complex interactions among several physical and biological factors, dictated by microhabitat characteristics. Habitat differences, such as different adult limpet densities (and thus, grazing pressure), surface rugosity, presence of mussel patches or exposure to wave action (among others), might explain to a certain extent the absence of clear peaks of recruitment to open rock. On the other hand, in a fast–growing species, with a brief annual spawning period, several year classes may be clearly evident in length–frequency distributions. However, if the spawning period is extended and growth (or secondary settlement or emergence from nurseries) is slow, pseudo–cohorts in the length–frequency distribution may overlap to such an extent that it is not possible to identify separate modes (King, 1995). This seems to be the case for *P. depressa* on the northern Portuguese shores.

Growth rates of *P. depressa* are thought to be high in Portuguese populations (Guerra and Gaudencio, 1986), and the absence of a distinct mode representing small–sized classes (< 0.5 cm) suggests that input of new individuals into the population is a continuous process. These findings were also supported by the analysis of the breeding cycle of *P. depressa* undertaken by Guerra and Gaudencio (1986), who found no marked annual patterns in the spawning periods. Another possible explanation for the non–existence of clear seasonal patterns – at least in the mussel zone – might be related with the fact that mussel beds are biologically unstable habitats, making the establishment of individuals, and especially juveniles, a matter of chance (Lewis and Bowman, 1975).

M. galloprovincialis and *P. depressa* are warm–water species in the centre of their distribution area. According to Lewis (1986) the well defined breeding seasons and settlement periods found near the northern limits of distribution tend to become less pronounced towards the south. Contrasting with these species, barnacles displayed a well defined settlement period during this study. The peak of settlement was in September, suggesting a summer breeding season. It is noteworthy that in this aspect the northern Portuguese populations of *C. montagui* follow the breeding pattern of those from the British Isles and not from those of the Mediterranean, which breed from February to early April (Crisp *et al.*, 1981). It is important to interpret these findings on the light of the biogeographic analysis carried out in Chapter 2. The northern Portuguese climate seems to be cold enough to permit the occurrence of essentially boreal species such as *Himanthalia elongata*, *Pelvetia canaliculata* and *Laminaria hyperborea*, as well as to restrict barnacle settlement to the summer months, similar to near their northern limit in European waters (Lewis, 1986; Burrows *et al.*, 1992). However, it also seems to be warm enough so as to permit a continuous reproduction of other intertidal species, like *Mytilus* and *Patella*. Both observations are in agreement with the existence of a smooth gradient in species composition and an interface between different biogeographic elements on the Portuguese coast.

The model developed to explain the dynamics of northern Portuguese intertidal mussel assemblages (figure 3.1) was shown to be wrong. Its main failure was the prediction of a decrease in mussel percentage cover during the winter months, when water motion (due to storms) is believed to have a pronounced effect over mussel beds (Paine and Levin, 1981; Sousa, 1984c; Suchanek, 1985). Yet, the absence of a seasonal pattern in the variation of mussel density was not a total surprise. Indeed, during a five–year study of *M. californianus* assemblages in Tatoosh Island and Mukkaw Bay (Washington State, USA), mussel density was found to be relatively constant, and no clear seasonal pattern could be perceived (Paine, 1974). Likewise, Seed (1969b) also observed that *M. edulis* populations in Yorkshire (UK) were very stable throughout the years.

Northern Portuguese intertidal assemblages of *M. galloprovincialis* cannot be directly compared with those studied by Dayton (1971) or Sousa (1979a,b), where the effectiveness of wave action was maximized by other factors (such as log battering and boulder turning, respectively) and displayed a sharp seasonal pattern. On the other hand, Paine and Levin (1981) showed that winter storms were the major force responsible for the creation of free space on *M. californianus* beds, but these mussels formed dense, multilayered beds, which are known to be less stable, and more likely to be torn from the rock surface by wave action, than the less dense, single–layered beds, of *M. galloprovincialis* observed in the present study (Harger and Landenberger, 1971; Paine, 1974; Paine and Levin, 1981).

Given the present results, one must be tempted to reject the hypothesis that winter storms are the main source of disturbance in intertidal mussel assemblages in northern Portugal. However, the analyses in Section 3.3.2 (p. 61) showed unambiguously that there was a significant increase in available space towards the end of the winter. Since this increase was followed by a simultaneous decrease in barnacle percentage cover, the creation of space could have been ascribed to a barnacle loss due to wave action. Barnacles, however, seem to be much more resistant to the effects of wave action than mussels, and since mussel density remained constant during the winter, a more complex explanation should be put forward to explain the observed shift in the percentage cover of barnacles and bare rock. Assuming that wave action during the winter months was effective in dislodging mussels, these must have been able to recover rapidly so as to maintain their occupancy levels. Mussel secondary settlement, which was analysed in a semi–quantitative way during the present work, seems to have followed the patterns described by Saldanha (1974) for the coast of Arrábida (Southern Portugal): size–frequency data from monthly samples showed that a peak corresponding to newly recruited juveniles (<5 mm) could be observed throughout the year. This pattern is widespread among other mussel species in the north Atlantic (Suchanek, 1981, 1985), where a more or less continuous primary settlement of plantigrads in the algal turf usually constitutes a reservoir of new individuals that invade the eulittoral at constant rates (Seed, 1969a). Thus, it is not unrealistic to think that newly recruited mussels can compensate losses by settling over barnacles, thus reducing the percentage cover of this species. The basis of this explanation depends on the known preference of mussels to settle over barnacles rather than on bare rock. Barnacles are known to facilitate the settlement of many organisms (e.g. Hawkins, 1981a,b; Hartnoll and Hawkins, 1985; Farrell, 1991; Kim, 1997; van Tamelen and Stekoll, 1997), and this is true for mussel secondary settlement on moderately exposed rocky shores (Dayton, 1971; Menge, 1976; Suchanek, 1985; Petraitis, 1987).

Several other problems arise in the re–definition of a new model to explain the dynamics of intertidal mussel assemblages in northern Portugal. If rates of mussel secondary settlement were constant (as suggested by the literature and qualitative data), and mussel loss significantly higher during the winter, the net result would be a decrease in mussel density during that period. In the present study, changes in mussel cover were not detected throughout the year, and even after an exceptional settlement of mussels, in March–April 1998, their average percentage cover remained constant.

Two simple explanations can be put forward to explain the stability of mussel occupancy: a) secondary settlement is not constant, being higher when dislodgement rate is higher or b) secondary settlement is constant and so is the dislodgement rate. At this stage, any quantitative information about secondary settlement rates of *M. galloprovincialis* would have been welcome. Both hypotheses have support in the literature, but they also have some flaws. In the North Atlantic populations of *M. edulis*, spawning was shown to occur virtually any time in the year (Seed, 1969b; Suchanek, 1985), and the same was true for *M. galloprovincialis* populations in southern Portugal (Saldanha, 1974). On the basis of such observations it is wise to admit that settlement rates should be more or less constant. If mortality rates were also constant and of equal magnitude, and new individuals settled preferentially on top of barnacles (as suggested by the present results), an increase in available space would be observed in all seasons (with the possible exception of summer, due to barnacle settlement). Furthermore, the increase in space would be accompanied by a simultaneous decrease in barnacle percentage cover, since new mussels would be settling or growing over barnacles. In the present study, neither of these changes was observed.

Alternatively, on the east coast of North America, Suchanek (1981) has reported a limited spawning period for *M. edulis* in the late autumn or early winter, which he thought to be an adaptation, since the main settling phase usually occurs after winter, when the number of settlement sites (storm–generated patches of bare rock) is higher. So, a limited settlement period in late winter and early spring would generally fit the observed results, provided that settlement rates could compensate for the losses caused by winter storms. Nevertheless, the effects of direct human impact on the mussel bed during the summer (which were evident in the field) were not detected. Trampling and scouring of mussel aggregates in search for bait for angling were observed in all shores, being particularly intense at Cabo do Mundo. Furthermore, on this shore a small oil–spill occurred in July 1998. The direct impact of the oil–spill was observed during subsequent sampling sessions, where considerable piles of empty mussel shells were spotted in the strandline. Since mussel percentage cover remained constant all over the year, there must have been some input of new individuals during or after these events, which supports the first hypothesis.

There is, however, a third way to interpret the present results, solving the former paradox by incorporating information from both hypotheses. Since evidence suggests that for most mussel populations spawning is continuous (Suchanek, 1985), and this seems not to be an exception for Portuguese populations of *M.*

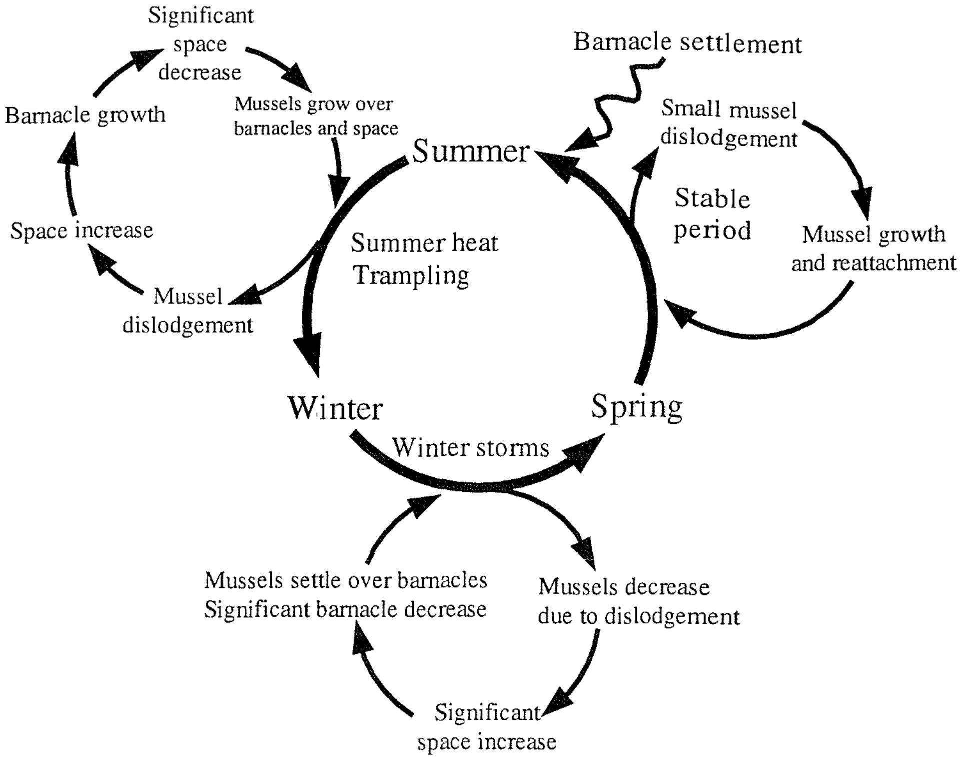


Figure 3.10: Modified model to explain the dynamics of mussel/barnacle assemblages on northern Portuguese moderately exposed rocky shores.

galloprovincialis (Saldanha, 1974), settlement should also be continuous, but it must vary in intensity throughout the year. According to Ardizzone *et al.* (1996) the input of new individuals is not the only way to counterbalance mortality. Petraitis (1995) showed that patches of mussels facing high rates of mortality could display no change in percentage cover as long as growth by the remaining survivors could fill the vacant space. Small mussels could easily double their size in one year, which was sufficient to withstand 60% mortality per year without a loss in percentage cover. Furthermore, Paine (1974) observed that even well–grown mussels (> 1 cm) that have been dislodged by wave action were able to return to the mussel matrix. Thus, a combined effect of a variable – but continuous – secondary settlement, a high growth rate and a high capacity to disperse within the mussel bed may have the ability to buffer losses due to dislodgement and ageing.

Figure 3.10 depicts a modified model to explain the dynamics of mussel assemblages, which incorporates data gathered during the present study, as well as some of the hypotheses discussed previously. Wave action during winter is still considered the main agent of disturbance. Mussel density remains constant, either by re–attachment, growth, and especially secondary settlement. Settlement of new individuals occurs on top of barnacles, resulting in a net increase in available space and decrease in barnacle percentage cover. During the calmer months of spring the rate of mussel mortality is supposed to be lower, and any loss is compensated mainly by growth or reattachment. Individual growth does not change patch size *per se* (Paine, 1974), and since reattachment of well–grown mussels is often done on the margin of well established patches, any increase in mussel percentage cover during the spring season should not be done at the expenses of barnacles alone, but must be evenly shared by both barnacles and space. In late summer, after the main barnacle settlement, there should be a reduction in available space and an increase in barnacle cover. Again, mussel mortality due to summer disturbances (which is supposed to be smaller when compared with the winter), should be compensated by growth or reattachment. Barnacle settlement, and subsequent growth, should override either the loss in barnacle cover due to mussel overgrowth and the creation of space due to mussel dislodgement.

The modified model still needs to go through a more robust testing phase. Despite being in a very raw state, and probably lacking in detail, it is nonetheless an important framework for the subsequent parts of this study. It acknowledges winter disturbances as the main controlling factor of mussel abundance, and integrates explicitly both recruitment data and species variability. However, the test of the whole model is beyond the scope of this work, in the sense that it would involve gathering new data sets for at least two more years to achieve such task. Nevertheless, it allows the making of simpler predictions that can be easily tested.

3.5 Conclusions

The following conclusions can be drawn from the previous results:

- Mussel assemblages displayed high levels of heterogeneity and variability at small spatial and temporal scales.
- Recruitment of both mussels and limpets was probably continuous throughout the year. On the contrary, barnacles displayed a distinct pattern of settlement, from June to October.
- The proposed model to explain the dynamics of mussel assemblages was shown to be wrong. Apparently winter storms do not alter mussel percentage cover, although there is a decrease in barnacle percentage cover and a simultaneous increase in space availability.

- The highly variable dynamics of these assemblages seem to buffer most of the effects of the considered disturbance events, including the effects of small–scale oil–spills and other human induced events.
- An alternative model was developed, integrating both species variability and recruitment data, as well as acknowledging winter disturbances as the main factor controlling mussel occupancy.

Chapter 4

Dynamics of Individual Mussel Patches

4.1 Introduction

Biological communities have multi–scale properties, and the observations made at different spatiotemporal scales usually bear very different, often diametrically opposed, results (Wu and Loucks, 1995). In the previous Chapter, the dynamics of the mussel/barnacle mosaic was studied at large spatial scales (shores and regions). The main goal of the previous analyses was to gain some insight about the factors that drive the mussel/barnacle mosaic in northern Portuguese shores. What prevents mussels from dominating the eulittoral zone? Disturbance, especially through wave action, was thought to be the principal factor responsible for such control (Paine and Levin, 1981; Sousa, 1984c; Suchanek, 1985). However, the hypothesis that mussel density would decrease during the winter season, when wave action is strongest (Costa, 1987), was shown to be wrong. Mussel dominance remained constant throughout the seasons, but behind this apparent 'stability' there were reasons to believe that this assemblage concealed a much more dynamic system. First, descriptive statistics showed that standard deviations of monthly samples were large, clearly indicating high levels of spatial heterogeneity. Second, the results of the statistical analyses have shown the existence of significant differences over time. Indeed, a high level of variability was found between sampling dates in each month, and although it did not prevent other differences from being detected, it was nevertheless significant for mussels, barnacles and space. Finally, the combined interpretation of the results for seasonal variation in mussels, barnacles and free space suggested that there was some significant 'creation' of space during the winter months which occurred, at least partially, at the expense of mussels.

The previous observations prompted a more detailed analysis of the dynamics of the mussel/barnacle mosaics, on a smaller spatial scale. Analyses at the patch scale are not abundant in the literature, especially if intertidal assemblages are considered. The pioneer work of Paine (1974), which was followed by model–based approaches (Levin and Paine, 1974; Levin, 1976; Paine and Levin, 1981), was carried out – coincidentally – on mussel assemblages. However, recent studies have focused mainly on the dynamics of algal patches on grazer driven assemblages, namely *Zostera* (Olesen and Sand-Jensen, 1994), *Cymodocea* (Marba and Duarte, 1995; Vidondo *et al.*, 1997) and *Fucus* (Hartnoll and Hawkins, 1985; Johnson *et al.*, 1997; Burrows and Hawkins, 1998; Johnson *et al.*, 1998). Paine and Levin (1981) developed a model that could explain and predict, with reasonable confidence, the dynamics of space creation on intertidal mussel beds, at several sites in the west coast of North America. Yet, the nature of the intertidal mussel assemblages in this region seems to be significantly different from those of northern Portuguese shores. Here, mussels do not form a compact – 100% cover – layer, where patches of bare rock (usually referred to as 'gaps') appear and disappear, driven by predictable external disturbance events. In the Portuguese eulittoral zone, the term 'patch' is more adequate for the mussels rather than the bare rock. In fact, mussels seldom occupy all the available space, and very often they form distinctly shaped aggregates of small size (≤ 500 cm^2), which appear, grow, coalesce, split, and eventually disappear.

The main goal of the present study was to find out whether (or not) the patterns observed previously were maintained at the patch scale level. To accomplish this task, the evolution of individual patches of mussels was followed at regular time intervals during a two–year period on three different shores. Direct analyses of patch birth, growth, shrinkage and loss rates were made to reveal the magnitude or importance of contribution of each of those processes to the overall gains and losses in area.

Because average mussel cover was found to be constant through time, it was expected that overall the settlement and growth of individuals would compensate for the losses caused by dislodgement and death. This was found to be the case on some similar systems (*Mytilus edulis* assemblages, east coast of North America), where growth alone was shown to be sufficient to withstand 60% mortality per year (Petraitis, 1995). Given these assumptions, two hypotheses were tested: 1) *gains and losses in patch area should be roughly equivalent within each season* and 2) *average gains and losses in area should be higher in the winter than in the other two seasons.*

4.2 Material and methods

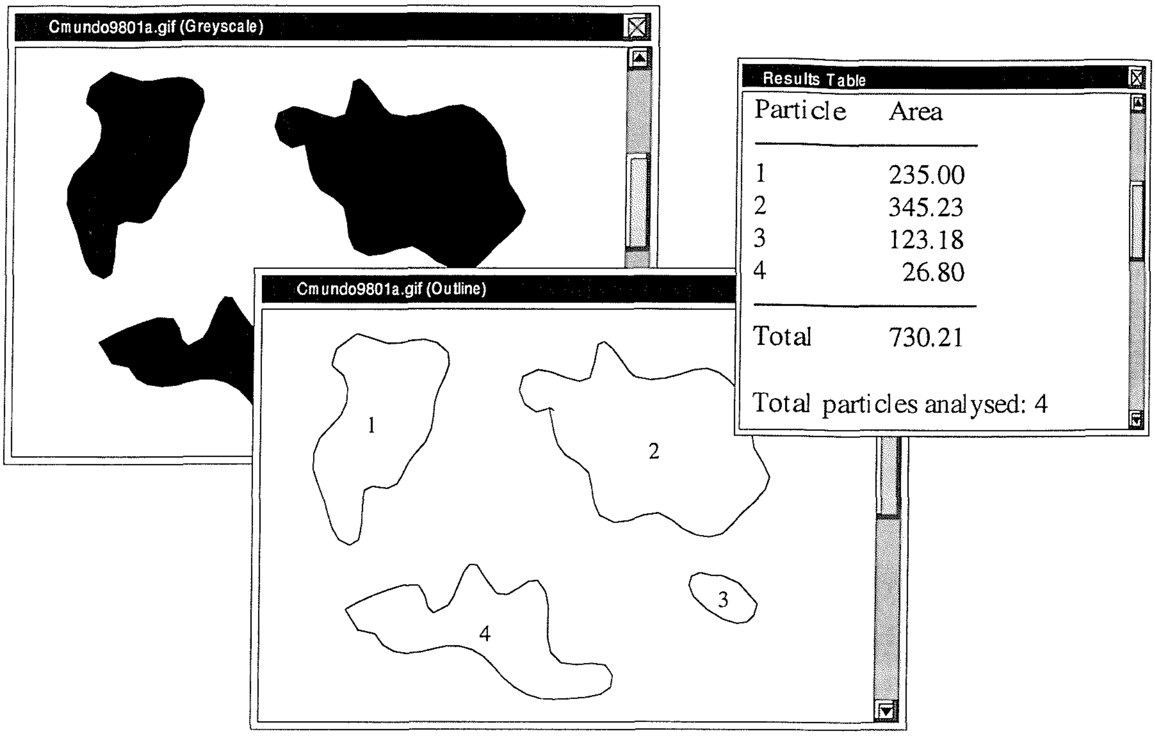
4.2.1 Data acquisition

Three shores were selected: Cabo do Mundo, Montedor and Moledo do Minho. In each shore, 15 fixed areas of about 60×40 cm were marked using stainless screws fastened into the rock with plastic plugs. The areas were selected so as to include clearly separated mussel patches of various sizes. A few 'areas' were lost during the two year survey, namely in Moledo do Minho and Cabo do Mundo, not only due to the loss of screw markers (in some cases because of a heavy overgrowth of mussels) but also due to the overturning of boulders caused by strong wave action. Thus, only 12 out of 15 areas per shore were used in the analyses. For practical considerations, and given the results in Chapter 3, three seasons were considered: Spring (April–June), Summer (July–October) and Winter (December–March). The sites were visited at regular intervals so as to take photos at the beginning and the end of each season. However, in this particular study, the same sampling date was used for the end and the beginning of consecutive seasons. Photos were taken with a 35mm SLR camera (Pentax MZ10, 50mm Macro Lens) using a colour slide film (100 ISO).

4.2.2 Image analysis

Slides were developed and digitized with a film scanner (Epson Filmscan 200) at 300dpi, resulting in images with approximately 800×600 pixels, and were stored in JPEG (Joint Photographic Experts Group) format. All images were treated with GIMP (GNU Image Manipulation Program Anonymous, 2000) before patch analysis. For each image, the contours of individual patches were outlined manually. The underlying image was then discarded and the resulting outlines were filled with black colour to maximize the contrast of the image. Images were scaled individually using the known distances between screws, and the detection of patches and area measurements were carried out automatically (figure 4.1) using ImageJ (Rasband, 2000). Seven images were available for each area on each shore, thus allowing the estimation of changes between a sequence of six seasons in two years.

After the identification of patches and area measurements, the patches present at the start of the study were labelled with characters (A, B, C, ... *n*). In the next season, if the patches persisted they were labelled with the same character, and if they split in several smaller patches the latter were labelled with the original patch name



Particle	Area
1	235.00
2	345.23
3	123.18
4	26.80
Total	730.21

Total particles analysed: 4

Figure 4.1: Example of automatic detection of patches and area analysis using ImageJ (Rasband, 2000).

plus a subscript (e.g., A_1, A_2, ...). A new subscript level was added each time a patch was split (e.g., A_{1_1}, A_{1_2}, ...). If two or more patches coalesced to form a new patch the latter was labelled with a new character and with the name of its precursors within parenthesis (e.g., X(A,B) meaning that patches A and B coalesced to form patch X). Patch names and sizes were saved in a data file, and a small program was developed to analyse automatically these data sets.

The following differences between each two consecutive seasons were computed: number of new, lost, split and coalescent patches; gains and losses in area due to new, lost, split and coalesced patches; gains and losses in area due to growth and shrinkage of persistent patches. Unfortunately, the analysis of individual patch history could not provide all the information concerning losses and gains in area. Patches can increase in size as a consequence of individual growth or due to newly settled individuals. On the other hand, they can decrease due to dislodgement, death or migration of individuals. If both gains and losses are similar, the net result will be a constant size through time. To detect such modifications, hereafter referred as ‘overall gains and losses’, it was necessary to deal explicitly with exact patch positions within a given coordinate system. Because the corners of the fifteen areas studied in each shore were

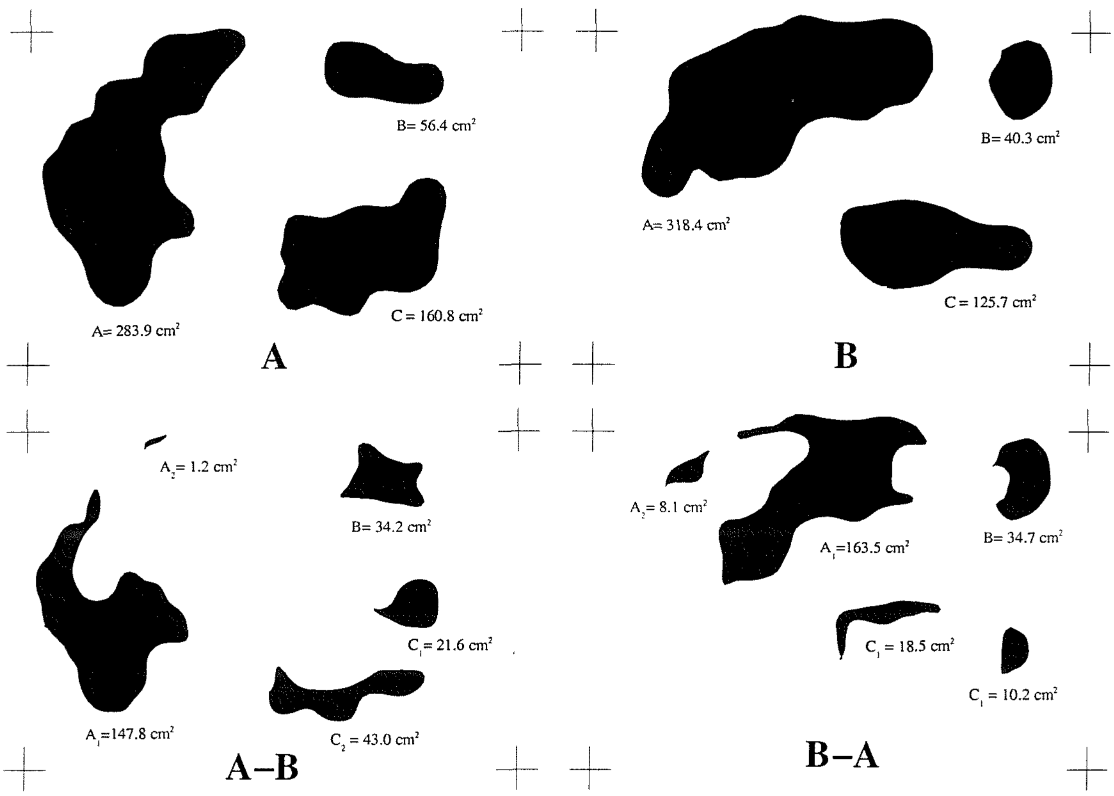


Figure 4.2: Example of image combination to assess overall gains and losses in area. Photos A and B were taken at consecutive dates. A-B depicts losses in area, while B-A depicts gains in area. Note that from A to B patch area decreased only 16.7 cm^2 (from 501.1 cm^2 to 484.4 cm^2) but real losses and gains in area were more than ten times higher (247.8 cm^2 and 235.0 cm^2, respectively).

marked with screws fastened into the rock surface, it was possible to delimit the exact boundaries of each area. Once scaled (that is, modified to have the same number of pixels either horizontally and vertically), the logical combination (subtraction) of two images of the same area resulted in a new image which bore the differences between the originals. Gains and losses in area were computed, changing the order in which the two images were combined (figure 4.2). The analysis of overall gains and losses could have been done at the patch scale. However, given the complexity of the resulting images, which often displayed a myriad of small patch fragments, it would have been a cumbersome task to assign each bit of lost or new area to individual patches, as was done for patch history analysis. Therefore, overall gains and losses were only estimated at each 'area' level ($\simeq$ 60$\times$40 cm).

4.2.3 Data analysis and hypotheses testing

4.2.3.1 Analysis of gains and losses in patch numbers and area

Several sources of gains and losses, either in patch numbers or in area, were considered in the present study. New patches, often small in size, can either be formed by direct settlement of new individuals (or reattachment of well-grown mussels) or by splitting of previously established patches. The former were referred to as 'new' or 'newly-born' patches, while the latter were called 'split' patches. Individual patches disappear mainly due to dislodgement, but also due to migration of individuals (Paine, 1974). Therefore, the terms 'dead' or 'lost' were used for vanished patches, whether they have actually been dislodged or their individual components migrated to other patches. Another cause of patch loss is when several patches lose their individuality to form a new – often bigger – aggregate. These were called 'coalesced' patches. Finally, patches that persist from one season to the other often grow (by growth of individuals or by settlement of new mussels) or shrink (by dislodgement of some individuals or migration), and these sources of variation were called 'growth' and 'shrinkage', respectively.

New patches always contribute to gains in area and number of patches, whilst dead patches contribute to losses in area and numbers of patches. Conversely, split patches contribute to gains in patch numbers and to a decrease in area, while coalesced patches often cause a decrease in patch numbers but an increase in area. Bar graphs were built for each pair of complementary variables, expressed as total number of patches (totals in the 12 fixed areas) and percentage cover. Gains and losses in area due to growth and shrinkage of patches were plotted separately, and were expressed as percentage cover only.

4.2.3.2 Hypotheses testing

The hypotheses that gains and losses in patch area would be roughly equivalent within each season, and that average gains and losses in area would be higher in the winter than in the spring and summer, were tested using an ANOVA model incorporating four factors (Table 4.1): changes (gains and losses), seasons (spring, summer and winter), years (1998 and 1999) and locations (Cabo do Mundo, Viana do Castelo and Moledo do Minho). Factors 'seasons', 'years' and 'changes' were considered fixed, whilst 'locations' was considered as a random factor. The use of 'years' as a fixed factor, contrasting with previous analyses (see Chapter 3) was necessary to allow for the inspection of differences among these two particular years, since it was shown

Table 4.1: Mean square estimates and degrees of freedom for the ANOVA model to estimate differences in absolute gains and losses in mussel occupied area, on different shores, seasons and years (computed after Underwood, 1997).

Factor	df	Mean square estimates
Changes (=C)	1	$\sigma^2_e + 60\sigma^2_{C\times L} + 180\sigma^2_C$
Locations (=L)	2	$\sigma^2_e + 120\sigma^2_L$
Seasons (=S)	2	$\sigma^2_e + 40\sigma^2_{L\times S} + 120\sigma^2_S$
Years (=Y)	1	$\sigma^2_e + 60\sigma^2_{L\times Y} + 180\sigma^2_Y$
C×L	2	$\sigma^2_e + 60\sigma^2_{C\times L}$
C×S	2	$\sigma^2_e + 20\sigma^2_{C\times L\times S} + 60\sigma^2_{C\times S}$
C×Y	1	$\sigma^2_e + 30\sigma^2_{C\times L\times Y} + 90\sigma^2_{C\times Y}$
L×S	4	$\sigma^2_e + 40\sigma^2_{L\times S}$
L×Y	2	$\sigma^2_e + 60\sigma^2_{L\times Y}$
S×Y	2	$\sigma^2_e + 20\sigma^2_{L\times S\times Y} + 60\sigma^2_{S\times Y}$
C×L×S	4	$\sigma^2_e + 20\sigma^2_{C\times L\times S}$
C×L×Y	2	$\sigma^2_e + 30\sigma^2_{C\times L\times Y}$
C×S×Y	2	$\sigma^2_e + 10\sigma^2_{C\times L\times S\times Y} + 30\sigma^2_{C\times S\times Y}$
L×S×Y	4	$\sigma^2_e + 20\sigma^2_{L\times S\times Y}$
C×L×S×Y	4	$\sigma^2_e + 10\sigma^2_{C\times L\times S\times Y}$
Residual	324	σ^2_e

previously that there was some significant variability between years.

Since the data sets were strongly non–independent, care was taken to avoid using measurements of the same patch (or derivatives) for the different levels of the factors considered in the analysis. Therefore, for each of the three shores, a 'pool' of patches was made using only patches present at the beginning of the survey and subsequent newly–born ones, but not those created by splitting or coalescence of other patches. From this pool, 10 patches were randomly allocated to each of the 12 combinations of changes/season/year. Absolute gains and losses in area were used, including null gains or losses (e.g., when by chance a selected patch did not increase or decrease in size in two consecutive seasons, a zero was used). Data were transformed using $log_{10}(X+1)$ transformation to achieve homoscedasticity (Underwood, 1997). Differences between levels of fixed factors (changes, seasons and years) were analysed using Student–Newman–Keuls (SNK) tests (Underwood, 1997).

The test of the two hypotheses using overall gains and losses was not possible because of lack of replication and non–independence of data. Since for each shore only 12 measurements were available (areas), and the ANOVA model required at least six combinations of years/seasons per shore, only two replicates were available. If a fourth factor was included, like factor 'changes' (gains and losses) in the previous

Table 4.2: Summary statistics for the two–year survey of mussel patches in three shores (numbers and averages are relative to the 12 fixed areas). 'New' means newly formed patches only, and 'All' and 'Total' refer to all analysed patches, including every instance of an individual patch in each season.

	Number of patches				Average size (cm^2)		
Site	Start	End	New	Total	Start	End	All
Cabo do Mundo	120	93	94	970	85	97	96
Viana do Castelo	94	115	60	955	104	82	80
Moledo do Minho	52	87	41	640	202	115	110
Total	266	295	195	2565			

analysis, there would be no replicates at all and, as a consequence, no estimate for the Residual term (Winer *et al.*, 1991). In this case, to proceed with further testing, the assumption that the residual variance was non–significant would have to be made. This is not a realistic assumption, especially when highly variable systems are considered (Underwood, 1997).

4.3 Results

Table 4.2 summarizes the results obtained during the two year survey in the three sampling sites. A total of 2565 individual patches (including patch instances) were analysed. Differences between shores were found at the start of the survey, with an obvious negative correlation between average patch size and the number of patches present. At Cabo do Mundo, 120 patches were found at the start of the survey, with an average size of 85 cm^2. In Viana do Castelo and Moledo do Minho the number of patches at the beginning of the study were smaller (94 and 52, respectively), but their average size was bigger (104 and 202 cm^2, respectively). The number of newly formed patches (excluding those created by splitting or by coalescence of other patches) was highest at Cabo do Mundo and smallest at Moledo do Minho. The trends in patch density and occupation were also different for the three sites. At Cabo do Mundo there was a decrease in the number of patches towards the end of the survey, but a corresponding increase in patch size. On the other two shores there was an increase in patch number and a decrease in average patch size. As shown in Chapter 2, Cabo do Mundo bears the highest density of mussels per unit area in the whole northern Portuguese coast, whilst Viana do Castelo and Moledo do Minho are within the average mussel densities found in this region. However, while at Cabo do Mundo and Viana do Castelo the density of mussels remained almost constant in the

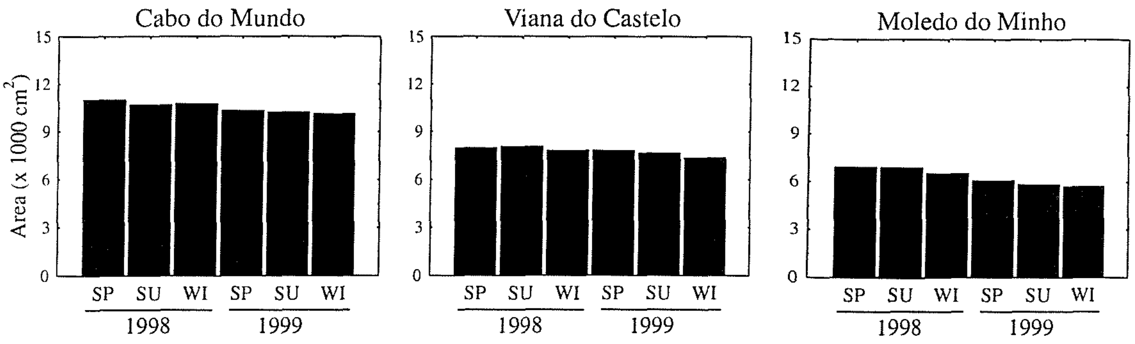


Figure 4.3: Seasonal variation of total area (sum of 12 sites) occupied by mussels in Cabo do Mundo, Viana do Castelo and Moledo do Minho.

surveyed areas, at Moledo do Minho there was a more pronounced decrease of density after the spring of the second year (figure 4.3).

4.3.1 Analysis of gains and losses in patch numbers and area

4.3.1.1 Variation in number of patches

Figure 4.4 depicts the seasonal variation in the number of new and lost patches. As expected, creation and disappearance of patches varied among seasons and shores (figure 4.4A). At Cabo do Mundo, most of the new patches appeared in the winter. This trend was also evident at Viana do Castelo, although on this shore the number of newly formed patches was much more constant throughout the seasons. On the other hand, on Moledo do Minho patch birth was higher during the spring. Patch loss showed a different pattern: whilst at Cabo do Mundo it was clearly higher in the spring, in the other shores there was a tendency to higher losses towards the second year. Overall, the number of newly–born and lost patches per season was more or less equivalent on the three shores (varying between 2 and 40, but rarely exceeding 15 per season) with the exception of the winter of the first year and the spring of the second year at Cabo do Mundo.

The processes of splitting and coalescence of previously formed patches (figure 4.4B) assumed a bigger importance in the creation and elimination of patches when compared to the effects of patch birth and loss. The number of new patches resulting from splitting varied between 10 and 50. In Cabo do Mundo the number of patches resulting from splitting was more or less constant (with the exception of the summer of the first year), decreasing towards the end of the second year. The high splitting rate in the summer of 1998 coincided with both a small oil spill, which killed

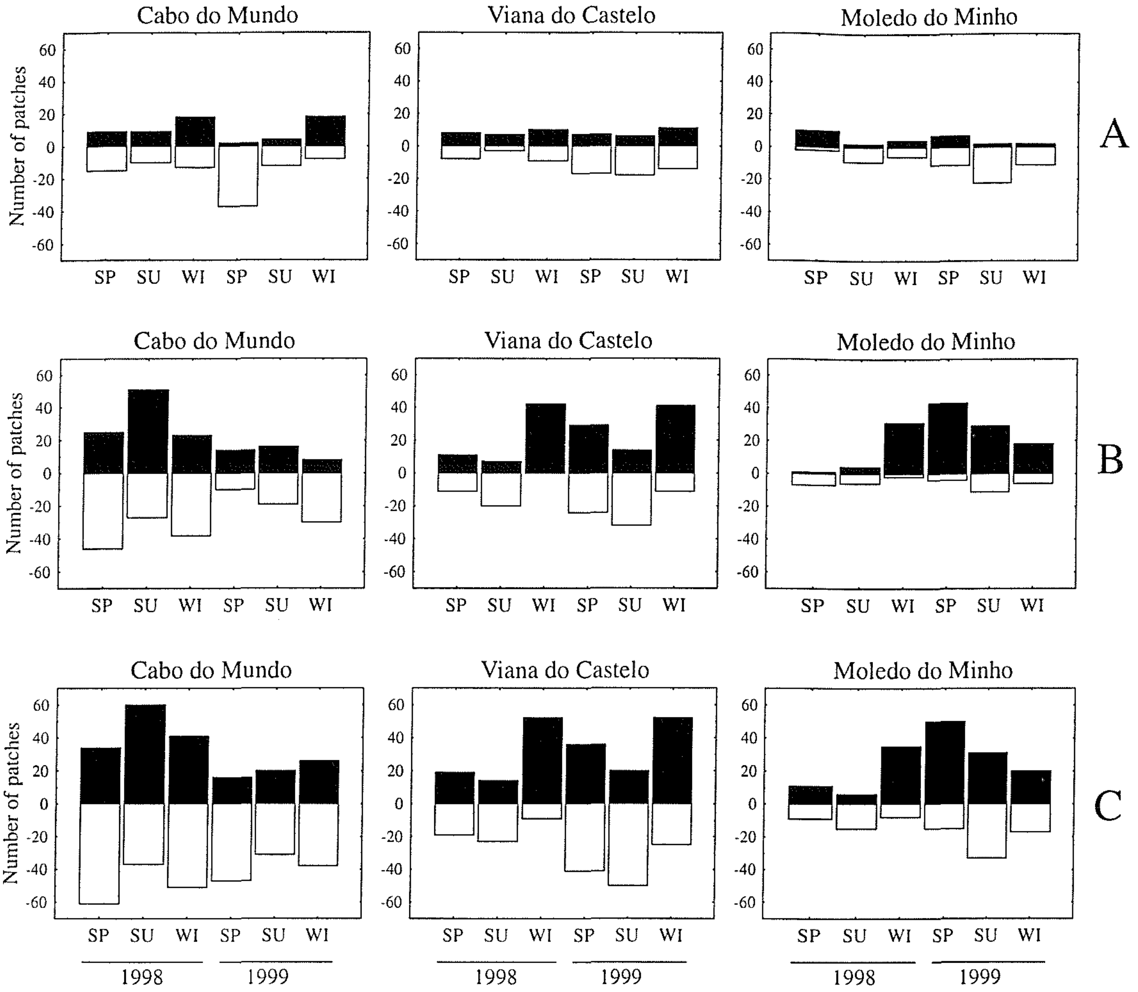


Figure 4.4: Seasonal variation of gains (black) and losses (white) in number of patches resulting from birth and loss (A), and splitting and coalescence of previously formed patches (B), respectively. The cumulative gains and losses are depicted in C.

several individuals, and severe damage caused by people scraping mussels in search of bait for fishing. At Viana do Castelo there was a higher rate of splitting during the winter months, while at Moledo do Minho there was again a trend towards an increase in splitting rates in the second year. Reduction in numbers of patches due to coalescence was considerable at Cabo do Mundo and Viana do Castelo, being similar in magnitude to the gains caused by patch splitting. Conversely, at Moledo do Minho the effects of coalescence were quite small when compared with the number of patches created by splitting. This fact can be explained by the specific characteristics of mussel patches on this shore, which had larger sizes and lower densities. The latter means that gaps between patches were also bigger, thus decreasing the likelihood of 'filling' such gaps. If the total number of new and lost patches is considered

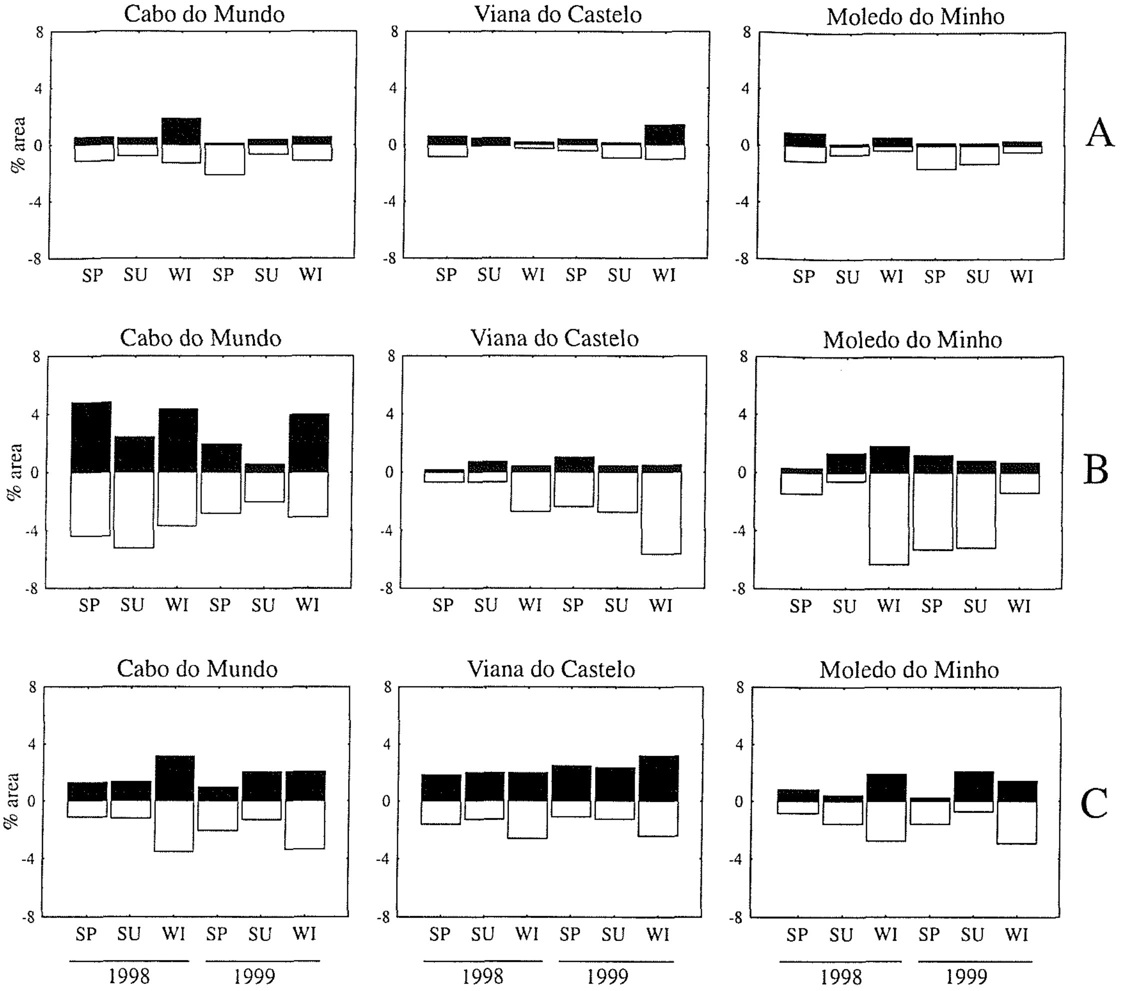


Figure 4.5: Seasonal variation of gains (black) and losses (white) in area resulting from newly–born and lost patches (A), coalescence and splitting of previously formed patches (B) and growth and shrinkage of patches (C), respectively.

(figure 4.4C), the magnitude of gains and losses at Cabo do Mundo was higher during the first year, while in the other two shores it was higher during the second year. These annual differences may have been responsible for the decrease in number of patches at Cabo do Mundo, and conversely, for the observed increase in patch number in the other two shores (see Table 4.2).

4.3.1.2 Gains and losses in area

Figure 4.5 depicts gains and losses in area resulting from the main sources of patch variation considered previously, plus growth and shrinkage of patches. Patch birth and loss (figure 4.5A) were clearly the least important sources of contribution to total gains and losses in area, seldom exceeding 2% of total occupied area. Given that the number of newly–born patches often reached 40 per season (figure 4.4A), newly–born patches were on average small in size, which is in agreement with other observations, since they were usually formed by clusters of very small individuals (secondary settlers) or by reattachment of few large individuals (Paine, 1974). Most importantly, these results suggest that dislodged patches were also of small size, which means that the bigger patches never disappeared completely. The other sources of patch variation had a more pronounced effect (figs. 4.5B and 4.5C). Patch splitting was responsible for losses in area that reached more than 4% on all shores, and was especially important at Moledo do Minho. Coalescence had a visible effect at Cabo do Mundo, but was much less important on the other shores. Once again, the differences in the contribution of coalescence for gains in area were probably related to patch density and size, as discussed previously. The contribution of growth and shrinkage of patches to total gains and losses in area was higher than that from newly–born and lost patches, and slightly smaller than that from splitting and coalescence. However, in this case there was a clear pattern of high rates of shrinkage during the winter months on all shores.

4.3.1.3 Total gains and losses in area

Figure 4.6 depicts the total variation of gains and losses in area as a result of individual patch history analysis (combined effects of patch birth, loss, splitting, coalescence, growth and shrinkage) and the analysis of overall gains and losses in area. As expected, the patterns of variation of gains and losses were similar for both types of analyses, but the magnitude of variation was much higher when overall gains and losses were considered. Moreover, differences between seasons were clearly marked in the latter case. Overall gains and losses were more or less of the same magnitude at Cabo do Mundo and Viana do Castelo and a clear difference between the winter and the other seasons was observed on both shores. Losses were higher than gains at Moledo do Minho, and this asymmetry was obviously linked with the observed decrease in total occupied area on this shore (figure 4.3).

4.3.1.4 Patch creation and survival

Survivorship of newly–born patches is depicted in figure 4.7. The results showed that most of the new patches died or were absorbed by bigger patches during the first season, loss rates being around 50%. In the first year, patches that were formed

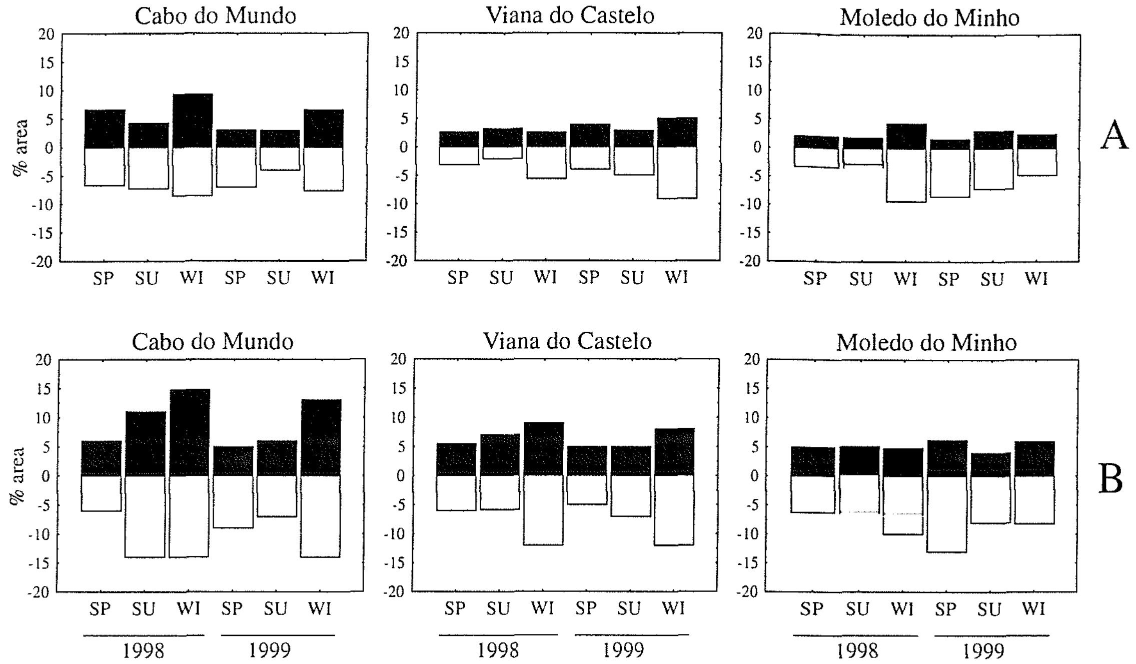


Figure 4.6: Cumulative gains (black) and losses (white) in area resulting from patch creation (birth, coalescence and growth) and disappearance (loss, splitting and shrinkage) (A) and overall gains and losses in area (B).

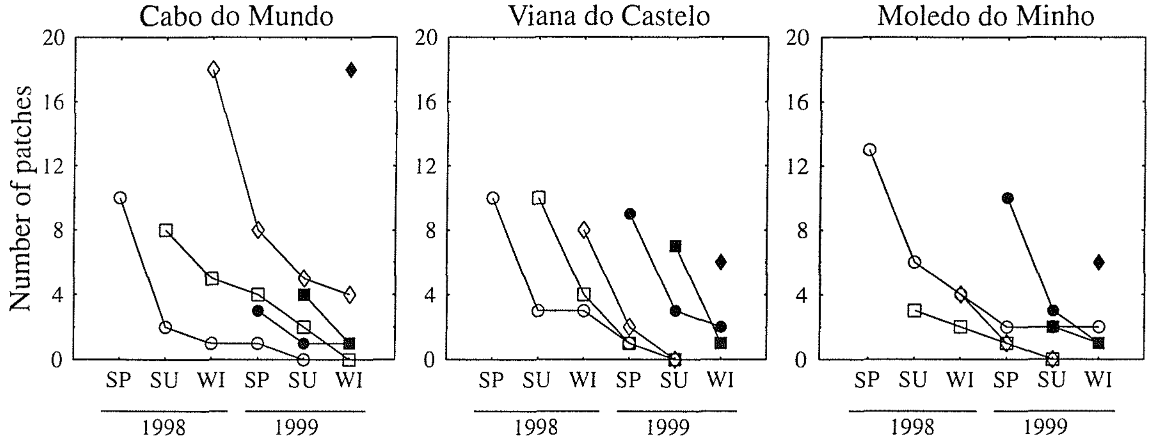


Figure 4.7: Number of newly–born patches per season and survivorship as individual patches in the three studied shores.

Table 4.3: Analysis of variance to test the effects of locations (shores), seasons, years and type of change (gain or loss) on mussel patch area.

Source of Variation	SS	DF	MS	F	P	Against MS
Changes (=C)	2.595	1	2.595	7.271	0.1135	C×L
Locations (=L)	5.374	2	2.687	8.783	**0.0002**	Residual
Seasons (=S)	1.408	2	0.704	0.219	0.8128	L×S
Years (=Y)	0.066	1	0.066	0.516	0.5536	L×Y
C×L	0.714	2	0.357	1.167	0.3135	Residual
C×S	1.647	2	0.823	1.450	0.3069	C×L×S
C×Y	0.012	1	0.012	0.022	0.8957	C×L×Y
L×S	12.852	4	3.213	10.502	< **0.0001**	Residual
L×Y	0.254	2	0.127	0.416	0.6602	Residual
S×Y	1.543	2	0.771	0.796	0.5282	L×S×Y
C×L×S	2.272	4	0.568	1.856	0.1109	Residual
C×L×Y	1.094	2	0.547	1.787	0.1715	Residual
C×S×Y	1.058	2	0.529	4.233	0.1014	C×L×S×Y
L×S×Y	3.878	4	0.969	3.169	**0.0138**	Residual
C×L×S×Y	0.500	4	0.125	0.408	0.8026	Residual
Residual	99.126	324	0.306			
Total	134.391	359				

in the spring disappeared by the summer of 1999, which means that at least some of them survived for more than 1.5 years. At Moledo do Minho, two of these new patches were still present in the end of the survey. Patches born in the summer of 1998 lasted until the summer (Cabo do Mundo and Moledo do Minho) or winter (Viana do Castelo) of 1999. Finally, patches formed in the winter of 1998 survived until the summer of 1999 (Viana do Castelo and Moledo do Minho), but at Cabo do Mundo some of them were still present in the end of the survey. Overall, there was a tendency for a decrease in patch life span from spring to winter: patches formed in the spring lasted longer than those formed in the winter of the same year. This trend may be correlated with an increasing harshness of physical conditions from spring to winter, as discussed earlier in the present study.

4.3.2 Hypotheses testing

The results of the analysis of variance for changes in mussel patch area among seasons, shores and years are depicted in Table 4.3. Homoscedasticity was achieved after $log_{10}(X+1)$ transformation (Cochran's C test=0.068, $P_{(\mathrm{v}=9,k=36)} > 0.05$). Since the third order interaction L×S×Y was significant, it was impossible to proceed with any tests at the higher levels. However, all other third order interactions were

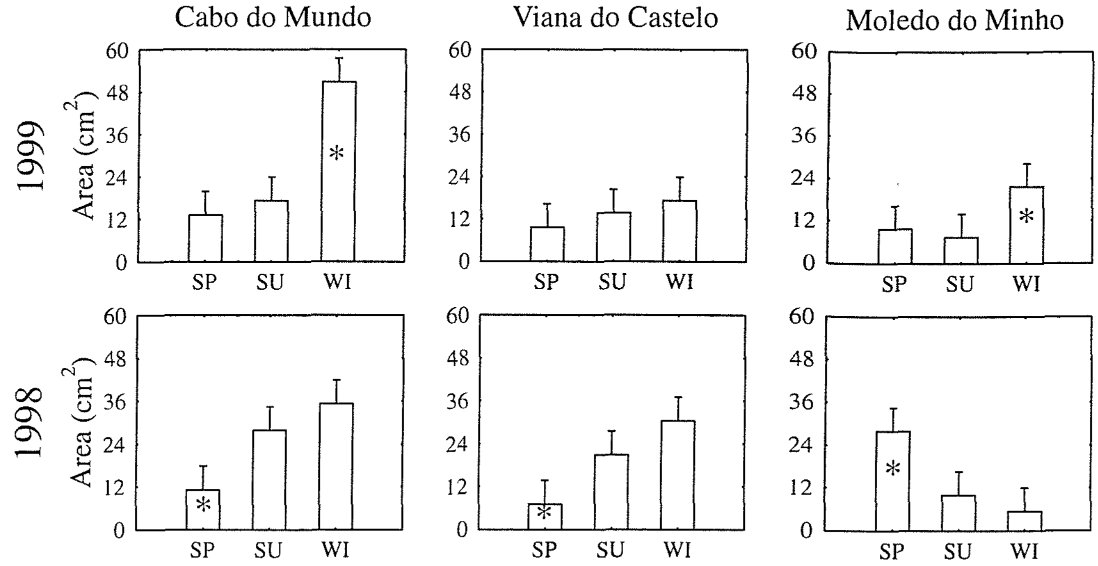


Figure 4.8: Multiple comparisons (SNK tests) after analysis of variance in Table 4.3. Graphics compare average changes (gains and losses) in patch area between three seasons, for each combination of location×year. Statistically significant differences are marked with *.

non–significant, suggesting that at least changes (average gains and losses in area) were consistent among shores, seasons and years. Although factor C (gains and losses in area) could not be tested directly as a consequence of the significant interaction L×S×Y, it is highly unlikely that there were significant differences between gains and losses in each combination of these factors. If there were differences between changes in area (such as loss rates higher than gain rates) they would have to be consistent over all other combinations of factors, otherwise they would be detected in third order interactions involving factor C. Thus, the assumption of similar changes in area was the most probable, and although care must be taken in making such an assumption, the graphical analysis of individual patches suggested that there was a clear symmetry between gains and losses in area.

The analysis of the interaction L×S×Y was done separately for the combinations of locations/years and locations/seasons. Figure 4.8 depicts the differences in average changes between seasons in each combination of shores/years. Changes in area during the winter were usually higher than in the other two seasons. The only deviation from such a pattern was observed at Moledo do Minho, in 1998, where spring changes were significantly higher than summer and winter changes. In most cases the SNK tests did not separate winter changes from the other two seasons. This could either be

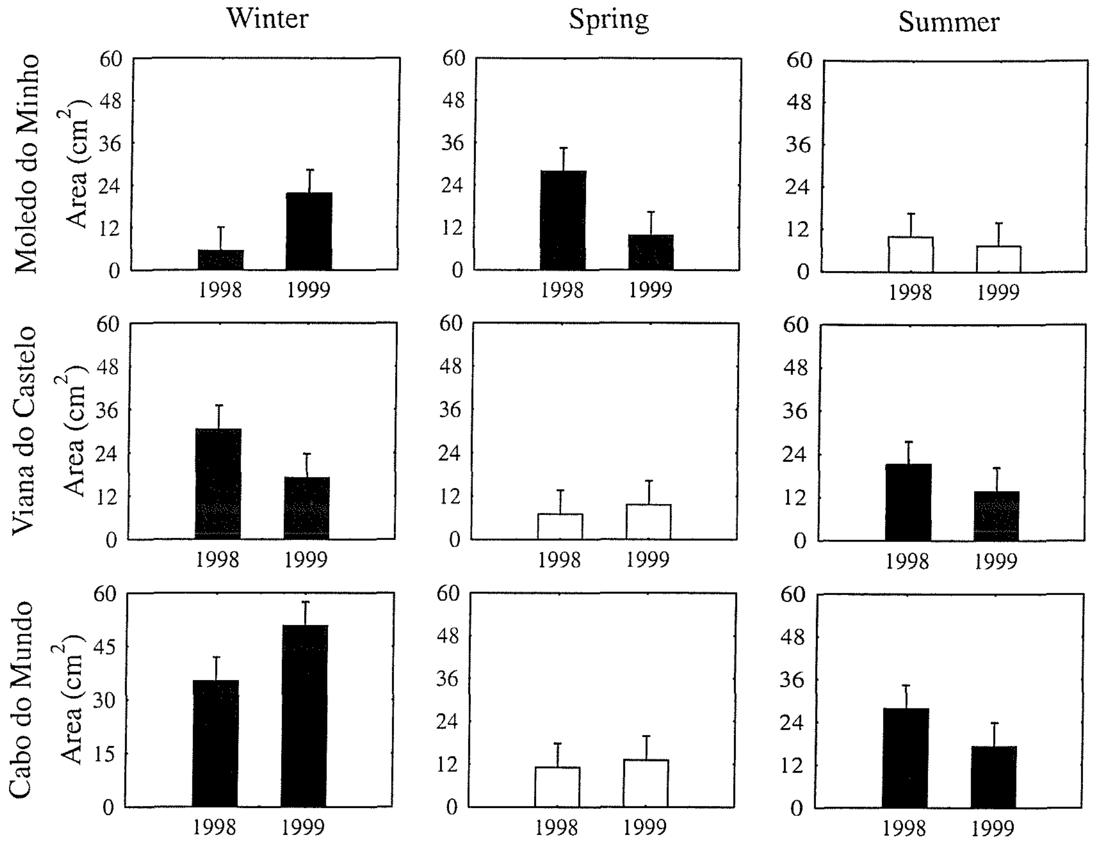


Figure 4.9: Multiple comparisons (SNK tests) after analysis of variance in Table 4.3. Graphics compare average changes (gains and losses) in patch area between two consecutive years, for each combination of location×season. Statistically significant differences are depicted in black.

a consequence of a real variation in patterns of change among seasons, as previously observed in individual patch history analyses, or simply the result of a lack of power of SNK tests (Day and Quinn, 1989). The hypothesis that rates of change were higher during winter months must be rejected because the observed patterns were not consistent between locations and years.

The results of SNK tests for the differences in average changes between years in each combination of shores/seasons are depicted in figure 4.9. As expected, there were significant differences between years, but these were not consistent among shores and seasons. Area changes during the winter were different on all shores, but while at Cabo do Mundo and Moledo do Minho the winter of 1999 seemed to be more severe than the winter of 1998, at Viana do Castelo this was reversed. Spring changes were only different at Moledo do Minho, with higher rates during the second year, and summer changes were different for Cabo do Mundo and Viana do Castelo, being higher during 1998 on both shores.

4.4 Discussion

The present results showed unequivocally that the dynamics of space occupation was much more variable at the patch scale than that observed at the shore scale. This was expected, in some sense, because it was shown earlier in this work that there was a high degree of variability either within shores or between sampling dates. Paine and Levin (1981) observed regional asynchronies in the dynamics of patch birth and loss in intertidal mussel assemblages in the northeast coast on North America. Although in that work the term patch was applied to free space rather than mussels, the processes driving mussel communities are supposed to be similar, the main difference being that in that region mussels monopolize space. Moreover, on the eastern coast of the British Isles, considerable differences in population age–structure of *M. edulis* were found among sites which appeared to be identical habitats. Those differences were thought to be the result of observing different populational stages in long term cycles of colonization, growth and denudation (Seed, 1969b).

There are several possible reasons, not mutually exclusive, to explain the highly variable patterns observed at the patch scale level and the temporal asynchronies between neighbouring populations. *Mytilus galloprovincialis* seems to be reproductively active throughout the whole year (Saldanha, 1974) like many other mussel species (Seed, 1969a). More importantly, it has two settlement phases (Saldanha, 1974), a widespread feature among mytilids (Bayne, 1964; Seed, 1969a; Suchanek, 1985). The primary settlers attach to algae on the lower shore for the first phase of their life, and constitute a pool that can recolonize the intertidal zone at relatively constant rates as secondary settlers (Bayne, 1964; Seed, 1969a). This ability to quickly recolonize denuded areas may have the power to buffer losses caused by natural mortality or external disturbances, and thus contribute to decrease heterogeneity in the system. However, settlement and/or recruitment of marine invertebrates is known to be a highly stochastic phenomenon, especially at larger temporal scales (see Underwood and Fairweather, 1989). Failures in mussel recruitment have been observed in several circumstances, and their effects on the age–structure of the assemblages were considerable (Seed, 1969b; Paine, 1974; Paine and Levin, 1981).

The age–structure of mussel patches usually determines their fate (Paine and

Levin, 1981; Svane and Ompi, 1993). As individual age increases, so does size, and in older patches big mussels tend to be crowded. Crowding is known to affect survivorship because it increases intraspecific competition, affecting individual ability to feed and to attach to the substratum (Peterson, 1982; Bertness and Grosholz, 1982). Secondary settlement, even at constant rates, is not a totally random process and young mussels are thought to settle preferentially in isolated aggregates or in the margins of older patches (Svane and Ompi, 1993). Although not deliberately studied, the latter behaviour was observed on all shores: very often patches of medium size (>400 cm^2) lost most of the inner – and older – mussels, leaving a thin outline composed of younger mussels that had settled on its margins. Thus, in the absence of drastic disturbance events, which can clear mussels from very large areas, age–structure of mussel aggregates is rather heterogeneous at scales higher than individual patches, and is quite homogeneous at the patch scale (Svane and Ompi, 1993). Therefore, mussel beds are a mixture of patches in different stages of succession and growth, and the selection of a particular spatial scale may have profound effects on subsequent results (Wu and Loucks, 1995). In the present study the operational scale was constrained by two factors: the area covered by the camera lens (about 60 × 40 cm) and film size. Since 12 areas were studied in each shore, the total area covered was about 3 m^2 and this may not have been enough to extract general patterns from the underlying variability.

Despite the observed variability, several important trends were still extractable from the available results. Patch birth did not contribute much to gains in area, and most of the new patches either disappeared in the first months or coalesced with other patches. Total patch dislodgement was observed mainly for small mussel aggregates, especially the newly formed ones. Patch splitting and shrinkage were the major sources of losses in area, and coalescence and growth were the most important sources of gains. These results suggest that large mussel patches are quite persistent, not always as individual units, but at least as part of a larger and more complex mosaic which rarely disappears completely. Therefore, during their life–time, mussel patches are split into smaller ones which are subsequently embedded into neighbouring aggregates. Apparently, the magnitude of the gains and losses in area associated to this phenomenon seems to be larger than what can be determined by the analysis of individual patch history (net differences in patch area).

Overall gains and losses, as defined in the methodology, were almost twice as high as apparent gains and losses determined from individual patch history. On the other hand, seasonal patterns were also more evident when overall gains and losses were analysed. At Cabo do Mundo and Viana do Castelo there were more changes in area occupation during the winter season than in the other two seasons, and this pattern was also consistent between years. The observed decrease in mussel area occupied at Moledo do Minho was probably related to the selection of the sites and the particular distribution of mussel patches on this shore. Whilst in the other locations mussel patches were very variable, both in size and in shape, at Moledo do Minho their boundaries were clearly defined, with circular or elliptical shapes, and since their density was smaller, gaps between patches were larger. These traits were obviously related with the lower rates of coalescence and, as a consequence, with overall patch persistency.

The hypothesis that changes (gains and losses) in area were consistently higher during the winter than during the other seasons was rejected on the light of the present results. Different patterns of change were observed at each shore and in each year. Nevertheless, the most different patterns of change were found at Moledo do Minho in 1998. Assuming that this was an unusual event, the remaining observations showed a clear trend towards higher changes during the winter (including Moledo do Minho in 1999) which may be the usual pattern of variation on these assemblages. Therefore, a combination of a lack of statistical power (small number of replicates) and the short time–scale of the experiment might explain the failure to detect consistent differences in patterns of change. Moreover, the statistical analyses were carried out using individual patch history data instead of overall gains and losses data. As stated earlier, the analysis of the latter revealed sharper patterns of seasonal variation than the former, but the quantity of information (replicates) was not enough to carry out an analysis of variance without a significant lack of power (Underwood, 1997).

Overall, and despite the results of the statistical analyses, the observations made suggest that during the winter months gains and losses in area are usually higher than in the other two seasons, which fits the model proposed in Chapter 3. However, this pattern does not seem to be regular, either between years or among different sites. The observed variation in patch gains and losses among shores and between years was probably the result of different population structures at the shore scale, allied with the short duration of the survey.

4.5 Conclusions

- The dynamics of mussel patch creation and loss are highly variable, both temporally or spatially.
- Patch splitting and shrinkage were the major processes of area loss, whilst coalescence and growth were the major processes of gains in area. Formation of new patches and dislodgement of patches had a minor contribution to those changes.
- Overall gains and losses at the area level were almost twice as high as cumulative gains and losses (due to birth, loss, split, coalescence, growth and shrinkage) observed at the patch scale. This suggests that mussel assemblages might be much more dynamic than what can be perceived at the patch scale or at the shore scale.
- Overall, gains and losses in area seem to cancel each other, which is in agreement with the stability of mussel percentage cover at the shore level observed in Chapter 3.

Chapter 5

Succession and Interaction Between Species

5.1 Introduction

The general patterns of variation of the intertidal mussel/barnacle mosaic were explored in the last two chapters, and an attempt was made to couple them with major external disturbance events that are believed to regulate the dynamics of these assemblages (Sousa, 1984c). When space is the major constraint to species survival and growth, the processes involved in the renewal of such a limited resource are essential for the persistence of several organisms (Connell, 1961b; Paine, 1966, 1974; Sousa, 1979a,b; Dayton, 1971; Paine and Levin, 1981; Ayling, 1981; Connell and Sousa, 1983; Sousa, 1984b; Chapman and Johnson, 1990; Blanchette, 1996). Disturbance provides the space for new colonizers and the hierarchical nature of species interactions dictates the pathway of succession (Sousa, 1984c). Because disturbance events vary over space and time, communities are best described as a mosaic of areas or patches differing in their state of succession and, therefore, in their species composition. Each of these patches can, in turn, influence the adjacent patches by providing propagules for further colonization, buffering environmental variation, and thus increasing the complexity of the system (Sousa, 1984b; Berlow, 1997). Stability or equilibrium within a patch is seldom or ever reached because disturbance (either physical or biological) is always resetting the system to a previous state (Wu and Loucks, 1995).

The mechanics of succession after disturbance have been addressed in several studies (e.g., Dayton, 1975; Farrell, 1991; Benedetti-Cecchi and Cinelli, 1994; Berlow, 1997; Benedetti-Cecchi, 2000). In temperate North–Atlantic intertidal ecosystems the first phase of succession after disturbance is usually characterized by the appearance of a thin mat of diatoms followed by ephemeral green algae that often monopolize the available space (Lubchenco and Menge, 1978; Southward and Southward, 1978; Sousa, 1979a,b; Hawkins, 1981b; Hawkins *et al.*, 1983; Benedetti-Cecchi and Cinelli, 1994; Benedetti-Cecchi *et al.*, 1996). Grazers play an important role in these ecosystems, and it is generally accepted that they can break inhibition by preventing ephemeral algal dominance in early stages, leaving some space for later colonists, and thus accelerating the successional pathway (see Sousa and Connell, 1992, for a review). But there is also evidence that grazing can also slow (Sousa *et al.*, 1981; Farrell, 1991; Sousa and Connell, 1992) or have no effect (Sousa, 1979b; Turner, 1983) upon succession. Therefore, in many situations the final outcome of a successional pathway after a disturbance event is not easily predictable.

For a given temporal scale of observation, a whole range of historic effects can influence variation in successional patterns and may have lasting effects (Berlow, 1997). These historic effects, which in most cases are not readily measurable, include both physical events (such as disturbance, environmental conditions, recruitment/dispersal events) and past biological interactions (such as facilitation/inhibition by earlier appearing species, consumption of early species, competition among earlier species). The outcome of species interactions often varies with local conditions, and historical events exert a strong influence over current processes by shaping the context in which they occur. Given the potential importance of interactions among past events and current processes, the patterns and mechanisms by which communities change during succession can be highly variable, complex and context–dependent (Connell and Slatyer, 1977; Paine and Levin, 1981; Sousa, 1984b; Connell *et al.*, 1987). Therefore, succession after disturbance is usually a contingent phenomenon (Berlow, 1997).

On northern Portuguese shores, the mussel/barnacle mosaic encompasses several species, including limpets (*Patella* spp.), trochids (*Gibbula umbilicalis* and *G. pennanti*), littorinids (*Littorina* spp.), dog–whelks (*Nucella lapillus*), sea–anemones (*Actinia equina*) and other less conspicuous animals and plants. Even if only the major species are considered, the web of possible direct and indirect interactions between them will still be very complex (figure 5.1).

Of all possible interactions between plants and animals on rocky intertidal shores and subtidal reefs, grazing has probably received the most attention (Foster, 1992; Raffaelli and Hawkins, 1996). On rocky intertidal shores, molluscs and sea–urchins are the most important grazers (Hawkins and Hartnoll, 1983b). Prosobranch limpets

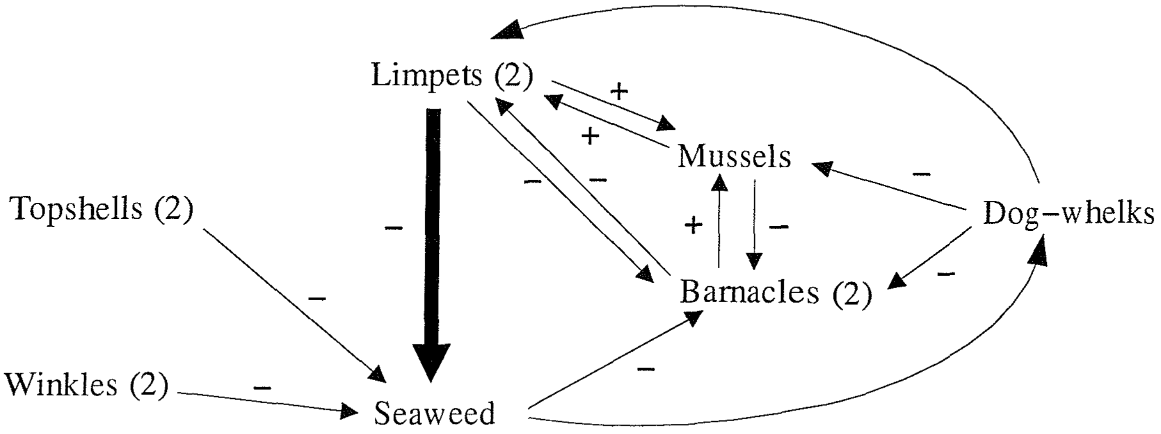


Figure 5.1: Web of putative interactions among species in northern Portuguese intertidal mussel assemblages. Number in parentheses refer to the number of species involved. -/+ indicate negative or positive effects, respectively.

are particularly important in some temperate regions (Branch, 1981), but trochids and littorinids also have been shown to play a significant role in the community structure (Menge, 1976; Lubchenco, 1978; Underwood, 1979; Petraitis, 1983; Norton *et al.*, 1990). The effects of limpets and trochids (and winkles) are, nonetheless, quite distinct. Limpets are generalist grazers and feed on the microflora and detritus available on the rock surface, preventing algal propagules from settling because they 'bulldoze' indiscriminately the rock surface (Dayton, 1971; Menge, 1976; Hawkins, 1983). Conversely, trochids and littorinids also feed upon large erect seaweed (especially ephemeral filamentous algae) and can break algal dominance at later stages of succession (Hawkins and Hartnoll, 1983b).

Although there are numerous examples of grazer exclusion experiments in the midshore, they were mainly carried out on systems dominated by barnacles and algae (e.g., Lubchenco, 1980; Hawkins, 1981a,b; Sousa *et al.*, 1981; Underwood and Jernakoff, 1981; Hawkins and Hartnoll, 1985; Petraitis, 1983; Underwood *et al.*, 1983; Underwood and Jernakoff, 1984; Farrell, 1989; Foster, 1990; Farrell, 1991; Benedetti-Cecchi and Cinelli, 1992a,b, 1993, 1994, 1997). Other authors attempted to replicate such experiments on mussel–dominated assemblages (e.g., Dayton, 1971; Menge, 1976; Sousa, 1984b; Berlow, 1997), but only few of these were carried out on eastern Atlantic shores where patellid limpets can be considered as keystone species (Hawkins *et al.*, 1992).

Experimental manipulation on rocky shores have provided some of the better examples of the effects of predation upon community structure (Connell, 1961a, 1970;

Paine, 1966, 1969, 1974; Dayton, 1971; Menge, 1976; Lubchenco, 1978; Lubchenco and Menge, 1978; Underwood *et al.*, 1983). The control of species diversity by the predatory dog–whelk *Nucella lapillus* on the mid and low rocky shores is perhaps one of the best known examples (Menge, 1976, 1978a,b, 1982, 1983; Lubchenco and Menge, 1978; Navarrete, 1996; Navarrete and Menge, 1996). Seed (1969b) considered the effects of predation by *Nucella* as the major structuring force in mussel assemblages, considering factors such as disturbance, physical stress and intraspecific competition as secondary, although he did no experimental manipulation to support such assumptions. However, recent evidence suggests that the effects of dog–whelks may have been overrated (Petraitis, 1990). On northern Portuguese shores, dog–whelks are relatively common and seem to be the most important predator of mussels in the midshore (Santos, 1997).

In Chapter 3, a new model was developed to explain the patterns of variation of the mussel/barnacle mosaic, after rejecting the hypothesis that mussel density varied seasonally, being lower during the winter months. The new model relied on the assumption that mussels grew preferentially on top of barnacles rather than bare rock, and that their density remained constant through time, while barnacle density decreased during the winter. Facilitation of mussel settlement by barnacles is not an unknown phenomenon (Petraitis, 1990). According to Dayton (1971), mussels are later colonists and require ephemeral algae, barnacles or byssal threads for secondary settlement, although they are capable of growing over all the other sessile species.

In this Chapter, the patterns of succession after disturbance are described, and some interactions between species are investigated. From the interactions previously outlined, three were selected for experimental analysis because of their paramount importance in the context of the assemblage under study: direct effects of grazers (*Patella*, *Gibbula* and *Littorina*) in the structure of the community, direct effects of predation by *Nucella lapillus* on mussels and facilitation of mussel settlement by barnacles. The analysis of succession after disturbance was done by following the evolution of species abundance in artificially cleared areas. Complete recovery from disturbance in similar systems can take as long as 8–10 years, mostly because the organisms involved have quite long life–spans, and their recruitment can be rather stochastic (Paine and Levin, 1981). Therefore, it was not expected to observe a total recovery of cleared areas within the limited time of the present study, and the experiments conducted were considered as preliminary. The main goal of these experiments was to analyse the patterns of recolonization of bare rock areas differing in size and position within a shore.

5.2 Material and methods

5.2.1 Succession after disturbance

Two experiments were conducted separately in two different shores. The first experiment consisted in following the recolonization of six cleared areas of different sizes: 30×30 cm and 70×70 cm. Four plots of each size were cleared in two shores (Aguda and Cabo do Mundo) and monitored regularly until the spring of 2000. The average denuded area size in a normal shore was computed from previous estimates of mussel and barnacle percentage cover and bare rock density, and is about 900 cm^2. The 70×70 cm areas were used to estimate recovery times for a large disturbance effect, such as the result of a patchy oil spill. The second experiment consisted in following species succession in six cleared areas of 30×30 cm at two different shore levels (upper and lower) within the mussel zone, in two shores (Cabo do Mundo and Viana do Castelo). Usually mussel densities decrease significantly towards the upper levels in the shore, which is thought to be a consequence of a combination of several physical factors (Seed, 1969a,b).

5.2.2 Species interactions

Of the three experiments planned – facilitation of mussel secondary settlement by barnacles, effects of grazers and effects of predators – only the first two were conducted successfully until the end of this work. Maintaining experimental structures on the shore proved to be a difficult task, either because of the harshness of the sea or because of (un)intentional destruction by humans. Cages were always destroyed and fences resisted longer, but were usually trampled or torn off deliberately, and had to be monitored and rebuilt at very small time intervals to be effective, even if only partially. Experiments without artefacts, such as the analysis of barnacle facilitation of mussel fixation, were the least problematic in terms of results, but even in this case some markers (stainless screws) were stolen.

5.2.2.1 Facilitation of mussel fixation by barnacles

The experiment was carried out on two shores (Moledo do Minho and Montedor). Sixteen small areas with about 10×10 cm, and with 100% of barnacle cover were selected randomly among the mussel patches. From these, eight were completely scraped so as to have only a smooth surface of bare rock. Each corner of the quadrats was marked with a stainless screw fastened to the rock with a plastic plug. Quadrats

Table 5.1: Mean square estimates and degrees of freedom for the ANOVA model to test facilitation of mussel fixation by barnacles in two shores, and in two different starting dates (computed after Underwood, 1997).

Factor	df	Mean square estimates
Shores (S)	1	$\sigma^2{}_e + 16\sigma^2{}_{S\times D} + 32\sigma^2{}_S$
Dates (D)	1	$\sigma^2{}_e + 16\sigma^2{}_{S\times D} + 32\sigma^2{}_D$
Treatment (T)	1	$\sigma^2{}_e + 8\sigma^2{}_{S\times D\times T} + 16\sigma^2{}_{D\times T} + 16\sigma^2{}_{S\times T} + 32A^2{}_T$
S×D	1	$\sigma^2{}_e + 16\sigma^2{}_{S\times D}$
S×T	1	$\sigma^2{}_e + 8\sigma^2{}_{S\times D\times T} + 16\sigma^2{}_{S\times T}$
D×T	1	$\sigma^2{}_e + 8\sigma^2{}_{S\times D\times T} + 16\sigma^2{}_{D\times T}$
S×D×T	1	$\sigma^2{}_e + 8\sigma^2{}_{S\times D\times T}$
Residual	56	$\sigma^2{}_e$

were monitored on a monthly basis, and both the number of mussels directly fixed into the barnacles or those invading it laterally (by growth of external patches) were counted.

The experiment was repeated six months later, to account for any differences in mussel secondary settlement. Both experiments were continued over nine months. The analysis of the data (either mussel direct fixation or lateral invasion) was done through a mixed ANOVA model (Table 5.1), including three factors. Both shores (S) and starting dates (D) were considered random factors, while the experimental treatment (T) was fixed. Since the model did not allow a direct test of factor T (due to the lack of a suitable term), the outcome of the analysis was dependent on the ability to pool S×T, D×T or both. Pooling was done after testing the significance of terms at $\alpha = 0.25$ (Underwood, 1997). Data were transformed with $log_e(X+1)$ to achieve homoscedasticity (Winer *et al.*, 1991).

5.2.2.2 Grazer effects

In a first phase the main goal of this experiment was to test the influence of two types of grazers – limpets and trochids – on the structure of the mussel assemblage. To address this problem, a three factorial asymmetrical model was used, combining grazer type (limpets and trochids), treatments (presence or exclusion of grazers) and locations. The experiment was carried out on three shores: Aguda, Cabo do Mundo and Moledo do Minho. Steel fences of 50×50 cm, with a height of 5 cm, were fastened into the rock substrate with stainless screws. In each shore, five replicates of each combination of treatments×grazers (+limpets +trochids, −limpets +trochids, +limpets −trochids, −limpets −trochids) plus five 'natural' plots (unfenced controls)

Table 5.2: Mean square estimates and degrees of freedom for the ANOVA model to test the effects of grazer exclusion on algal growth, at three different shores and in three different starting times (computed after Underwood, 1997).

Factor	df	Mean square estimates
Shores (S)	2	$\sigma^2{}_e + 15\sigma^2{}_{S\times D} + 45\sigma^2{}_S$
Dates (D)	2	$\sigma^2{}_e + 15\sigma^2{}_{S\times D} + 45\sigma^2{}_D$
Treatment (T)	2	$\sigma^2{}_e + 5\sigma^2{}_{S\times D\times T} + 15\sigma^2{}_{D\times T} + 15\sigma^2{}_{S\times T} + 45A^2{}_T$
S×D	4	$\sigma^2{}_e + 15\sigma^2{}_{S\times D}$
S×T	4	$\sigma^2{}_e + 5\sigma^2{}_{S\times D\times T} + 15\sigma^2{}_{S\times T}$
D×T	4	$\sigma^2{}_e + 5\sigma^2{}_{S\times D\times T} + 15\sigma^2{}_{D\times T}$
S×D×T	8	$\sigma^2{}_e + 5\sigma^2{}_{S\times D\times T}$
Residual	108	$\sigma^2{}_e$

were randomly placed in the mussel/barnacle zone. All experiments were maintained for nine months, after which they were abandoned and the fences removed. Regular visits were made to rebuild damaged fences and to kill the limpets that were able to cross undamaged fences. Percentage cover of every algal species was recorded using a quadrat with 100 divisions.

Unfortunately, the fences proved to be ineffective for excluding trochids. Fortnightly visits to the exclusion sites showed that trochids were able to invade the exclusion areas easily, even when these were not destroyed or damaged. Therefore, this part of the experiment was abandoned due to the high costs, both in time and money, of maintaining these experimental plots, and grazer effects on the structure of mussel assemblages were only studied for limpets using a less complex ANOVA model (Table 5.2).

Shores (S) and starting dates (D) were considered random factors, while the experimental treatment (T) was fixed. As in the mussel fixation experiment, the proposed model did not allow a direct test of factor T due to the lack of a suitable term, and the outcome of the analysis was dependent on the ability to pool S×T, D×T or both. Multiple comparisons between levels of treatments were carried out using SNK tests (Underwood, 1997). Data were transformed with $log_e(X+1)$ to achieve homoscedasticity (Winer *et al.*, 1991; Underwood, 1997).

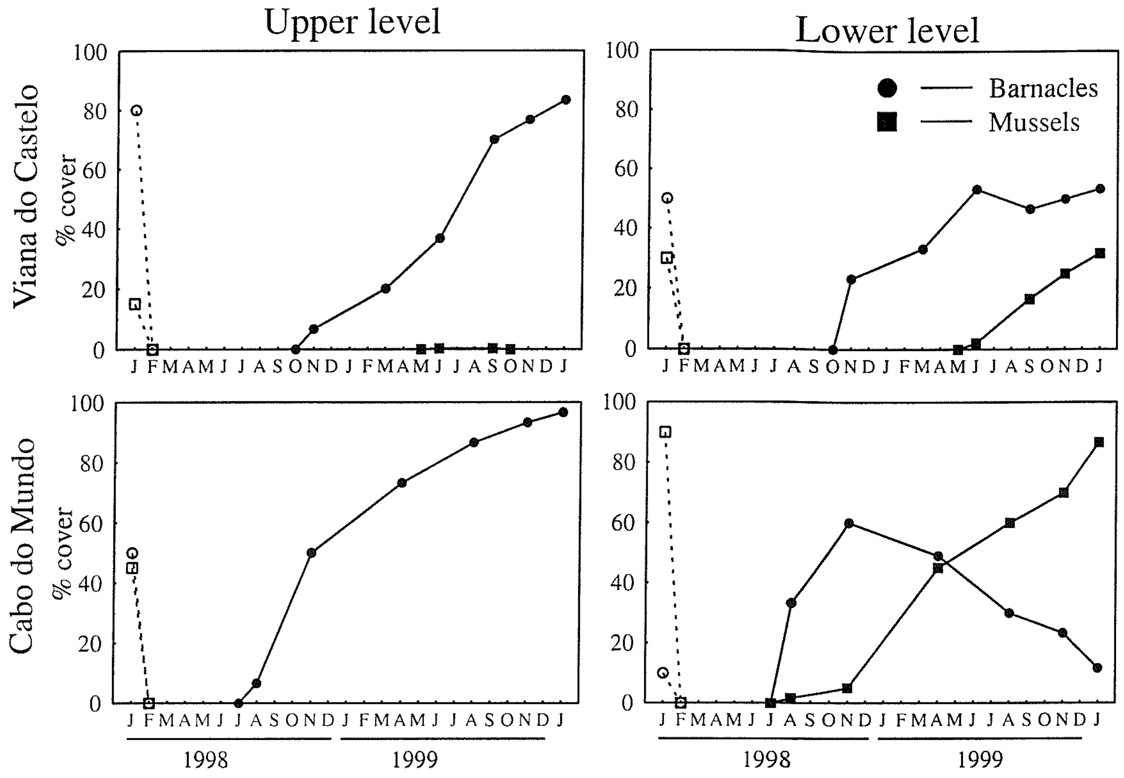


Figure 5.2: Patterns of succession in cleared experimental plots (30×30*cm*, n=6) made at two different levels in the mussel zone, at two different shores. Open symbols indicate pre–scraping percentage cover and closed symbols indicate post–scraping percentage cover. All experiments started in January 1998.

5.3 Results

5.3.1 Succession after disturbance

5.3.1.1 Differences between shore levels

Figure 5.2 depicts the recolonization after total clearing of space at two different shore levels. The bare rock stayed denuded until the summer after clearing, when barnacle settlement started (see Chapter 3, figure 3.9). Barnacle density increased rapidly after that, mainly due to the subsequent growth of settled individuals. In the upper level of the mussel zone, barnacles reached almost 100% cover by the end of the second year after clearing. Mussel density never recovered in this zone, although at Viana do Castelo, some sporadic settlers appeared during the spring–summer of the second year, but they were not observed after then.

At Cabo do Mundo, mussel recovery started very early in the lower level of the mussel zone, while at Viana do Castelo it only started in the spring of 1999. This difference was probably related with the different densities of mussels in both shores. At Cabo do Mundo mussels reached almost 100% cover, the clearing areas being almost completely surrounded by mussels. In contrast, at Viana do Castelo the initial average density of mussels was only 20–30%. Thus, at Cabo do Mundo lateral growth was enough to fill up the cleared areas, while at Viana do Castelo mussel recovery was dependent on the direct fixation of individuals and subsequent subsistence of patches. Nevertheless, by the end of the second year of the experiment the average densities of mussels were similar to those before the clearings were made.

5.3.1.2 Differences between size of cleared areas

If size of cleared areas is considered (figure 5.3), the patterns of succession are quite similar. Barnacles started settling in the summer of 1998 and rapidly dominated the cleared areas, reaching between 80–100% cover at Aguda and to a less extent at Cabo do Mundo. The difference can be explained by a stronger mussel fixation (secondary settlement) on the latter shore, mainly because the density of mussels is much higher there (initial average cover of 55%) when compared to Aguda (initial average cover of 30%), and the pool of secondary settlers must also be higher. Overall, recovery after clearing was faster at Cabo do Mundo thanat Aguda, because in this shore the percentage cover of mussels in the end of the experiment was still far from its initial value.

An interesting phenomenon was observed in the larger denuded areas: before barnacle settlement, and mostly during the late winter and spring after clearing, a considerable development of ephemeral algae (*Ulva* and *Enteromorpha*) was observed. This difference may be explained by the fact that the clearing of rock surfaces was complete, killing all major grazers (limpets) enclosed in the boundaries of the plots. Limpet recovery was quite fast, but was obviously quicker in small areas than in bigger ones, and in the latter the grazing pressure may have been reduced significantly allowing the development of ephemeral algae.

5.3.2 Species interactions

5.3.2.1 Facilitation of mussel fixation by barnacles

Trends in mussel recolonization of cleared and barnacle dominated areas are shown in figure 5.4. If direct settlement is considered (figure 5.4A), small mussels ($<$ 0.5

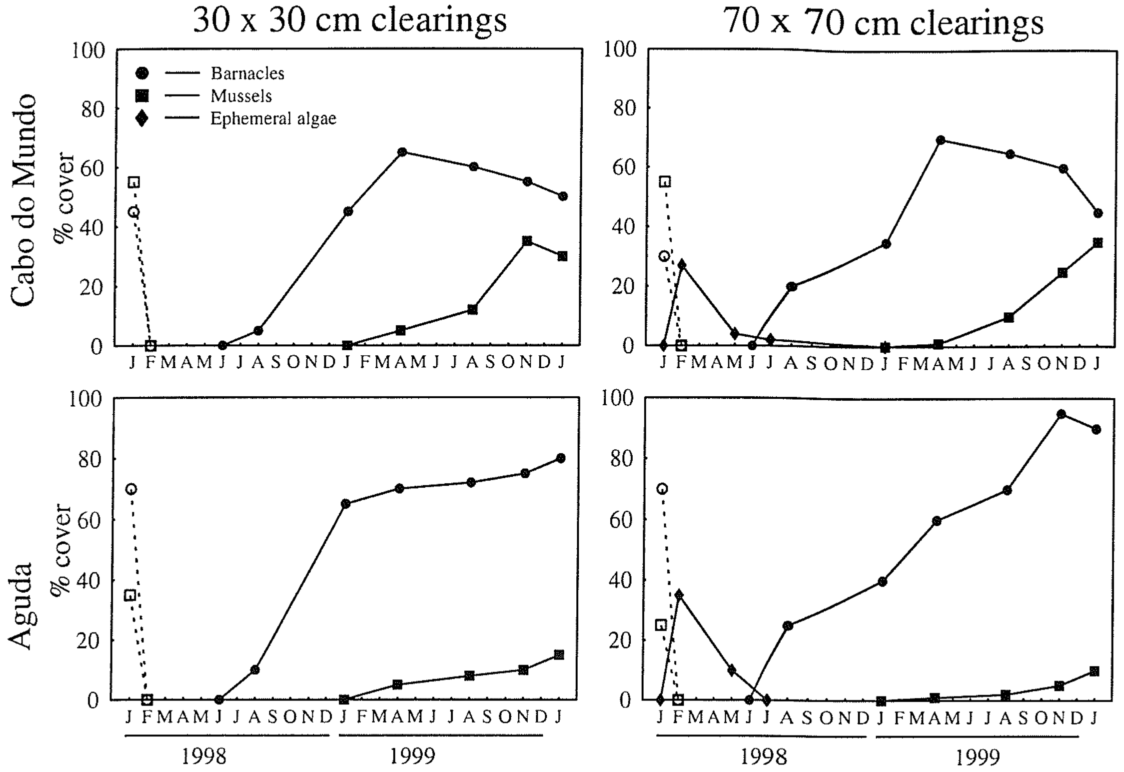


Figure 5.3: Patterns of succession in cleared experimental plots (n=6) of different sizes made at the mussel zone, at two different shores. Open symbols indicate pre–scraping percentage cover and closed symbols indicate post–scraping percentage cover. All experiments started in January 1998.

cm) started settling right after the beginning of both experiments (February 1999 and September 1999) and their number increased rapidly only in barnacle covered areas. While at Moledo do Minho the increase of fixed mussels was consistent over time, at Montedor there was a significant decrease after October 1999 for no apparent reason. However, by the end of the experiment the number of directly fixed mussels increased again. Very few mussels settled in the cleared areas of both shores, and those that were able to do it, settled on the few available crevices in the denuded rock surface.

Patterns of lateral invasion were slightly different from those of direct settlement (figure 5.4B). Lateral invasion was observed in cleared and barnacle dominated areas. While at Montedor the number of lateral invaders was negligible in both types of areas, at Moledo do Minho these numbers were significant even in cleared areas, although there was a higher rate of invasion in barnacle covered areas than in the cleared ones.

Table 5.3 shows the results of the ANOVAs carried out for mussel direct

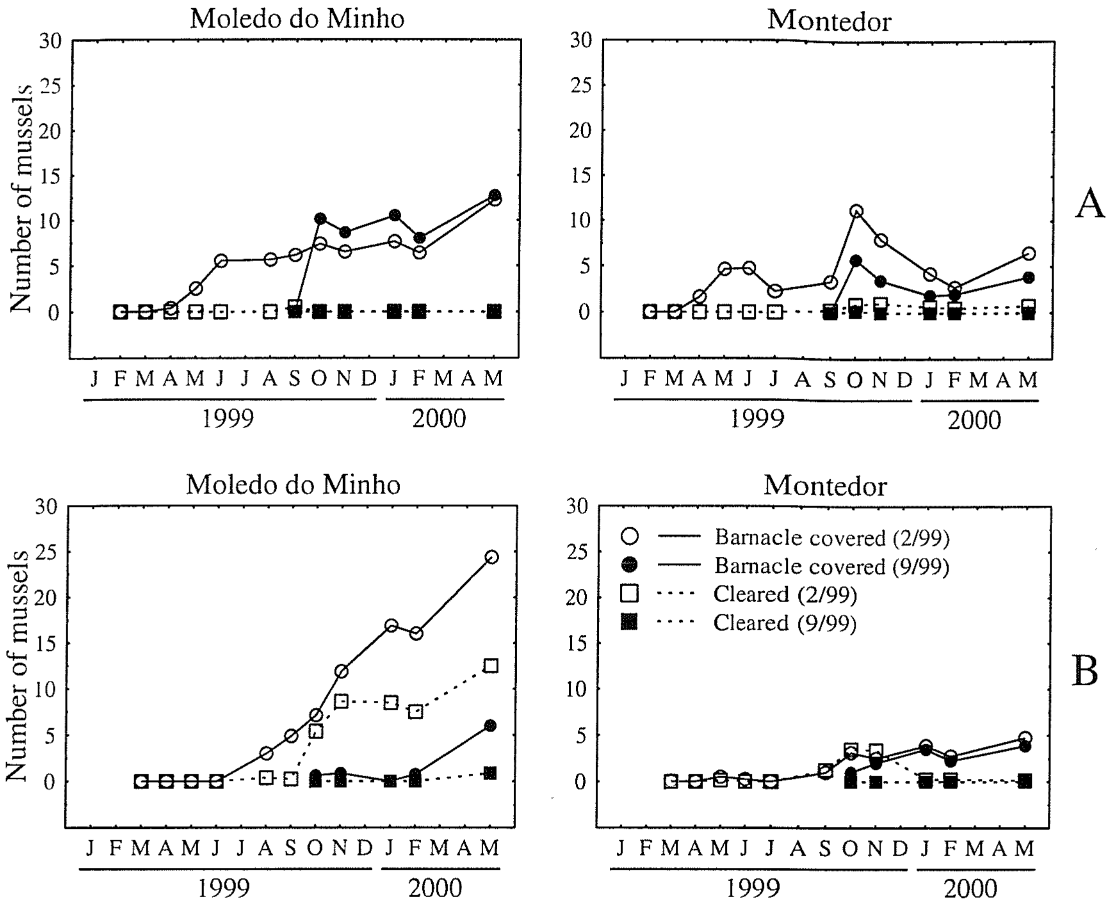


Figure 5.4: Trends in mussel recolonization of cleared and barnacle covered areas by direct fixation (A) and lateral invasion (B). Data values are averages of eight replicates used for each treatment in two experiments with different starting dates.

fixation and lateral invasion. Homoscedasticity was achieved for both direct fixation (Cochran's C test = 0.26, $P_{(v=7,k=8)} > 0.05$) and lateral invasion data (Cochran's C test = 0.22, $P_{(v=7,k=8)} > 0.05$) after $log_e(X + 1)$ transformation. In both cases it was possible to pool several terms to test for differences among Treatments. The results showed that there were significant differences among treatments (scraped and unscraped areas), but no differences among shores or dates. Therefore, after the nine months of each experiment, there was a higher fixation of mussels and higher rates of lateral invasion in the areas covered by barnacles than in the bare rock surfaces (figure 5.5), suggesting that barnacles facilitate mussel secondary settlement on smooth rock surfaces.

Table 5.3: Analysis of variance to test for differences in mussel direct fixation (A) and lateral invasion (B) over barnacle covered areas and bare rock. Significant tests depicted in bold.

A –Direct fixation

Source of Variation	SS	DF	MS	F	P	Against MS
Shores (=S)	0.968	1	0.968	1.061	0.4546	S×D
Dates (=D)	0.444	1	0.444	0.487	0.6228	S×D
Treatments (=T)	27.505	1	27.505	22.36	**0.0200**	*
S×D	0.912	1	0.912	1.379	0.2479	Residual
S×T	0.733	1	0.733	0.625	0.5914	S×D×T
D×T	1.805	1	1.805	1.539	0.4133	S×D×T
S×D×T	1.172	1	1.172	1.773	0.1936	Residual
Residual	37.036	56	0.661			
Total	70.575	63				

* Tested against pooled SS of S×T, D×T and S×D×T, MS=1.23 with v = 3

B – Lateral invasion

Source of Variation	SS	DF	MS	F	P	Against MS
Shores (=S)	0.807	1	0.807	6.799	0.2324	S×D
Dates (=D)	0.176	1	0.176	1.483	0.4178	S×D
Treatments (=T)	6.165	1	6.165	7.401	**0.0100**	*
S×D	0.119	1	0.119	0.138	0.7113	Residual
S×T	0.317	1	0.317	0.775	0.5661	S×D×T
D×T	0.402	1	0.402	0.981	0.5416	S×D×T
S×D×T	0.410	1	0.410	0.478	0.4926	Residual
Residual	48.038	56	0.858			
Total	56.433	63				

* Tested against pooled SS of S×T, D×T, S×D×T and Residual, MS=0.833 with v = 59

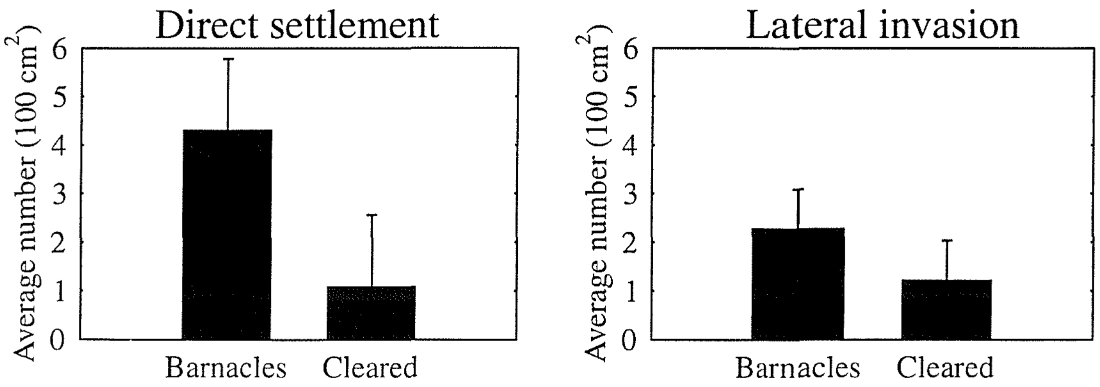


Figure 5.5: Average number of mussels (untransformed) present on barnacle covered and cleared areas due to direct settlement or lateral invasion, after analyses of variance (Table 5.3).

Table 5.4: Analysis of variance to test for the effects of treatments (exclusion of grazers, fenced and unfenced controls) on algal growth on three different shores, at three different starting dates. Significant tests depicted in bold.

Source of Variation	SS	DF	MS	F	P	Against MS
Shore (=S)	825.220	2	412.610	1.366	0.3196	S×D
Date (=D)	633.092	2	316.546	8.077	**0.0005**	Residual
Treatment (=T)	11863.234	2	5931.617			NT
S×D	1208.191	4	302.048	7.707	**<0.0001**	Residual
S×T	887.431	4	221.858	2.433	0.1291	S×D×T
D×T	1714.133	4	428.533	10.935	**<0.0001**	Residual
S×D×T	729.348	8	91.168	2.326	**0.0237**	Residual
Residual	4232.460	108	39.189			
Total	22093.108	134				

5.3.2.2 Grazer effects

The initial goal of the experiment was to compare the effect of grazer exclusion on perennial and ephemeral algal growth, carrying out separate analyses for each of the major species found (*Mastocarpus stellatus*, *Laurencia pinnatifida*, *Corallina mediterranea*, *Ceramium* spp., *Porphyra* spp. and *Ulva/Enteromorpha* (hereafter referred as ephemeral green algae). However, both the successional pathways and the final species composition differed drastically between shores and starting dates. The effects of grazer exclusion were also quantitatively different for each situation, ranging from insignificant ephemeral algal growth to almost 70% cover of perennial algae.

As mentioned earlier, fences were not able to exclude trochids, and the rate of damage (either by humans or by the sea) implies that exclusion of limpets was never total. Moreover, a considerable number of small limpets (<0.5 cm) were always found within fences, even when these were untouched. Their effect may not have been as strong as that of adults, but it should not be disregarded. Nevertheless, the differences observed while monitoring the experiments suggest that at least a significant reduction of grazing pressure was achieved. It was decided to analyse differences in total algal growth rather than in different species, and to interpret the results carefully.

Table 5.4 depicts the results of the ANOVA for the limpet exclusion experiments. Homoscedasticity was achieved after $log_e(X+1)$ transformation (Cochran's C test=0.16, $P_{(v=4,k=27)} > 0.05$). The significant S×D×T interaction suggested that differences between treatments were not consistent among shores and starting dates, and SNK tests were computed separately for the fixed factor (treatments) in each

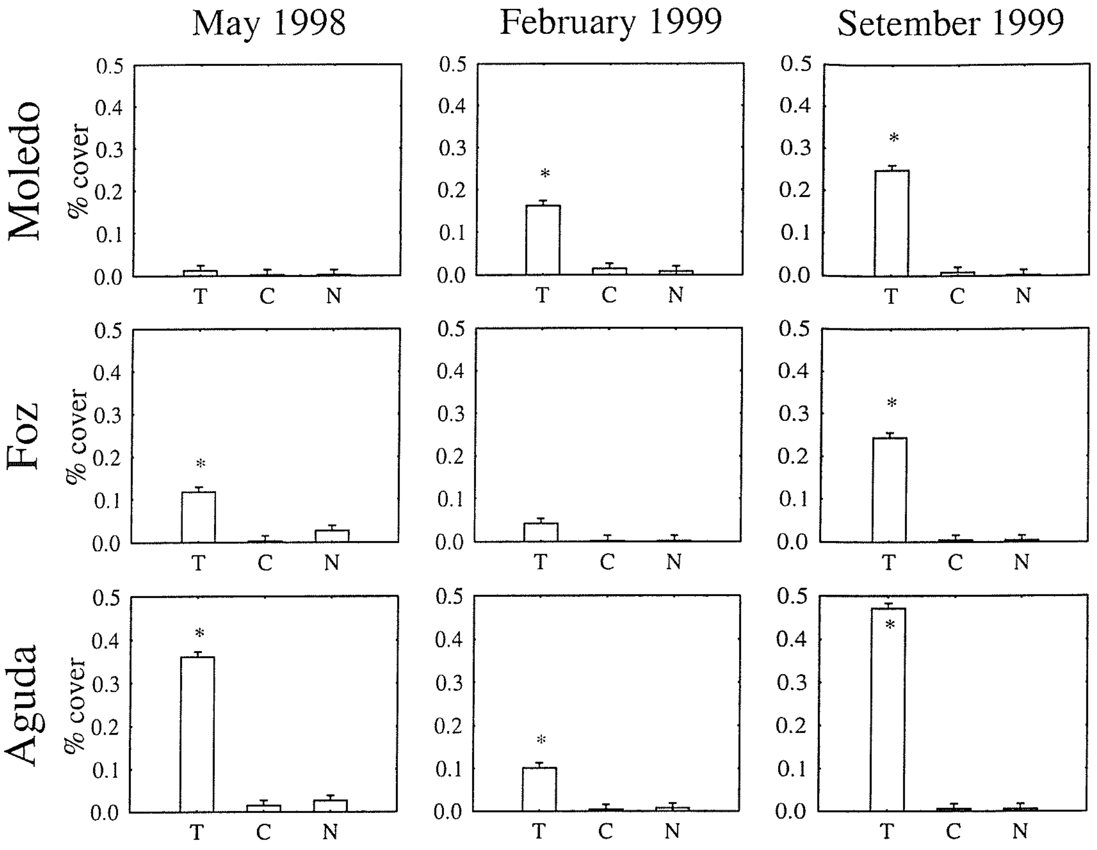


Figure 5.6: Multiple comparisons (SNK tests) after analysis of variance in Table 5.4. Graphics compare average percentage cover of algae between three treatments (T - exclusion: C - fenced; U - unfenced controls) for three different shores, and at three different starting dates. Statistically significant differences are marked with *.

combination of shores/starting dates (Underwood, 1997).

Multiple comparisons (figure 5.6) showed that in seven out of nine cases the effect of grazer exclusion was similar, producing a significant increase in total algal growth where limpets were excluded. This pattern was not observed in the first experiment at Moledo do Minho, and in the second experiment at Foz do Douro. While in the former there was no algal growth in limpet exclusion areas, at Foz do Douro algae grew on some of the five exclusion areas but were totally absent in the remainders. SNK tests were not able to detect differences in these cases, most probably due to the small number of replicates. Overall, results showed that the effect of limpets was significant, preventing most algae from growing in the midshore among mussels, independently of the time of exclusion.

A detailed inspection of the variation of algal growth after limpet removal

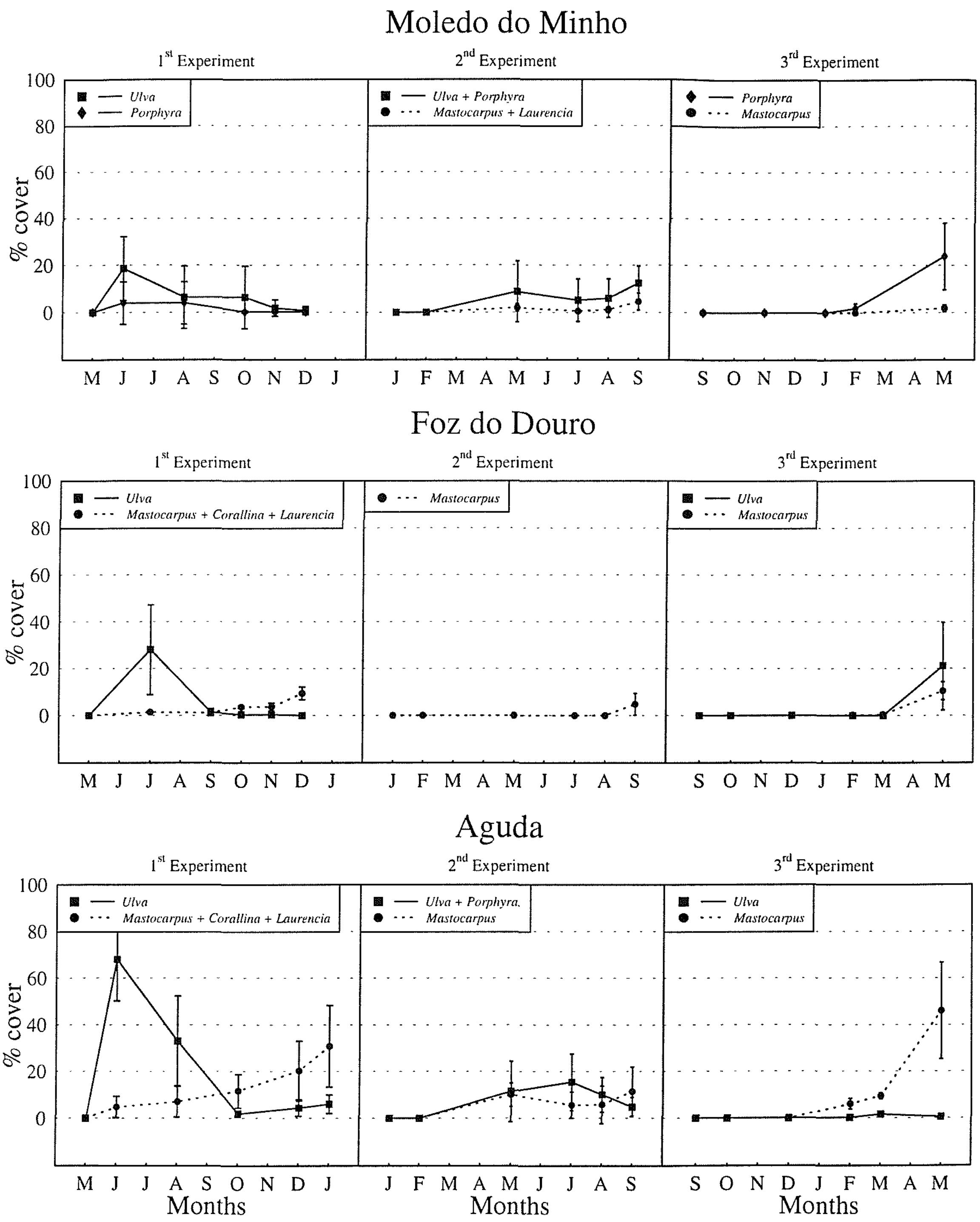


Figure 5.7: Variation in percentage cover of major algal species after limpet exclusion in three shores and three different starting dates. For the sake of simplicity, only the data for exclusion areas is shown. The growth of algae in fenced and unfenced controls was always <10%, and in most cases <5%.

showed that the patterns of succession were far more complex than expected (figure 5.7). Of the three shores considered, Aguda showed the most consistent results, independently of starting date: in all three experiments the final result was a well grown layer of perennial algae, always with *Mastocarpus stellatus.* In the first and second experiments *Mastocarpus* reached an average of 11% cover, but while in the former other two other algal species appeared (*Laurencia* and *Corallina*), in the latter only *Mastocarpus* was present. The difference may have been related to the fact that the end of the second experiment coincided with the summer months, when both human activity and especially air temperatures were higher. In the third experiment the final average density of *Mastocarpus* alone was about 45%, leaving only mussels and a small percentage of barnacles uncovered.

At Foz do Douro, apart from the second experiment where insignificant algal growth was observed, the exclusion of limpets had almost the same qualitative effect as in Aguda. Again, *Mastocarpus* was the major perennial species fixed in exclusion areas, reaching 10% in the third experiment. In the first experiment it reached 5%, while *Corallina* and *Laurencia* had a final percentage cover of 2.5% each. However, at the end of this experiment there was a considerable growth of both *Laurencia* and *Corallina* in unfenced controls at levels little different from the exclusions.

At Moledo do Minho differences in limpet exclusion areas were only observed in the last two experiments. However, instead of perennial algae, the most abundant algal species in the end of the experiments were ephemeral ones, especially *Porphyra* (with a final average percentage cover of 12% and 23% , respectively). *Mastocarpus* never reached more than 4%, and *Laurencia* only reached 1%. Another interesting observation is that, contrasting with perennial algae and ephemeral green algae, *Porphyra* grew preferentially over mussels and not on bare rock or dead barnacles. Given that *Porphyra* mats were rare or absent in fenced and unfenced controls, the result suggests that the effect of small limpets, which are the major grazers that wander over mussels, may have a stronger effect on algal growth than previously expected.

An interesting phenomenon was the development of green algal cover during the first stages of succession in the first experiment, which was more evident at Aguda (were in some cases green algae covered almost all exclusion areas), but also quite visible at Foz do Douro and Moledo do Minho. This ephemeral algal growth was not observed in the other experiments, which can be explained by the difference in starting dates. According to Ardré (1971) the emission of zooids by most of the species of ephemeral green algae was observed all year round, but was highest during the spring and autumn. Thus, when limpets are excluded in early spring these algae have a superb opportunity to settle and grow, and ultimately to monopolize all the available space.

5.4 Discussion

Patterns of succession observed after rock surface clearings followed roughly the trends of those described in the literature for similar assemblages (Dayton, 1971; Paine and Levin, 1981; Sousa, 1984b; Tokeshi and Romero, 1995; Berlow, 1997). Although the experiments were carried out during a short period of time, when compared to other published data (e.g., Paine, 1974; Berlow, 1997), their results suggest that recovery might be faster than expected. Patterns of succession differed slightly with patch size and position. In the lower zone of the mussel belt total recovery was practically attained at both studied sites, whilst in the upper zone it was far from being complete by the end of the study. Such difference is obviously related with two factors: lower availability of recruits in the upper zones, where mussel densities are smaller, and physical constraints, which are thought to set the upper limit of the mussel belt (Seed, 1969a,b). On the other hand, larger cleared areas displayed a considerable ephemeral algal growth right after denudation, contrasting with smaller areas where the first colonizers were barnacles. In mussel assemblages, initial patterns of colonization depend on area size and season of creation (Paine and Levin, 1981). The growth of ephemeral algae in larger denuded areas is attributable to a decrease in grazer pressure after clearing, and a slower recovery of grazers in these areas (Sousa, 1984c,b).

After the development of a thin coat of diatoms, followed in some cases by the growth of ephemeral green algae, the next colonizers were always the barnacles (mainly *C. montagui*, but also some *C. stellatus*). Because during the course of this study barnacle settlement was always high, most of the cleared areas were partially or even completely covered by barnacles by the end of the clearing experiments. Barnacles were previously shown to enhance mussel fixation (Petraitis, 1990). During this study it was demonstrated that a barnacle cover enhanced both direct settlement and lateral invasion of mussels from the margin of established patches. Field observations showed that empty barnacle shells provided a shelter for very small mussels that settled within or between them, either as isolated individuals or forming small clusters. These clusters of mussels, which seldom reached more than 1 cm^2, were formed by only a few individuals weakly connected, but their importance as precursors of new and well established patches is unknown. During the course of the experiment, none of these small patches lasted more than a couple of months, but it was possible to perceive a high individual mobility, either within each plot, or from them to the nearby mussel patches (Paine, 1974).

Direct fixation of mussels in cleared surfaces was seldom observed. Conversely, lateral invasion from nearby patches was also observed in cleared surfaces, but was significantly smaller than in areas where barnacles were present. Surface rugosity was not analysed during this study, although it is known to enhance mussel fixation (Petraitis, 1990). However, because on the northern Portuguese shores the most common substrate consists of smooth, or partially smooth, granite surfaces with few crevices and fissures, this factor was not considered in these preliminary experiments.

Limpets play an important role in the structure of the community. Although total exclusion was not attained during the experiments, the effects of a reduced grazing pressure were evident in most of the cases. The succession of species within exclusion areas was similar, but less complex, than that described by Sousa (1984b) for a comparable assemblage on the Pacific coast of North America. Furthermore, succession of species was faster than in that work, where ephemeral green algae dominated at least during a full year, and later colonists only appeared after 7–11 months and attained dominance three years later. In the present study, later colonists were always red seaweed, and no *Fucus* species were observed in exclusion plots. *Mastocarpus* was the most important perennial algal species developing after limpet exclusion, although at Foz do Douro and Moledo do Minho it has never attained a significant percentage cover as it did in Aguda.

Variability in the final outcome of the experiments was probably a consequence of their short duration, but also of different local settings and historical effects (Berlow, 1997). In Foz do Douro the small development of *Mastocarpus* might have been the result of a lack of propagules, since the species was restricted to a few individuals in the lower shore, but in Moledo do Minho it was very abundant in the lower eulittoral, often blanketing considerable portions of the rock surface. The failure of *Mastocarpus* to colonize the midshore zones at Moledo do Minho must be explained by other factors such as physical constraints. During this study, it was observed that, in Moledo do Minho, wave action alone was able to turn and drag very large boulders ($>1\ m^3$). Since the rock surface is particularly smooth in this shore, drag might be much higher than in shores where the surface is more broken, and may inhibit the settlement of some algal sporelings (Vadas *et al.*, 1990; Blanchette, 1997).

Either ephemeral and perennial algae that appeared after limpet exclusion settled over barnacles or denuded rock surface, with the exception of *Porphyra* which was observed to form a dense mat over mussels in Moledo do Minho. By the end of the experiments mussel density remained the same, even when they were covered by *Porphyra*, which suggests that there are no short–term effects of algae over mussels. However, in the longer term these algal mats might interfere with mussel feeding and growth and promote patch loss (Dittman and Robles, 1991). On the other hand, the results of these experiments also suggested that limpets might enhance indirectly the development of mussel patches by facilitating barnacle settlement (Hawkins, 1983). Limpets prevented ephemeral algae from monopolizing the space during late spring and early summer, which is exactly when barnacle settlement occurs. The enhancement of barnacle settlement by limpets was previously demonstrated in similar assemblages (Hawkins, 1983; Petraitis, 1983) or lower on the shore (Underwood *et al.*, 1983), but a formal test should be carried out in Portuguese shores.

Mastocarpus dominance was observed to last beyond the end of the experiments and the removal of fences. In many cases, the few fronds developed in exclusion plots survived for a couple of months, after which they became dry and wizened, disappearing during the harsher winter months. An interesting observation was that the higher the density of *Mastocarpus* the more time they survived after removal of fences. At Aguda, at the end of the third experiment (May 2000), the plots were scraped to analyse differences in species diversity caused by the changes in community structure after limpet exclusion. However, the holdfasts of *Mastocarpus* remained and two months later a new and dense canopy of this seaweed was present in every plot. By this time, limpet density was already at 'normal' levels due to the removal of fences. Thus, the susceptibility of *Mastocarpus* to physical conditions may depend on its density, which in turn affects their capacity to retain moisture and to stand drag caused by wave action (Blanchette, 1997). It seems that, after reaching an 'escape–size' (Hawkins and Hartnoll, 1983b; Hartnoll and Hawkins, 1985), which may just be the presence of a well developed holdfast, the canopy of *Mastocarpus* might last for a long period of time, probably interfering with the dynamics of the mussel/barnacle patches.

The effect of littorinids and trochids on macroalgae growth was not analysed. The high cost/benefit ratio to maintain and effectively exclude these grazers made it impracticable to carry on with such experiments. The succession patterns observed during the first experiment suggested that the effects of trochids and littorinids were at least buffered by those of limpets, since in the plots where limpets had been excluded, but where trochids and littorinids were present, a green algal mat developed like in the plots where all grazers had been removed. Littorinids prefer ephemeral green algae (Lubchenco, 1978; Hawkins and Hartnoll, 1983b; Petraitis, 1983) while trochids, such as *Gibbula*, feed on perennial red and brown algae. *Gibbula umbilicalis*, in particular, was found feeding on *Mastocarpus* fronds. Apart from some observations after the massive kills of trochids as a consequence of large oil spills (see Hawkins and Hartnoll, 1983b, for a review) no direct manipulations of *Gibbula* were made. Therefore, their role in later stages of succession should be investigated in detail.

The effect of dog–whelks on mussels was also not analysed due to logistic constraints. Nevertheless, the premise that dog–whelks regulate the density of mussels is based in two assumptions (Menge, 1976): *Nucella* is the only predator found in large enough densities to control mussel abundance and mussels are the preferred prey of dog–whelks. The validity of the first assumption has already been questioned (Edwards *et al.*, 1982), and the basis of the second assumption has never been seriously evaluated (Petraitis, 1990). The idea that dog–whelks prefer mussels over all other prey species comes from both laboratory and field observations (see Crothers, 1985, for a review), but most studies failed to correct for bias caused by different handling times (Fairweather and Underwood, 1983). In a recent work, Petraitis (1990) concluded that the predatory activity of *Nucella* was not enough to provide direct regulation of the distribution and abundance of *M. edulis* in the eastern coast of North America.

On the northern Portuguese shores dog–whelks are relatively common, but they were seldom found in densities equivalent to those observed by Connell (1961a), Petraitis (1987) or Berlow (1997). Their abundance is proportional to mussel density, and in shores like Cabo do Mundo, where mussels cover more than 50% of the rock surface, dog–whelks could reach more than 100 individuals per square metre, although their distribution in the shore was patchy (Santos, 1997). In all shores, it was common to find at least one or two adult dog–whelks in medium sized patches of mussels ($\simeq$ 400 cm^2). Their effect over these patches is obviously dependent on the time they spent in each patch or on the rate of movement between patches, a question that should be investigated in detail. Most of the dog–whelks that were found feeding, were doing so on mussels rather than on barnacles. Even considering that handling times are very different for the two prey species (Petraitis, 1990), field observations suggest that mussels should be a better choice when their abundance is high, because on the northern Portuguese shores barnacle species grow packed in a thin layer, never reaching the size of their conspecifics in other latitudes. Other putative predators, such as birds (gulls), crabs and starfishes are rare, but the effect of fishes (especially blennids and labrids) on mussels, should not be disregarded.

These results, coupled with those from the analysis of succession patterns, reinforce the idea that barnacles play an important role in the patch dynamics of mussel assemblages (Sousa, 1984b). Mussel recovery after disturbance seems to be highly dependent on barnacle cover and, as a consequence, it will depend on the successful recruitment of barnacles during the summer months. The recolonization of denuded space, either by direct fixation or by lateral invasion, will always be slower until the next barnacle settlement and subsequent growth. Therefore, the time of disturbance occurrence will obviously set the speed of recovery of the system (Sousa, 1984c; Berlow, 1997).

5.5 Conclusions

The following conclusions can be drawn from the previous results:

- Succession after disturbance varies with patch size and position within a shore.
- Patterns of succession are similar, but less complex, than those found in comparable assemblages.
- Grazers seem to play an important role in community structure, preventing algae from developing in the mussel zone. Their indirect effects on mussel fixation, growth and survival, either by enhancing barnacle settlement or by preventing epiphytes from growing over mussels should be investigated in detail.
- Barnacles enhance mussel fixation and seem to play an important role in the patch dynamics of the mussel assemblage.

Chapter 6

Oil Spill Impact Assessment

6.1 Introduction

The detection of human influences on the abundance of populations involves many problems, but two are paramount in designing sampling programmes: spatial and temporal variability and their interaction (Underwood, 1991, 1992, 1993, 1994). At any single location there is a considerable small–scale spatial variability which must be overcome by adequate sampling effort, use of correct size of sampling units and appropriate transformations to homogenize variances. On larger scales, there is variation from place to place in response to deterministic factors, such as environmental gradients or biological interactions, and stochastic events such as recruitment variability. Small–scale patterns of variability also differ from place to place. These factors can be overcome by hierarchical designs (Underwood, 1997).

Temporal variability, which is essential to measure when trying to detect impacts of human activities, also presents challenges. Many natural populations display complex temporal variability patterns, so that their abundances are very noisy (Underwood, 1991). This problem is complicated since natural populations also display a marked lack of concordance in their temporal trajectories from one place to another, even when closely adjacent. This results in considerable statistical interaction between changes in mean abundance from time to time and differences from place to place (Underwood, 1994). Therefore, the principal challenge posed in field assessments of environmental impacts is to isolate the effect of interest from the noise introduced by natural variability. If the magnitude of an impact is small relative to natural variability, it will be difficult to detect with any degree of confidence. Thus, it is imperative to use suitable analyses as well as to consider statistical power in planning and interpreting environmental impact assessment studies.

The rationale behind the analyses used to detect environmental impacts has been the subject of considerable discussion. According to Underwood (1991) much, if not all, of the focus of monitoring in most habitats is on the detection of changes in the mean abundance, size or diversity of species. Yet, sampling designs used to detect such changes are often oversimplistic and based in poor logic. Most studies lack any kind of replication, whether spatial or temporal, and conclusions have often been drawn on the basis of subjective interpretation rather than by using proper data sets and statistical techniques.

Before–After–Control–Impact (BACI) designs were introduced by Green (1979) in the first attempt to solve the logical problems inherent to these kind of analyses. The BACI design included both spatial and temporal measurements of variability: one sample was taken before and after the putative impact, at an impacted site and at an undisturbed (control) site. The model, itself, was a simple two–way crossed ANOVA, and the focus of the analysis was on the interaction between the two factors: an impact was expected to change the pattern of variability in the affected site, thus causing a statistically significant interaction. Unfortunately, the BACI design is compromised due to the lack of replication of sampling times and sites (Hurlbert, 1984; Underwood, 1994). Any difference from before to after the potential disturbance is very likely to occur between two times of sampling in two different sites, thus causing the interaction to be significant, and may not be related to any kind of human activity.

Bernstein and Zalinski (1983) and Stewart-Oaten *et al.* (1986) improved the BACI design by adding appropriate temporal replication, and suggested a non regular frequency of sampling to avoid coincidences with natural cycles. But the so called BACIP (Before–After–Control–Impact–Paired) design still suffered from unreplicated spatial variability (Underwood, 1991, 1994). Stewart-Oaten *et al.* (1986) acknowledged the problem, and suggested that the model was still applicable if one condition was met: it was absolutely necessary that the temporal variation of density of species followed similar patterns at the control and impacted sites before the impact. According to Underwood (1994) this is not a wise assumption and will seldom be true for many natural populations.

The problem of spatial replication arises because in most cases it is impossible to 'replicate' the impact. An impact, such as an oil spill, can affect a considerable area, but sampling different sites within that area cannot be taken as spatial replication of that impact. Since the sites were affected by the same event, using them as independent measurements of an oil spill induced effect is nothing but pseudo–replication (Hurlbert, 1984). This problem was solved with the recent development of 'beyond BACI' designs (Underwood, 1991, 1992, 1993, 1994). Beyond BACI includes both replicated control sites as well as different sampling times. The analysis is said to be asymmetrical because the impacted site is not replicated. However, by doing a clever repartition of the variance components, and focusing on interactions, it is possible to detect unambiguously any impact that causes changes in the patterns of variability of populations, provided that such changes are bigger than the underlying natural variability (Underwood, 1993, 1994).

Beyond BACI can lead to significant advances in the detection of impacts associated with anthropogenic disturbance because it acknowledges the importance of spatial and temporal sampling designs, thus ensuring unconfounded detection of such impacts. However, and despite the logical robustness of this design, its use seems not to be widespread: in the last decade, and excluding the works of (Underwood, 1993, 1994), seven published papers addressed the use of beyond BACI for environmental impact detection, but only four of them effectively used the method (Gray *et al.*, 1996; Glasby, 1997; Roberts *et al.*, 1998; Lardicci *et al.*, 1999). The lack of employment of beyond BACI analysis as a method for detecting environmental impacts might be a consequence of its apparent complexity, of the inability to set up compatible sampling strategies, or both.

An important concept in statistical hypotheses testing is statistical power, which is the probability that a test will correctly detect an effect of a specified magnitude, provided that this effect exists. Since statistical hypotheses testing is often used in environmental monitoring and impact assessments to test some null hypothesis (e.g., that there is no effect of an oil spill on the average density of a marine species), power analysis should be used in the design of such analyses. There are several methods available to include statistical power analysis in the design of impact assessments or monitoring programmes, yet they are rarely used. Instead, designs are often based on historical precedents or other non-statistical criteria. As a result, statistical power is often low for environmental analyses, meaning that such studies have little chance of correctly detecting specified effects, even if they actually exist (Peterman, 1990).

Unfortunately, beyond BACI analyses are quite complex and rely on the outcome of many statistical tests which are performed in a stepwise manner. The computation of the power of each of these tests would be a laborious task. Moreover, there are serious problems in the computation of statistical power for tests involving interactions (Winer *et al.*, 1991). Statistical power is a function of α (probability of Type I error), number of replicates, sample variance and size of effect (also known as 'effect size'). The first two parameters are known and the third can be estimated from a previous analysis of variance, being equivalent to the error or residual terms. The effect size is usually unknown, but is defined as the amount of variation added to a given variance component as a result of an effect. In many situations, it is possible to estimate this amount for main factors before the analysis is actually done. However, if interactions are considered, there will be a range of possible effect sizes because in this case two or more factors are involved. The lack of a theoretical body that allows to anticipate the amount of variance added to an interaction term as a result of some impact (or effect) makes it impossible to use *a priori* statistical power analysis to improve beyond BACI designs (Underwood, 1994).

According to Peterman (1990), *a posteriori* power analysis should be done whenever a test fails to reject the null hypothesis. This is particularly important in environmental impact studies, because failing to detect an impact due to the low power of the analysis can lead to severe ecological consequences, since in these cases no mitigating measures will be considered. Therefore, caution must be taken when an impact is not detected by any statistical technique. In the case of beyond BACI designs, the problems described for *a priori* power analysis also apply to *a posterior* power analysis. Moreover, it is not feasible to calculate statistical power for each of the several tests involved in the analysis due to the complexity of the stepwise procedures used to detect the effects of an impact. It is more realistic to consider overall power, hereafter referred as *efficiency*, that is, the number of times a given model succeeds in detecting impacts when they occur. This approach can be accomplished in two different ways: a) by the use of re–sampling techniques using real data; b) by simulating populations with the same degree of variability as the ones studied, and then simulating impacts of known magnitude in an impacted population.

During this study, the sampling strategy was chosen to provide data for the analysis of variability of mussels, barnacles and limpets, and simultaneously to acquire data for before/after impact assessment on mussel assemblages. In this Chapter, beyond BACI analysis was used to detect the putative effects of a small oil spill that occurred in June 1998, affecting one of the studied shores (Cabo do Mundo). The origin of the oil spill is still unknown, but official sources estimated that the two tons of refined oil came from inland, probably caused by an illegal or accidental discharge in an untreated sewage effluent. The power of the analyses was tested using both bootstrapping and simulation techniques, since they give complementary information.

6.2 Material and methods

6.2.1 The model

Since most of the oil spills that occur on the northern Portuguese coast are small in extent, it was necessary to develop a specific beyond BACI model that anticipated the particular effects of such impacts. Small–scale oil spills seldom affect whole shores. Patchy oil deposition will most likely produce a differential mortality of organisms at the spatial scale, thus increasing the variance within the impacted site when compared to undisturbed sites. The model used in this work (Table 6.1) is derived from those proposed by Underwood (1993, 1994) but goes further by including an extra factor to account for spatial variability within each shore. This is achieved by nesting sites within locations. The interpretation of the results is straightforward, and is made according to the rules expressed in Table 6.2. The focus of the analysis is on the higher order interactions that measure the variability of the parameter being used (density, percentage cover) through time and space. An interaction will be statistically significant if the patterns of variability (e.g., the variation of the parameter with time) differ among the levels of a given spatial scale (sites or shores).

Small oil spills will decrease (or increase) the mean density of species in the impacted shore. If the effect of the impact is not sustained and the affected species recover rapidly after the disturbance, the impact is called a 'pulse impact' (Bender *et al.*, 1984; Underwood, 1991, 1992). Pulse impacts alter the normal pattern of variability over short periods of time, and may be detected as a significant T(Aft)×I interaction in the analysis. In the present model, the smallest scale of analysis measures the variability among sites, which are nested within shores. A small and patchy oil spill will decrease the density of some populations in some of the sites within the impacted shore, leaving the others untouched. This effect will produce a different pattern of variability in some sites within the impacted shore, and will come out as a significant T(Aft)×Si(I) interaction.

For the impact to be unambiguously detected several other conditions must apply. First, the patterns of variability in the sites of the impacted shore should be similar before the impact (that is T(Bef)×Si(I)/Residual should not be significant). If they are different, which is most probably the case for natural and variable populations, there should be a statistical difference between the patterns of variation before and after the impact. Because there is no way to know if an impact will increase or decrease the variability of populations, differences between T(Aft)×Si(I) and T(Bef)×Si(I) should be tested with a two–tailed test. Second, there must be no difference in the patterns of

Table 6.1: General beyond BACI model used in the present study. B=Before vs After; I=Impacted; C=Control; Sh=Shores; Si=Sites; T=Times (Sampling times). Repartitioned sources of variance are depicted in bold.

Source of variation	df	Estimates
B	1	Before *vs* After impact (Not used)
L	$l-1$	Differences between locations (Not used)
I vs C	1	Differences between impacted and control locations
Among C	$l-2$	Differences among control locations
B×L	$l-1$	-
B×I	1	Variability patterns of impacted location from before to after
B×C	$l-2$	Variability patterns of control locations from before to after
Si(L)	$l(s-1)$	Differences between sites within locations (Not used)
Si(I)	$s-1$	Variability between sites of impacted location
Si(C)	$(l-1)(s-1)$	Variability between sites of control locations
B×Si(L)	$l(s-1)$	-
B×Si(I)	$s-1$	Variability patterns of sites in impacted location from before to after
B×Si(C)	$(l-1)(s-1)$	Variability patterns of sites in control locations from before to after
T(B)	$2(t-1)$	Differences between sampling times (Not used)
T(B)×L	$2(t-1)(l-1)$	-
T(B)×I	$2(t-1)$	-
T(Bef)×I	$(t-1)$	Variability patterns of impacted location before the impact
T(Aft)×I	$(t-1)$	Variability patterns of impacted location after the impact
T(B)×C	$2(t-1)(l-2)$	-
T(Bef)×C	$(t-1)(l-2)$	Variability patterns of control locations before the impact
T(Aft)×C	$(t-1)(l-2)$	Variability patterns of control locations after the impact
T(B)×Si(L)	$2l(t-1)(s-1)$	-
T(B)×Si(I)	$2(t-1)(s-1)$	-
T(Bef)×Si(I)	$(t-1)(s-1)$	Variability patterns of sites in impacted location before the impact
T(Aft)×Si(I)	$(t-1)(s-1)$	Variability patterns of sites in impacted location after the impact
T(B)×Si(C)	$2(t-1)(l-2)(s-1)$	-
T(Bef)×Si(C)	$(t-1)(l-2)(s-1)$	Variability patterns of sites in control locations before the impact
T(Aft)×Si(C)	$(t-1)(l-2)(s-1)$	Variability patterns of sites in control locations after the impact
Residual	$2tsl(n-1)$	-
Total	$2tsln-1$	-

Table 6.2: Rules used for the interpretation of the results obtained using the beyond BACI model depicted in Table 6.1.

1 An impact, at the smallest possible scale, will be detected as a different pattern of variability among sampling times before and after the impact, in the impacted shore.
T(Aft)×Si(I)/Resid. IS significant
T(Bef)×Si(I)/Resid. NOT significant
OR If significant **T(Aft)×Si(I)≠T(Bef)×Si(I) (2-tailed test)**
AND **T(Aft)×Si(C)/Resid. NOT significant**
OR If significant **T(Aft)×Si(C)=(Bef)×Si(C)**

2 If ALL the above interactions are NOT significant
2a An impact at the next scale up on time would be detected if:
B×Si(I)/T(B)×Si(I) IS significant
B×Si(C)/T(B)×Si(C) NOT significant
OR If significant **B×Si(I)≠B×Si(C)**

2b An impact at the next scale up on space would be detected if:
T(Aft)×I/T(B)×Si(Sh) IS significant
T(Bef)×I/T(B)×Si(Sh) NOT significant
OR If significant **T(Aft)×I≠T(Bef)×I (2-tailed test)**
AND **T(Aft)×I≠T(Aft)×C (2-tailed test)**
AND **T(Bef)×I=T(Bef)×C (2-tailed test)**

3 If ALL the above tests are NOT significant, an impact at the next spatial scale will be detected as a difference between B×I and B×C. These tests depend on being able to pool (i) T(B)×Sh, (ii) B×Si(Sh) or (iii) BOTH. Therefore:
B×I/B×Si(Sh) (i), /T(B)×Sh (ii), or /T(B)×Si(Sh) (iii) IS significant
B×C/T(B)×Sh (i), B×Si(Sh) (ii) or T(B)×Si(Sh) (iii) NOT significant
OR If significant **B×I≠B×C (2-tailed test)**

4 If ALL tests above are NOT significant, a small–scale impact (patchy) will increase the variability in the impacted shore and will be detected if **Si(I)≠Si(C) (2-tailed test)**

variability among the sites of the control shores. This is measured by the interactions T(Bef)×Si(C) and T(Aft)×Si(C), for before and after the impact respectively, and if both interactions are significant they should be similar.

If the oil spill affects the whole 'impacted' shore, decreasing species density evenly, there will be no differences in the patterns of variability among the sites of the impacted shore (T(Aft)×Si(I) will not be significant). In this case, if the patterns of variation among all shores are similar (T(B)×Si(Sh) is not significant) then it is possible to proceed with the analysis at a higher spatial or temporal scale. At the next spatial scale, an impact should be detected if it causes a change in the average patterns of variability in the impacted shore. Therefore, T(Aft)×I should be significant and T(Bef)×I should be not significant. Again, if there are interactions before the impact (T(Bef)×I is significant) then T(Aft)×I should differ and be bigger than T(Bef)×I. Moreover, the patterns of variability after the impact should differ between the impacted and control sites (T(Aft)×C should be different from T(Aft)×I), but must be similar before the impact (T(Bef)×C/T(Bef)×I should not be significant).

At the next temporal scale, an impact should cause a change in the patterns of variability of the impacted sites from before to after. This is measured by B×Si(I), and this interaction must be significant. In the control sites, the pattern of variability from before to after should be non–significant or, if significant, B×Si(C) should be different and smaller than B×Si(I). If none of these interactions are significant the analysis proceeds at the largest spatiotemporal level, using the average variation from before to after the impact on the impacted and control shores. B×I should be significant, meaning that a change occurred from before to after the impact in the impacted shore, and B×C should be non-significant or, if significant, it should be different and smaller than B×I. It is worth noticing that the tests of B×I and B×C depend on being able to pool T(B)×Sh, B×si(Sh) or both (Underwood, 1997).

If all tests fail to detect the effect of an impact, and no interactions are significant, the hypothesis that an impact increases (or decreases) the variance in the impacted site could be tested. In the present study a small–scale oil spill would increase the variance within the impacted shore, because by being patchy it would cause differential mortality at a small spatial scale. If this is true, the two–tailed test Si(I)/Si(C) should be significant because the variation in the impacted site must be bigger than in the control sites.

6.2.2 Data acquisition

The five sampling times before and after the impact were selected randomly from the data sets presented in Chapter 3. Since on some of the dates it was impossible to sample all the four shores, and the analysis requires samples taken at the same times, there were 21 sampling times left to use in the analysis (ten before and eleven after the impact). The random selection of five out of ten (or eleven) samples allowed for gaps of more than one month between consecutive samples, thus decreasing the probability of non–independent estimates of percentage cover of mussels and density of limpets. Non–independence of data is probably the most important problem of any experimental design. It brings up positive or negative correlation among estimates, and invalidates most of the statistical tests performed over the data (Winer *et al.*, 1991; Underwood, 1981).

This problem was addressed in Chapter 3, and the same considerations are applied here. The sampled sites (within each shore) were large in extent, ranging from 150 m^2 to 600 m^2. At each sampling time ten quadrats (50×50 cm) were used to estimate percentage cover of mussels and density of limpets, thus covering an area of 2.5 m^2. This area is much smaller (less than 5%) than the smallest site (from the 16 used in all four shores), and the probability of sampling the same area covered by previous quadrats is also very small, even considering continuous sampling over time. Furthermore, this probability was subsequently reduced, since the selection of sampling times for the analysis was randomly made from a larger set, and most of the sampling times used were not consecutive. Nevertheless, if there is a considerable degree of non-independence between sampling times, it will increase the probability of Type I error, thus affecting the overall beyond BACI analysis by producing false significant interactions.

Another important aspect to be considered is homoscedasticity. Homogeneity of variances is one of the least important assumptions of ANOVA, and these analyses were shown to be quite robust to departures from that assumption (Underwood, 1981, 1997). Heterogeneity of variances can be a serious problem if the data are unbalanced (different number of replicates per level of treatment) and/or the number of replicates is small, which is not the case for the present analysis. Heterogeneity of variances can lead to excessive Type I error, thus increasing the number of significant tests, but it is not clear how it affects the overall beyond BACI analysis, because that depends on the outcome of several statistical tests. Given the stepwise nature of the tests, it is probable that in some cases heteroscedasticity can even improve the overall analysis. Beyond BACI models are designed in such a way that the probability of detecting impacts is increased. Repartitioned sources of variance are tested against non–repartitioned ones, when in fact there are no true tests for them (see Winer *et al.*, 1991; Underwood, 1997). When dealing with the detection of environmental impacts, otherwise inappropriate tests may be the most acceptable way of making a mistake because it may lead to the detection of an impact when, in fact, there was none (Underwood, 1991). This reasoning has been termed the *'precautionary principle'* (see Glasby, 1997) and it increases the likelihood that any mistakes that are made will favour the environment. To achieve homoscedasticity, data were transformed using *arcsine* transformation for percentage cover of mussels and *square root* transformation for limpet density (Underwood, 1997).

6.2.3 Power analyses

6.2.3.1 Bootstrap analysis

Bootstrapping (Efron, 1979) is a widely used re–sampling technique which was developed to compute confidence intervals for parameter estimates when the underlying distribution of the data is unknown. This technique can be easily applied to solve several other problems, namely to estimate the reliability of the results produced by complex analyses (e.g., Saitou and Nei, 1987). In the case of this study, the variable of interest is the efficiency of the beyond BACI model under the observed population variability. Thus, the main question is: *how likely is the beyond BACI model to detect impacts when the variability of the populations is similar to that observed during this study?* As shown earlier, the estimates of mussel and limpet abundance were quite variable within each site, shore and sampling time. This variability, which is measured by the interactions in the model, may cause the analysis to fail to detect an impact or, conversely, to detect impacts when none has occurred. Unfortunately, the distribution of these data values is unknown and difficult to model mathematically. The bootstrap method solves this problem by taking advantage of modern computing power: a 'bootstrap distribution' of values is built from the real data by replicating each individual value several times. The new data values, which to all intents and purposes have an 'infinite size', are then re–sampled (with replacement) and analysed repeatedly, producing multiple 'bootstrap estimates'. Provided that the real data sets are representative of the populations under study, the percentage of analyses that detected an impact will be a reasonable estimate of the overall efficiency (or power) of the model. Therefore, for each Site×Shore×Sampling combination a pool of 10,000 values was created, based on the ten estimates obtained in the field. These pools were then re–sampled (10 replicates) and a beyond BACI analysis was performed over these new data sets. The procedure was repeated 10,000 times and the results were expressed as percentage of impacts detected.

6.2.3.2 Simulation of impacts

Because simulation techniques are time consuming and computer intensive, only mussel percentage cover data were used in the simulations. Multiple sets of four populations were created by means of Monte–Carlo simulation, based on two parameters: within site variability (W) and between sampling times variability (S). The parameter W represents the average site variability (sites being nested in shores) per sampling time, and is estimated by the Mean Square (MS) of the Residual term in the beyond BACI model. To keep the number of simulations to a minimum this parameter was fixed and was set to the value of the Residual MS of the beyond BACI analysis for mussel percentage cover with untransformed data (W=0.008). The parameter S represents the variability of average percentage cover between sampling times, but it has no direct equivalent in the beyond BACI model. Therefore, the value of S regarding the actual mussel percentage cover data is unknown. Increasing S increases the differences of average percentage cover between sampling times, and results in very interactive populations, while decreasing S decreases the differences between sampling times and reduces the degree of interactions in the system.

A preliminary simulation, using different values of S, showed that the value of this parameter for the studied populations was around 0.0012. Because this approximation was estimated by comparing the shapes of the resulting graphs with those built from real data, 10 values of S were used in the simulations, ranging from 0.0004 to 0.0022 with steps of 0.0002. Since the true magnitude of the impact was also unknown, 10 levels of impact effect were used, ranging from zero (no impact) to a 90% decrease in population density. Ten thousand simulations were done for each combination of impact effect and S, and the results, expressed as percentage of detected impacts, were summarized in a contour plot.

6.3 Results

6.3.1 Beyond BACI analyses

The results of the beyond BACI analyses are depicted in Table 6.3 for both mussels and limpets. Homogeneity of variances was achieved for mussel percentage cover (Cochran's C=0.0214, $P_{(\mathrm{v}=9,k=160)} > 0.05$), and density of limpets (Cochran's C = 0.0215, $P_{(\mathrm{v}=9,k=160)} > 0.05$) after *arcsine* and *square root* transformation, respectively. In the case of mussel data, T(Bef)×Si(I) and T(Aft)×Si(I) were both significant, but not different from each other (F=0.30, P=0.97). This means that the patterns of mussel percentage cover variability were different from site to site within the impacted shore, but they were maintained from before to after the impact. The same applies to control shores, as T(Bef)×Si(C) and T(Aft)×Si(C) were significant, but not different from each other (F=0.80, P=0.66). Therefore, at the sites level, no differences were observed that could be attributable to a putative effect of the oil spill.

Figure 6.1 depicts the patterns of variability of mussel percentage cover on each site at the four shores studied. It is clear that these patterns were similar from

Table 6.3: Beyond BACI analysis of mussel percentage cover variation in four shores. B = Before vs After; I = Impacted; C = Control; Sh = Shores; Si = Sites; T = Times (Sampling Times). Significant terms are marked with *.

		Limpets			Mussels		
Source of variation	df	SS	MS	F	SS	MS	F
B	1	5320.51	5320.51		22.99	22.99	
Sh	3	14175.70	4725.23		22922.41	7640.81	
I vs C	1	10754.70	10754.70		9487.31	9487.31	
Among C	2	3421.00	1710.50		13435.10	6717.55	
B×Sh	3	89.46	29.82		1242.29	414.10	
B×I	1	49.29	49.29		11.49	11.49	
B×C	2	40.17	20.09		1230.80	615.40	
Si(Sh)	12	837.98	69.83		3254.51	271.21	
Si(I)	3	495.22	165.07		1973.04	657.68	
Si(C)	9	342.76	38.08		1281.47	142.39	
B×Si(Sh)	12	775.38	64.61		3235.59	269.63	
B×Si(I)	3	249.39	83.13		2950.30	983.43	
B×Si(C)	9	525.99	58.44		285.29	31.7	
T(B)	8	1035.84	129.48		13679.04	1709.88	
T(B)×Sh	24	1395.80	58.16		6683.33	278.47	
T(B)×I	8	600.03	75.00		1786.87	223.36	
T(Bef)×I	4	460.77	115.19		1499.42	374.86	
T(Aft)×I	4	139.26	34.81		287.45	71.86	
T(B)×C	16	795.77	49.74		4896.46	306.03	
T(Bef)×C	8	640.84	80.11		4357.80	544.73	
T(Aft)×C	8	154.93	19.37		538.66	67.33	
T(B)×Si(Sh)	96	2710.43	28.23	**5.51***	9777.24	101.85	**3.20***
T(B)×Si(I)	24	1214.36	50.60		3278.59	136.61	
T(Bef)×Si(I)	12	886.34	73.86	**14.42***	2524.71	210.39	**6.60***
T(Aft)×Si(I)	12	328.02	27.34	**5.33***	753.89	62.83	**1.97***
T(B)×Si(C)	72	1496.06	20.78		6498.65	90.26	
T(Bef)×Si(C)	36	212.79	5.91	1.15	3619.78	100.55	**2.16***
T(Aft)×Si(C)	36	1283.27	35.65	**6.96***	2878.87	79.97	**2.51***
Residual	1440	7377.74	5.12		45803.91	31.81	
Total	1599	33718.82			106621.31		

before to after the impact, both on the impacted and on the control shores. Patterns of variability were less interactive at Aguda and Viana do Castelo, while they differed more at Cabo do Mundo and Moledo do Minho. The next logical step was to proceed with the analysis at the shore level, but since the interaction T(B)×Si(Sh) was significant, no further tests were possible (Underwood, 1997).

In the case of limpets, patterns of variability on the impacted shore (T(Bef)×Si(I) and T(Aft)×Si(I)) were significant but not different from each other (F=0.394, P=0.94). In contrast, patterns of variability on the control shores were not significant before the impact ((Bef)×Si(C) non–significant), but were significant after the impact (T(Aft)×Si(C) was significant). These results are not straightforward since they

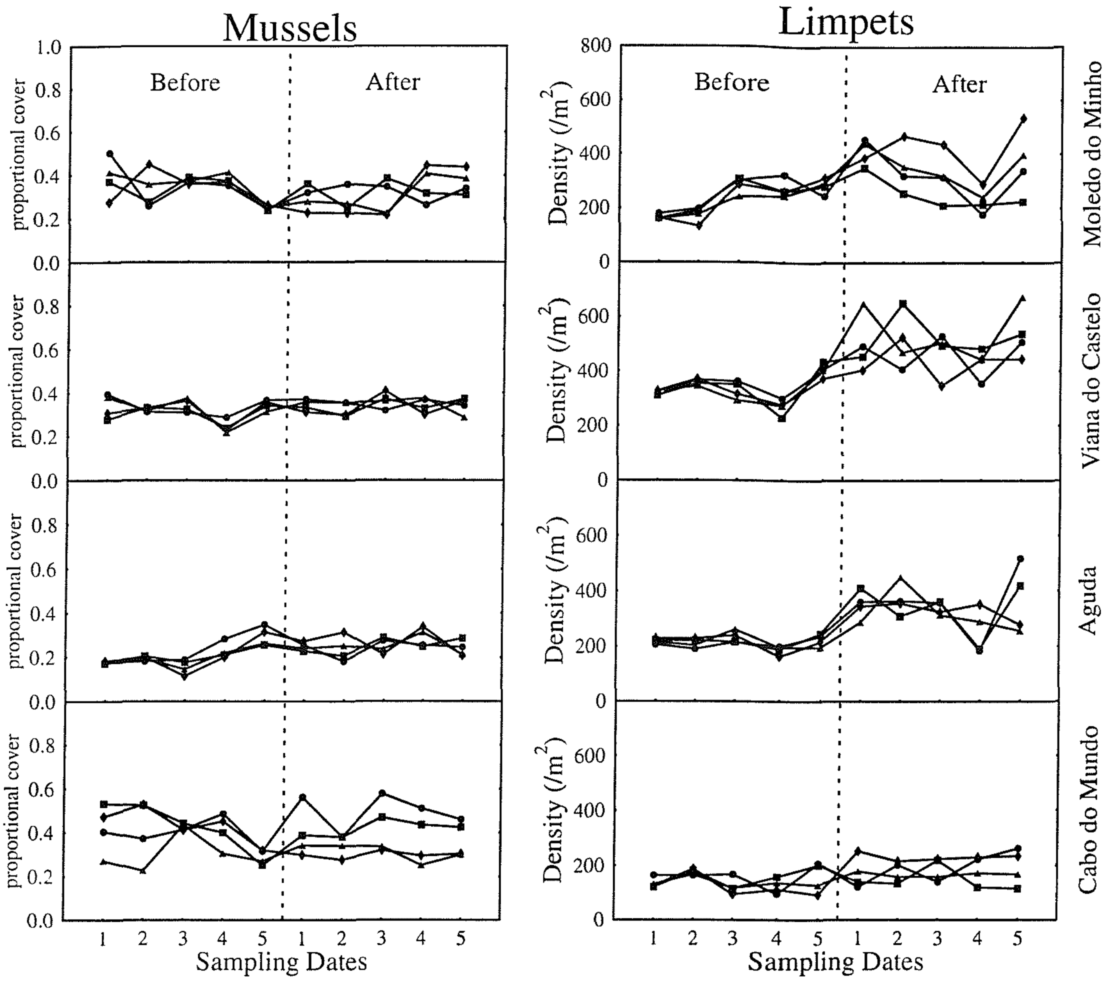


Figure 6.1: Patterns of variation of proportional cover of mussels and density of limpets on the shores studied. Cabo do Mundo was the impacted shore. Lines represent variation of average (n=10) percentage cover or density on each of the four sites sampled at each shore.

suggest that on the control shores the patterns of variability of limpets at the site level were similar before the impact, but changed drastically after it. In figure 6.1 it is possible to observe that at Cabo do Mundo (impacted shore) the patterns of variability were similar from before to after, in contrast with the control shores where there was a general increase in limpet density after the impact. These changes are obviously not impact–related, since the control shores are far away from the impact site (the nearest site, Aguda, is located 15 Km south). Moreover, changes in the patterns of variability of limpets were not observed on the impacted shore. Such a scenario could be a consequence of an impact if, for example, a widespread increase in limpet density was coincident with the oil spill, and the higher mortality of limpets in the impacted

Table 6.4: Bootstrap analyses of beyond BACI model for mussel and limpet data. The beyond BACI was carried out at different Type I errors to gain some insight into the effect of this on the outcome of the analyses.

	Type I error prob. (α)			
Species	0.05	0.1	0.2	0.3
Mussels	29.5%	32.1%	26.5%	21.2%
Limpets	3.3%	5.2%	6.7%	7.0%

shore would cancel the effect of such increase. For this to be true, the patterns of variability before the impact would have to be similar in both impacted and control shores, which was not the case, since T(Bef)×Si(I) is significantly different from T(Bef)×Si(C) (F=12.49, $p < 0.01$). Thus, the observed results are most probably related to the high variability of limpet data, rather than to an unlikely widespread increase in limpet density which was not observed on the impacted shore because of the effect of the oil spill. Once again, and according to the rules depicted in Table 6.2, no further tests were possible.

The results showed that the patterns of variability of both mussel percentage cover and density of limpets were very different at the smallest spatial and temporal scales and, as a consequence of this, no detectable effect of the oil spill was observed on the two species.

6.3.2 Power analysis

6.3.2.1 Bootstrap analysis

The results of the bootstrap analyses (Table 6.4) showed that the percentage of detected impacts was small, being higher for mussels than for limpets. In both cases, only homoscedastic data sets were analysed. In the case of mussels, the percentage of successful detections varied about 30%. Using an $\alpha = 0.1$ produced a slightly better result, but higher values of α decreased the efficiency of the model by 5–10%. In the case of limpets the detection rate was about 3%, and increased using higher Type I error probabilities, but never surpassed 10%.

6.3.2.2 Simulation analysis

The results of the simulation analysis are depicted in figure 6.2. The graph shows that overall efficiency is higher for a narrow range of S (0.0006–0.0009) and decreases for both very variable or unvariable populations. Another important aspect is that the

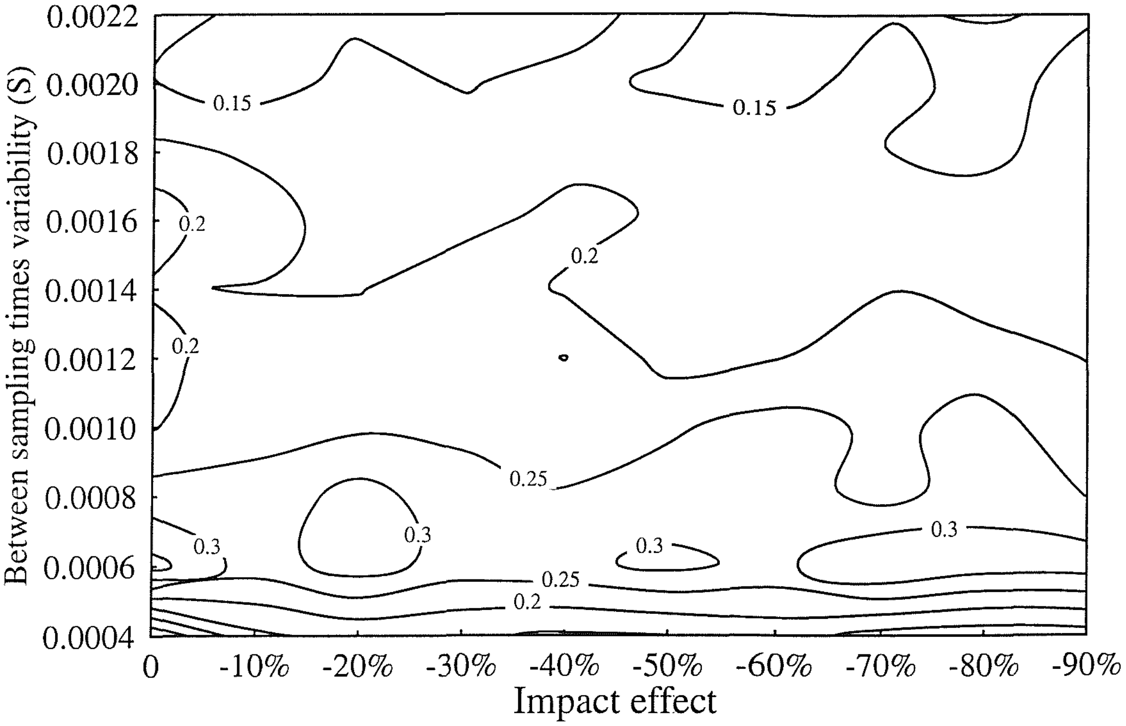


Figure 6.2: Efficiency of beyond BACI model for several magnitudes of impact and S (between sampling times variability), expressed as proportion of analyses that detected an impact.

magnitude of the impact does not seem to have any effect on the overall efficiency of the analysis. For a 50% reduction in percentage cover, the power of the model is still very low, although for some values of S it should be higher than 30%. These results are in agreement with those from the bootstrap analysis. If, as suggested earlier, the real value of S is around 0.0012, then the corresponding efficiency will vary around 20–25%, which is quite close to the bootstrap estimate of the efficiency for an $\alpha = 0.05$ (29.5%).

6.4 Discussion

The beyond BACI model developed in this study was not able to detect the effects of the oil spill that affected mussels and limpets on the shore of Cabo do Mundo. Both populations were shown to be very variable, either spatially (between sites within a shore) or temporally (between sampling times). It is noteworthy that, in the case of mussels, the patterns of variation were consistent over the period of time considered in the analysis (thus, from before to after the impact) in the control and impacted shores. This was not the case for limpets, but the differences between patterns of variation from before to after the impact in the control sites might have been caused by the nature of the data, as suggested before. Given that the apparent effects of the impact were observed directly in the field (mussel mortality), several reasons can be invoked to explain why the analyses failed to detect them. *A posteriori* power analyses have revealed that the beyond BACI model was not powerful enough in the present situation because the estimated power values, for both limpet and mussel data, were well below 40%. According to Peterman (1990) a test is considered to be powerful when it is able to reject a false null hypothesis in, at least, 80% of the cases. However, the lack of power may not be only a consequence of poor replication or an inadequate sampling design.

As suggested by the simulation of impacts, the power of the model is expected to be higher if the magnitude of the impact causes more than a 50% change in the populations being monitored. Moreover, the results of the simulation analysis should be viewed as a raw approximation of the efficiency of the beyond BACI model in real circumstances. The algorithm used to generate data sets did not account for heterogeneity between sites, sampling times and shores, that is, W and S were the same for all shores, and only average densities within shores were different. Heterogeneity will obviously increase the overall variability, producing very 'interactive populations' and reducing the efficiency of the analysis. On the other hand, impact effects were described as decreasing a population to some proportion of its natural abundance. Thus, impact effects were multiplicative rather than additive, and they should have been analysed by transforming data to logarithms (Underwood, 1992). However, this was not possible, since *arcsine* transformation of percentages was necessary to achieve homoscedasticity. Finally, a considerable number of undetected impacts was associated with cases where the 'impacted' population had a small percentage cover average (which was set randomly). Obviously, the effect of a 10% reduction in populations with 10% or 80% percentage cover would be very different, and this might have decreased the overall efficiency estimates, at least for higher impact effects.

The lack of power of environmental sampling programmes, and in particular those using BACI analyses, might be a major problem. However, according to Underwood (1994), highly interactive populations are characterized by large natural fluctuations from time to time and place to place. To persist at all, these populations must probably be resilient and able to recover from non–anthropogenic disturbances and natural fluctuations in recruitment and mortality. In such populations, for human impacts to be biologically meaningful, they must be very large, or they will not move the abundances out of their natural range of variation. Thus, the only effects of human disturbances that are going to matter are the very large ones. In the present study, field observations after the impact suggested that the effect of the impact was very small. Several empty mussel shells were observed piled on the strandline, but very few limpet shells were found. This can probably mean that the direct mortality caused by the oil deposition on the shore was higher for mussels than for limpets. No published evidence exists for the resistance of the two species to oil deposition, but this observation is supported by the results of the bootstrap analyses. Coincidentally, or not, the power of the model for the detection of the oil spill effects on limpets was much smaller than for mussels, which might be related to a lower mortality of the former species.

There were several ways to improve the beyond BACI model used (Underwood, 1992, 1993, 1994). Increasing the number of replicates per site might have reduced the variability within sites (W), and would provide a better estimate for the Residual MS. However, since this source of variance is always used as a denominator in the F tests, it would only increase the power of the individual tests, and consequently increase the probability of detecting significant interactions, either among controls and impacted sites. This is not important in the present situation, because most of the interactions were significant (with the exception of the T(Bef)×Si(C) for the limpets).

A better way to increase the efficiency of the model would be to use more sampling times before and after the impact, because in some cases the high variability between sampling times is associated with the low number of replicates. Decreasing this variability (S) is known to increase the power of the model (see figure 6.2), especially when the magnitude of the impact is considerable. The problem is that in many cases there is not much point in trying to decrease S because it is already a good estimate of the variability between sampling times (populations are very variable through time). The results presented in the previous chapters showed that, at least as far as mussels are concerned, there was a high degree of temporal (and spatial) variability. Furthermore, a large number of consecutive sampling times should be avoided because of non–independence of data (Underwood, 1992). In the present study, the number of sampling times was not a limiting factor. Several combinations of different numbers of sampling times were tried, but it was impossible to get homoscedastic data sets using more than five sampling times before and after the impact. Finally, the best way to increase the efficiency of any BACI model is to use a large number of control locations. Even when the populations are very interactive, a large number of locations will produce a better estimate of the patterns of variability at undisturbed locations, which will be contrasted against the impacted site. All these issues are obviously related with the cost–benefits of the monitoring programmes developed to assess human–induced impacts on natural populations. In the case of this study, the number of replicates used is well above that found in other studies (e.g., Glasby, 1997; Roberts *et al.*, 1998; Lardicci *et al.*, 1999), which does not imply that it was enough. The number of control sites (three) is close to the minimum acceptable, but for the amount of data to be collected, and given the logistic constraints common to many medium or long–term monitoring programs, it was almost impossible to have more than a few locations.

The failure to detect impact effects as a consequence of high population variability is not uncommon. Lardicci *et al.* (1999) analysed the influence of a coastal power station thermal discharge on spatial variability of meiobenthic and macrobenthic community abundance in the Gulf of Follonica (Western Mediterranean) using beyond BACI designs. The analysis showed that heated effluent seemed not to influence assemblage structure or the spatial distribution of the studied taxa. Abundance and variability of the benthic assemblages either did not exhibit significant differences between impact and control locations or the control locations were as different from each other as they were from the impacted location. The authors conclude that the assemblage abundances in the impacted location were within the range of spatial variability encountered naturally elsewhere. In the same manner, Glasby (1997) compared post–impact data for marinas and undisturbed locations in estuarine systems and found that for certain taxa there were differences between control locations and marinas. However, for most of the analysed species the large variability among controls masked any existing differences between them and the impacted sites, and the analyses failed to detect any effect of the human activity in marinas on the epibiotic fauna and flora.

As suggested by Underwood (*pers. comm.*), when a complex beyond BACI model is unable to detect an impact at the smallest scales because the populations being analysed are very interactive, the analysis should be carried out using a simpler model and omitting some spatial (or temporal) scales. This procedure was followed using the simplest beyond BACI model (Underwood, 1993) after excluding factor 'sites', and using 40 replicates per combination of Shore×Sampling Time but, once more, no impact was detected (results not shown here).

Contrasting with other works (Glasby, 1997; Roberts *et al.*, 1998; Lardicci *et al.*, 1999), in the present study the impact of the oil spill was only analysed for two important macrofaunal representatives: mussels and limpets. According to Underwood (1994), there is no reason to avoid the use of more than a few species when dealing with environmental impacts. The analyses of impact effects on several species or taxonomic groups is desirable, if not mandatory, because in most cases the nature of the impact might have a different effect on different organisms. Mussel assemblages are known to encompass a wide variety of smaller animals and plants (see Suchanek, 1985), which might be more sensitive to the physical and toxic effects of the deposited oil than the bigger species, that can stand very harsh conditions, at least for a considerable period of time.

In a different context, Osenberg *et al.* (1994) found that in long–term studies, both chemical–physical parameters and individual–based biological parameters (e.g., body size) were more consistent through time than population–based parameters (e.g., density). Overall, few of the population and chemical–physical parameters provided adequate power given the time constraints of most studies, and they advocate that a greater emphasis should be put on individual–based parameters. The work of Osenberg *et al.* (1994) was developed using a different variant of BACI (called BACIP) which does not explicitly account for interaction between populations (Underwood, 1992), but their findings may be also true for the beyond BACI analyses.

Probably, the best way to assess environmental impact changes is to use all the available techniques of analysis, as different approaches examine different components of the assemblages and are therefore more likely to detect any effects (Underwood and Peterson, 1988; Warwick, 1993). This approach was used successfully by Roberts *et al.* (1998), who were able to detect the effects of sewage outfalls on several sessile organisms, by using a combination of beyond BACI analyses (Underwood, 1992) and Multidimensional Scaling (Clarke and Warwick, 1994).

6.5 Conclusions

- No direct effects of the impact on mussel percentage cover or on limpet density were detected.

- The variability patterns of mussels and limpets in the impacted location were within the range of spatial and temporal variability found in undisturbed locations and, overall, were very large. These might have been responsible for the failure to detect the impact.

- The beyond BACI model used seems not to be very powerful, at least for small impact effects.
- Combined results of power analyses and field observations suggest that the mortality caused by the oil spill was very small when compared to the natural variability of the studied populations.

Chapter 7

General Discussion

7.1 Biogeography of northern Portuguese shores

The open nature of the Portuguese coast, where inlets and large estuaries are absent, allied to most of the sites facing westwards against the prevailing northwest swells, determines the exposed or moderately exposed nature of its rocky shores. Although subjected to intense human pressure, especially in the last five decades, the northern shores still retain many interesting features. The similarities between these shores and those of the northeast Spain (Niell, 1977; Anadón, 1981; Anadón and Niell, 1981; Fernández and Niell, 1981; Anadón, 1983; Bárbara and Cremades, 1993), the French Brittany (Fischer-Piétte, 1956) and the southwest of England (Crisp and Southward, 1958; Lewis, 1964) are striking when compared with the warm–temperate/subtropical shores of the southern Portuguese coast.

The main differences between northern and southern shores occur at the lower eulittoral level, as a consequence of the presence of large brown macrophytes (and also some red seaweed) that were absent from the south. These differences, which had been stressed earlier by Ardré (1970, 1971), have been accentuated since then because the southern borders of some northern species have shifted northwards. Shifts in species borders along the Iberian coast were observed previously by Fischer-Piétte (1956, 1957, 1958, 1960, 1963) and more recently by Arrontes (1993). However, the first attempt to link species distribution with climatic gradients along the Portuguese coast was made by Ardré (1971). The relation between shifts in marine species boundaries and climate change has been addressed recently in several works (e.g., Fields *et al.*, 1993; Barry *et al.*, 1995; Southward *et al.*, 1995; Sagarin *et al.*, 1999).

Most, if not all studies, predict poleward shifts in ranges of species in response to a putative warming trend. For example, Southward *et al.* (1995) found that in the

Table 7.1: Principal northward retreats and expansions of intertidal species observed by comparing the results of this work with early literature. Distances (in Km) are approximate.

NORTHWARD RETREATS				
Species	Previous limit	Reference	Actual limit	Dist.
Himanthalia elongata	S. M. do Porto	Ardré (1970)	Angeiras	200
Pelvetia canaliculata	Peniche	Rodrigues (1963)	Cabo do Mundo	250
Laminaria hyperborea	Baleal	Ardré (1970)	Figueira da Foz	100
Laminaria saccharina	Afife	Santos (1994)	?	-
NORTHWARD EXPANSIONS				
Species	Previous limit	Reference	Actual limit	Km
Siphonaria pectinata	Baleal	Nobre (1940)	Viana do Castelo	300
Onchidella celtica	Peniche	Nobre (1940)	Vila Chã	250

English Channel warm–water species increased in abundance and cold–water species declined during periods of ocean warming (1920–1960 and 1981–1995), whereas the opposite occurred during a colder period (1960–1981). In Southern California, Barry *et al.* (1995) compared two surveys conducted at the same intertidal site 60 years apart, and observed a general increase in southern invertebrate species and a decrease in northern species. Furthermore, northwards shifts have been documented for other animals, such as birds (Thomas and Lennon, 1999) and butterflies (Parmesan, 1996).

During the present study, northward retreats were observed for some intertidal species, but the number of expanding southern species was relatively small, contrasting, for example, with the findings of Sagarin *et al.* (1999), where almost half of the southern species found in a single site were local additions resulting from range expansions. The two southern species depicted in Table 7.1 were absent from the northern Portuguese coast in the early 1940s (Nobre, 1940), but could be found on the northeast Spanish coast (in the case of *Siphonaria*) or on the southwest coast of the United Kingdom (in the case of *Onchidella*). On the Portuguese coast, the main problem is that distributions of species were not well documented before the 1960s (Ardré, 1970), in the case of algae, or much later (e.g., Saldanha, 1974; Santos, 1994) in the case of marine invertebrates. On the other hand, the absence of quantitative information and the different taxonomic nomenclature used in earlier works add another level of confusion when comparisons are made with recent data. For example, the distribution of *Pelvetia canaliculata* during the 1950s and 1960s is still far from being clear, since Fischer-Piétte (1959) described its southern limit in Oporto (which is similar to its present situation) and a few years later Rodrigues (1963) and Ardré (1970) observed this species near Peniche, almost 200 Km south.

If small invertebrate species (amphipods, isopods, etc.) are considered, the number of northward extensions of southern species increases slightly (Santos, 1994). But there still remains the question of whether these species have actually extended their range northwards, when compared to the 1940s, or if they were just not recorded earlier.

As pointed out by Sagarin *et al.* (1999) there are several possible explanations for the differences found between sites when comparisons at large time scales are made. These include, among others, community shifts due to short–term population variations, changes in upwelling intensity, vertical shifts in intertidal distribution that can confound interpretation of geographic range shifts, anthropogenic changes, and, obviously, climate change. To assess whether shifts in ranges of species were caused by a general increase in average air and sea surface temperatures, or if they resulted from sporadic events or short–term climatic oscillations, it is necessary to rule out each of the competing hypotheses on the basis of strong climatic data and proper information about distribution of species and their life–history. Experimental work, like transplantation of northern organisms to southern sites where they existed before might give a clue about the factors that are operating at these large spatial scales (Hoffman and Blows, 1994).

7.2 Patch dynamics of the mussel/barnacle assemblage

Despite the outlined latitudinal changes in species composition, the northern Portuguese rocky shores can still be viewed as an homogeneous unit. Apart from the highly diversified lower eulittoral zone, mussels and barnacles dominate the midshore. Only in very particular situations do other conspicuous species occur. Therefore, the mussel/barnacle mosaic may be considered a general feature of exposed or moderately exposed northern Portuguese rocky shores. Further south mussels seldom dominate the eulittoral, being replaced either by barnacles or by *Pollicipes*. This might be better explained by differences in substrate type and topography, which might be unsuitable for mussel fixation and growth, associated with chance events (settlement, secondary recruitment), rather than by climatic differences between the northern and southern regions. The Portuguese coast is located in the centre of the distribution range of *M. galloprovincialis* and, even in the southernmost parts of Portugal, mussels can occasionally reach densities similar to those found in some of the northern sites.

On the northern Portuguese coast, the mussel/barnacle assemblage displayed highly variable patterns, both at the spatial and temporal scales. Unlike other similar assemblages, where the effects of disturbance by wave action were clearly seasonal

(Paine, 1974; Paine and Levin, 1981), the populations studied displayed no apparent seasonal patterns at the shore scale. Thus, the hypothesis that mussel abundance decreased during the winter months was rejected and an alternative model had to be proposed. The new model was based on the observation that space was freed during the winter and barnacle density decreased simultaneously, while mussel density remained constant. Since mussels are more easily dislodged by wave action than barnacles (Denny, 1983), the model predicts that mussel losses should be higher during the winter but are compensated by growth and/or secondary settlement over barnacles.

The analysis of the variation of mussel occupancy at the individual patch scale also revealed complex patterns, differing from shore to shore. However, when overall gains and losses were used some seasonal trends were discernible. At least on two shores the magnitude of gains and losses was clearly higher during the winter months, but even so the general patterns of variation were different among shores and years. The weight of these localized differences on the outcome of the statistical analyses was most probably a consequence of the short duration of the surveys. Overall, the limited time–scale of this study (three years) might not have been enough to observe medium or long–term cycles that probably occur. Disturbance during the winter may not be always effective in clearing space, as observed on some of the studied shores. Moreover, the cycles of *space creation* → *barnacle settlement* → *mussel settlement* may not be synchronized on all shores. It is essential to proceed with the survey of the dynamics of the mussel/barnacle assemblage if such cycles are to be studied. One important question is whether the sampling strategy used during this study should be maintained or modified. The present results showed that spatial variability was high at any spatial scale within all shores (from the patch scale to the shore scale) and differences between shores were almost always significant. Therefore, for monitoring purposes, subsequent sampling might be improved by reducing the number of sampled sites within shores – or even by eliminating this spatial scale – and by including more shores in the survey. The number of replicates (quadrats) can also be reduced to 20–30 per shore (see Hawkins *et al.*, 1986).

7.3 Succession and interactions among species

Any comparisons between the mussel assemblages on the northern Portuguese shores and those described in other studies (Seed, 1969a,b; Paine, 1974; Menge, 1976; Paine and Levin, 1981; Berlow, 1997) should be made with caution. In the Pacific coast

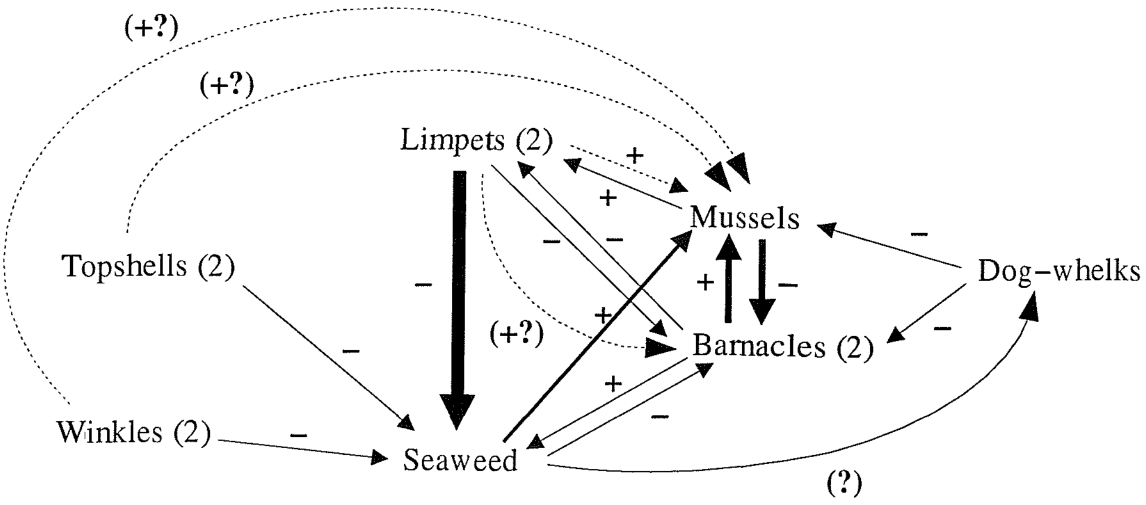


Figure 7.1: Web of putative interactions among species in northern Portuguese intertidal mussel assemblages, modified from figure 5.1. -/+ indicate negative or positive effects, respectively. Dotted lines indicate possible indirect interactions.

of the USA the main predators of mussels are starfishes (Paine, 1974, 1984) and mussels (*M. californianus*) often dominate the shore entirely. In the early stages of succession the most important competitors are *Pollicipes* and *Balanus*. On the Atlantic coast of the USA the main predators are dog-whelks (Menge, 1976, 1983, but see Edwards *et al.*, 1982) and mussels (*M. edulis*) seldom reach the densities found in the Pacific coast. On both coasts the major grazer species are restricted to littorinids and small acmaeid limpets. By contrast, in the northeast Atlantic mussels (*M. edulis* or *M. galloprovincialis*) form a mosaic with barnacles (*Chthamalus* and *Semibalanus*) and the main predators are dog-whelks (*Nucella lapillus*). Along with topshells and winkles, patellid limpets are very common and thought to be major structuring agents on these communities (Hawkins and Hartnoll, 1983b). Figure 7.1 depicts the possible interactions among species on the northern Portuguese rocky shore mussel assemblages.

Succession in cleared patches was unexpectedly simple and much faster than in other mussel assemblages (Paine and Levin, 1981; Berlow, 1997). It followed roughly the facilitation model proposed by Connell and Slatyer (1977) and Farrell (1991), where early colonists became extinct in time either because they are removed by physical or biological disturbance, or because they are excluded by competition with later species. The limited time–scale of the experiments conducted during this study does not permit to test the consistency of these patterns through time. For example, Berlow (1997) found that even in very simple systems, like the *M.*

californianus assemblages of the pacific coast of the USA, where the relative absence of macroalgae reduces the complexity of interactions, different mechanisms of succession appeared to be operating at different times and with different species. The combination of these processes suggested that, overall, the entire successional process in the community was chaotic and complex, magnifying even the smallest stochastic variation in recruitment, disturbance events, environmental conditions, and other variables. Nevertheless, Berlow also suggested that, despite its complexity, the system revealed consistent and repeatable patterns of succession, mainly as a consequence of some strong interactions that had the ability to dampen stochastic variation during succession. Among these were the competitive ability of mussels to dominate the shore and the facilitation of mussel settlement by barnacles.

On the northern Portuguese shores mussel occupancy might be more dependent on barnacle density than previously expected. Mussels are known to settle in all types of substrate, although they prefer rougher surfaces than smoother ones (Seed, 1969b; Suchanek, 1985; Petraitis, 1990). Barnacles increase surface rugosity, as demonstrated by Petraitis (1990), who showed that mussel recruitment was three times larger on resin castings of barnacles rather than on smoother granite surfaces. Berlow (1997) found that mussel settlement in the absence of barnacles appeared to be an 'all or none' phenomenon, depending on the local patterns of substrate rugosity. Mussels only take advantage of barnacles as a settling substrate when these grow as a thick and compacted layer, increasing rugosity due to empty shells and interstices among individuals. Because barnacles may take at least one or two years to reach this stage, even when settlement during summer is high, the effects of a putative barnacle settlement failure on mussel percentage cover may take well over two or three years to be observable.

In the present study, limpets were shown to prevent the growth of both ephemeral and perennial algae in early and later stages of succession, respectively. In cleared plots, where grazing pressure was temporarily reduced, a green algal mat (*Ulva*, *Enteromorpha*) developed rapidly, but this pattern varied with the time of clearing and position within a shore. Exclusion of limpets allowed several macroalgae to develop in the midshore, either over barnacles, mussels or on bare rock, although the results varied among shores and dates. These differences were probably related with propagule availability (Sousa, 1984b), since the main differences between the studied shores were found at the lower eulittoral, where most of the macroalgal species live. It is important to understand what is the effect of ephemeral species (*Ulva*, *Enteromorpha*, *Porphyra*) and perennial macroalgae (*Mastocarpus*, *Corallina* and *Laurencia*) in subsequent successional stages. Ephemeral algae may inhibit barnacle settlement (Sousa, 1979b; Hawkins, 1983; Underwood *et al.*, 1983) but also improve mussel secondary settlement (Seed, 1969b; Dayton, 1971; Menge, 1976; Suchanek, 1978; Turner, 1983; Suchanek, 1985). As discussed previously, barnacles are thought to be important in later stages of succession, by facilitating mussel secondary settlement, which means that interactions that prevent them from settling might affect mussel secondary settlement in a later stage. Thus, knowing the strength of these two interactions is essential if any predictions are to be made (Paine, 1980; Menge *et al.*, 1994).

The web of interactions depicted in figure 7.1 is far from being fully tested. Many direct interactions were derived from literature (e.g., Connell, 1961a,b; Paine, 1974; Menge, 1976; Lubchenco and Menge, 1978; Lubchenco and Gaines, 1981; Hawkins, 1983; Hawkins and Hartnoll, 1983b; Hartnoll and Hawkins, 1985; Farrell, 1991; Hawkins *et al.*, 1992; Sousa and Connell, 1992; Berlow, 1997) and need further confirmation by means of field manipulations. Indirect interactions were also based on field observations and need confirmation as well.

The experimental analysis of the effect of dog–whelk predation on mussels was abandoned due to the high damage caused to the cages. A recent experiment, made during the spring of 2000, produced no conclusive results because there was a high recruitment of mussels into cages, which buffered any putative effects of dog–whelk predation. Although the key stone status of dog-whelks has been challenged recently (Petraitis, 1990), it is important to know whether *Nucella* can actually control mussel densities in the northern Portuguese rocky shores, or just play a minor role modulating mussel populations.

The knowledge of direct and indirect effects of limpets on barnacles also assumes a particular importance. Although not tested during the present study, negative effects of limpets on barnacles ('bulldozing') were not detected, because barnacle settlement appeared to be normal in cleared plots, even after limpet invasion. On the other hand, the indirect positive effect of limpets on barnacle settlement, by preventing ephemeral algae from growing in the first phases of succession, might be important in late successional stages, especially for mussel secondary settlement.

7.4 Models and the prediction of oil spill impact effects

One of the aims of the present work was to understand the effects of small oil spills on the mussel/barnacle assemblages and to be able to predict, at least partially, the successional pathways after these 'pulse' disturbances. The beyond BACI approach failed to detect any effects of the oil spill that occurred in the summer of 1998, either on mussel percentage cover or on limpet densities. These results were expected because both species displayed high levels of variability through time. Most probably the mortality caused directly or indirectly by the oil spill was within the natural range of variability of both populations.

The knowledge gained with the analysis of mussel/barnacle patch dynamics at several spatial and temporal scales can be easily coupled with the information about successional patterns after disturbance, interaction among species and recruitment/settlement of main species, and permits to make some interesting predictions that, ultimately, can be confirmed experimentally.

The oil spill occurred in early summer, during the barnacle settlement season. Even assuming that most of the younger barnacles were killed by the deposited oil, the main peak of barnacle settlement was after that event, at mid July and August (figure 3.9, Chapter 3). Thus, the settlement rates observed after the oil spill were probably enough to compensate for the losses of previously settled barnacles.

If the oil spill had occurred at the end of the barnacle settlement season, and assuming that it would kill a large proportion of the newly settled individuals, the effects of such impact on the patch dynamics of the mussel/barnacle mosaic would only be visible much later – possibly two or three years after the impact. The reason for such a prediction is because mussels prefer empty shells of old barnacles as a settlement substrate, and not small and isolated individuals. Therefore, new barnacles only provide a suitable substrate for mussel fixation at least two years after their settlement, when they begin to form a thick and compact layer. In the meantime, mussels will use mainly the older barnacles for secondary settlement (figure 7.2).

The final outcome of such a scenario will depend on the proportions of mussels and barnacles before the impact, and especially on the age–structure of the barnacle population. If old barnacles are rare, this substrata will run out quickly, and mussel losses due to dislodgement will have to be compensated only by direct settlement onto the bare rock or by the lateral growth of surviving mussel patches. Since the results of this study suggest that both ways are less effective than direct fixation on barnacles, an accentuated decrease of mussel percentage cover is predictable.

Another interesting aspect that can be derived from the present results is that small oil spills might be beneficial for mussels by killing barnacles and thus increasing the proportion of a suitable substrate for secondary settlement. Even if both barnacles and mussels are killed equally by an oil spill, secondary settlement

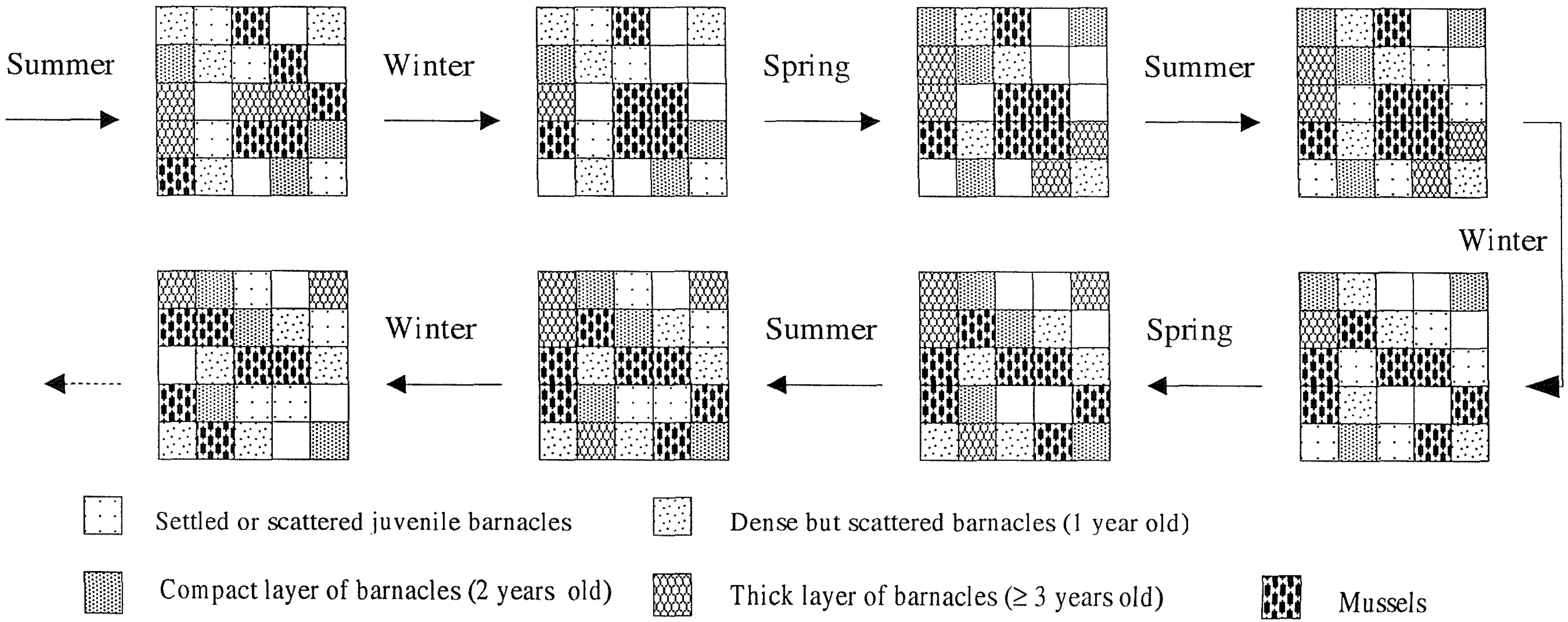


Figure 7.2: Schematic representation of the dynamics of a mussel/barnacle mosaic. For the sake of simplicity, gains and losses in area occupied by mussels were restricted to the winter season. Changes in area occupied by mussels also occur, to a lesser extent, during the spring and summer.

of mussels will be improved provided that the small mussels which live in the lower shore and sublittoral fringe can escape the effects of such impact. This is only possible because, as discussed previously, it seems that these small mussels can invade the midshore at constant rates during the whole year (Seed, 1969b).

Finally, if limpets had been killed massively the effects would have been more drastic. Depending on the time of the year, a dense cover of ephemeral green algae or of perennial red macroalgae would develop, interfering in unknown ways with the re–establishment of both mussels and barnacles (but see Southward and Southward, 1978).

7.5 Final remarks

As stressed throughout this Chapter, the models proposed here are far from being fully tested. Therefore, they should be considered as a first step in the understanding of the complex processes that drive the mussel/barnacle assemblages.

As suggested by Wu and Loucks (1995), natural disturbance (wave action, in this case) was explicitly incorporated as an important structuring force in this type of communities, and its effects were analysed at several spatial scales. The importance of disturbance as a structuring agent of natural communities might, however, be overrated (Petraitis *et al.*, 1989). In many cases, disturbance is seen as a simple mechanism resetting or renewing some limited resource (see Sousa, 1984c). But disturbance events often alter death and birth rates, through direct or indirect ways. They can kill individuals or affect competitors and resource levels in ways that alter survival and fecundity of other species. The processes that govern patch diversity – immigration and extinction – will ultimately depend on species–specific abilities to endure competition or resist disturbance (Petraitis *et al.*, 1989).

The present results suggest that disturbance by wave action may not be consistently effective among different shores and years, but further observations should be made to confirm this. When, by chance, the effects of wave action are minor or non–existent, interaction among species will assume a particular importance and will dictate the pathways of succession, often producing unexpected results. The new patches will, in turn, influence future succession, by providing propagules, shelter to other animals, or by preempting space (Sousa, 1984c; Petraitis *et al.*, 1989).

To fully understand such outcomes, a good knowledge of interactions among species and species–specific characteristics and responses is needed. Many assumptions made during this study still need further testing and/or confirmation, and a considerable effort should be put on the analysis of subtle interactions among species if a strong predictive capability is to be achieved (Benedetti-Cecchi, 2000).

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Appendix A

Sites × Species matrix

Table A.1: Species abundance on the studied shores. 0 - Absent; 1 - Observed (one individual); 2 - Rare; 3 - Frequent; 4 - Common; 5 - Very abundant; 6 - Dominant. This scale (adapted from Raffaelli and Hawkins, 1996) differs for each organism according to the method used to estimate their abundance. Sites labeled with * were sampled by Santos (1994). Labels of sites are as in figure 2.3.

Species	MO*	MO	VP	AF*	MN*	MN	VI*	VI	MI*	MI	VC*	VC	AN*	AN	CM*	CM	OP*	OP	VA*	VA	AG*	AG	BU*	BU	SP*	NA	PE	CO	ER	MA	CR	VIs*	SM*	SM	BA*
Gelidium sesquipedale	0	3	3	4	5	5	5	5	4	4	3	3	2	2	0	0	1	1	2	2	0	0	0	0	0	2	2	0	2	3	2	0	0	0	3
Porphyra umbilicalis	3	3	2	0	2	3	0	2	2	4	1	2	3	3	3	3	1	1	2	2	2	2	3	3	1	2	2	3	3	1	1	0	2	2	0
Asparagopsis armata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	2	2	1	0	2	3	2
Calliblepharis ciliata	1	2	2	0	3	3	2	2	1	1	1	2	0	1	0	0	0	0	0	0	0	2	0	0	0	0	0	0	1	0	0	0	0	0	0
Calliblepharis jubata	4	4	3	5	3	3	3	3	2	2	3	3	4	4	1	1	0	0	2	2	3	3	1	2	0	0	2	0	1	0	0	1	0	0	2
Plocamium cartilagineum	0	2	2	0	0	2	0	2	0	1	0	2	0	0	0	2	0	1	0	0	0	2	0	2	1	2	1	2	2	2	2	1	0	0	3
Gymnogongrus crenulatus	0	2	2	0	1	2	0	3	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gymnogongrus grifithsiae	0	0	0	0	0	2	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Callophyllis laciniata	1	2	2	0	1	2	1	3	0	0	3	3	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	2	0	0	0
Chondrus crispus	6	6	3	4	5	5	6	6	4	4	3	4	4	3	4	3	3	3	2	2	2	3	3	3	0	2	2	0	1	1	1	0	0	0	0
Gigartina acicularis	1	2	2	4	2	3	2	3	3	4	1	2	3	3	0	0	0	1	0	0	0	2	3	3	2	1	2	2	3	2	2	2	0	0	1
Gigartina pistillata	0	2	3	3	2	2	2	2	3	3	3	3	3	3	3	3	0	0	0	0	1	1	1	1	5	1	1	0	2	2	0	0	0	0	1
Mastocarpus stellatus	1	2	2	4	4	4	2	3	4	4	4	4	3	3	3	3	3	3	4	4	2	2	1	2	3	2	2	0	2	1	2	2	0	0	0
Corallina elongata	4	3	3	3	4	4	4	4	3	3	4	4	3	3	3	3	4	4	4	4	4	4	4	4	3	5	5	3	5	4	5	1	0	2	3
Jania rubens	0	2	1	0	1	1	0	1	0	1	2	2	0	0	0	0	0	2	0	0	0	1	0	1	1	2	3	2	2	0	0	0	0	0	3
Lithophyllum incrustans	3	3	4	1	4	4	3	3	4	4	2	2	1	1	6	6	5	5	4	4	6	6	3	3	3	3	3	2	3	3	3	3	0	2	3
Lithophyllum lichenoides	1	1	2	2	3	3	3	3	2	2	1	1	0	0	0	0	0	0	0	0	0	0	0	2	0	1	3	1	2	3	3	0	0	0	5

Table A.1: Species abundance on the studied shores (continued).

Species	MO*	MO	VP	AF*	MN*	MN	VI*	VI	MI*	MI	VC*	VC	AN*	AN	CM*	CM	OP*	OP	VA*	VA	AG*	AG	BU*	BU	SP*	NA	PE	CO	ER	MA	CR	VIs*	SM*	SM	BA*
Palmaria palmata	1	2	1	0	2	2	0	2	0	1	3	3	0	0	0	2	0	0	0	2	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0
Gastroclonium ovatum	2	3	2	0	2	3	2	3	2	2	1	2	2	2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Lomentaria articulata	3	3	2	0	3	3	2	4	3	3	3	3	2	2	1	1	3	3	3	3	1	1	2	2	1	2	0	1	0	2	1	0	2	2	0
Callithamnion tetragonum	3	3	0	0	0	0	2	2	0	0	0	0	0	0	3	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ceramium sp.	1	1	2	0	1	1	3	3	3	3	5	5	4	4	4	4	0	0	0	0	4	4	3	3	1	1	2	1	1	2	2	2	0	0	0
Halurus equisetifolius	0	2	1	0	0	1	0	2	0	1	4	4	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1
Delesseria sanguinea	1	1	0	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chondria coerulescens	1	3	2	0	1	3	0	3	1	2	0	3	1	2	0	2	1	1	0	1	2	2	1	1	0	0	1	0	1	0	0	1	0	0	1
Laurencia pinnatifida	4	4	3	1	3	3	4	4	3	3	4	4	4	4	3	3	2	2	3	3	3	3	3	3	2	2	2	2	3	2	2	0	4	5	1
Polysiphonia sp.	1	2	2	2	3	2	2	2	3	3	2	2	3	3	3	3	0	1	0	1	0	2	0	2	2	1	2	1	1	0	2	4	0	2	0
Pterosiphonia complanata	3	3	3	0	2	2	3	3	3	2	5	5	1	2	0	0	4	4	0	0	3	3	0	0	1	0	2	0	0	1	0	2	0	1	1
Laminaria hyperborea	1	2	2	0	4	4	0	3	0	1	0	2	0	0	1	2	3	3	0	0	0	0	3	3	0	0	0	0	0	0	0	0	0	0	0
Laminaria ochroleuca	3	2	2	4	4	2	0	0	4	3	4	3	3	3	3	3	4	4	1	1	1	1	0	2	0	0	2	0	1	2	0	0	0	0	0
Laminaria saccharina	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Saccorhiza polyschides	4	4	5	0	5	5	4	4	4	4	5	5	4	4	3	3	0	0	4	4	2	2	5	5	0	2	3	2	2	2	2	0	0	0	3
Stypocaulon scoparium	0	2	1	0	0	2	0	1	3	3	0	0	4	4	0	0	0	0	0	0	0	0	0	0	1	0	1	0	2	0	1	1	0	0	0
Cladostephus spongiosus	0	1	0	0	0	2	0	1	2	2	1	1	3	3	0	0	0	0	0	0	1	2	0	1	0	1	2	0	0	2	0	0	0	0	3
Dictyopteris polyploides	0	2	2	0	1	2	0	0	2	2	0	1	4	4	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	2	0	2	0	0	3
Dictyota dichotoma	0	2	1	0	1	1	2	0	2	2	0	0	3	3	0	0	0	0	0	0	2	2	1	1	2	0	1	2	4	1	2	1	0	0	1
Padina pavonia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Ascophyllum nodosum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0
Fucus spiralis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	2	0	0	0	0	0	2	2	0	2	2	2	1	2	3	5	1	2	2
Fucus vesiculosus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0
Pelvetia canaliculata	2	3	2	0	5	5	1	2	0	2	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0
Himanthalia elongata	6	6	3	3	6	6	3	4	4	4	3	3	3	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bifurcaria bifurcata	1	2	1	2	1	2	1	2	2	2	2	2	2	3	2	2	1	1	0	0	0	1	0	2	0	2	2	3	2	3	3	0	3	4	6
Cystoseira baccata	0	2	1	1	1	2	0	2	2	2	4	4	2	2	3	3	0	0	0	1	2	2	0	2	2	1	1	1	0	2	1	2	0	0	3
Cystoseira tamariscifolia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	2	2	0	1	0	4
Halidrys siliquosa	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ulva spp.	5	5	3	4	5	5	4	4	4	4	3	3	4	4	3	3	1	1	3	3	3	3	4	4	3	4	3	3	5	3	3	4	3	3	4
Codium tomentosum	1	1	2	2	3	3	2	2	3	4	3	3	3	3	4	3	3	3	3	3	3	3	1	1	2	2	2	1	3	2	2	0	3	3	5
Codium adhaerens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	1	2	1	0	2	3	3

Table A.1: Species abundance on the studied shores (continued).

Species	MO*	MO	VP	AF*	MN*	MN	VI*	VI	MI*	MI	VC*	VC	AN*	AN	CM*	CM	OP*	OP	VA*	VA	AG*	AG	BU*	BU	SP*	NA	PE	CO	ER	MA	CR	VIs*	SM*	SM	BA*
Scinaia furcelata	0	2	1	0	0	3	0	2	0	1	0	2	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Schizymenia dubyi	0	2	1	0	0	2	0	2	0	1	0	0	0	0	0	1	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Gracillaria multipartita	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dumontia contorta	0	2	2	0	0	1	0	2	0	2	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Halichondria panicea	1	1	2	2	3	3	1	1	1	1	2	2	0	0	0	0	4	4	3	3	0	0	1	1	1	2	1	2	0	2	1	0	1	1	0
Hymeniacidon perleve	2	2	3	2	3	3	0	0	1	1	1	1	1	1	1	1	2	2	4	4	2	2	2	2	2	2	3	2	2	0	2	0	4	4	0
Actinia equina	3	3	2	2	3	3	4	4	4	4	3	3	3	3	4	4	3	3	2	2	2	2	2	2	3	3	2	3	3	4	3	0	4	4	1
Anemonia viridis	1	1	3	2	1	1	1	1	3	3	2	2	0	0	3	3	3	3	0	2	4	4	1	1	3	2	0	2	2	3	2	0	0	1	1
Actinothoe sphyrodeta	1	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1	2	2	1	1	2	2	0	0	0	0	0	0	0	0	0	0	0
Cereus pedunculatus	0	0	0	0	0	0	1	1	0	0	1	1	0	0	3	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Tealia felina	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Anthopleura thallia	0	1	2	0	0	1	0	2	0	2	0	1	0	0	2	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	4	1
Bunodactis verrucosa	1	1	2	0	1	1	0	0	2	2	1	1	2	2	3	3	0	0	0	0	1	1	1	1	0	1	2	2	0	0	0	0	0	0	1
Sabellaria alveolata	3	4	3	3	4	4	4	4	4	4	5	5	6	6	4	4	3	3	5	5	5	5	6	6	2	2	1	2	1	2	2	0	3	3	2
Pollicipes pollicipes	3	3	2	0	3	3	1	1	0	0	1	1	0	0	1	1	3	3	2	2	1	1	4	4	5	3	3	2	5	3	3	0	0	0	0
Chthamalus montagui	4	6	4	4	6	6	5	6	6	5	5	5	4	6	4	6	5	6	4	3	3	5	4	5	4	5	5	4	6	4	4	4	3	4	4
Chthamalus stellatus	3	4	2	2	3	4	2	4	2	3	1	2	1	1	3	4	2	2	2	2	3	1	2	1	1	1	2	2	1	2	2	2	0	1	2
Balanus perforatus	4	4	2	3	4	4	3	3	1	1	2	2	1	1	3	3	3	3	4	4	1	1	4	4	2	2	2	1	2	1	2	0	4	4	1
Fissurella graeca	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Patella rustica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	2	3	3	3	0	2	3	3
Patella vulgata	3	3	3	1	2	2	3	3	2	2	0	0	1	1	2	2	1	1	1	1	2	2	1	1	1	1	2	1	2	1	1	2	0	0	0
Patella depressa	3	4	5	3	4	4	4	5	3	3	3	3	3	3	4	3	3	4	3	3	2	2	2	2	3	2	3	3	3	3	3	3	0	0	2
Patella ulyssiponensis	3	3	4	2	4	4	4	4	2	2	2	2	1	1	3	3	3	3	2	2	3	3	1	1	3	3	4	3	3	2	3	3	2	2	3
Helcion pellucidum	4	4	2	3	4	4	4	4	2	2	4	4	2	2	4	4	0	0	2	2	1	1	3	3	2	1	1	0	1	0	1	0	0	0	0
Gibbula umbilicalis	2	2	3	4	3	3	4	4	4	4	3	3	3	3	4	4	4	4	4	4	4	4	3	3	2	3	3	3	2	3	2	2	0	0	4
Gibbula pennanti	0	2	2	0	0	2	0	3	0	2	0	3	0	2	0	2	0	2	0	1	0	3	0	2	2	2	1	2	1	2	2	0	0	1	2
Gibbula cineraria	0	0	2	1	2	2	1	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Monodonta lineata	3	3	3	0	3	3	4	4	3	3	0	0	1	1	2	2	1	3	1	2	1	3	0	0	1	2	2	3	2	3	2	0	0	1	2
Calliostoma zizyphinum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Littorina littorea	0	0	0	0	0	0	1	2	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0
Littorina saxatilis	3	3	3	2	3	3	4	4	4	4	1	1	0	0	4	4	4	4	1	1	0	0	0	3	2	2	3	2	3	3	2	0	0	0	2
Littorina obtusata	0	0	0	4	3	3	0	0	3	3	0	0	0	0	2	2	0	0	4	4	0	0	0	0	2	0	0	0	0	0	0	5	0	0	0

Table A.1: Species abundance on the studied shores (continued).

Species	MO*	MO	VP	AF*	MN*	MN	VI*	VI	MI*	MI	VC*	VC	AN*	AN	CM*	CM	OP*	OP	VA*	VA	AG*	AG	BU*	BU	SP*	NA	PE	CO	ER	MA	CR	VIs*	SM*	SM	BA*
Melaraphe neritoides	3	3	3	1	5	5	5	5	3	3	6	6	4	4	4	4	5	5	1	1	0	0	3	3	4	3	5	4	3	4	4	2	5	5	4
Trivia europaea	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Ocinebrina erinacea	0	0	0	0	0	0	0	0	0	0	1	1	0	0	2	2	0	0	1	1	1	1	0	2	0	0	0	0	0	0	0	0	0	0	1
Ocinebrina edwardsii	0	0	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1	0	1	0	1	1	0	0	0	3
Nucella lapillus	3	3	3	2	3	3	4	4	2	2	3	3	3	3	5	5	3	3	3	3	4	4	4	4	0	3	3	3	2	3	2	0	3	2	4
Nassarius reticulatus	0	0	2	1	2	2	1	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	2	0	1	0	0	1	1	3	0	0	0
Nassarius incrassatus	0	0	0	0	0	0	0	0	3	3	1	1	1	1	1	2	1	1	1	1	1	1	0	0	2	1	2	1	3	2	3	0	0	0	0
Onchidella celtica	0	0	0	0	0	0	0	0	0	0	1	2	0	0	0	3	0	2	1	0	0	1	0	1	0	1	2	1	1	2	2	0	0	0	1
Siphonaria pectinata	0	0	0	0	0	0	0	1	0	0	0	2	1	1	0	3	0	2	0	1	0	0	0	1	1	2	2	3	2	3	3	0	2	2	3
Mytilus galloprovincialis	5	5	4	4	6	6	6	6	5	5	5	5	4	4	6	6	5	5	3	3	6	6	4	4	2	3	4	4	3	4	3	0	5	4	4
Asterina gibbosa	0	1	2	0	0	2	0	2	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0
Marthasterias glacialis	2	2	3	1	5	5	4	4	2	2	1	1	3	3	2	2	1	1	1	1	1	1	0	0	1	2	3	2	1	2	2	0	0	0	0
Asterias rubens	1	1	2	0	0	2	0	1	2	2	1	1	3	3	1	1	1	1	0	0	1	1	3	3	1	1	1	2	1	1	1	0	0	0	0
Paracentrotus lividus	1	1	3	3	4	4	3	3	3	3	2	2	3	3	3	3	3	3	2	2	3	3	1	1	3	2	2	1	2	3	2	0	0	0	0
Verrucaria maura	5	5	3	0	6	6	6	6	2	2	4	4	0	0	4	4	4	4	1	1	0	0	3	3	3	3	4	2	3	3	3	2	1	1	3
Lichina pygmaea	2	2	3	0	4	3	4	4	4	4	0	0	0	0	2	2	3	3	0	0	0	0	0	1	2	2	3	0	2	2	3	0	2	2	4

Appendix B

Similarity breakdown analysis

After an ordination and an ANOSIM analysis, the usual question is: *what are the species responsible for the resulting structure*? Several techniques were developed for such purpose, but the most analytical way of achieving this is by the use of SIMPER analysis (Clarke and Warwick, 1994). The first step is to compute the *average dissimilarity* $\bar{\delta}$ between all pairs of inter–groups samples and then break this average down into the separate *contributions from each species* to $\bar{\delta}$.

For the Bray–Curtiss dissimilarity δ_{jk} between two samples j and k, the contribution from the ith species, $\delta_{jk}(i)$, can be defined as

$$\bar{\delta}_{jk}(i) = 100 \times |y_{ij} - y_{ik}| / \sum_{i=1}^{p} (y_{ij} + y_{ik}) \tag{B.1}$$

where p is the total number of species. $\delta_{jk}(i)$ is then averaged over all pairs (j,k), with j in the first and k in the second group, to give the *average contribution* $\bar{\delta}_i$ from the ith species to the overall dissimilarity $\bar{\delta}$ between groups j and k.

There are many pairs of samples making up the average $\bar{\delta}_i$, and a useful measure of how consistently a species contributes to $\bar{\delta}_i$ across all such pairs of samples is the *standard deviation* $SD(\delta_i)$ of the $\delta_{jk}(i)$ values. If $\bar{\delta}_i$ is large and $SD(\delta_i)$ small, then the ith species not only contributes much to the dissimilarity between the groups being analysed, but also does so consistently in inter–comparisons of all samples in the two groups. According to Clarke and Warwick (1994), those species which have a large $\bar{\delta}_i / SD(\delta_i)$ ratio can be considered good *discriminating species*.

Table B.1: Dissimilarity breakdown for the species contribution to the differences between northern and central regions. Only the 30 topmost species are shown. The best discriminating species (Ratio $\geq$ 2.00) are in bold.

	Average Scores					
Species	Centre	North	Av. Term	Ratio	%	Cum. %
Himanthalia elongata	0.00	3.60	1.29	2.00	3.35	3.35
Verrucaria maura	2.20	3.80	0.87	1.49	2.26	5.61
Gelidium sesquipedale	0.80	2.93	0.86	1.64	2.25	7.86
Saccorhiza polyschides	2.40	4.20	0.78	1.35	2.04	9.89
Melaraphe neritoides	2.50	4.20	0.77	1.31	2.02	11.91
Chondrus crispus	2.30	4.40	0.76	1.41	1.98	13.89
Ceramium sp.	1.60	2.93	0.75	1.35	1.96	15.85
Gigartina pistillata	1.00	2.47	0.75	2.35	1.94	17.79
Pterosiphonia complanata	1.50	2.47	0.72	1.41	1.88	19.67
Laminaria ochroleuca	1.40	2.60	0.71	1.66	1.84	21.52
Helcion pellucidum	1.50	3.33	0.70	1.67	1.83	23.34
Littorina saxatilis	1.70	2.73	0.69	1.39	1.79	25.13
Pollicipes pollicipes	2.80	1.33	0.67	1.32	1.75	26.88
Lichina pygmaea	1.10	2.27	0.67	1.36	1.73	28.61
Calliblepharis jubata	1.30	2.87	0.66	1.41	1.73	30.34
Marthasterias glacialis	0.90	2.73	0.66	1.50	1.71	32.05
Gastroclonium ovatum	0.10	1.87	0.64	2.13	1.67	33.71
Lithophyllum incrustans	4.20	3.33	0.60	1.21	1.56	35.27
Polysiphonia sp.	0.90	2.40	0.57	1.52	1.48	36.75
Pelvetia canaliculata	0.00	1.67	0.57	1.11	1.48	38.23
Laminaria hyperborea	1.20	1.47	0.57	1.31	1.48	39.71
Mytilus galloprovincialis	4.10	5.20	0.55	1.35	1.42	41.13
Monodonta lineata	1.40	2.33	0.55	1.43	1.42	42.55
Halichondria panicea	1.90	1.20	0.54	1.26	1.41	43.96
Gigartina acicularis	1.20	2.07	0.54	1.34	1.40	45.36
Littorina obtusata	1.00	1.07	0.53	0.97	1.39	46.75
Sabellaria alveolata	4.20	4.27	0.53	1.51	1.39	48.13
Anemonia viridis	2.30	1.67	0.52	1.27	1.35	49.48
Cystoseira baccata	1.00	2.00	0.50	1.20	1.31	50.79
Stypocaulon scoparium	0.10	1.33	0.49	0.87	1.28	52.07

Table B.2: Dissimilarity breakdown for the species contribution to the differences between northern and southern regions. Only the 30 topmost species are shown. The best discriminating species (Ratio $\geq$ 2.00) are in bold.

	Average Scores					
Species	South	North	Av. Term	Ratio	%	Cum. %
Himanthalia elongata	0.00	3.60	1.24	2.00	3.16	3.16
Chondrus crispus	1.00	4.40	1.19	2.50	3.03	6.20
Patella rustica	2.80	0.00	0.97	6.97	2.49	8.68
Helcion pellucidum	0.60	3.33	0.95	2.52	2.43	11.11
Sabellaria alveolata	1.60	4.27	0.94	2.40	2.40	13.51
Calliblepharis jubata	0.60	2.87	0.82	1.86	2.10	15.61
Siphonaria pectinata	2.60	0.53	0.75	2.26	1.90	17.51
Pterosiphonia complanata	0.60	2.47	0.72	1.43	1.85	19.36
Pollicipes pollicipes	3.20	1.33	0.70	1.42	1.79	21.14
Sacchoriza polyschides	2.20	4.20	0.70	2.61	1.78	22.92
Laminaria ochroleuca	1.00	2.60	0.67	1.53	1.71	24.63
Verrucaria maura	3.00	3.80	0.66	1.59	1.69	26.32
Gelidium sesquipedale	1.80	2.93	0.66	1.42	1.68	28.00
Gastroclonium ovatum	0.00	1.87	0.64	2.22	1.64	29.64
Fucus spiralis	2.00	0.27	0.62	2.09	1.60	31.23
Mastocarpus stellatus	1.40	3.07	0.61	1.51	1.57	32.80
Lomentaria articulata	0.80	2.53	0.61	1.84	1.56	34.36
Ceramium sp.	1.60	2.93	0.59	1.41	1.51	35.87
Gigartina pistillata	1.00	2.47	0.57	1.47	1.46	37.34
Pelvetia canaliculata	0.00	1.67	0.55	1.11	1.40	38.74
Mytilus galloprovincialis	3.60	5.20	0.55	1.81	1.40	40.14
Lichina pygmaea	2.00	2.27	0.55	1.28	1.40	41.53
Nassarius incrassatus	2.20	0.87	0.54	1.65	1.38	42.91
Onchidella celtica	1.60	0.40	0.50	2.34	1.28	44.19
Dictyota dichotoma	2.00	1.13	0.49	1.29	1.26	45.45
Asparagopsis armata	1.40	0.00	0.49	2.86	1.24	46.69
Codium adhaerens	1.40	0.00	0.48	3.00	1.24	47.93
Laminaria hyperborea	0.00	1.47	0.48	1.12	1.22	49.15
Stypocaulon scoparium	0.80	1.33	0.48	1.09	1.22	50.37
Lithophyllum lichenoides	2.40	1.47	0.48	1.27	1.22	51.59

Table B.3: Dissimilarity breakdown for the species contribution to the differences between central and southern regions. Only the 30 topmost species are shown. The best discriminating species (Ratio $\geq$ 2.00) are in bold.

	Average Scores					
Species	South	Centre	Av. Term	Ratio	%	Cum. %
Patella rustica	2.80	0.00	1.19	8.26	3.32	3.32
Sabellaria alveolata	1.60	4.20	1.11	1.66	3.08	6.40
Lithophyllum lichenoides	2.40	0.30	0.91	2.31	2.53	8.93
Bifurcaria bifurcata	2.60	0.70	0.83	1.90	2.32	11.24
Melaraphe neritoides	4.00	2.50	0.83	1.32	2.31	13.55
Siphonaria pectinata	2.60	0.70	0.83	1.95	2.30	15.85
Sacchoriza polyschides	2.20	2.40	0.70	1.51	1.95	17.81
Littorina saxatilis	2.60	1.70	0.66	1.63	1.83	19.64
Pterosiphonia complanata	0.60	1.50	0.65	1.09	1.81	21.45
Ceramium sp.	1.60	1.60	0.65	1.96	1.80	23.25
Chondrus crispus	1.00	2.30	0.65	1.77	1.80	25.05
Lichina pygmaea	2.00	1.10	0.64	1.31	1.78	26.83
Balanus perforatus	1.60	2.80	0.62	1.40	1.73	28.56
Dictyota dichotoma	2.00	0.80	0.62	1.24	1.72	30.28
Halichondria panicea	1.20	1.90	0.60	1.36	1.68	31.96
Lomentaria articulata	0.80	2.10	0.60	1.48	1.68	33.63
Lithophyllum incrustans	2.80	4.20	0.60	1.11	1.67	35.31
Codium adhaerens	1.40	0.00	0.59	3.12	1.65	36.96
Fucus spiralis	2.00	0.80	0.59	1.36	1.63	38.59
Mastocarpus stellatus	1.40	2.60	0.58	1.15	1.62	40.21
Verrucaria maura	3.00	2.20	0.58	1.19	1.62	41.82
Gigartina acicularis	2.20	1.20	0.57	1.46	1.59	43.41
Anemonia viridis	1.80	2.30	0.57	1.34	1.58	44.99
Nassarius incrassatus	2.20	0.90	0.57	1.53	1.58	46.57
Laminaria ochroleuca	1.00	1.40	0.56	1.16	1.56	48.13
Gelidium sesquipedale	1.80	0.80	0.56	1.32	1.56	49.68
Asparagopsis armata	1.40	0.10	0.55	2.30	1.54	51.22
Pollicipes pollicipes	3.20	2.80	0.55	1.23	1.53	52.75
Jania rubens	1.40	0.70	0.54	1.27	1.50	54.25
Monodonta lineata	2.40	1.40	0.54	1.39	1.50	55.75

Appendix C

Size–frequency data for *Patella depressa*

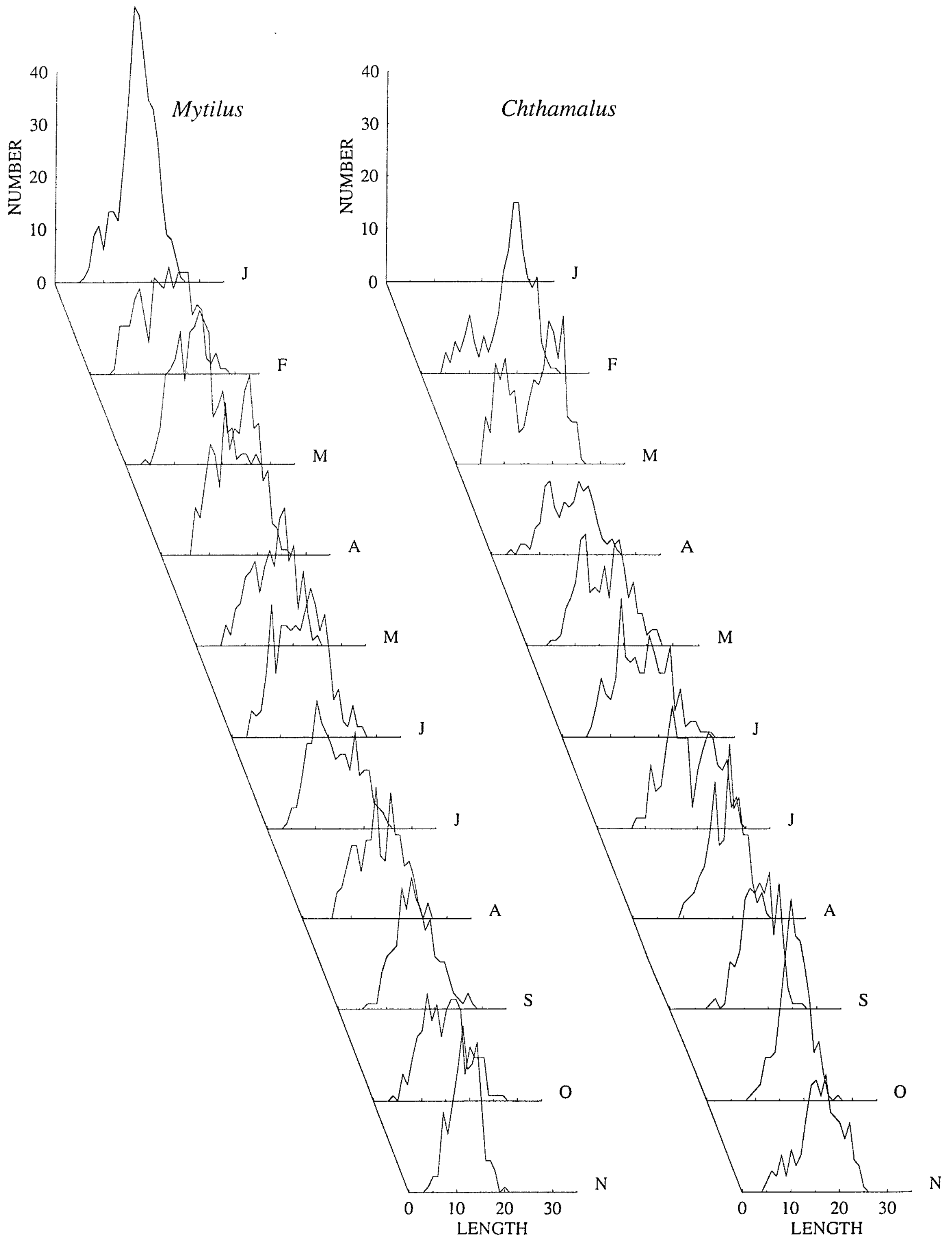

Figure C.1: Size–frequency distributions for the populations of *Patella depressa* in the barnacle and mussel zones at Aguda.

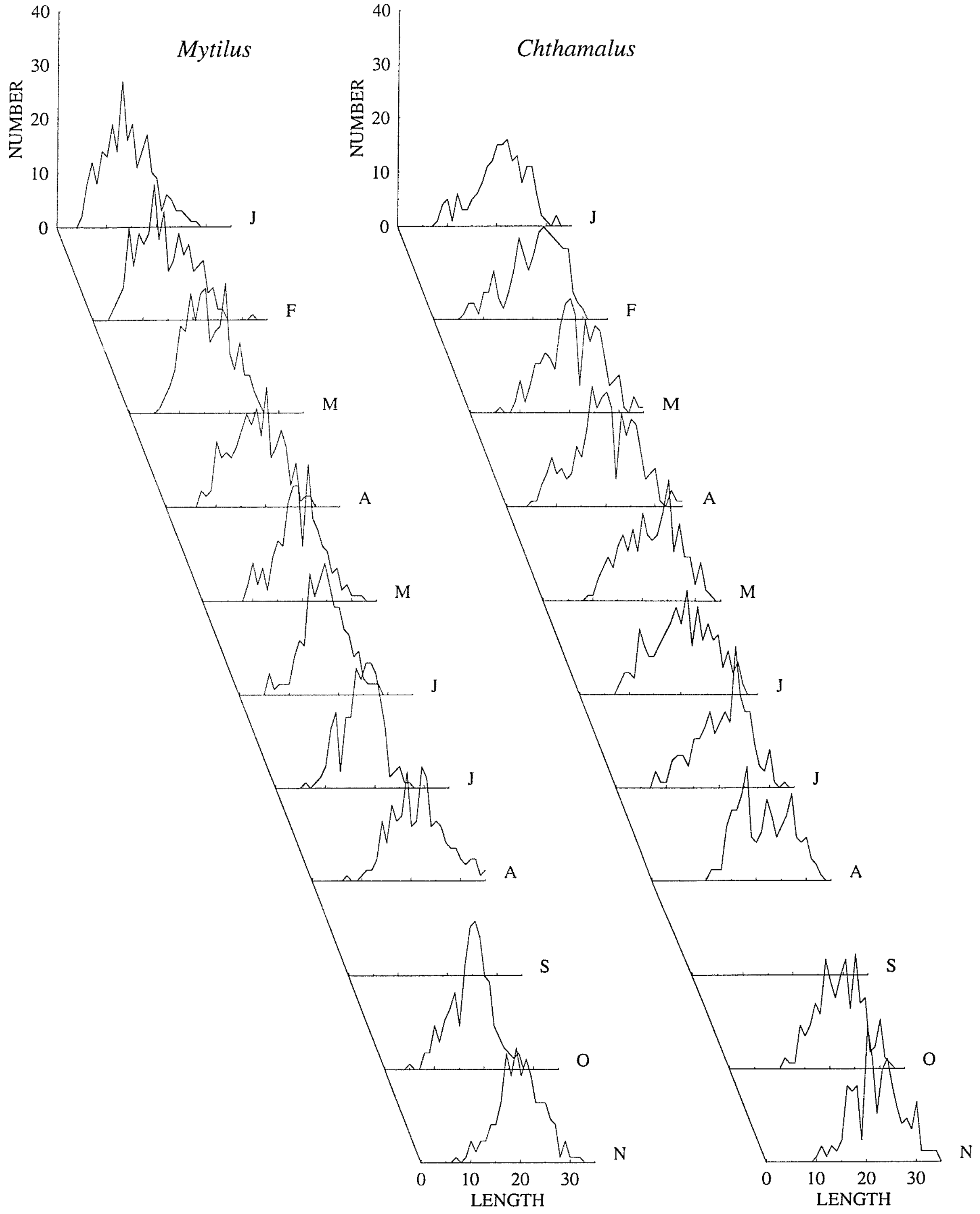

Figure C.2: Size–frequency distributions for the populations of *Patella depressa* in the barnacle and mussel zones at Oporto.

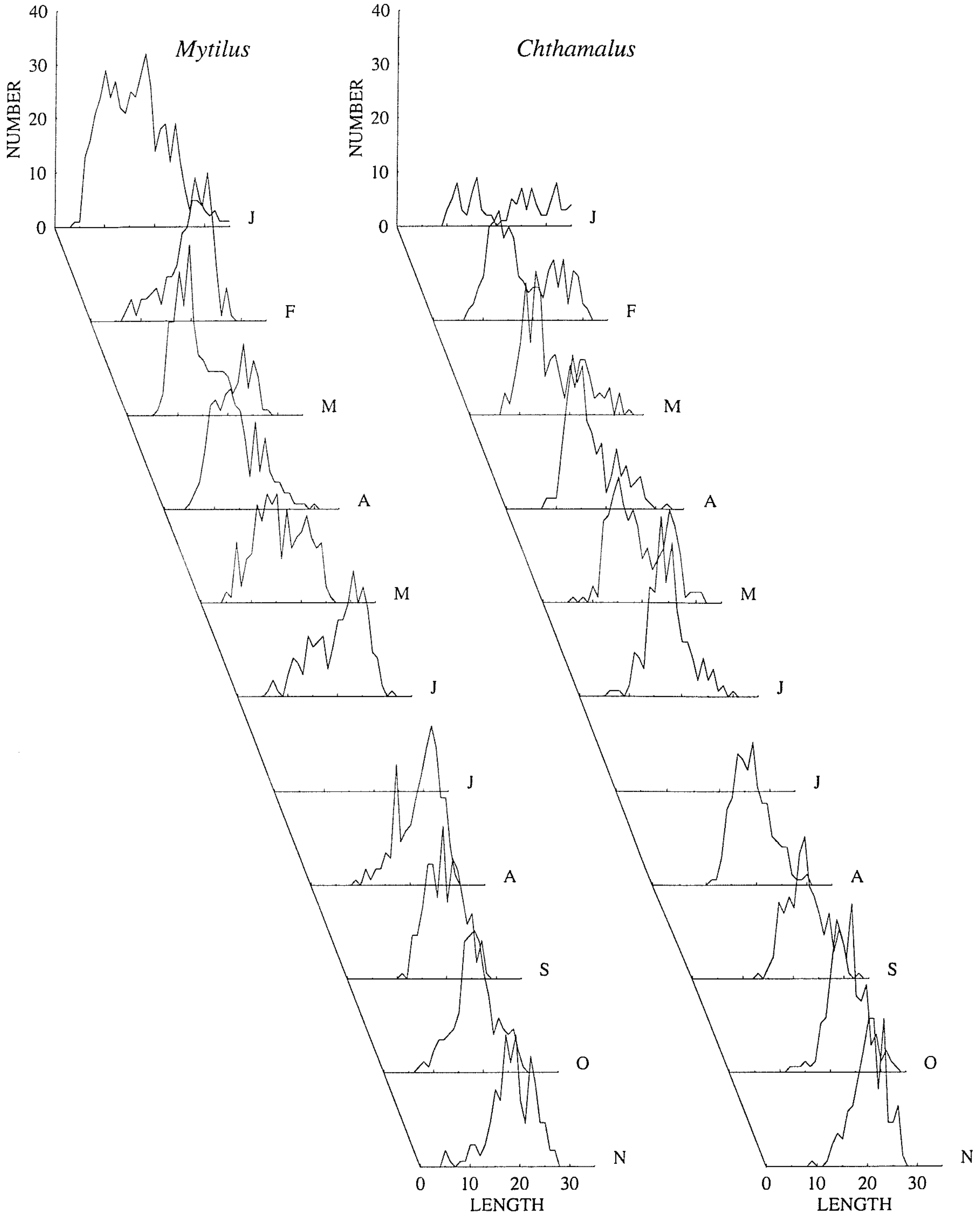

Figure C.3: Size–frequency distributions for the populations of *Patella depressa* in the barnacle and mussel zones at Cabo do Mundo.

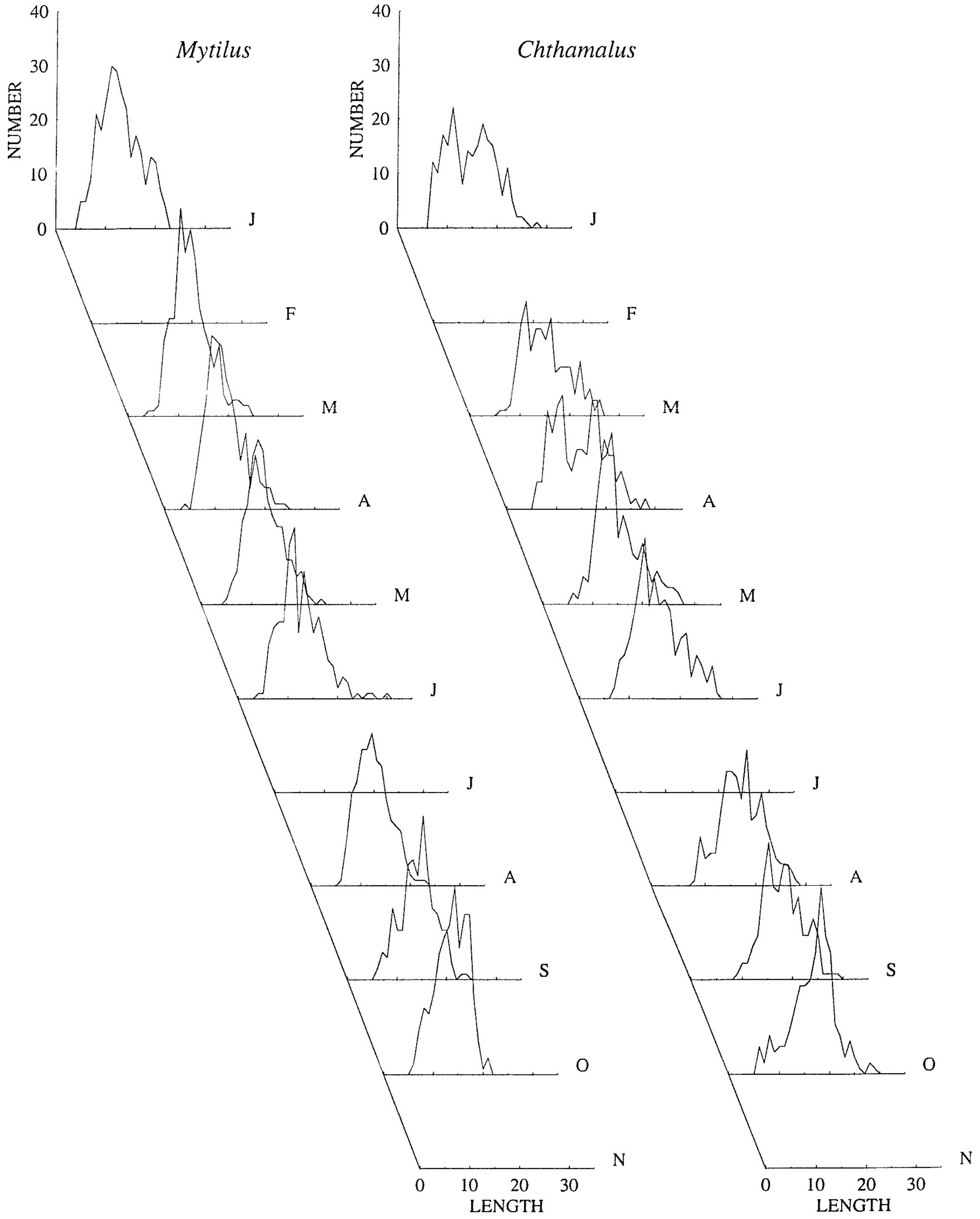

Figure C.4: Size–frequency distributions for the populations of *Patella depressa* in the barnacle and mussel zones at Viana do Castelo (North).

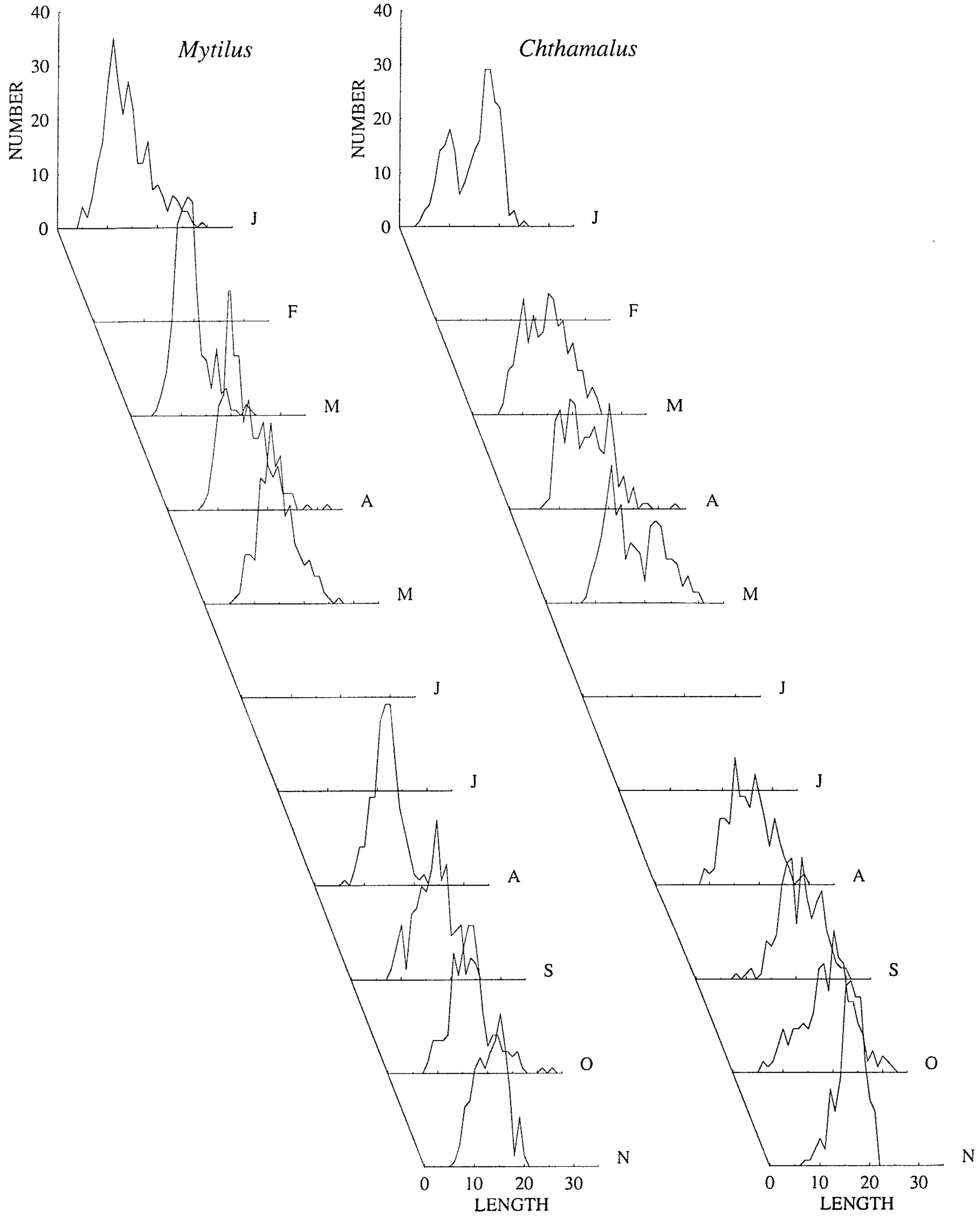

Figure C.5: Size–frequency distributions for the populations of *Patella depressa* in the barnacle and mussel zones at Moledo do Minho.