COMMUNITY STRUCTURE AND DYNAMICS OF THE AZOREAN ROCKY INTERTIDAL: EXPLOITATION OF KEYSTONE SPECIES

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COMMUNITY STRUCTURE AND DYNAMICS OF THE AZOREAN ROCKY INTERTIDAL: EXPLOITATION OF KEYSTONE SPECIES

by

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Community structure and dynamics of the Azorean rocky intertidal: exploitation of keystone species

Gustavo Oliveira de Meneses Martins

Abstract

Experimental work has shown the importance of grazing by patellid limpets in structuring intertidal assemblages. Little is known, however, about the effects of a large-scale and chronic removal of limpets. Here I investigate the ecology of *Patella candei*, a seldom-studied limpet endemic to Macaronesia, and how its long-term fishery impacts the Azorean rocky intertidal. The specific aims of this thesis are to: examine the processes that affect the distribution of limpets in the Azores at a range of spatial scales; investigate the role of grazing by *P. candei* in structuring the Azorean rocky intertidal and if its harvesting has impacted the dynamics and functioning of this ecosystem. The distribution of limpets was variable at a range of spatial scales. At the scale of islands, inter-island variation in harvesting intensity affected the abundance and size structure of populations of limpets as well as the balance between grazers, algae and barnacles. Stocks of limpets showed clear signs of exploitation and there was evidence that current legislation, including limpet protected zones, have been largely ineffective in protecting these populations. At smaller spatial scales, substratum micro-topography influenced the distribution and survival of limpets. I also showed that the experimental provision of microhabitats could be used as a measure to mitigate the effects of coastal urbanisation, whilst promoting a local enhancement of the stocks of limpets. Overall my results provide evidence for the population and community level effects of limpet harvesting and show that limpet harvesting has a strong impact on the structure and functioning of the Azorean rocky intertidal.

Estrutura e dinâmica das comunidades do intertidal rochoso Açoreano: exploração de espécies chave

Gustavo Oliveira de Meneses Martins

Resumo

O relevante papel que as lapas desempenham nas comunidades intertidais tem sido reforçado em diversos trabalhos experimentais. Todavia, pouco se sabe sobre os eventuais efeitos da sua remoção de uma forma crónica e em larga escala. No presente trabalho, investiga-se a ecologia de *Patella candei*, uma espécie pouco estudada e endémica da Macaronésia, e de que forma a sua exploração afecta o intertidal Açoreano. Neste sentido, o presente trabalho tem como objectivos: examinar os processos que influenciam a distribuição espacial das lapas; investigar o papel de *Patella candei* nas comunidades do intertidal rochoso Açoreano; e se a sua sobre-exploração tem afectado a estrutura e funcionamento deste ecossistema. A distribuição de lapas foi variável a diferentes escalas espaciais. À escala das ilhas, a abundância de lapas variou de acordo com a intensidade de exploração, resultando em diferenças no balanço entre herbívoros, algas e cracas. O presente estudo mostra que as populações de lapas apresentam sinais evidentes de exploração e que as actuais medidas de conservação têm sido claramente ineficazes. A uma menor escala espacial, a microtopografia do substrato influenciou de forma significativa a distribuição espacial das lapas. O presente estudo vem também revelar que a provisão experimental de microhabitats pode ser usada como medida de mitigação dos impactos da urbanização, promovendo o aumento populacional de lapas. Em síntese, os resultados apresentados mostram que a exploração de lapas no Açores tem impactos ao nível da estrutura populacional das lapas que se repercutem na estrutura e funcionamento da comunidade.

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Author's Declaration

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CHAPTER 1

General introduction

General introduction

1.1. Thesis overview

Many coastal locations with long established human populations have a tradition of local exploitation of marine resources including those in the littoral zone. Arguably the largest anthropogenic impact in the Azorean intertidal is the overexploitation of the keystone patellid grazers (Hawkins et al. 1999). In the archipelago of the Azores, heavy exploitation of limpets (*Patella* spp.) for human consumption over more than 30 years has caused extensive decline of these populations (Santos et al. 1990, Morton et al. 1998, Hawkins et al. 2000). Experimental work on the importance of top down control by intertidal grazers (e.g. Menge et al. 1999, Thompson et al. 2004), and specifically on patellid limpets throughout NW Europe (e.g. Hawkins et al. 1992, Jenkins et al. 2005) strongly suggest that patellid exploitation is likely to have a strong impact on community structure of Azorean rocky shores.

The ways insular systems differ from continental shelves are diverse. Oceanic islands provide isolated patches of intertidal habitat with communities, which are often simpler and less resilient than those found on their mainland counterparts (Williamson 1981). The isolation and relatively small size of most oceanic islands in comparison to mainland coastal systems make them highly susceptible to degradation and ecosystem disruption (Hawkins et al. 1999). Potential causes of such fragility include the generally low and stochastic nature of benthic recruitment in a dispersive island environment and the often frequent and pervasive nature of human resource exploitation. The majority of marine benthic invertebrates, including most of the major space occupiers (e.g. mussels, barnacles), grazers (e.g. limpets, top-shells) and predators (e.g. crabs) of the rocky intertidal have a complex life cycle that encompasses separate planktonic and bottom dwelling phases, linked by a settlement event (Thorson, 1950). Larvae released into the water column by benthic adults are dispersed away from the local population by physical transport in the water column (see Morgan 2001 for review) In such open systems, local reproductive output may have little or no impact on local recruitment (Sponaugle et al 2002, Jenkins 2005) especially in dispersive environments such as exposed headlands and isolated islands. Interactions between coastline topography, water circulation, the dispersal of larvae and their subsequent recruitment are not well understood (but see Archambault & Bourget 1999). Evidence suggests that self-recruitment increases with isolation and that isolated islands will on average receive lower levels of recruitment, owing to dispersive larval loss, than equivalent mainland sites (Cowen et al. 2000). This is notable even on islands quite close to the coast. For instance, Crisp & Southward (1958) commented on absences and reductions of common species with respect to larval dispersal on the Isles of Scilly, UK (45 km from the mainland) and Ushant, France (20 km from the mainland), while Hawkins & Hiscock (1983) showed similar reductions in abundance of several gastropod species from the island of Lundy (18 km from the mainland)

This suggests that a decrease in reproductive output due to exploitation may have disproportionate impacts on the maintenance of insular populations The absence or reduced abundance of certain species as a result of low recruitment will inevitably influence community composition and possibly function (Connolly & Roughgarden 1998)

1.2. The Azores archipelago

1.2.1. Physical environment

The Archipelago of the Azores is located in the North Atlantic (Fig. 1.1) and occupies an area of approximately 2344 km^2 along the Mid-Atlantic Ridge running WNW-ESE. The archipelago comprises nine islands and several islets being divided into 3 groups: western group (Corvo and Flores), central group (Faial, Graciosa, Pico, São Jorge, and Terceira), and eastern group (São Miguel and Santa Maria). Each island was formed by different volcanic eruptions, which makes islands a mosaic of differing ages. As whole, the Azores is geologically young with islands ranging between <1 Myears (Pico Island) and 8 Myears (Santa Maria). The archipelago is composed of volcanic rocks, mainly basalt s.l., although fossileferous limestone also occurs in Santa Maria (Morton et al. 1998).

The coastline is steep with high cliffs falling directly into the sea alternating with small rocky beaches. Sandy beaches are uncommon. Islands are surrounded by deep water (>1000 m) within a few miles of the coast, and are exposed to frequent swell and surge. Sheltered areas are rare except for a few bays and harbours.

The Azores lies in the warm temperate region with the ocean playing a major influence on the climate. As such, relative humidity is commonly above 70% (Neto 1997). According to CLIMAAT (2008), rainfall is high and can reach up to 1000 mm yr^{-1}, whilst air temperature is regular with little daily and yearly fluctuations with a mean monthly temperature of 20-24°C during summer and 14-15°C during winter. Islands are exposed to strong winds, which predominantly blow from SW, W and NW in the central and eastern groups, and from SE, E and NE in the western group.

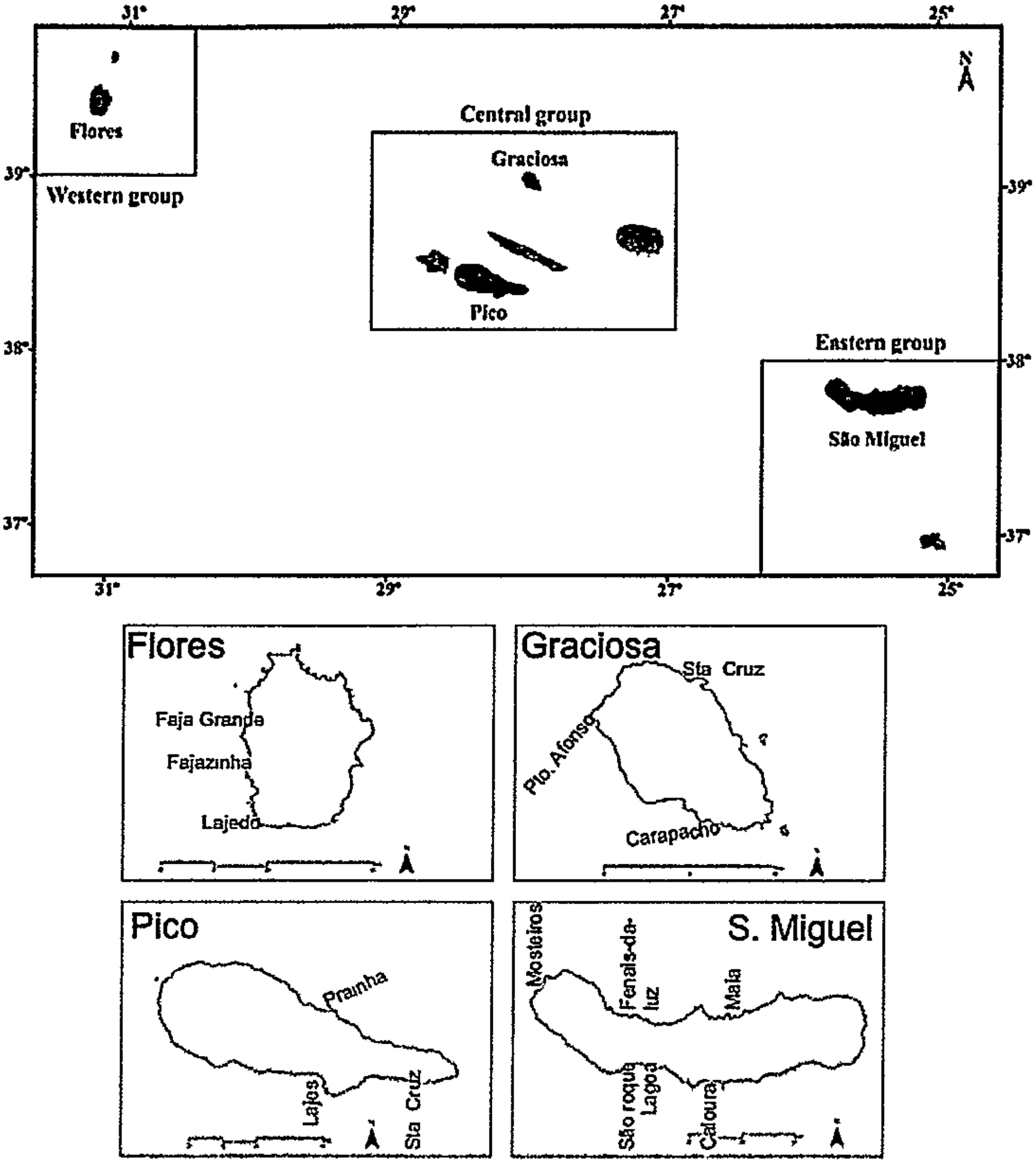

Figure 1.1. The archipelago of the Azores showing the islands and locations where work has been made during the present study Flores Fajã Grande – 39°27'N, 31°15'W, Fajazinha – 39°25'N, 31°15'W, Lajedo – 39°22'N, 31°,15'W, Graciosa Santa Cruz – 39°05'N, 29°00'W; Carapacho – 39°00'N, 27°58'W, Porto Afonso – 39°03'N, 28°04'W, Pico Lajes – 38°23'N, 28°15'W; Prainha – 38°28'N, 28°12'W, Santa Cruz – 38°23'N, 28°05'W, São Miguel Lagoa – 37°44'N, 25°35'W, Caloura – 37°44'N, 25°30'W; Mosteiros – 37°53'N, 25°49'W, Maia – 37°50'N, 25°23'W, Fenais-da-Luz – 37°49'N, 25°38'W, São Roque – 37°44'N, 25°38'W.

The tidal cycle is semi-diurnal with maximum amplitude smaller than 2 m. For São Miguel, where the majority of work described in this thesis took place, the maximum amplitude recorded was 1.89 m, while mean amplitudes for neaps and spring tides are 0.65 m and 1.44 m, respectively (Neto 1997). Seawater temperature is similar to that of the air with a mean annual temperate of 16 °C in winter and 19 °C in summer.

In North Atlantic there is a clockwise oceanic circulation. The Gulf Stream flows eastward and forms two smaller branches at around 40° N: the North Atlantic Current (NAC) and the Azores Current (AC) (Morton et al. 1998). Each of these branches splits into further branches. The Azores archipelago is influenced by these two currents: the NAC is a north-west current passing north of the Azores, whilst the AC flows predominantly to the east passing south of the archipelago (Morton et al. 1998). There are some changes in the intensity and direction as these currents flow with season although the general regime is from west to east. Within the archipelago of the Azores, coastal currents are complex and directly related to the submarine topography. A current with higher density and salinity flows from the Mediterranean at about 900 m depth in the reverse direction (Morton et al. 1998).

1.2.2. The biota

The fauna and flora of the Azores originated from both the East and West coasts of the Atlantic although the latter are less common. The greater affinity of Azorean biodiversity to the East Atlantic has been shown for many taxa including fish (Santos et al. 1997), crustaceans (Costa 1994), opistobranchs (Wirtz 1998) and algae (e.g. Titley & Neto 1995, Titley & Neto 2006). According to the present-day clockwise current this seems a paradox, however, some authors suggest that colonisation of the Azores by European species took place mostly in a period where dominant currents were in an anti-clockwise gyre, which existed before the closure of the strait of Panama 3-4 Myrs ago (Morton et al 1998)

Due to the isolation, and geological history of the Azores, some groups of marine animals and plants are poorly represented in terms of species richness and, except for molluscs, there is a low percentage of endemism when compared to other Macaronesian archipelagos (Morton et al 1998, Ávila et al 2008) Recent environmental changes associated with the last glaciation and variation in the sea level may account for the local disappearance of several species and for the overall low level of endemism recorded in the Azores (Briggs 1966, Ávila et al 2008) Notable absences include mussels (although these are sporadically recorded within harbours), large brown algae (e.g kelp forests) and seagrass beds.

In the rocky intertidal, three broad vertical areas can easily be distinguished although there is some overlap due to frequent swell (Hawkins et al 1990a, Neto 2000) The upper shore is characterised by two littorinids *Littorina striata* King 1832 and *Melarhaphe neritoides* L. 1758, *Verrucaria* sp and *Lychina* sp. are also common although the latter rarely is abundant

At mid-shore heights, the chthamalid barnacle *Chthamalus stellatus* Poli 1791, is the major space occupier except in very sheltered conditions (e g inside harbours). Other abundant barnacles the NE Atlantic, the *Semibalanus balanoides* L. 1767 and *C montagui* Southward 1976, do not occur in the Azores *Patella candei* D'Orbingly 1840 is the dominant grazer at this height and its abundance generally increases with exposure to wave-action Under moderately exposed conditions, an algal association between the turf-forming *Gelidium microdon* Kutzing 1849 and the fucoid *Fucus spiralis* L 1753 becomes common forming scattered patches

The upper zone of the lower shore, is dominated by turf-forming species including *Caulacanthus ustulatus* (Mertens ex Turner) Kützing 1843 (among others). At this height, *Patella aspera* Röding 1798 can be seen in patches cleared of algae. The predatory whelk *Stramonita haemastoma* L. 1766 is also frequent although rarely abundant and is commonly seen feeding on barnacles. The crab *Pachygrapsus marmoratus* Fabricius 1787 may be very abundant, especially on boulders. Towards the low water mark, articulated coralline algae become the dominant taxa. Small patches of *Stypocaulon scoparium* (L.) Kützing 1843 can be seen scattered among these. *Cystoseira* spp. can also form dense patches in the more exposed locations.

During extreme low water tides, the sea-urchins *Paracentrotus lividus* Lamark 1816 and *Arbacia lixula* L. 1758 may become exposed to air and abundant in moderately exposed and sheltered conditions. As exposure increases, the large barnacle *Megabalanus azoricus* Pilsbry 1916 can also be seen forming dense aggregations.

Rock pools are not particularly abundant on these shores. However, when present their biota can vary greatly from pool to pool. In some of these, space is completely dominated by individuals of *Cystoseira* spp. and *Sargassum* spp. Other pools can be largely dominated by erect corallines with many filamentous (e.g. *Cladophora* sp.) and foliose (*Ulva* spp.) algae interspersed within it. Other pools can still be dominated by encrusting coralline algae and sea-urchins.

In the present work, species identification was done following guides of Maggs & Hommersand (1993), Hayward & Ryland (1995), Morton et al. (1998), Carrillo & Sansón (1999), Algaebase (2006), and Neto et al. (2006). Where appropriate, species authorities are given on species first mention.

1.3. The patellid limpets in the Azores

In the archipelago of the Azores two species of limpets occur (Fig 1 2) There has been much confusion regarding the taxonomy of limpets, particularly those from the Macaronesian islands (Corte-Real et al. 1996). In this study, I will adopt names suggested by Hawkins and co-authors who have examined the morphological and genetic structure of limpet populations in the Macaronesian archipelagos (Corte-Real et al. 1996, Weber & Hawkins 2002, 2005)

In the Azores archipelago *Patella candei gomesii* Drouët (locally denominated as "lapa-mansa") belongs to the *P candei* complex, which is exclusive to Macaronesia. *P c gomesii* is an endemic subspecies of the Azores (Weber & Hawkins 2002) occurring in the mid and high shore and also subtidally, especially on boulders (Hawkins et al 2000) *P c gomesii* has a depressed and rounded form, very smoothly ribbed with an obtuse and blunted apex. Externally, it is pinkish, grey to brown (Weber & Hawkins 2002). This subspecies is morphologically plastic revealing two habitat morphs the "smooth limpet" and the "fly limpet" characteristic of the eulittoral zone and of the higher exposed shore areas, respectively (Hawkins et al 1990b) These two ecomorphs are, considered genetically the same population and data on the reproductive cycle of the two morphs emphasized this aspect (Cúrdia et al 2005) According to Martins et al (1987), *P c gomesii* spawns throughout the year, without synchronized resting periods. However, recent work using histological techniques showed that this subspecies has synchronous spawning of both genders with a peak spawning event occurring in late summer (Cúrdia et al. 2005), a result that is in concordance with other species of *Patella* in the NE Atlantic Studies on aspects of the biology suggest that this species may not be a protandrous hermaphrodite (Menezes 1991) as previously thought (Martins et al 1987) According to Menezes (1991), a shell length of 10 mm corresponds to the size of first sexual maturation in *P. c. gomesii*. From here onwards I will refer to this species as *P. candei* alone.

Figure 1.2. Dorsal and ventral views of *Patella aspera* (on the left) and *P. candei* (on the right). Note the darker foot colour of *P. candei* and the lighter foot colour on *P. aspera*.

The other patellid species present in the Azores, *P. aspera* Lamarck, has a broad distribution. Although *P. aspera* is often regarded as the name formerly used for *Patella ulyssiponensis*, genetic differences occur between individuals from the Macaronesia islands and those from continental Europe (Webber & Hawkins 2005). These authors suggest that *P. ulyssiponensis* should designate the continental individuals, whilst *P. aspera* should be referred to individuals from the Macaronesia. *P. aspera* (locally designated as "lapa-brava") is mostly found in the low intertidal of exposed shores though it can occur in the infralittoral (Thompson 1979). It is usually larger than *P. c. gomesii* and has an orange or yellow foot. Its shell is lighter in colour, thicker and more irregular (with well defined ridges) compared to *P. c. gomesii* and it is commonly covered by algae. According to the MarLIN (2006) database and to Thompson (1979), *P. aspera* is a protandrous hermaphrodite. At 20 mm shell length all mature individuals are males, while from 20 mm to full size the number of females increases until at 55 mm where 70% of the mature individuals are female. Maturation of gonads starts in May-June each year and spawning takes place around the beginning of October in the British Isles (Thompson 1979). Larvae can spend from 2 to 10 days in the water column during which they have the potential to disperse over 10 km (Thompson 1979). However, according to Martins et al (1987), contrasting results were obtained for *P. aspera* in the Azores with gamete release occurring in the winter with a peak in January and the time of first spawning corresponding to the shell size of 20-25 mm.

1 3.1. The exploitation of *Patella* in the Azores

In the Azores, shores have been exploited for food since the islands were first colonised and many shellfish populations are currently overexploited including lobsters (*Scyllarus arctus* L. 1758 and *Scyllarides latus* Latreille 1803), barnacles (*Megabalanus azoricus*) and limpets (*Patella* spp.) (Morton et al. 1998). Commercial harvesting of seaweeds (e.g. *Pterocladiella* sp. and *Gelidium microdon*), which are collected for agar (Santos & Duarte 1991) was also common a few years ago This activity has declined although recreational harvesting of seaweeds (e.g. *Porphyra* spp., *Laurencia* spp) for food still occurs at low levels

Arguably the largest anthropogenic impact in the Azorean intertidal is the over-exploitation of the keystone patellid grazers (Hawkins et al 1999). Exploitation of limpets in the Azores has probably been taking place since human colonisation of the islands in the 15th Century (Ferraz et al 2001). Limpet harvesting in the Azores was moderate until the 1980's and was mainly for self-consumption. However, introduction of snorkelling and scuba diving in the early 1980's together with the increase of limpet's commercial value (e g. tourism) led to a prompt increase in limpet exploitation in the archipelago (Ferraz et al 2001) Exploitation intensity varies among islands having been greater in the eastern group, especially in the largest and most populated island of the archipelago, São Miguel. Official statistics show the highest collection of limpets took place in 1984 with 94 tons collected in São Miguel, whilst a total of only 3 tons were collected across the whole of the remainder of the Azores (Martins et al. 1987). Such intense harvesting contributed to the decline of limpets in the archipelago and its fishery collapsed in 1988 (Santos et al. 1990). Limpet harvesting was prohibited in 1989, though in 1990 non-commercial catch quotas were established for the western group (Flores and Corvo) (Menezes et al. 1991). In 1993, the government of the Azores declared a period - between the 1st of October and the 31st of May - during which limpet harvesting is prohibited. Outside this period, limpets can be caught above a minimum size of 3 and 5 cm (maximum shell length) for *P. candei* and *P. aspera* respectively to a maximum of 1 kg $person^{-1}$ day^{-1}. Moreover, within each island, areas were created where limpet harvesting is prohibited throughout the whole year (D.R.R. 14/93/A Diário da República - I Série B, 178). Studies carried out during the period of 1993-98 indicated some recovery of stocks in the central and western groups (Ferraz et al. 2001). In contrast, populations of limpets in the eastern group remained low and are virtually absent.

Most studies concerning the exploitation of limpets in the Azores are based on commercial declared catches. However, recreational and subsistence harvesting of limpets is intense and generalised across the archipelago (Martins pers. obs.). This type of harvesting is often not considered for statistics or managerial purposes although its impact can be high (e.g. Dye et al. 1994). Furthermore, because such studies often use CPUE (in g/min) as a data source, the natural density of limpet populations on the shore has seldom been recorded.

Given the potential impact that the exploitation of limpets can have in the structure and functioning of Azorean intertidal communities, it is surprising that so little is currently known, about the processes such as recruitment, growth and mortality rates, predators, grazing, the effects of wave-exposure, substratum topography that may influence the biology and ecology of these shores, particularly for *P. candei*, an endemic species to the Macaronesian archipelagos

1.4. Human exploitation of marine biotic resources

Rocky shores worldwide are typically open systems, with steep environmental gradients supporting diverse communities of animals and plants (Thompson et al. 2002) Their accessibility to man has rendered them vulnerable to a variety of impacts Human activities can greatly shape marine ecosystems and their effects are usually viewed as negative (Castilla 1999) The ways human activities can influence the structure of marine ecosystems are diverse (Thompson et al 2002), including the exploitation of marine resources (e g Botsford et al. 1997, Castilla 1999), pollution (e g Bishop et al. 2002, Terlizzi et al 2002) and recreational activities (e g Milazzo et al. 2002, Airoldi et al 2005a).

Many locations worldwide with long established human populations have a tradition of local exploitation of marine resources including those in the littoral and in some localities this has been taking place since prehistoric times (Siegfried et al. 1994) Two main attributes distinguish man from natural predators· predation by man is usually facultative rather than obligate, and man is a tool-using predator (Hockey 1994) Although, the harvesting of marine biotic resources was historically done mainly for self-consumption, the latest technological advances (e g. scuba) and the high commercial value commonly attained by targeted species have led to disproportionate increase in pressure on these communities. This has prompted a considerable amount of research, which generally showed that the removal of key species could dramatically change the structure and probably the function of marine ecosystems (see Castilla 1999 and references therein). This raised concern among managers, politicians, biologists and the general public.

In an attempt to protect and foster the sustainable exploitation of marine stocks, a suite of strategies has been put in place in many localities among which the establishment of quotas, minimum harvesting sizes or no-take marine areas are the most common. Despite this effort, many marine fisheries worldwide continue to decline or have collapsed due to over-fishing (Botsford et al. 1997, Jackson et al. 2001, Hilborn et al. 2003, Myers & Worm 2003). Updated estimates indicate as much as 29% of the world's fisheries have either collapsed or are no longer viable, and this level is predicted to increase in the next decades (Worm et al. 2006).

1.4.1. Population-level effects of exploitation

Evidence for the effect of humans, as top predators, in the rocky intertidal comes chiefly from South Africa and Chile (Moreno et al. 1984, Hockey & Bosman, 1986, Oliva & Castilla 1986, Durán et al. 1987, Griffiths & Branch 1997, Castilla 1999, Lasiak 1999 and Siegfried 1994 for review). Exploitation rapidly prompts the reduction of the number and mean size of target populations; this has been demonstrated for a variety of intertidal organism (see Griffiths & Branch 1997 and references therein). Exploitation causes the removal of larger animals leading to a decrease in the mean size of the population (e.g. Branch 1975a, Lasiak 1993, Branch & Moreno 1994). In the Azores too, a decrease of up to 2 cm was recorded in the mean size of limpets between 1983 and 1986 (Martins et al. 1987). The combined effect of reduced abundance and size due to exploitation likely diminish the reproductive output of target populations (e.g. Dadzie et al 2007, Harding et al. 2007, LaPlante & Schultz 2007) In addition, size truncation of exploited populations may be detrimental for protandrous hermaphrodite species where the removal of larger animals will largely target females

Besides the abovementioned effects, exploitation can also influence population dynamics, inertia (the capacity of a population to resist disturbances) or resilience (the capacity of a population to recover from disturbances) For instance, the size truncation of target populations skews population structure towards lower size classes As a consequence, population dynamics becomes chiefly dominated by the immature stages (e.g recruitment or early post-recruitment dynamics), which are naturally more variable than adult stages. Such elevation of variability may affect species' ability to endure stochastic disturbances or climate change (Hsieh et al 2006, Anderson et al 2008) In addition, exploitation of target species to levels where population size is decreased below a critical point may also be detrimental Allee effects may result in reproductive and recruitment failure and thus constraining the resilience of target populations (Courchamp et al. 2008) In addition, the reduction of population size may lead to lower genetic diversity (e.g Hauser et al 2002), whilst smaller populations will be more susceptible to loss of genetic diversity due to genetic drift (e g Allendorf & Luikart 2007)

Individual growth and mortality rates in exploited populations may also be expected to vary as a result of changes in the intensity of density-dependent competition (Creed et al 1996, 1997). For example, Crisp (1960) demonstrated that intense intraspecific competition could lead to a severe reduction in growth rate of barnacles. Additionally, Hawkins (1983) showed that recruitment of *Semibalanus balanoides* only occurred where conspecifics were present on the substrata For algae, growth of germlins declines with increasing density (Choi & Norton 2005). Evidence that intraspecific competition occurs among limpets is also widespread as been shown for *Patella vulgata* (e.g. Boaventura et al. 2002a), *P. depressa* (e.g. Boaventura et al. 2002a, Boaventura et al. 2003), *Cellana tramoserica* (e.g. Creese & Underwood 1982, Fletcher 1984, Keough et al. 1997), *P. cochlear* (e.g. Branch 1975b) and *Notoacmea petterdi* (e.g. Creese 1980). Generally, increased mortality and reduced growth were found with increasing densities of conspecifics. Where studied, the magnitude of intraspecific competition also varied among size-classes (e.g. Keough et al. 1997, Boaventura et al. 2003). Hence, it is logical that a reduction in limpet density due to overexploitation in the Azores could lead to substantial decrease in intraspecific competition and hence changes in the population structure and dynamics. To some extent, the predicted changes, i.e. higher growth rates, may initially benefit the population to override the effects of exploitation. However, as the number of limpet diminishes, Allee effects could affect the recovery of over-exploited populations and might lead to extinction (Stephens et al. 1999, Courchamp et al. 2008).

1.4.2. Community level effects of exploitation

There is a broad recognition of the importance of top-down processes in structuring rocky intertidal communities (see Menge et al. 1999, Menge 2000a for review). Fishing, when targeting keystone species, usually leads to severe changes in the community structure followed by a local change in diversity and shifts in dominance (e.g. Durán & Castilla 1989, Sala et al. 1998, Pinnegar et al. 2000, Shears & Babcock 2002, Guidetti 2006, Guidetti & Sala 2007). For instance, Guidetti (2006) showed that in the Mediterranean Sea, the density of exploited fish species, namely *Diplodus* spp., was greater inside no-take marine reserves. *Diplodus* spp. are the main predators of the sea-urchins *Paracentrotus lividus* and *Arbacia lixula*, whose grazing activities are responsible for the creation of barrens (areas where space is dominated by coralline encrusting algae and characterised by low species richness) As became clear, increased predation (by fish) on a keystone species (sea-urchins) within the reserve increased diversity by preventing monopolisation of space (Paine 1974, Castilla & Durán 1985), which resulted in the development of an exuberant and diverse algal assemblage and associated macrofauna.

The above example also highlights the importance of indirect effects in regulating marine communities (the effect of *Diplodus* spp on the algal assemblage), which can be comparable to those of direct interactions (see Menge 1995 for review). By changing the interplay of direct and indirect interactions, the removal of organisms from a system can have profound effects on structure of marine communities leading to a cascade of changes (see Bianch & Moreno 1994, Hughes 1994, Leinaas & Christie 1996, Benedetti-Cecchi et al 1998, Gagnon et al 2004, Scheffer et al 2005 for review) and from which the recovery will depend on the ecosystem resilience (Castilla et al 1994, Hughes et al 2005). In addition, fishing of large consumer species can either increase or dampen spatial variability of their prey depending on the mean effect size of the removal (Benedetti-Cecchi 2000a)

1 4 2 1 Community level effects of limpet exploitation

Limpets are not consumed in large numbers except in a few locations worldwide and there is, therefore, little information on how this fishery affects community structure (but see Moreno et al. 1984) However, the role of limpets in structuring intertidal communities has long been recognised (see Branch 1981, Lubchenco & Gaines 1981, Hawkins & Hartnoll 1983 for reviews). For instance, experimental removal of limpets from the shore dramatically enhances algal growth and can raise the upper vertical limit of many seaweeds (e.g. Underwood 1980, Underwood & Jernakoff 1984, Branch 1985, Jernakoff 1985, Dungan 1986, Van Tamelen 1987, Farrell 1988, Benedetti-Cecchi & Cinelli 1992, Scheibling 1994, Bulleri et al. 2000, Benedetti-Cecchi et al. 2001a, Boaventura et al. 2002b, Arrontes et al. 2004, Jenkins et al. 2005, Coleman et al. 2006, Jonsson et al. 2006, Davies et al. 2007). In addition, limpets commonly affect the abundance of barnacles (Denley & Underwood 1979, Branch 1981, Underwood et al. 1983, Hawkins 1983, Miller & Carefoot 1989). Grazing by limpets can kill small barnacles by smothering or physically knocking them from the substratum (bulldozing). However, for larger barnacles, grazing can enhance survival through removal of algae that would otherwise overgrow them. At mid-shore heights, limpets, algae and barnacles interact strongly on many rocky intertidal shores and the assemblage is maintained by a set of direct and indirect interactions between all players (e.g. Hawkins & Hartnoll 1983, Jara & Moreno 1984, Dungan 1986, Van Tamelen 1987, Benedetti-Cecchi 2000b). For instance, by directly removing algae, limpets indirectly favour the recruitment of barnacles. At certain densities, barnacles in turn interfere with limpets foraging activity. This indicates that a complex suite of interactions between all players in a system affects the maintenance of the structure of communities and that under certain conditions species activities can even negatively affect themselves (see Fig. 1.3 below).

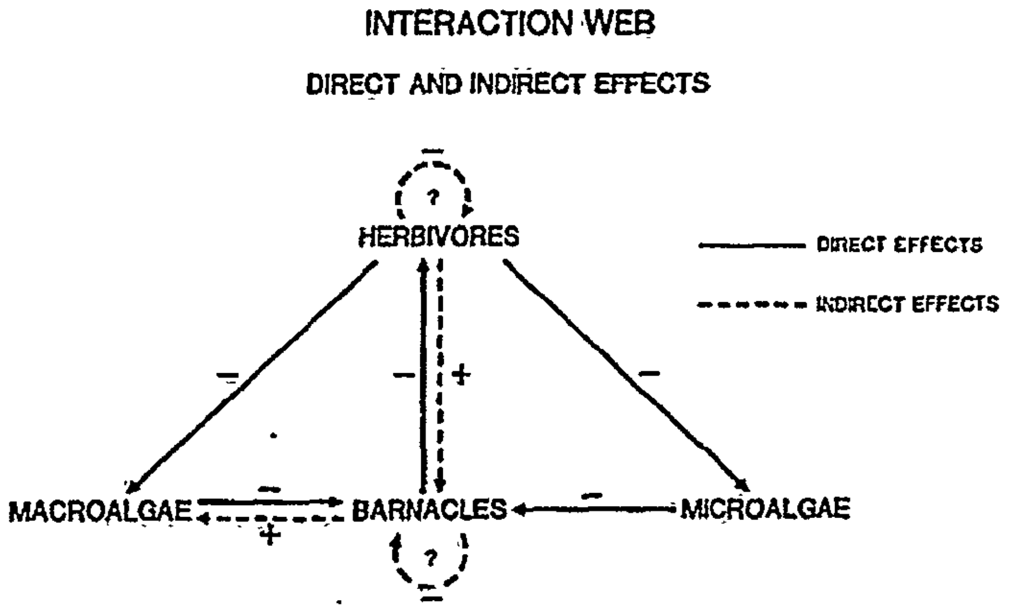

Figure 1.3. Interaction web model between limpets, algae and barnacles (In: Van Tamelen 1987)

Indirect effects of limpets in the rocky intertidal are not limited to barnacles For example, by limiting the settlement of canopy algae (e g Jenkins et al 1999) grazing can promote the growth of turf-forming algae (Benedetti-Cecchi et al 2001b) Furthermore, spatial variability in the distribution of limpet grazing (Johnson et al 2008) likely affects spatial community structure resulting in a mosaic of differing assemblages (Johnson et al 1998a)

Owing to the abovementioned, the commercial harvesting of limpets may be expected to have strong effects on the structure and function on Azorean mid-shore rocky intertidal community

1.5. Summary of chapter aims

The present study aims to examine the role of the patellid limpet *P. candei* in structuring the mid-shore rocky intertidal community in the Azores and how the harvesting of limpets may impact community structure. The role of *P. candei* in structuring Azorean rocky intertidal communities has never been examined. Although much experimental work on the top-down effect of limpets on European rocky shores suggests that the harvesting of limpets likely has a strong impact on Azorean intertidal community structure, examples also exist showing that the role of limpets may be spatially or temporally variable and hence not pervasive as generally thought (Benedetti-Cecchi et al. 2001a, Bertness et al. 2006, Bazterrica et al. 2007).

Until today, much work done on Azorean marine coastal systems has been dominated by taxonomic and biogeographic descriptions of the fauna and flora present in these islands and little is currently known about the processes that shape these communities. To my knowledge, no study has yet compared the community structure among islands at a hierarchy of spatial scales. Because different ecological processes generate variability at different scales, examination of patterns across a range of spatial scales is a fundamental step before explanatory models for these patterns can be proposed (Underwood & Chapman 1996, Hewitt et al. 2007). This gap motivated an initial description of the scales of spatial distribution of intertidal populations (Chapter 2), showing that Azorean shores are largely dominated by processes operating at the larger scale of islands and at the smaller scale of metres.

Following this, I tried to identify the processes that most likely affect the distribution of limpets at the relevant spatial scales. During field observations, it was noted that a large number of animals were commonly associated with particular substratum features, among which pits were the most common. The effect of substratum topography in the distribution of marine animals, in general, is widely recognized (Chapman 1994, Underwood 2004) and has also been shown for limpets (Hawkins and Hartnoll 1982, Gray and Hodgson 1998) These features are thought to ameliorate environmental conditions (e g desiccation) enhancing the survival of intertidal animals, especially juvenile stages The spatial distribution of such topographic features can also affect the structure of intertidal communities by affecting the distribution of key species (e.g. Johnson et al 1998b) Chapter 3, thus examines the effects of pits in determining the small-scale patterns of distribution of *P candei*, while examining the potential use of substratum complexity in enhancing the stocks of limpets on an artificial seawall In contrast, Chapter 4 examines the effects of variable regime of limpet harvesting at the scale of islands in structuring mid-shore communities, whilst in Chapter 5 the intra-island distribution of limpets in regards to the presence (or absence) of legislative protection is examined

Chapter 6 describes a suite of experimental studies used to examine the effects of limpet harvesting at population and community levels In Chapter 4, it became clear that São Miguel Island (the Island with the largest history of limpet exploitation), has an average mid-shore algal percentage cover of 56 3 ± 4 1 (mean ± SE), whilst at Flores (Island with the lowest history of limpet exploitation) algae are restricted to 25 9 ± 3 7 This suggests that the reduced abundance of limpets in São Miguel has led to an upward extension of macroalgae Notably turf-forming species are the dominant growth form at mid-shore levels in São Miguel, whilst at Flores the barnacle *Chthamalus stellatus* secures most of the space at this height Following this, experimental work was done to ask 3 general questions: (i) does the upward extension of turf-forming algae affect subsequent limpet recruitment due to space pre-emption? (ii) are limpets able to regain the space back in the event of harvesting cessation? and (iii) is the current number of limpets able to control algal growth?

The final chapter (Chapter 7) combines results from the above chapters and discusses their implications for the ecology of Azorean rocky shores.

CHAPTER 2

Rocky intertidal community structure in oceanic islands: scales of spatial variability

Rocky intertidal community structure in oceanic islands: scales of spatial variability

2.1. Abstract

There is a clear bias in the literature on island ecology towards terrestrial rather than marine systems, which have remained comparatively poorly studied. Marine populations are typically open and local production may have little impact on local recruitment such that long-distance dispersal is an important determinant of population ecology. Since oceanic islands form discrete patches of habitat surrounded by a structurally different environment I hereby tested the general hypothesis that processes operating at the scale of islands have a greater influence on these populations than the processes operating at smaller, within-island scales. A hierarchical design examined the patterns of abundance and distribution of conspicuous taxa at 3 tidal heights at a range of spatial scales ranging from metres to hundreds of kilometres apart in the rocky intertidal of the Azores. Both uni- and multivariate analyses showed that at the largest scale (islands), significant variation was detected in the lower and mid shore communities, but not on the upper shore. Along the vertical gradient of immersion there was a trend for increasing small-scale patchiness towards the top of the shore. The processes that can generate these patterns are discussed. This study corroborates the suitability of the analytical tools used here to examine patterns of distribution over a range of spatial scales and its applicability in the field of island marine ecology.

2.2. Introduction

Ecological systems are naturally complex and inherently variable and there is an increasing appreciation that better knowledge of this variability is crucial for understanding the ecological processes structuring these systems. Because different ecological processes generate variability at different scales, examination of patterns across a range of spatial scales is a fundamental step before explanatory models for these patterns can be proposed (Underwood & Chapman 1996, Hewitt et al 2007) The development of analytical approaches, such as hierarchical designs and estimates of variance components, allow variability to be examined at a range of spatial scales from very small variability at the scale of the sampling unit, to large geographic comparisons (Underwood 1997).

Rocky intertidal communities have been extensively studied and have proved to be tractable systems for experimental ecology, contributing much toward our general understanding of population and community ecology. There is an extensive literature on most aspects of assemblage structure, including manipulative experiments to test models about competition (e.g Connell 1961), predation or herbivory (e.g Paine 1974, Coleman et al 2006) More complex designs have tested models on the interplay between physical and biological factors (e g. Thompson et al 2004). Furthermore, there has been considerable analysis of spatial and temporal scales of variability of intertidal populations over the last decade (Underwood & Chapman 1996, Benedetti-Cecchi 2001, see Fraschetti et al 2005 for review)

Habitat loss and fragmentation are among the principal factors leading to biodiversity loss (Pimm & Raven 2000), prompting considerable research on the study of habitat patchiness Archipelagos form highly fragmented habitats surrounded by a structurally different system and are useful to test ecological hypotheses that can be of relevance to a range of other patchy habitats including marine protected areas, seamounts, and freshwater lakes In recent years island ecology has been dominated by island biogeography theory based on MacArthur & Wilson (1967), which is based on the assumption that the number of species on islands results from the balance between immigration and extinctions, the former influenced by the distance from the mainland and the latter by the effect of island area acting on population size. Thus, a common approach has been to count the number of species on islands of differing sizes and relate these patterns of species richness to the geographical or physical attributes of islands (Báldi & McCollin 2003). However, the model of island biogeography has been fraught with difficulties owing to the accumulation of contradictory results and the study of island ecology has more recently embraced a meta-population approach (Lomolino 2000, Báldi & McCollin 2003). Although the importance of carrying out work over a greater range of spatial scales in the study of islands has been stressed (e.g. Whittaker 2000), these have remained scarce. In contrast to the literature on terrestrial ecosystems, marine island ecology has lagged behind (but see Tuya & Haroun 2006, Cornell et al. 2007).

A suite of analytical procedures is now available to ecologists that allow us to examine patterns of distribution at a range of spatial (or temporal) scales. The few studies that have applied these methodologies to marine island ecology (e.g. Ramírez et al. 2005, Tuya & Haroun 2006) have provided valuable insights into the processes shaping these populations. Hence one of the principal objectives of this study was to identify the relevant scales of variation in order to help focus our attention on the physical and biological factors that most probably influence these systems.

In addition, oceanic islands form patches of habitat surrounded by a structurally different oceanic environment. In such open systems larval retention is probably low and local production may have little impact on local recruitment (Hughes et al. 1999, Swearer et al. 1999). Since the majority of intertidal animals and plants have at least a short planktonic phase during their life-cycle, and because the capability to disperse over long distances is a strong determinant of the biogeography of sessile marine organisms which vary noticeably among species (Johnson et al. 2001), it has been suggested that the processes operating at larger-scales may play a key factor in the population biology and in structuring marine island communities Thus, as a second objective of this study, I examined the proposition that regional-scale processes are central in structuring marine island communities and that this will be detected by greater variability at the scale of islands rather than at the smaller within-island scale

2.3. Materials and methods

2 3 1 Study site and community

The present study was done at 4 islands of the Azorean archipelago Flores, Graciosa, Pico and São Miguel (see Fig 1 1). The present study was carried out at 3 shore heights corresponding to distinct communities. low shore algal dominated levels (1.20 ± 0.10 m above Chartum Datum (CD)), mid shore levels (1.90 ± 0.10 m above CD) at the boundary between the turf-forming algae and barnacle/rock cover, and high shore animal dominated levels (2 50 ± 0 10 m above CD) towards the upper limit of limpets and barnacles Heights were determined in relation to low water using levelling poles. The most abundant organisms throughout the archipelago were turf-forming algae lower on the shore and the chthamalid barnacle *Chthamalus stellatus* higher up. Among patellid limpets, *Patella candei* was the most common grazer at mid shore levels whereas *P aspera* was also present on the low shore *Fucus spiralis* formed scattered clumps at mid shore levels, while *Sargassum* spp. and *Cystoseira* spp. were commonly found in rock pools High shore grazers included the littorinids *Littorina striata* and *Melarhaphe neritoides*

2.3.2. Sampling design

A hierarchical design was adopted to examine patterns of species distribution at 4 islands separated by 120 to 515 km. Islands were randomly selected but stratified to encompass at least one island per group (western, central and eastern) and hence cover the whole archipelago.

Within each island, 3 exposed locations (km's apart) were selected at random. Within each location, 3 sites (10's m apart) comprising a stretch of coast of 20 m were randomly selected and 5 replicate quadrats (m's apart) of 25 × 25 cm randomly placed on well-drained rock were used at each tidal level at each site. Digital photography was used to rapidly assess community structure and hence allow for a high level of geographical coverage and replication. Photographs were analysed by overlaying 50 random points and recording the organisms beneath. The lack of abundant erect algae allowed this approach to accurately determine percentage cover of major space occupiers. The abundance of coralline turf (e.g. *Corallina elongata* Ellis & Solander 1786, *Jania* spp.), coarsely branched algae (e.g. *Gelidium* spp., *Osmundea* spp.), foliose algae (*Ulva* spp.), canopy-forming algae (*Fucus spiralis*) and the barnacle *Chthamalus stellatus* were expressed as percentage cover. Mobile invertebrates such as gastropods were counted and expressed as number per quadrat. Organisms that were scarce at the levels examined (e.g. encrusting and erect corallines, *Melaraphe neritoides*) or difficult to identify against a black basaltic background (e.g. the encrusting alga *Ralfsia* sp.) were not analysed.

2.3 3 Data analysis

2 3 3 1 Univariate analysis

To examine patterns of spatial variation I used a 3-way fully nested analysis of variance (ANOVA) for each tidal height Factors were island (random, 4 levels), shore (random, 3 levels) and site (random, 3 levels) with 5 replicates Cochran's test was used to check homogeneity of variances and transformations applied where necessary (Underwood 1997). Occasionally, heterogeneity of variances persisted after transformation. In these cases, analysis was done on untransformed data since ANOVA is robust to departures from this assumption where replication is high (Underwood 1997). However, a more conservative p-value (< 0.01) was used

Mean square (MS) estimates were used to assess the variation associated with each scale This was done by dividing the difference between the MS of the term of interest and the MS of the term hierarchically below, by the product of the levels of all terms below that of interest Negative estimates of variation were removed from the analysis and all the other values were recalculated following the procedure described by Fletcher & Underwood (2002) Estimates of spatial variation were reported as actual variances to guarantee independence and allow comparisons with other habitats, but also as percentages to better ascertain the magnitude of each scale contribution to patterns of distribution

2 3 3 2 Multivariate analysis

To examine patterns of assemblage structure at different spatial scales the same general procedure as described for the univariate analysis was applied but using a distance-based multivariable analysis of variance (PERMANOVA, Anderson 2001)

The multivariate pseudo-variance components can be considered as analogues to the univariate ANOVA estimators (Anderson MJ pers. comm.) and these were used to calculate the components of variation associated with each term in a similar way as described for the univariate analysis. Graphical representation of the centroids for sites used non-metric dimensional scaling (MDS). All multivariate analyses were performed on untransformed data, using Bray-Curtis dissimilarity measures and 999 permutations.

2.4. Results

2.4.1. Univariate analysis

2.4.1.1. Low shore community

The lower shore community was dominated by algal turf assemblages mainly composed of coralline (e.g. *Corallina* spp.) and coarsely branched (e.g. *Gelidium* spp.) algae. Macroinvertebrates were scarce and restricted to a few individuals of *P. aspera*. Three morphological groups of algae were considered for analysis. These differed significantly in their patterns of spatial variability (Fig. 2.1, Table 2.1). Coralline turfs and coarsely branched algae showed significant variation at both small and large spatial scales, but for both, the scale of island was responsible for most of the overall variability (Table 2.4). Mean percentage cover varied among islands from 35 to 78% and from 13 to 59% in coralline turfs and coarsely branched algae respectively (Fig. 2.1). In contrast, foliose algae showed no variation at this spatial scale (Table 2.1) but had high variability at the smaller scale of quadrats (see Table 2.4).

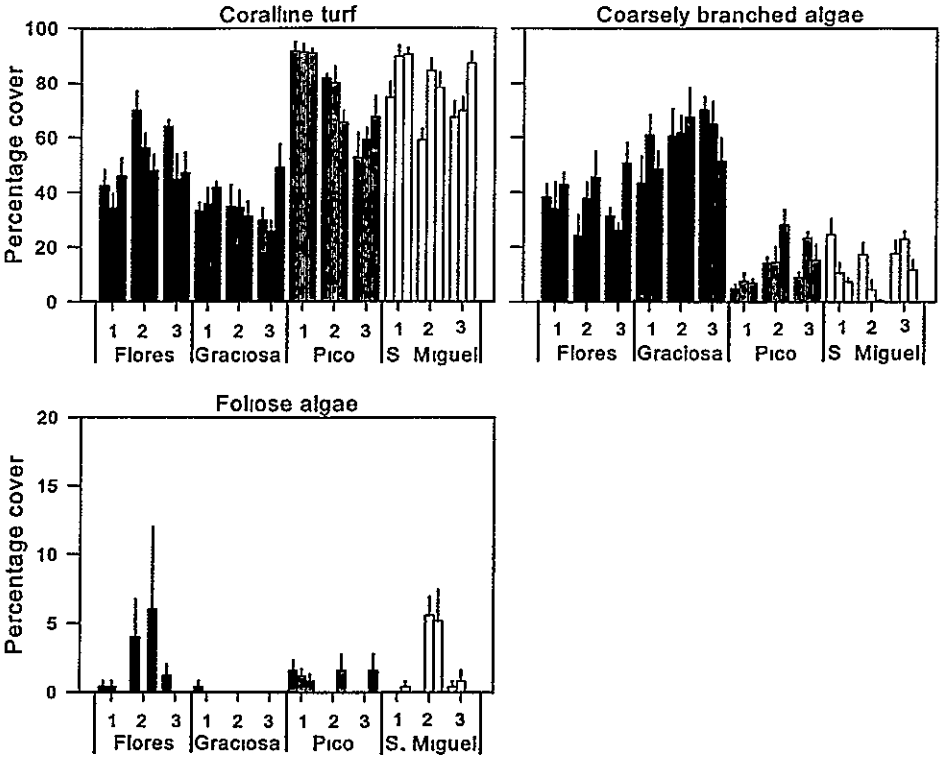

Figure 2.1. Mean (+SE) abundance of algal morphological groups on the lower shore at a hierarchy of spatial scales Within each island, the abundance of algae is shown for each of the three shores (km apart) surveyed (numbered). Flores. 1 - Fajã Grande, 2 - Lajedo, 3 – Fajãzinha, Graciosa: 1 - Porto Afonso, 2 - Santa Cruz, 3 – Carapacho, Pico· 1 - Prainha, 2 - Lajes, 3 - Santa Cruz; São Miguel: 1 - Lagoa, 2 - Caloura, 3 - Mosteiros For each shore, there are three vertical bars, each representing one of the three sites (metres apart) surveyed

2 4 1 2 Mid shore community

The mid shore community structure was a mixture of both algae and animals (Figs 2 2 and 2 3) These formed a mosaic structure consisting of algal patches, mainly composed of coarsely branched algae and in few locations of *Fucus spiralis*, interspersed among patches of barnacles and bare space Limpets were the main grazing gastropods and were found in algal-free patches

Table 2.1. 3-way fully-nested ANOVA comparing the abundance of lower-shore taxa at a hierarchy of spatial scales: islands (Is), shores (Sh) and sites (Si).

		Coralline turf		Coarsely branched		Foliose algae	
Source	df	MS	*F*	MS	*F*	MS	*F*
Is	3	$1.9E^4$	13.8**	$2.1E^4$	49.05***	22.43	0.71
Sh (Is)	8	$1.4E^3$	3.45**	$4.3E^2$	1.31	31.71	3.33*
Si (Is × Sh)	24	$4.0E^2$	2.68***	$2.3E^2$	1.93**	9.53	1.08
Residual	144	$1.5E^2$		$1.7E^2$		8.87	
Transformation		none		none		none	
Cochran's		$C = 0.08$		$C = 0.10$		$C = 0.56$**	

Here and afterwards, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, E = ×10

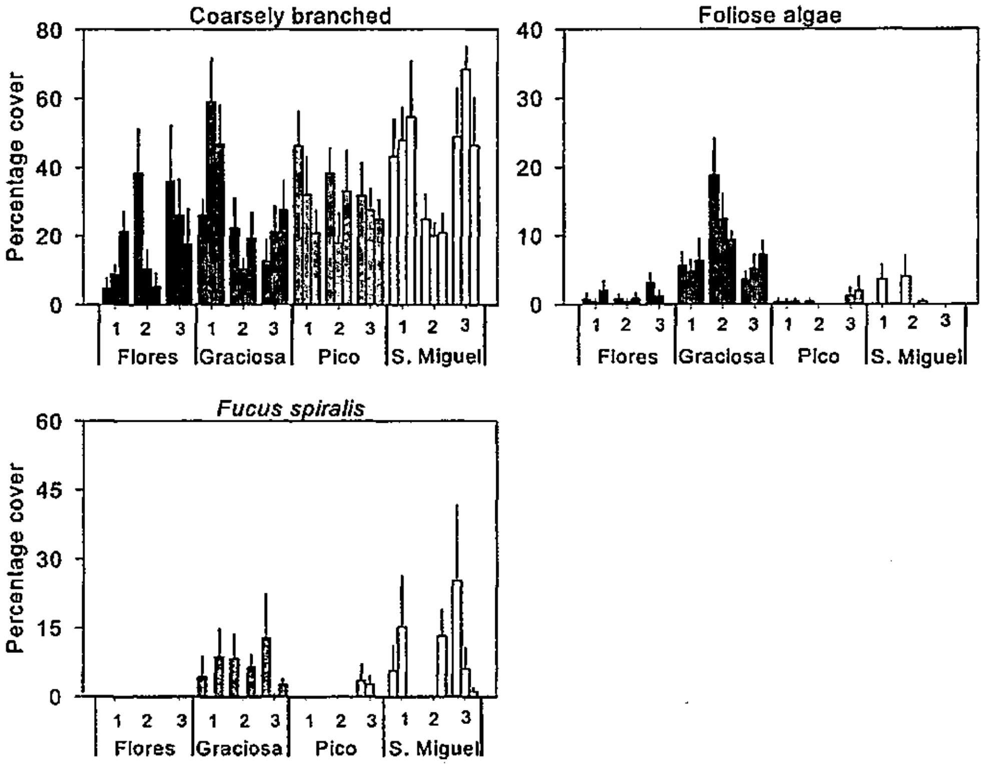

Figure 2.2. Mean (+SE) abundance of algal morphological groups on the mid shore at a hierarchy of spatial scales. Legend as in Fig. 2.1

Among the algae, 3 morphological groups were relatively abundant but differed significantly in their patterns of distribution (Fig. 2.2, Table 2.2) Coarsely branched algae showed no significant variation at either the scale of island or site (Table 2 2) and most variability was present at the scale of quadrats (see Table 2.4). In contrast, foliose algae and *Fucus spiralis* showed significant variation at the scale of islands ranging in cover between 1 and 8% and 0 and 7%, respectively (Fig 2 2, Table 2.2), but for both, the scales associated with most variation differed. Whilst for foliose algae most of the variation was similarly associated with both the larger (38%) and smaller (45%) spatial scales, for *F spiralis* the processes operating at the smaller scale of quadrats had much greater influence (86%) on the patterns of distribution (see Table 2.4)

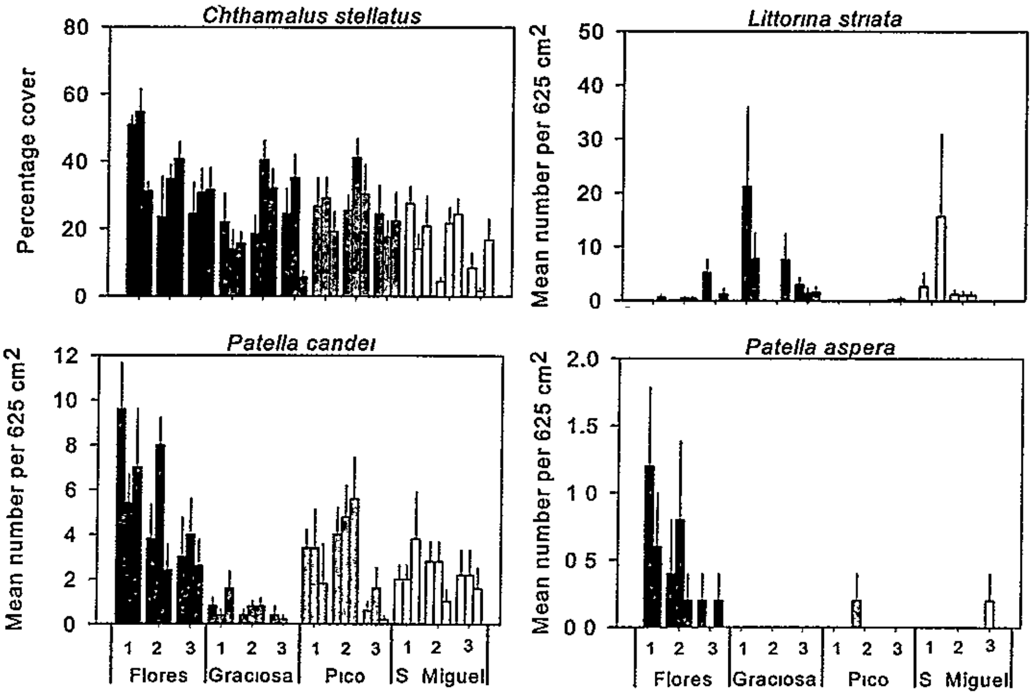

Figure 2.3. Mean (+SE) abundance of macroinvertebrates on the mid shore at a hierarchy of spatial scales Legend as in Fig 2.1

Table 2.2. 3-way fully-nested ANOVA comparing the abundance of mid-shore taxa at hierarchy of spatial scales: islands (Is), shores (Sh) and sites (Si).

		Coarsely branched		Foliose algae		*Fucus spiralis*	
Source	df	MS	*F*	MS	*F*	MS	*F*
Is	3	4.1E^{3}	1.87	27.6	12.8**	9.53	14.3**
Sh (Is)	8	2.2E^{3}	3.91*	2.15	4.09**	0.66	0.34
Si (Is × Sh)	24	5.5E^{2}	1.29	0.52	1.03	1.96	2.39***
Residual	144	4.3E^{2}		0.51		0.82	
Transformation		none		Sq-Rt		Ln (x+1)	
Cochran's		$C = 0.09$		$C = 0.12$		$C = 0.12$	
		C. stellatus		*Patella aspera*		*Patella candei*	
Source	df	MS	*F*	MS	*F*	MS	*F*
Is	3	3.2E^{3}	4.56*	1.67	7.35*	153.1	3.99
Sh (Is)	8	7.0E^{2}	1.79	0.23	1.11	38.3	4.33**
Si (Is × Sh)	24	3.9E^{2}	1.97**	0.21	1.23	8.6	1.23
Residual	144	2.0E^{2}		0.17		7.17	
Transformation		none		none		none	
Cochran's		$C = 0.10$		$C = 0.28$**		$C = 0.13$	
		Littorina striata					
Source	df	MS	*F*				
Is	3	189.5	1.68				
Sh (Is)	8	112.6	1.27				
Si (Is × Sh)	24	88.5	1.23				
Residual	144	72.0					
Transformation		none					
Cochran's		$C = 0.46$**					

Patterns of spatial distribution differed substantially among invertebrates (Fig. 2.3). The barnacle *Chthamalus stellatus* showed significant variation at the scale of islands ranging in mean cover between 16% (São Miguel) and 36% (Flores) (Fig. 2.3, Table 2.2). Significant differences were also detected at the scale of sites (Table 2.2).

Heterogeneity of variances meant that at a more conservative p-value, there was no significant variation associated with any scale for *P aspera* (Table 2 2). However, patterns of distribution of the conspecifc *P candei* differed among shores (Fig 2.3, Table 2.2). For all mid-shore invertebrates, despite significant effects of island and site, the greatest proportion of spatial variation was associated with the smallest scale of quadrats (see Table 2 4)

2 4 1 3 High shore community

On the animal dominated high shore, erect algae were reduced to a few plants of *Ulva rigida C* Agardh 1823 but these were mostly restricted to pits or crevices. *P. candei* was the only limpet found at this tidal height but its abundance was low. The analysis was limited to the 2 most abundant species *Chthamalus stellatus* and *Littorina striata* (Fig 2.4). Both species showed similar patterns of spatial distribution with significant differences evident at the scales of shore and site, but not at the scale of islands (Table 2 3) For both species, a greater proportion of variability was associated with the smaller scale of quadrats, whilst intermediate levels of variation were found at the scales of shore and site (see Table 2.4)

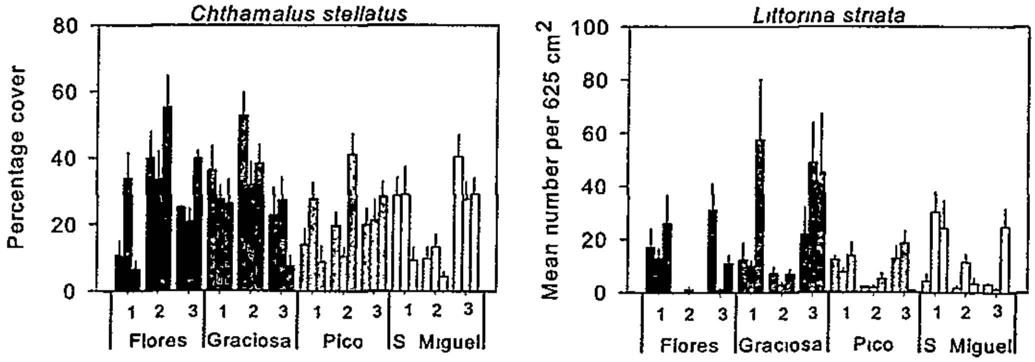

Figure 2.4. Mean (+SE) abundance of macroinvertebrates on the upper shore at a hierarchy of spatial scales Legend as in Fig 2 1

Table 2.3. 3-way fully-nested ANOVA comparing the abundance of taxa on the upper-shore at a hierarchy of spatial scales: islands (Is), shores (Sh) and sites (Si).

		Chthamalus stellatus		*Littorina striata*	
Source	df	MS	*F*	MS	*F*
Is	3	1106.2	0.67	5.96	0.58
Sh (Is)	8	1647.5	3.15*	10.22	2.97*
Si (Is × Sh)	24	523.8	3.18***	3.44	3.77***
Residual	144	164.8		0.91	
Transformation		none		Ln (x+1)	
Cochran's		$C = 0.08$		$C = 0.11$	

Table 2.4. Univariate estimates of variance associated with each scale (islands, shores, sites and quadrats) and the respective percentage contribution. Bold values denote contributions greater than 50% of overall variability.

	Island		Shore		Site		Quadrat	
	var	%	var	%	var	%	var	%
Lower shore								
Coralline turf	392.9	**60**	65.4	10	50.1	8	149.0	23
Coarsely branched	464.4	**69**	6.8	1	32.1	5	172.6	26
Foliose algae	0.0[a]	0	1.31	13	0.13	1	8.87	**86**
Mid-shore								
Coarsely branched	42.0	7	107.5	18	24.6	4	430.0	**71**
Foliose algae	11.6	38	4.55	15	0.61	2	13.84	45
Fucus spiralis	9.46	9	0.0a	0	5.9	5	95.4	**86**
Chthamalus stellatus	55.5	18	20.7	7	38.7	12	199.3	**63**
Patella aspera	<0.1	0	0.0[a]	0	0.0[a]	0	1.41	**100**
Patella candei	2.6	21	2.0	16	0.3	3	7.2	**60**
Littorina striata	1.7	2	1.6	2	3.4	4	71.7	**91**
Upper shore								
Chthamalus stellatus	0.0[a]	0	65.1	22	71.8	24	164.8	**55**
Littorina striata	10.1	2	63.2	14	85.8	20	277.5	**64**

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[a] Negative values were eliminated from the model following Fletcher & Underwood (2002).

2 4.2. Multivariate analysis

Significant variation in the assemblage structure was detected at all spatial scales both on the lower and mid shore tidal heights (Fig 2 5, Table 2 5) In contrast, the structure of higher shore assemblages was similar among the 4 islands examined, although there was significant variation at smaller spatial scales. Variability at the largest spatial scale was high lower on the shore but decreased with increasing shore height (Table 2 6). Residual variation, however, was low at the bottom of the shore but high at both the mid and high shore assemblages.

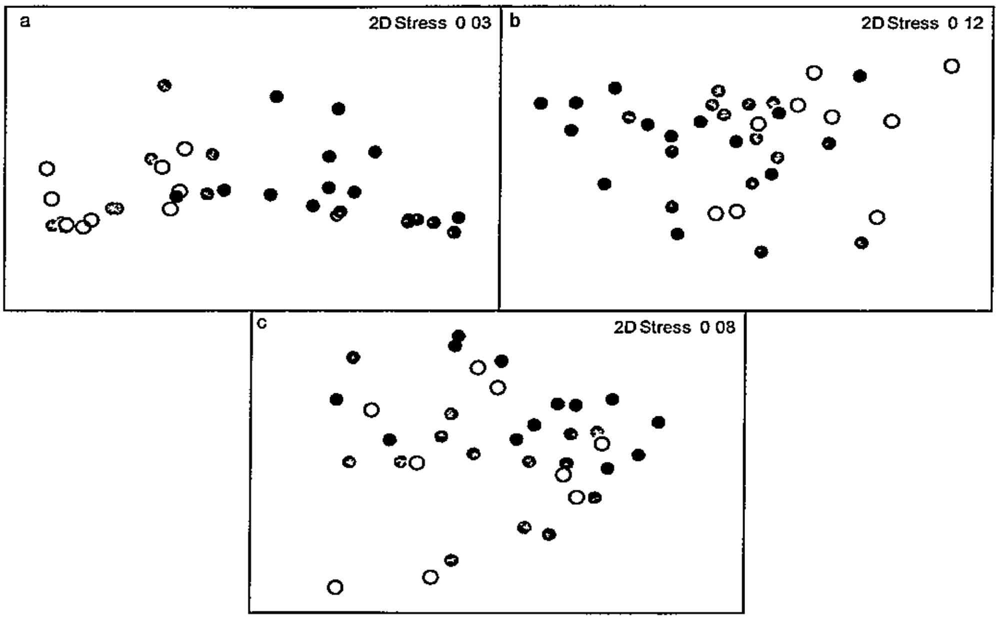

Figure 2.5. MDS ordination representing the community structure on the a) low, b) mid, and c) high shore tidal heights at a hierarchy of spatial scales. Each circle represents the centroid for that site. (Flores – black, Graciosa – dark grey, Pico – light grey, São Miguel – white)

Table 2.5. 3-way fully-nested PERMANOVA comparing the assemblage structure at a hierarchy of spatial scales on each tidal height.

		Lower shore		Mid shore		Upper shore	
Source	df	MS	*F*	MS	*F*	MS	*F*
Is	3	$2.3E^4$	21.48**	$1.5E^4$	4.11**	$4.2E^3$	0.57
Sh (Is)	8	$1.1E^3$	2.22*	$3.6E^3$	2.03*	$7.4E^3$	2.90**
Si (Is × Sh)	24	$4.8E^2$	2.29**	$1.8E^3$	1.69**	$2.5E^3$	2.65**
Residual	144	$2.1E^2$		$1.0E^3$		$9.6E^2$	

Table 2.6. Multivariate estimates of pseudo-variance associated with each scale (islands, shores, sites and quadrats) and the respective percentage contribution. Bold values denote contributions greater than 50% of overall variability.

	Island		Shore		Site		Quadrat	
	var	%	var	%	var	%	var	%
Lower shore	483.2	**62**	38.8	5	53.9	7	209.7	27
Mid shore	247.3	16	120.7	8	144.4	9	1044.1	**67**
Upper shore	0.0a	0	263.0	17	315.8	21	959.1	**62**

Legend as in Table 2.4

2.5. Discussion

The structure of rocky intertidal communities in temperate oceanic islands has received far less attention than that on mainland coastlines. Characterization of spatial (or temporal) scales of variation is a preliminary step to subsequent experimental test of hypotheses. Identification of appropriate scales can centre our attention on the most relevant processes (Benedetti-Cecchi 2001), while integrative studies including manipulative experiments across identified significant scales of variation are an important means of scaling up from local manipulative experiments (Hewitt et al. 2007). Moreover, partitioning natural variability across a range of spatial scales is useful for comparisons with other studies and habitats, provided that similar scales are used.

Much experimental work has provided evidence of the small-scale processes influencing rocky intertidal populations. For instance, small-scale variation may result from spatial differences in pre-recruitment processes such as the dispersal of larvae or propagules (e.g. Bobadilla & Santelices 2005), recruitment itself (e g. Coleman 2003), post-recruitment processes such as grazing (e g. Benedetti-Cecchi et al 2001), competition (e.g. Steneck et al. 1991), or mortality (e g Jenkins et al 2001) and physical stress mediated by small-scale spatial differences in topographic features of the substratum (e g. Underwood 2004) and disturbances (e g Sousa 1979). A high level of small-scale variation seems to be an intrinsic feature of most marine habitats including soft-sediment habitats (e g. Ysebaert & Herman 2002), rock pools (e g Metaxas & Scheibling 1993), coral reefs (e.g Hughes et al 1999), or seagrass beds (e g. Piazzi et al. 2004) Whilst many studies on marine systems provide evidence of the pervasive nature of small-scale spatial variability (see Fraschetti et al. 2005 and references therein), few have examined naturally fragmented and isolated habitats such as islands

Oceanic islands typically form discrete patches of habitat In such open systems, larvae produced by benthic adults and released to the water column are dispersed away through physical transport and local larval retention may be minimal (Hughes et al 1999, Swearer et al 1999) Since recruitment is a key process in structuring marine populations (reviewed by Caley et al. 1996), it is suggested that patterns of oceanic current transport will be a key process in structuring island populations Although the experimental manipulation of large-scale processes is fraught with difficulties, their influence on population dynamics can be ascertained by examining the scale at which most variability is associated For instance, work in the Canary Islands has detected significant variation in the abundance of several taxa at the scale of islands (Ramírez et al. 2005, Tuya & Haroun 2006), which were linked to regional-scale differences in the productivity of coastal waters. This has also been shown in fragmented terrestrial systems, where an important proportion of variation is also commonly detected at the scale of landscapes (e.g. Saab 1999).

In this study, there was significant variation among islands for most taxa in the lower and mid shore but not higher on the shore. Lower shore algal dominated communities were mostly influenced by processes operating at the scale of islands as was clear by the great variability associated with this scale. At mid shore heights, however, despite significant variation among islands, there was a greater proportion of variability at the scale of the sampling unit, except for foliose algae, which showed similar levels of variability associated with both the smallest and largest scales. Both univariate and multivariate analyses concurred with these patterns suggesting that along the vertical gradient of emersion, there is a trend for a decreasing influence of processes operating at larger-scales with increasing shore height. This may be the result of differences in the dispersal ability between the lower shore algal dominated assemblages (Bobadilla & Santelices 2005) and the higher shore animal dominated communities (Johnson et al. 2001). However, higher shore assemblages were notably dominated by the barnacle *Chthamalus stellatus* and the grazing mollusc *Littorina striata*. Both species have planktonic larvae and hence can disperse over large spatial scales. In fact, genetic evidence indicates that, at least for *L. striata*, there is larval exchange among islands (De Wolf et al. 2000). This highlights the potential influence that large-scale processes (e.g. currents) may have on the distribution of these animals and it is, therefore, odd that large-scale variation was not detected in the present study. A more likely explanation could be that the influence of large-scale factors on higher shore populations was masked by an interaction between the increased environmental harshness towards the top of the shore, which tends to lead to greater patchiness (Underwood & Chapman 2000), and the reduced time during which these populations are influenced by the marine environment. This pattern was clear in populations of *C stellatus*, which showed a broad vertical distribution At the lower limit of its distribution, there was significant variation at the largest and smallest spatial scales However, toward the upper limit of distribution, variation significantly increased at the smaller spatial scale

The rocky intertidal of the Azores is characterised by hard basaltic shores exposed to high wave action with sheltered areas restricted to harbours and any few nutrients that run-off from land are quickly lost in the vastness of the sea, while its isolation limits any such influence from the nearest land mass (Morton et al 1998) In addition, the islands of the Azores encompass little latitudinal variation, with similar climate among islands Thus, the rocky intertidal of the Azores forms a rather uniform habitat with few obvious gradients in the physical environment. In this scenario, the sources for the large-scale variation in the distribution and numbers of rocky intertidal animals and plants are probably related to the seasonal variation in the intensity and direction of currents, the time that larvae can spend in the water column and their ability to find suitable substratum for colonisation Examination of the temporal and spatial patterns of settlement and recruitment could greatly benefit our understanding regarding the dynamics of these populations However, the possibility that other processes could also produce significant variation in the structure of intertidal populations at the larger scale of islands must not be discarded For instance, there is evidence suggesting that the influence of anthropogenic activities (e g fishing) can change the abundance of exploited species among islands (Tuya et al. 2006) In the present study, this could well be the case for patellid limpets (see Chapter 4), which are harvested at dissimilar levels on different islands (Hawkins et al. 2000).

In conclusion, it is clear that variability is an intrinsic feature of oceanic islands. Significant variation was detected at all spatial scales examined indicating the complexity of insular intertidal systems. As hypothesised, the processes operating at the larger scale of islands played an important role in structuring these populations. This was, however, most pronounced on the lower algal dominated communities suggesting an interaction between the processes affecting the horizontal (e.g. currents, coastal productivity) and vertical (e.g. environmental harshness) patterns of distribution. The pervasive nature of small-scale variability was also confirmed in this study, but this was more pronounced higher in the shore as a result of increased physical stress. This study emphasises the need to use complex analyses to realistically describe patterns of variability. This can be achieved by using an integrative approach involving uni- and multivariate analysis of hierarchical spatial (or temporal) scales of variation and analysis of associated variance components and should be applied in a range of ecological studies relevant to the field of island ecology.

CHAPTER 3

Small-scale patterns of distribution of *Patella candei*:

Influence of microhabitats

Small-scale patterns of distribution of *Patella candei*: Influence of microhabitats

3.1. Abstract

It is widely recognised that microhabitats are important for a variety of marine organisms. Here I examined the influence of microhabitats on the distribution and survival of the exploited limpet *Patella candei* on natural shores before determining the effect of introducing such habitats to an artificial seawall. On natural shores individuals were associated with pits (a natural feature of volcanic rocky shores). Animals inhabiting pits showed reduced mortality and were smaller than those on open rock. Microhabitat utilisation was similar over the vertical range of distribution of *P. candei*. Following observation of natural patterns, we applied this knowledge by experimentally drilling pits at varying densities and sizes in a seawall that had been constructed with simple topographical complexity. Overall, the number of animals increased in areas with experimentally increased microhabitat area. There was evidence that this was the result of immigration (larger animals) but also of increased recruitment. The number of recently recruited animals increased with pit density but this was not the result of increased microhabitat area per se. Larger animals were limited by the size of pits but did not seem to respond to increased density of larger pits. Overall, our results indicate that microhabitats influence the distribution and survival of *P. candei* and the kind of modification here applied to artificial habitats can be easily applied to mitigate their impacts on natural systems or to enhance the stocks of locally exploited species.

3.2. Introduction

Coastal systems are highly productive but their accessibility has rendered them susceptible to a variety of anthropogenic impacts (Thompson et al. 2002) and there is increasing appreciation that a wide range of human activities have altered or degraded coastal marine ecosystems. Exploitation of living marine resources is one such activity, which, through direct and indirect effects can affect the trophic structure of marine ecosystems (e.g. Botsford et al 1997, Castilla 2000)

The management of fisheries has mainly been via restrictive or precautionary measures, among which, the establishment of quotas, minimum catch sizes or the implementation of no-take marine reserves and closed seasons are the most common In addition, alternative and more proactive measures such as the deliberate release of cultured animals have increased in recent years (Booth & Cox 2003) despite some concern that this measure may have negative effects, for instance, by changing the genetic diversity of wild populations or introducing diseases (Bartley et al 2006, Bell et al 2006)

The deployment of artificial structures that increase habitat complexity in marine habitats or confer protection to certain life stages have been widely used with the purpose of enhancing fishery resources or the rehabilitation of habitat loss Successful examples exist for the stock enhancement in populations of rock lobsters (Butler & Herrnkind 1997, Briones-Fourzán et al 2007, Herrnkind et al 2007), fish (Santos & Monteiro 1997, Leitão et al. 2008) and algae (Choi et al 2002, Oyamada et al 2008) The materials conventionally used as artificial reefs are mostly concrete blocks although other materials (e g waste vehicle tires) have also been tested The potential use of such structures in enhancing the stocks of intertidal sedentary or sessile species (e.g limpets, goose barnacles) has, however, been largely overlooked.

The deployment of artificial structures in coastal areas is, however, controversial Worldwide urbanisation has resulted in substantial proportions of the coast being replaced by artificial structures such as marinas, breakwaters or seawalls (e g. Sydney Harbour, Austialia – Airoldi et al 2005b, Chapman 2006, Goodsell et al

2007) and much work has shown that coastal defence structures are poor surrogates for the natural habitats they replace (Chapman 2003, Chapman & Bulleri 2003, Moschella et al. 2005, Chapman 2006) and their impacts can extend to adjacent systems (Kelaher et al. 1998, Martin et al. 2005, Goodsell et al. 2007, Clynick et al. 2008). The predicted increase in storm frequency and sea-level rise due to global warming, as well as increased demands for renewable energy is however likely to exacerbate the number of artificial structures that will be deployed in coastal habitats (Thomson et al. 2002, Booth & Cox 2003). Modifications to existing and proposed coastal engineering structures offer an opportunity for integrative management between the need to protect coastal areas or generate energy and stock enhancement (Moschella et al. 2005).

Conservation of disturbed systems requires a sound understanding of the life history and ecology of the target species. Intertidal animals such as limpets experience extreme environmental conditions during the low tide period (e.g. Lewis 1964) associated with thermal and desiccation stresses (Harley 2003). These animals, especially upper shore species, usually have high physiological tolerances (e.g. Wolcott 1973) and exhibit a range of morphological (e.g. Vermeij 1973, Branch & Marsh 1978) and behavioural (e.g. Garrity 1984, Williams & Morritt 1995) adaptations which help to reduce the effects of environmental stress. The selection of particular habitats such as crevices or pits can greatly reduce physical stress (Jones & Boulding 1999) for example allowing species to survive higher on the shore. Microhabitats are topographic features and are considered important refugia for a wide range of intertidal organisms by dampening environmental extremes (Fairweather 1988, Gray & Hoddson 1998) and providing protection from predation (Bertness et al. 1981, Garrity 1984). Microhabitats can be provided by physical features such as crevices (Fairweather et al. 1984, Gray & Hodgson 1998) and pits (Chapman 1994, Underwood 2004), or biological features such as the tests of living or dead barnacles (Underwood & McFadyen 1983, Bros 1987) and engineering species (Crowe 1996, Thompson et al. 1996) Microhabitats ameliorate environmental conditions by reducing thermal and desiccation stresses during the low tide period (Gray & Hodgson 1998). Hence they can be key features for the recruitment and survival of many species of marine molluscs including limpets (e.g. Hawkins & Hartnoll 1982, Gray & Hodgson 1998) and snails (e.g Catesby & McKillup 1998). This is especially the case for juvenile stages, which show less resistance to environmental stress (Branch & March 1978). The majority of man-made structures (seawalls, breakwaters, pilings) typically lack the habitat complexity of natural shores and this is widely recognised as the main factor affecting the assemblages they support (Chapman 2003)

In the present study, I examined the influence of microhabitats in the distribution and survival of *P. candei* on natural shores Following this, I tested the general hypothesis that under the model that microhabitat provision affects the distribution and survival of *P candei* on natural shores, I would predict that in areas of a seawall with experimentally added microhabitats the number of limpets would increase a proportion to the extent of increase of provision of microhabitat and that a greater number of limpets would survive adverse conditions

3.3. Materials and methods

3.3 1 Study sites

Observational work was undertaken on two moderately exposed rocky platforms on the south coast of São Miguel Island (37°50'N, 25°15'W) Lagoa and Caloura (see Chapter 2 for community description), whilst the experimental study used a steep seawall consisting of large regular-sized blocks of natural rock at São Roque constructed in 2005. Although the seawall was made up of natural rock (basalt), its surface was smooth and lacked the micro-topographic complexity of the surrounding natural rocky shores (substratum rugosity, estimated as the difference in length of 5 replicate 100 mm aluminium sheets moulded to the substratum. Seawall - 3.1 ± 0.6 mm (mean ± SE), and natural shore - 18.5 ± 1.8 mm. 2-way ANOVA: significant main effect of habitat (seawall vs. natural shore) $F_{1,17}$ (pooled) = 28.87, $p < 0.001$, unpublished data).

3.3.2. Sampling design

3.3.2.1. Observational study

Patterns of distribution of *P. candei* were examined during May 2006 at two shore heights well within its vertical range of distribution and where its abundance is greatest: at approximately 1.5 m above Chart Datum (CD) and at approximately 2.2 m above CD. At each location, 3 sites, each being a stretch of coast of approximately 20 m in length and separated by at least 50 m were chosen. At each tidal height, 6 replicate quadrats of 25 × 25 cm were deployed at random within areas of well-drained bedrock. The size of the quadrat considered was a compromise between the need to sample relatively large number of animals (for analytical purposes) and the size of natural patches free of algae typically found lower on the shore. Smooth areas of rock with clearly identifiable pits were selected on both shores. At the lower sampling level, turf-forming algae monopolised much of the space preventing extensive colonisation by limpets. Therefore, quadrats were located within randomly selected patches that were free of algae. All limpets were counted, measured (maximum shell length) and their position (inside pits vs. open rock) recorded. In the present study, pits were small round-shaped holes that clearly protruded into the bedrock with an average depth of 10-

12 mm. Many retained water or were dampen when the tide was out Each quadrat was photographed to estimate the cross-sectional area of the different habitat types (pits vs open rock). The area of the pits' walls was then added For this, we considered pits as cylinder-like structures and hence the area of the walls could be estimated by multiplying the perimeter of the pit (calculated from the photographs) by pit mean depth In addition, the depth and maximum length of inhabited pits were also recorded in situ for latter reference

Mortality was assessed towards the upper shore levels where limpets were most common and where the importance of microhabitats in providing refuge from desiccation was expected to be largest At each location and within each habitat (pit and rock) twenty limpets ranging in size between 10 and 15 mm shell length were marked with coloured nail-varnish in March 2007 Ideally, mortality would have been estimated at a range of animal sizes (from recently recruited 0 5 mm animals up to 40 mm adults) It was not possible, however, to tag smaller individuals and larger animals were scarce due to exploitation. Marked individuals were relocated fortnightly During each visit, nearby areas were carefully searched for animals that had migrated Relocated limpets were counted, whereas missing limpets were considered dead The layer of nail-varnish was renewed on each visit The mark done on animals was still clear during each visit suggesting that missing individuals could be attributable to mortality rather than to the fact of marks being washed off.

3 3 2 2 Habitat enhancement

Following the results of the observational study, which showed the importance of pits for the survival of smaller animals, the use of pit provision in enhancing the recruitment of limpets through modification of coastal engineering was investigated A topographically simple seawall where pits were generally absent was used, on which two sites were selected 200 m apart at mid-shore levels.

At each site twenty areas of 25 × 25 cm were marked and randomly assigned to a 2-way orthogonal design including the factors pit size (small and large) and pit density (lesser and greater) with five replicates per treatment. Within each area, eight and sixteen evenly spaced pits were drilled in the lesser and greater density treatments, respectively. The lesser density treatment corresponded to the average pit density recorded in the observational study, while the greater density treatment corresponded to twice that number. Small pits had 12 mm diameter and 10 mm depth and covered an area, which corresponded to approximately 6% and 12% of the substratum in the lesser and greater density treatments, respectively. Large pits, 24 mm in diameter and 10 mm in depth, corresponded to approximately 15% and 30% of the substratum in the lesser and greater density treatments, respectively. The sizes of experimental pits were within the range of those used by limpets on the two rocky shores and the modal limpet size class of 10-15 mm (see Chapter 4) suggests that the sizes of experimental pits were suitable for majority the of the population. Pits were drilled during late November and early December 2006 prior to the main settlement period of limpets. An additional set of 5 replicate controls (no pits drilled) was randomly selected at each location. Prior to the start of the experiment, the animals present on the exposed surface of the seawall were manually removed from within and approximately 50 cm around each quadrat. Sampling was done 4 months later in March 2007 and consisted of counting and measuring all limpets within each quadrat and recording their position (pits vs. open rock). Each plot was carefully inspected for small limpets (< 5 mm).

3 3.3 Data analysis

On natural shores, I tested the hypothesis that limpets would be associated with pits using replicated *G*-tests of goodness-of-fit The additive properties of *G*-tests allowed me to test for generality of the limpet-habitat association among locations and sites. For the advantages of this test over the traditional χ^2 tests of goodness-of-fit see Sokal & Rohlf (1995) and McDonald (2008) Analyses were run separately for the upper and lower shore data. Yates correction was used in individual *G*-tests of goodness-of-fit to correct for small sample sizes (Sokal & Rohlf 1995, Quinn & Keough 2002) However, the non-corrected *G*-values were retained for the tests of generality as the Yates correction affect the way *G*-values are added up (McDonald 2008) For each site, the expected proportions for the test were calculated using the average per quadrat area of each habitat

To test the hypothesis that the limpet-microhabitat association strength would vary over the vertical range of limpet distribution I used analysis of variance (ANOVA) on the per quadrat percentage of inhabiting limpets to the per quadrat pit area ratio. Data were log-transformed prior to the analysis Data were tested using 3-way mixed model ANOVA with habitat (fixed, 2 levels), location (random, 2 levels) and site (random, 3 levels and nested within location).

Mortality of limpets inhabiting pits and on open rock was compared using the exact binomial test for goodness-of-fit (Sokal & Rohlf 1995, McDonald 2008) on the surviving animals after 10-weeks. Data were analysed separately for each location

The Kolmogorov-Smirnov test was used to examine for differences in the size of limpet in pits and on open rock For this particular test, data were grouped among sites within each location and tidal height

On the seawall, an ANOVA was used to test the general hypothesis that limpets would aggregate in areas where microhabitats were experimentally added. Since the number of areas with experimental pits (4 treatments) was greater than controls, a 2-way asymmetrical ANOVA was used. This was done by using the sum of squares from two independent ANOVA's: one run with all treatments together (1 control plus 4 treatments) and the other run without the control. This allows distinguishing between the variation associated with controls and that of treatments, which can then be contrasted with one degree of freedom (see Underwood 1997 for further detail on asymmetrical designs). Thus, a 2-way asymmetrical ANOVA was used with 2 factors: site (random, 2 levels) and treatments (fixed). The per quadrat total number of limpets, that is the number of animals inhabiting experimental pits and those on open rock, was used in this analysis. Partitioning of the mean squares among the different treatments (pit size and pit density) was not done, as this was not relevant for the hypothesis being tested. The effects of various treatments in the numbers of inhabiting animals are examined below. Prior to analysis, Cochran's test was used to test for homogeneity of variances and transformations applied where necessary (Underwood 1997).

To test the hypothesis that pit size and pit density would affect the number of inhabiting limpets a 3-way ANOVA was used with site (random, 2 levels), pit size (fixed, 2 levels) and pit density (fixed, 2 levels). This analysis contrasts with the previously described in that only limpets that were inside pits were considered for the analysis. Because of the nature of the different treatments they differed in the areal proportion of the quadrat represented by pits, which could affect interpretation of results. To examine if animals were responsive to the area of microhabitat per se the number of limpets inside pits was correlated against the per quadrat areal proportion of pits.

3.4. Results

3 4 1. Observational study

A total of 457 animals were recorded on natural shores. Significant heterogeneity among individual *G*-tests indicates that the ratios differ among sites both at the upper and lower shore levels (Table 3.1) and hence data should not be analysed by looking for each site separately. Individual tests (sites) showed highly significant *G*-values indicating that limpets were inside pits more frequently than would be expected by chance. Analysis of the limpet-pit association strength (Fig 3.1, Table 3 2) showed that significant variation occurred among sites corroborating the significant heterogeneity found in the previous analysis. There was, however, no significant variation between upper and lower shore levels. Thus, the hypothesis that the importance of microhabitats increases with increasing physical harshness must be rejected

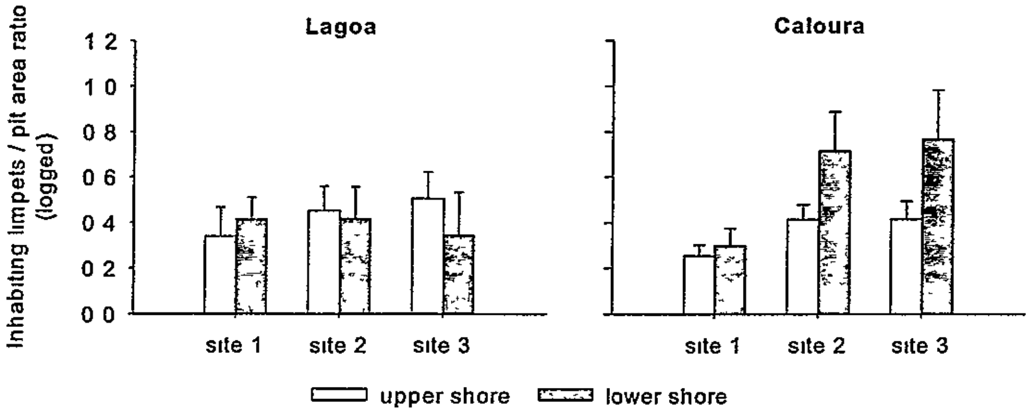

Figure 3.1. Ratio of the per quadrat (625 cm^2) number of *Patella candei* inhabiting pits to the area of pits (+SE) estimated on the lower and upper shore levels in the two studied locations

Table 3.1. Replicated *G*-tests of goodness-of-fit testing for the association of *Patella candei* with microhabitats at 3 sites within each of two natural shores.

Shore height	Location	Site	Pits	Rock	df	*G*-value	p
Upper	Lagoa	1	28	14	1	260.66	< 0.001
		2	19	5	1	232.04	< 0.001
		3	35	3	1	493.17	< 0.001
	Caloura	1	24	2	1	212.30	< 0.001
		2	16	3	1	207.53	< 0.001
		3	31	7	1	389.00	< 0.001
	Total				6	1873.01[a]	< 0.001
	Pooled		153	34	1	1788.93[a]	< 0.001
	Heterogeneity				5	84.09[a]	< 0.001
Lower	Lagoa	1	35	15	1	392.41	< 0.001
		2	24	15	1	414.97	< 0.001
		3	37	25	1	477.87	< 0.001
	Caloura	1	23	2	1	242.65	< 0.001
		2	48	4	1	875.50	< 0.001
		3	31	9	1	556.78	< 0.001
	Total				6	3037.64[a]	< 0.001
	Pooled		198	70	1	2775.98[a]	< 0.001
	Heterogeneity				5	261.66[a]	< 0.001

[a] Yates correction was applied to all tests except where marked. The un-corrected values of individual *G*-tests (not shown) were added to calculate the total *G*-value (McDonald, 2008).

Analysis of limpet mortality showed that the number of relocated limpets decreased more with time for those on open rock in the two locations (Fig. 3.2). At Lagoa, the difference in numbers of relocated limpets after 10 weeks was significant different between the two habitats (Exact binomial test for goodness-of-fit $p < 0.01$) being greater in pits, thus suggesting that animals in pits have reduced mortality. At Caloura, however, the result was not significant (exact binomial test for goodness-of-fit, $p = 0.082$), although the number of relocated limpets was substantially lower on open rock.

Table 3.2. ANOVA testing for differences in the *Patella candei*-pit association strength (per quadrat proportion of inhabiting limpets / per quadrat pit area) upper and lower on the shore

Source	df	MS	*F*	p	*F*-ratio
Location = L	1	0.0787	0.24	> 0.64	S (L)
Site (L) = S (L)	4	0.3230	3.29	< 0.05	Residual
Shore height = H	1	0.0004	0.02	> 0.92	L × H
H × L	1	0.0235	0.47	= 0.53	H × S (L)
H × S (L)	4	0.0498	0.51	> 0.73	Residual
Residual	60	0.0983			
Transformation		none			
Cochran's test		$C = 0.24$			

The size of limpets also differed between habitats being smaller for those inhabiting pits (Fig 3.3) Significant variation was recorded lower on the shore at both locations (Lagoa $D = 0.79$, $p < 0.001$, Caloura $D = 0.43$, $p < 0.01$). Upper on the shore, significant variation was also detected at Lagoa ($D = 0.53$, $p < 0.004$) At Caloura, there were few animals with which to perform the test but it is clear that the size of inhabiting pits was also smaller than those on open rock (Fig 3.3). Overall, limpets were smaller inside pits and reached a lower maximum size. mean shell length (± SE) inside pits was 12.2 mm (0.3) compared to 16.9 mm (0.5) on open rock.

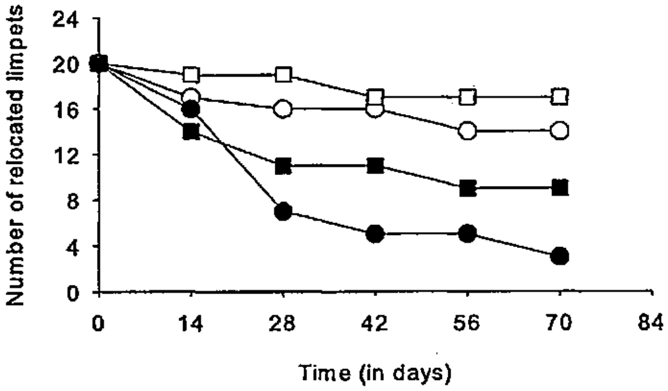

Figure 3.2. Number of marked *Patella candei* relocated at fortnight intervals. Twenty animals were initially marked in each of the two habitats (pits - open symbols, open rock – black symbols) on two shores: Lagoa (circles) and Caloura (quadrats).

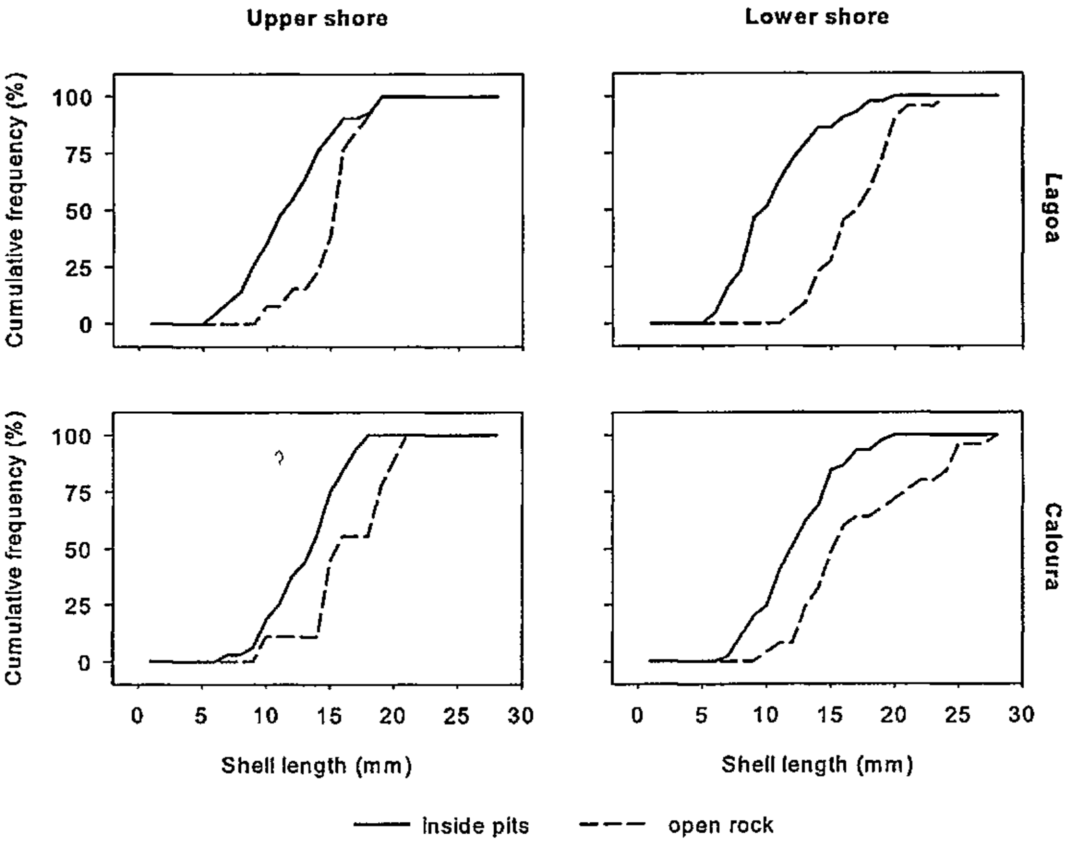

Figure 3.3. Size structure of the populations of *Patella candei* that were inside pits and on open rock. Analysis was done separately for the upper and lower shore populations. Data were grouped among the 3 sites within each of the two locations.

3 4.2. Habitat enhancement

In the seawall, limpets generally aggregated in areas where experimental pits were added (Fig. 3.4). The overall greater density of limpets in these areas was probably the result of direct recruitment (as indicated by the presence of recently recruited animals) and immigration (indicated by the presence of larger animals) The numbers of recently recruited (<5 mm) and immature (6-10 mm) animals were significantly greater among quadrats with added holes when compared to the control although this only became evident at site 2 (Fig 3.4, Table 3 3) At site 1, there was no measurable recruitment; this was probably the consequence of the bloom of green algae of the genus *Ulva* that occurred just after the start of the experiment and which may have been an effect of limpet removal thereby possibly limiting limpet recruitment through space pre-emption (Benedetti-Cecchi et al , 1999). The larger mature animals (≥11 mm) also tended to aggregate in areas with experimental pits, but this was not significant (Fig. 3.4, Table 3.3) as there was much variability among replicate quadrats Larger animals were most likely immigrants from nearby areas (especially the vertical and more protected sides of the boulders where limpets were more common) and such variability could be a consequence of natural variation in the abundance of nearby limpets

The effects of pit size and density on the number of animals inhabiting pits revealed variable results according to size-class Generally, the number of recently recruited animals (at site 2) increased with increasing pit density, while the abundance of larger mature individuals was limited by pit size (Fig 3.5, Table 3 4). There was no relationship between the number of limpets and the per quadrat areal proportion of pits for both the recently recruited and juvenile animals (data not shown), suggesting that the significantly greater number of recruits in the high pit density treatments was not the direct result of increased area of microhabitat per se In contrast, larger mature animals responded significantly to increased microhabitat area (site 1 $F_{1,18} = 18\ 42$, $r = 0.71$; $p <$

0.001; site 2: $F_{1,18} = 23.02$, $r = 0.75$, $p < 0.001$). This effect was, however, most pronounced among treatments varying in pit size than among treatments varying in pit density (Fig. 3.6). For example, increasing the density of large pits meant doubling the area of available pits yet there was no increase in limpet density. This indicates that above a certain area of large pits (between zero and that in the lesser density treatment) addition of larger pits does not increase the number of larger animals.

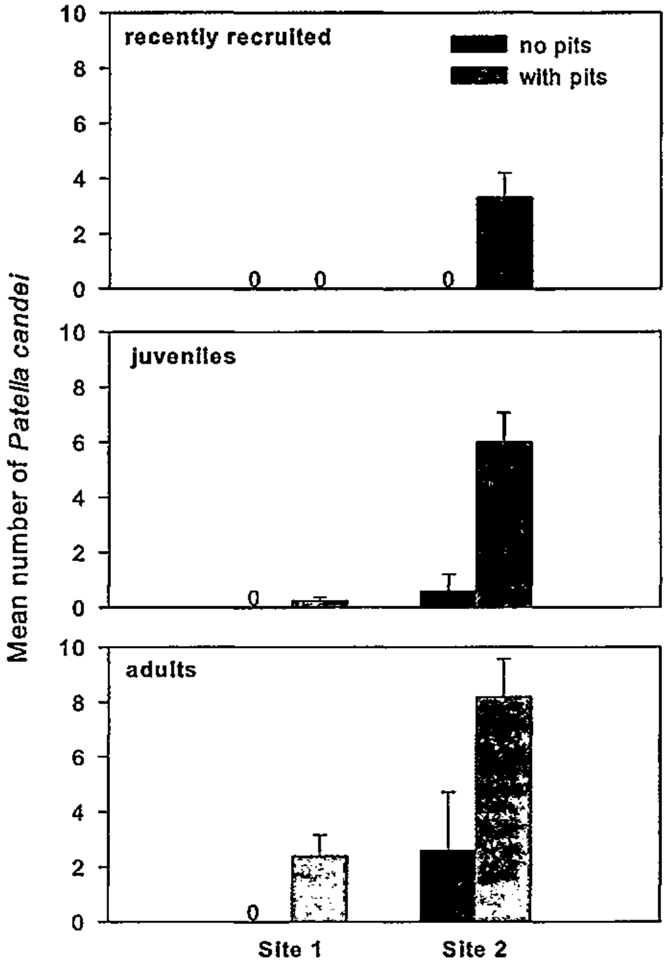

Figure 3.4. Mean (+SE) number of *Patella candei* on a seawall in areas where pits were experimentally added (n = 20) and in control areas (no pits added, n = 5). Data include all animals: those that were both inside pits and on open rock within experimental areas.

Table 3.3. Asymmetrical ANOVA comparing the abundance of *Patella candei* (includes both animals inside pits and on open rock) between controls (no experimental pits) and treatments (with experimental pits). C = control, T = treatments

		0 – 5 mm		6 – 10 mm		≥11 mm	
Source	df	MS	*F*	MS	*F*	MS	*F*
[a] Site	1	10 39	44 64***	16 32	43 72***	228 98	0 44
[d] Among all	4	1 03	1 00	1 46	1 42	146 33	10 07*
[c] C *vs* T	1	2 59	1 00	3 84	1 38	108 05	3 64
[b] Among T	3	0 51	1 00	0 66	1.49	159 09	16 76*
[a] Site × Among all	4	1 03	4 41**	1 03	2.75*	14 53	0 03
[a] Site × C *vs* T	1	2 59	11 13**	2 78	7 45**	29 65	0 06
[a] Site × Among T	3	0.51	2 17	0 44	1 19	9 49	0 02
Residual	40	0 23		0 37		13 01	
Transformation		Ln (x + 1)		Sq-Rt		none	
Cochran's test		*C* = 0 33*		*C* = 0 33 ns		*C* = 0 31 ns	

[a] tested over the Residual, [b] tested over Site × Among T, [c] tested over Site × C *vs* T, [d] tested over Site × Among all

Table 3.4. ANOVA examining the effect of pit density and size on the number of *Patella candei* in experimental areas where pits were added Data only includes animals found inside pits

		0 – 5 mm		6 – 10 mm		≥ 11 mm	
Source	df	MS	*F*	MS	*F*	MS	*F*
[a] Site = S	1	12 98	44 59***	16 56	47 70***	129 60	12 67**
[d] Pit Size = PS	1	0 08	1 00	0 61	39 02	409 60	6 06
[c] Pit Density = PD	1	1 22	1 00	0 66	0 74	12 10	4 84
[a] S × PS	1	0 08	0 28	0 02	0 04	67 60	6 61*
[a] S × PD	1	1 22	4 20*	0 90	2 58	2 50	0 24
[b] PS × PD	1	0 21	1 00	1 17	1 29	0 90	9 00
[a] S × PS × PD	1	0 21	0 73	0 91	2 61	0 10	0 01
Residual	32	0 29		0 35		10 23	
Transformation		Ln (x + 1)		Sq-Rt		none	
Cochran's test		*C* = 0 33 ns		*C* = 0 36 ns		*C* = 0 35 ns	

[a] tested over the Residual, [b] tested over S × PS × PD, [c] tested over S × PD, [d] tested over S × PS

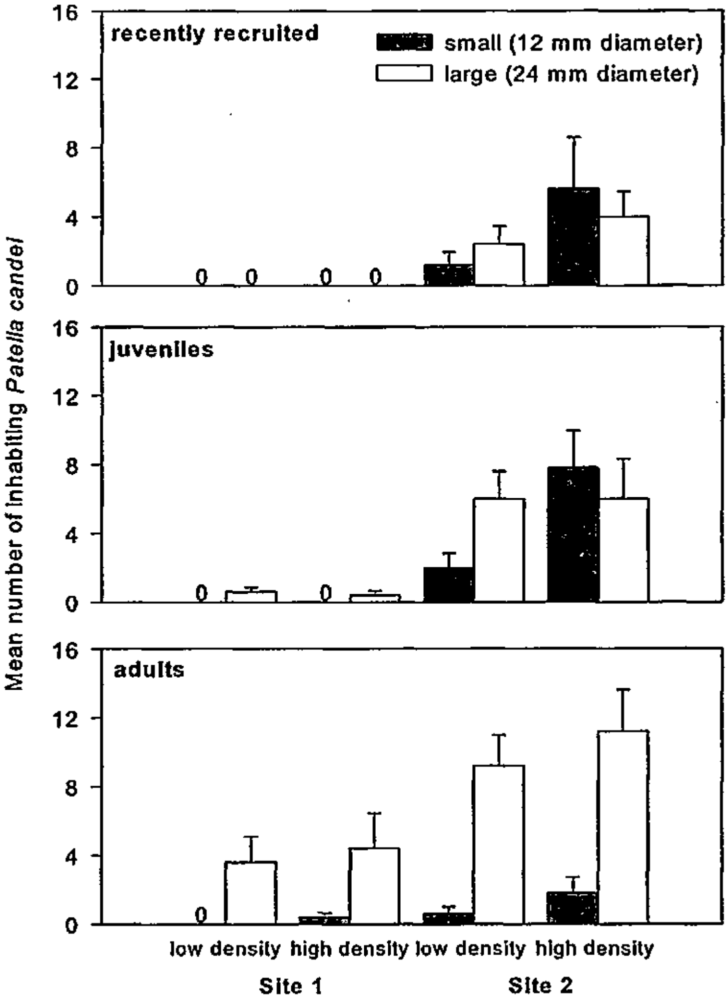

Figure 3.5. Mean (+SE, n = 5) number of *Patella candei* on a topographically simple seawall in experimental areas where pits were added. Data only includes animals found inside pits.

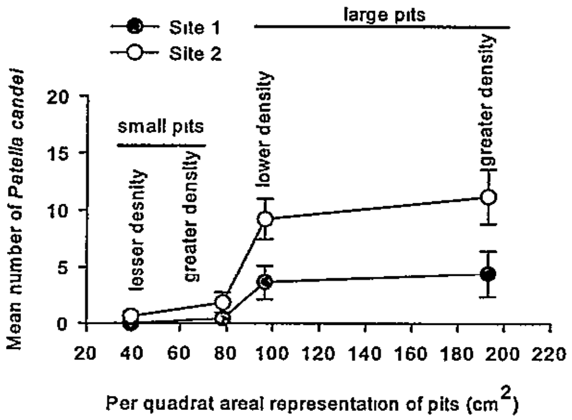

Figure 3.6. Mean (±SE, n = 5) number of the larger mature *Patella candei* that were found inside pits in relation to the per quadrat areal proportion of pits.

3.5. Discussion

As expected, our study indicated as in many other upper shore intertidal gastropods (Catesby & McKillup 1998, Gray & Hodgson 1998), *P candei* benefits from the protection provided by microhabitats On natural shores, all hypotheses, but one, were supported Thus, patterns of distribution were influenced by microhabitats, with limpets significantly associated with pits Those individuals inhabiting pits showed reduced mortality and were of smaller size than those found on open rock The exception was that microhabitats did not become increasingly important higher on the shore as hypothesised Results showed no clear pattern over the range of vertical distribution examined, with variable results among sites This was surprising given the perceived increasing benefit of refugia with increasing height on the shore as a consequence of increased emersion stress. The level of predation intensity over the vertical gradient of the Azorean shores is unknown and it is possible that the threat of predation at low tidal levels from for example, *Stramonita haemastoma* and grapsid crabs may make acquisition of refugia by low shore limpets as important as high on the shore where the threat of desiccation or heat stress is probably the main driving force.

For instance, in SW England Silva et al. (2008) showed that predation by crabs can have a significant effect on the lower shore population sizes of *Patella vulgata.*

Another complicating factor is the existence of two ecomorphs - a more conical and taller shell higher on the shore and a flatter shell lower on the shore (Hawkins et al. 1990b). Such different morphologies are thought to confer animals differential physiological tolerance to environmental stress (Lowell 1984, McMahon 1990, De Wolf et al. 1997) and could have also influenced the results observed. Further experimental work would be needed to disentangle the effects of predation and morphological-physiological plasticity in determining the patterns of distribution for *P. candei.*

This study shows that modifications made to a man-made structure promoted an increase in numbers of limpets in areas with experimentally increased microhabitat area. Analysis done in animals differing in size suggests that this was not just an aggregative effect. That is, animals moving from areas with low microhabitat areas to areas with increased microhabitat area (e.g. larger animals). The significant greater number of recently recruited animals in areas with experimental pits compared to controls indicates that microhabitat provision contributes to a local increase in limpet abundance by enhancing recruitment, or by reducing the mortality of recently recruited animals. Analyses of the distribution of limpets 11-months after set up showed that areas where pits had been drilled still supported larger populations of limpets although this pattern was not statistically significant. At this time, there were no individuals < 5 cm present indicating that the distribution patterns initiated during recruitment had probably persisted as the individuals grew (Appendix A). The distinction between an aggregative effect and a real effect on population size is paramount to evaluate the success of such modifications in coastal engineering in enhancing the stocks of exploited populations. The numbers of recently recruited animals increased with increasing pit density in both the smaller and larger pit size treatments However, the number of these animals did not increase with increasing microhabitat area (across all treatments) This suggests that factors other than microhabitat area per se are affecting the settlement of larvae. For instance, the greater overall substratum complexity (number of microhabitats) in the greater density treatments may increase small-scale variations in water flow at the substratum-water interface that could indicate larvae suitable sites for settlement (Kohler & Wahl 1999) In contrast, there was a significant increase in the number of larger mature individuals with increasing microhabitat area per se. This effect was, however, mostly caused by differences in area between treatments varying in pit size rather than pit density. This suggests that the use of microhabitats by larger limpets is, obviously, limited by the size of pits In addition, the number of larger animals did not increase with increasing density of larger pits suggesting that above pit densities greater than that used in the lesser density treatment, factors other than microhabitat area (e g. food or space availability) limit the abundance of larger limpets. Larger animals often occurred isolated in each pit suggesting that competition among the larger animals is high (Boaventura et al 2003)

While there is an increasing demand to defend coastlines worldwide, integrated coastal management requires that this must be done in ways that promote the sustainability of natural marine systems Ecologists have long been accused of producing little in the way of applied science that is crucial for managers to make informed decisions (Underwood 1995, 1998 for discussion). Here I show that basic knowledge derived from simple studies such as the description of patterns of species distribution in combination with experimental marine ecology can provide information of applied interest that can inform ecologists and fishery and coastal managers (Castilla 2000). The modifications made in the present study (see also Moschella et al 2005, Moreira et al 2007) could easily be incorporated into coastal engineering by either moulding pits into the surface of concrete materials or by choosing natural rock with complex topography. The choice of appropriate substrates or ways to modify them to better mimic local conditions (as in this study), in addition to implementation of optimal spatial configuration and design of artificial structures, may help to mitigate the impacts of coastal urbanisation or the construction of marine renewable energy devices promoting the sustainability of marine organisms.

Changes to the local abundance of limpets are likely to have important consequences for population and community levels. For instance, the bloom of *Ulva* recorded at site 1 in the seawall may have been driven by the removal of limpets prior to the start of the experiment, which subsequently affected animal recruitment via space pre-emption (Benedetti-Cecchi et al. 1999). In contrast, the increase in recently recruited animals in areas with experimental pits, at least at site 2, will likely influence local population dynamics such as increasing local reproductive output, an important factor for exploited species. At the community levels, consequences may also be expected as suggested by much experimental work done on the role of patellid limpets in structuring intertidal communities (e.g. Hawkins et al. 1992, Jenkins et al. 2005, Coleman et al. 2006). In addition, since limpets tend to aggregate in areas with pits, the spatial distribution of microhabitats may also influence the spatial structure of mid shore communities. This was evident one year following the start of the experiment with clear halos free of algae around inhabited pits.

The present study focused on only one habitat type and species. The types of natural microhabitats may be as diverse as the number of species in a system and may vary from location to location. From an integrated coastal management point of view aimed at promoting the sustainability of marine natural systems as a whole, the results obtained here are limited. However, as a rule-of-thumb it could be argued that designing man-made structures to mimic local habitats as closely as possible represents the best strategy for mitigating the impacts of these structures on natural systems (Moschella et al. 2005) Increasing habitat heterogeneity – the number of different components of habitats (Matias et al. 2007) – will diversify the set of niches that can be exploited by different species, or within species, by different life-history stages

CHAPTER 4

Exploitation of rocky intertidal grazers: population status and potential impacts on community structure and functioning

Exploitation of rocky intertidal grazers: population status and potential impacts on community structure and functioning

4.1. Abstract

A wide range of anthropogenic activities is impacting on the ecology of coastal areas. Exploitation of marine resources is one such activity, which through cascading trophic effects, can have influences well beyond that of the target species. I investigated the mid-rocky shore community structure of the Azores archipelago, a seldom-studied habitat, and where there is a local tradition of exploiting limpets, the main intertidal grazers. Limpet population structure differed among islands and there was an inverse relationship between the abundance of larger limpets and the human population per coastal perimeter, but not the associated catch data. At small scales of resolution (quadrats), there was a negative relationship between the cover of algae and limpets and a positive relationship between barnacles and limpets. This relationship was also apparent at the larger scale of islands as a function of the gradient of exploitation. Results show how natural habitat fragmentation may be useful where the experimental test of hypothesis is not possible and provides evidence for the trophic cascading effects of organism removal at landscape scales.

4.2. Introduction

The rocky intertidal is a highly productive system supporting diverse assemblages of plants and animals. However, its accessibility to humans has rendered it susceptible to a variety of anthropogenic impacts (Thompson et al. 2002). Human populations have a long tradition of exploiting intertidal resources and concern about the effects of this disturbance has prompted much research, for example in Chile and South Africa (see Siegfried 1994 for review). At these localities, exploitation was shown to cause a reduction in the abundance and mean size of exploited species (e.g Branch 1975a, Castilla & Durán 1985). In addition, there is increasing evidence that the effects of fishing can extend well beyond the exploited species through cascading trophic effects (Castilla 1999, Scheffer et al. 2005) that can change community structure and the functioning of ecosystems at landscape scales of resolution (Durán & Castilla 1989, Lindberg et al. 1998, Castilla 1999)

The majority of rocky intertidal benthic invertebrates have complex life cycles that include planktonic and bottom dwelling phases, linked by a settlement event (Thorson 1950). Larvae released by benthic adults into the water column are dispersed by physical transport (Morgan 2001) in such a way that, in open systems (e.g. islands, headlands), local production can have little impact on local recruitment (Caley et al. 1996) The replenishment of benthic populations is largely dependent on the supply of new individuals, which is a function of the abundance of planktonic larvae, the behaviour and physical processes bringing larvae into contact with the substratum, and the availability of suitable sites for settlement (Minchinton & Scheibling 1993) Anecdotal evidence suggests that fragmented habitats such as islands typically receive lower recruitment than the mainland, and this is evident even on islands quite close to continental coasts (e g Crisp & Southward 1958) The relatively small size and the strong currents that characterise oceanic island environments reduce larval retention (Swearer et al 1999), resulting in a greater larval loss, and hence lower recruitment Thus, in these highly dispersive insular habitats, a reduction in reproductive output as a consequence of the removal of mature animals is likely to render island populations more susceptible to exploitation than would be expected elsewhere (Roberts & Hawkins 1999) In the Canary Islands, for instance, intense exploitation of rocky intertidal limpets led to a dramatic reduction in these populations as well as to the local extinction of *Patella candei candei* (Côrte-Real et al 1996, Navarro et al. 2005)

In the Azores, littoral organisms (e.g. barnacles, seaweeds and limpets) have been exploited since the islands were first colonised in the 15th century. Arguably, one of the largest anthropogenic impacts on these shores has been the exploitation of patellid limpets (Hawkins et al. 2000), which are gathered for food at both commercial and recreational levels. The economic value of limpets rose steadily in the 1980's leading to a dramatic increase in exploitation. However, the extent of exploitation differed among islands, being greatest in São Miguel (the largest and most developed island), and least in the islands of the western group (Flores and Corvo) (Table 4.1). This fishery reached its peak in 1984 with a harvest of 97,000 kg, of which 94,000 kg were collected on São Miguel alone (Santos et al. 1990). Such intense harvesting prompted a marked decline in the limpet populations on São Miguel (Martins et al. 1987, Santos et al. 1990, Hawkins et al. 2000) and the fishery collapsed in 1985. In 1993 legislation was passed to protect this resource. Limpet no-take areas were created whereas a seasonal harvesting restriction from November to May was applied elsewhere jointly with and minimum legal catch sizes of 30 and 50 mm shell length for *Patella candei* and *P. aspera,* respectively. Ferraz et al. (2001) reported some limpet population recovery in 1998 in the western and central groups of islands but not in São Miguel. Although informative, these studies did not consider limpet density, since they were based on captures per unit time (but see Hawkins et al. 1990a).

Hence limpets are used as model species in this work as they represent an economically important resource and because they are considered key organisms whose role in structuring the rocky intertidal is widely recognised. For instance, experimental evidence has shown that limpets, and particularly patellid limpets in the NE Atlantic, have a strong top-down influence on the structure of the rocky intertidal (e.g. Hawkins et al. 1992, Coleman et al. 2006) suggesting that a reduction in limpet abundance as a consequence of over-exploitation is likely to have strong community level effects through direct and indirect interactions (e.g. Van Tamelen 1987). In addition, whilst most experimental work has been done at small spatial scales (e.g. quadrats), differences in the exploitation regime among islands may allow us to examine the impacts of harvesting at landscape scales.

Table 4.1. Commercial exploitation of limpets (*Patella* spp., in 10^3 kg) in the Azores from 1974 to 2005. n.a., not available.

	Period			
	1974-1989[a]	1993-1998[b]*	2000-2005[c]	Total
Flores	0.14	0.63	0.39	1.16
Graciosa	0.03	0.63	2.49	3.15
Pico	1.40	0.63	1.59	3.62
São Miguel	n.a.	627.00	0.00	627.00

[a] Ferraz et al. 2001, [b] Santos et al. 1990, [c] Azorean Regional Statistics Service (SREA)

* Landings represent approximate values as these were derived from a graph (Santos et al. 1990), where there was separate data for São Miguel but all other islands were grouped. Therefore, the estimated landings for Flores, Graciosa and Pico correspond to the difference between the two series, divided by 8 islands.

The main purpose of the present study was to evaluate the limpet population structure across the Azores archipelago. I tested the proposition that the fragmented and isolated nature of these islands makes it possible to examine the impact of different exploitation regimes as a function of each island's fishing history. The hypothesis that there is a decrease in limpet density and maximum size toward the eastern islands, reflecting greater fishing effort was examined as was the potential effects that grazer exploitation may have on the structure of mid-shore assemblages.

4.3. Materials and methods

4.3.1. Study sites and community

The present study uses the same data as that used in Chapter 2 but restricts the analysis done to mid-shore tidal heights (1.90 ± 0.1 m above CD) where populations of *Patella* spp. attain maximal densities (Hawkins et al. 1990a, Chapter 2). The analyses done on the density of *P. candei* and *P. aspera* are as in Chapter 2. However, for simplicity in the analysis of results I hereby repeat both the correspondent figures and tables.

The study focused on the two patellid species present on these islands: *P. aspera* and *P. candei*. The former is a slow-growing protandrous species that can attain large sizes. The latter is a faster growing more opportunistic species. It is gonochoric and attains maximal sizes smaller than *P. aspera* (Martins et al. 1987) (see Chapter 1 for further descriptions).

4.3.2. Sampling design

As abovementioned, sampling design is described in full in Chapter 2. The exception is that here I also consider for analysis the biomass and size structure of patellid populations. As such, all limpets within replicate quadrats were measured to the nearest mm using Vernier callipers. The biomass of *P. candei* was estimated using a previously calculated relationship between biomass and shell length (biomass (g) = 0.0001 × shell length (mm)$^{2.79}$, $r^2 = 0.96$, Appendix B). The biomass of *P. aspera* was not considered as there were insufficient animals from which a robust relationship could be estimated. The cover of algae and barnacles was assessed as in Chapter 2. However, analysis of the algal cover only considered erect algae. In addition, as patellid limpets are commonly considered generalist grazers (do not graze over specific algal species), the cover of each algal species was summed in each replicate quadrat and algae are analysed as a single group

4.3.3. Data analysis

Two approaches were used to test the general hypothesis that the population structure of limpets differs among islands The abundance and biomass of limpets were analysed using a 3-way mixed model analysis of variance (ANOVA) as in Chapter 2, but here islands were considered fixed as the present study tested specific hypothesis following islands exploitation regime (Table 4.1). Hence, the ANOVA had the following factors: island (fixed factor, 4 levels), location (random factor, 3 levels, nested within island), and site (random factor, 3 levels, nested within location and island) with five replicates. As before, prior to analysis data were checked for heterogeneity of variances using Cochran's test and transformations were applied where necessary, following Underwood (1997) In one particular case (density of *P. aspera*, see Table 4 2), transformations were unsuccessful in removing heterogeneity However, ANOVA is relatively robust to heterogeneous variances in large designs (Underwood 1997) and hence, untransformed data were analysed Student-Newman-Keuls (SNK) tests were used to compare means within significant factors. In addition, the chi-square test of association was used to test the null hypothesis of no association between the frequency of *P. candei* (there were not sufficient data for the analysis of *P aspera*) in different size-classes and islands Visual analyses were made using 5 mm size-classes (see Fig. 4.2) which corresponds to half the shell length that *P candei* is able to attain in its first year (Menezes 1991). However, data had to be grouped in 10 mm size-classes for the χ^2 test in order to reduce the number of zeros and the number of cells with less than 5 observations (Quinn & Keough, 2002). In this analysis, the 6 animals larger than 30 mm were lumped together in the largest size-class (>20 mm).

In order to examine if differences among islands could be attributed to the islands' regime of exploitation, the total number of *P. candei* and the number of larger individuals (>20 mm) in each island was regressed against catch rates (see Table 1). However, since data from landings is potentially underestimated (e.g. does not include illegal harvesting), data were also regressed against the number of islanders per coastal perimeter. This index provides an indirect estimate of potential exploitation in each island.

The role of patellid limpets in structuring the rocky intertidal in the NE Atlantic is well documented (see introduction, Chapter 1). To test the hypothesis that changes in the abundance of limpets may lead to changes in the dominance of mid-shore assemblages between macro-algae and barnacles, we used both ANOVA and correlation analyses. ANOVA's were used as above to test for differences in the abundance of algae and barnacles among islands. Since there is no experimental evidence of the direct or indirect effect of limpets on the community structure in the Azores, correlations were used to examine the relationship between the abundance of limpets and the abundance of macro-algae and barnacles. Probabilities were adjusted by Bonferroni correction. Finally, in order to examine if differences in the abundance of limpets among islands can lead to changes in the structure of mid-shore assemblages at landscape scales, the mean limpet abundance of each island was correlated with the mean cover of algae and barnacles, respectively.

4.4. Results

4 4 1. Population level effects

The two species of limpets, *P candei* and *P aspera,* differed greatly in abundance and distribution The former was common in the rocky intertidal of all islands, whilst *P aspera* was restricted to a few individuals in Flores, being nearly absent in the remaining islands

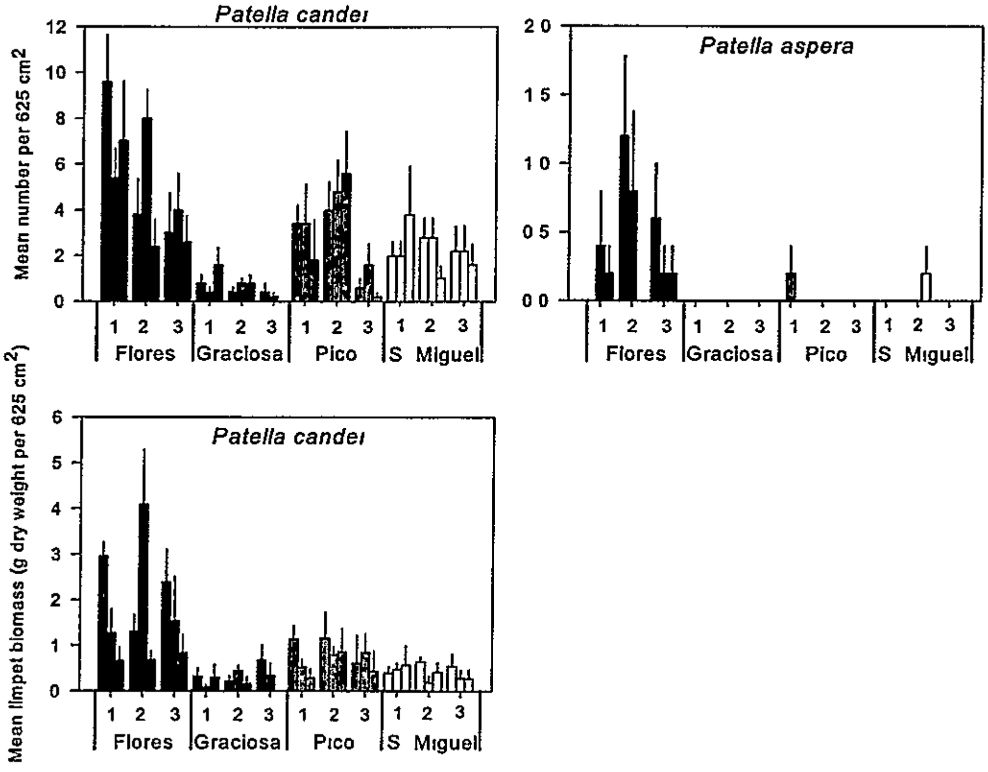

Figure 4.1. Mean (+SE) limpet abundance and biomass at a hierarchy of spatial scales Within each island, the abundance of algae is shown for each of the three shores (km apart) surveyed (numbered). Flores 1 - Fajã Grande, 2 - Lajedo, 3 – Fajãzinha, Graciosa 1 - Porto Afonso, 2 - Santa Cruz, 3 – Carapacho, Pico 1 - Prainha, 2 - Lajes, 3 - Santa Cruz, São Miguel 1 - Lagoa, 2 - Caloura, 3 - Mosteiros For each shore, there are three vertical bars, each representing one of the three sites (metres apart) surveyed

Table 4.2. Patterns of limpet abundance and biomass at a hierarchy of spatial scales: Island (Is, fixed), Location (Lo, random and nested within islands) and Site (Si, random and nested within locations and islands).

		Density				Biomass	
		Patella candei		*Patella aspera*		*Patella candei*	
	df	MS	*F*	MS	*F*	MS	*F*
Is	3	153.07	3.99	1.67	7.35*	1.96	6.58*
Lo (Is)	8	38.33	4.33**	0.23	1.11	0.30	2.46*
Si (Is × Lo)	24	8.56	1.23	0.21	1.23	0.12	1.51
Residual	144	7.17		0.17		0.08	
Transformation		none		none		Sq-Rt	
Cochran's test		$C = 0.14$		$C = 0.28$**		$C = 0.13$	

Although the hypothesis that the abundance of *P. candei* differs among islands was rejected (Table 4.2), it was very close to significance (p = 0.0521). This and the fact that a large proportion of the overall variability was indeed associated with the scale of islands (analysis of the components of variation, see Chapter 2) suggests that a significant test for islands may have been masked by the low power of this test (see degrees of freedom in Table 4.2) and by the significant effect among locations – the denominator of the *F*-test for islands. Despite this, there was significant variation in the biomass of *P. candei* among islands (Fig. 4.1, Table 4.2). SNK tests showed a significantly higher biomass of *P. candei* in Flores (1.75 ± 0.25, mean ± SE) than in the remaining 3 islands among which there was no variation, ranging between 0.28 ± 0.06 in Graciosa, 0.42 ± 0.07 in São Miguel and 0.74 ± 0.13 g in Pico (Fig. 4.1). There was significant variation in the abundance of *P. aspera* among islands: at Flores, it attained mean densities of 0.4 ± 0.1 (mean ± SE), whilst it was virtually absent in the remainder of the 3 islands (Fig. 4.1, Table 4.2).

There was small-scale intra-island variation for both the abundance and biomass of *P candei* (Fig 4 1, Table 4 2) This probably reflects natural variability in recruitment or small-scale variation in biological (e.g. competition) and physical (substratum microtopography, see Chapter 3) factors. However, it could also be the result of spatial variation in the intensity of limpet exploitation within islands At present, no data is available that would allows to ascertain the causes of this variability and since these were considered random factors, this variation is not further discussed.

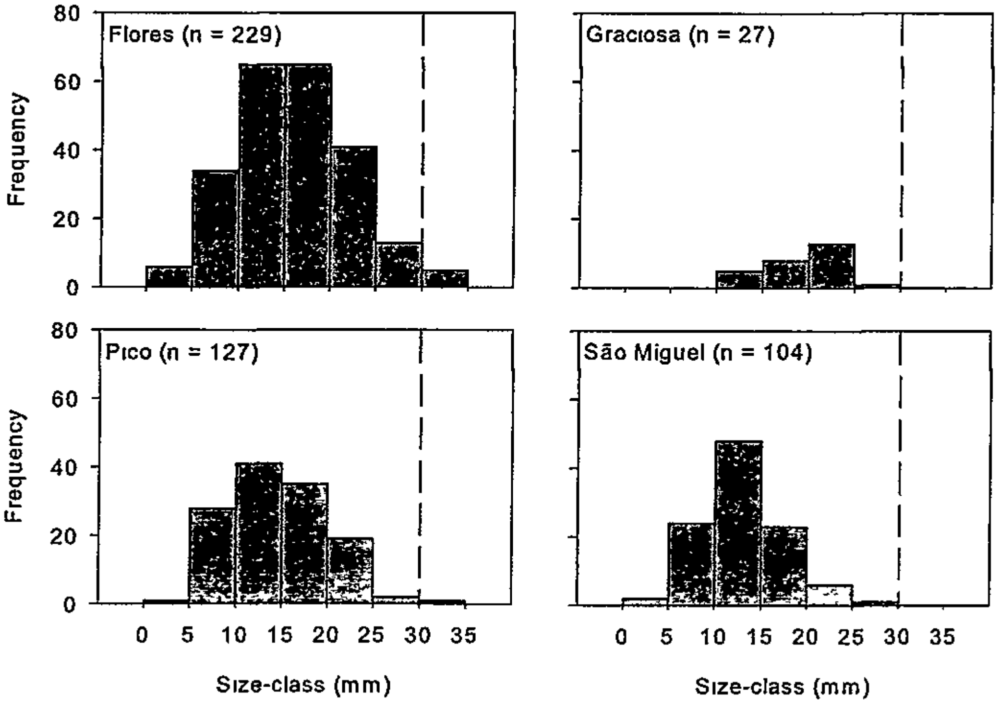

Figure 4.2. *Patella candei* Size-frequency histograms for each island Dashed line indicates the minimum legal catch size For each island, data were pooled among all the shores (and sites) surveyed

Analysis of the frequency of limpets in each size-class (Fig 4 2) showed a normal distribution with a modal size class of 10 to 15 mm in 3 of the islands It should be noted that in all islands, out of 487 limpets recorded only 6 were found to be larger than the legal catch size (30 mm) and of these 5 were recorded in Flores A significant association was detected between the frequency of limpets in each size-class and islands ($\chi^2 = 35.98$, df = 6, $p < 0.001$). Inspection of the relative chi-square values (Table 4.3) shows important contributors to this pattern were a greater number of large limpets in Graciosa than expected and a lower number in São Miguel. To a lesser extent, there were also fewer small limpets (<10 mm) in Graciosa than would be expected.

Table 4.3. *Patella candei.* χ^2 test of association between the frequency of limpets at different size-classes and islands.

Size-class (mm)		Flores	Graciosa	Pico	São Miguel
0-10	Observed	40	0	29	26
	Expected	44.7	5.3	24.8	20.3
	χ^2 contribution	0.5	5.3	0.7	1.6
11-20	Observed	130	13	76	71
	Expected	136.4	16.1	75.6	61.9
	χ^2 contribution	0.3	0.6	< 0.1	1.3
> 20	Observed	59	14	22	7
	Expected	48.0	5.7	26.6	21.8
	χ^2 contribution	2.5	12.3	0.8	10.0

The number of islanders per coastal perimeter was a better predictor of the abundance of *P. candei* across the archipelago than the level of limpet catches. The number of larger animals decreased with increasing island population (Fig. 4.3) whilst no correlation was found with the catch data ($F_{1,2} = 4.71$, $r^2 = 0.70$, $p > 0.16$). However, the total number of limpets per island (including animals of all sizes) did not correlate with either the island population ($F_{1,2} = 0.41$, $r^2 = 0.17$, $p > 0.58$) nor the catch data ($F_{1,2} = 0.004$, $r^2 < 0.01$, $p > 0.95$).

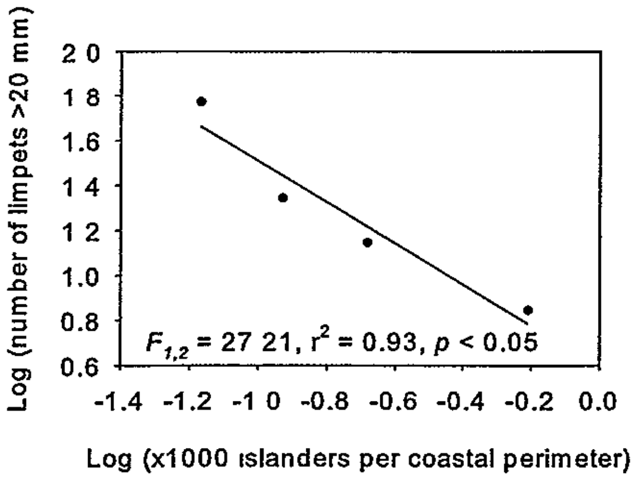

Figure 4.3. *Patella candei* Regression analysis between the number of limpets greater than 20 mm (shell length) and the number of islanders per coastal perimeter

4.4.2 Community level effects

There was significant variation in the abundance of algae at the scale of islands and sites (Table 4.4). At the larger scale of islands, the percentage cover of algae ranged between 25.9 ± 3.7 (mean ± SE) at Flores and 56.3 ± 4 1 (mean ± SE) at São Miguel (Fig 4 4) A similar pattern of distribution was observed for barnacles with significant variation at the largest and smallest scales (Table 4 4) The abundance of barnacles was greatest at Flores, 35.9 ± 2.6 (mean percentage cover ± SE) and lowest at São Miguel, 15 5 ± 2 0 (mean percentage cover ± SE), whereas intermediate levels were recorded for Pico and Graciosa with 26 3 ± 2 3 and 23.1 ± 2 4 (mean percentage cover ± SE), respectively (Fig 4 4) As with limpets (see above), significant variation at the smaller scale of sites among algae and barnacles is probably the result of natural variability (i e recruitment, competition for space)

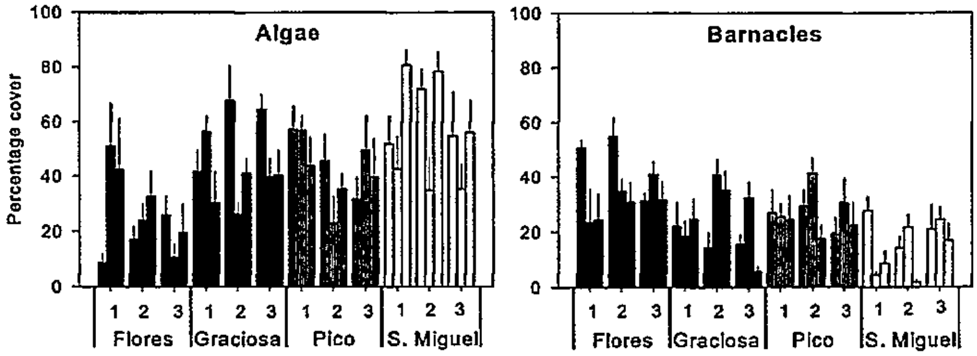

Figure 4.4. Mean (+SE) algal and barnacle abundance at a hierarchy of spatial scales. See legend in Fig. 4.1 for further details.

Table 4.4. Patterns of algal and barnacle abundance at a hierarchy of spatial scales. See table 4.2 for nomenclature.

		Algal cover		Barnacle cover	
	df	MS	*F*	MS	*F*
Is	3	57.13	5.53*	3.2E3	4.56*
Lo (Is)	8	10.33	1.77	7.0E2	1.79
Si (Lo × Is)	24	5.83	1.72*	3.9E2	1.97**
Residual	144	3.40		1.9E2	
Transformation		Sq-Rt		none	
Cochran's test		$C = 0.08$		$C = 0.10$	

There was a significant negative correlation between the abundance of limpets and the percent cover of algae ($F_{1,178}$ = 10.88, r = 0.24, $p < 0.01$), although the correlation coefficient was weak. In contrast, a clearer relationship was detected between the maximum cover of algae and the density of limpets (Fig. 4.5). Similarly, whilst barnacle cover was weakly correlated with limpet density ($F_{1,178}$ = 19.51, r = 0.31, $p < 0.001$), there was a strong positive correlation between the density of limpets and minimum cover of barnacles (Fig. 4.5). In addition, the percent cover of barnacles was inversely correlated with the cover of algae ($F_{1,178}$ = 239.26, r = 0.76, $p < 0.001$).

This 3-way relationship between limpets, algae and barnacles differed among islands and would likely have consequences for mid-shore community structure as islands supporting a greater abundance of limpets (e g Flores) tended to support mid-shore assemblages with greater abundance of barnacles. In contrast, at lower abundances of limpets (e g. São Miguel), islands tended to support algal-dominated mid-shore assemblages (Fig. 4.6)

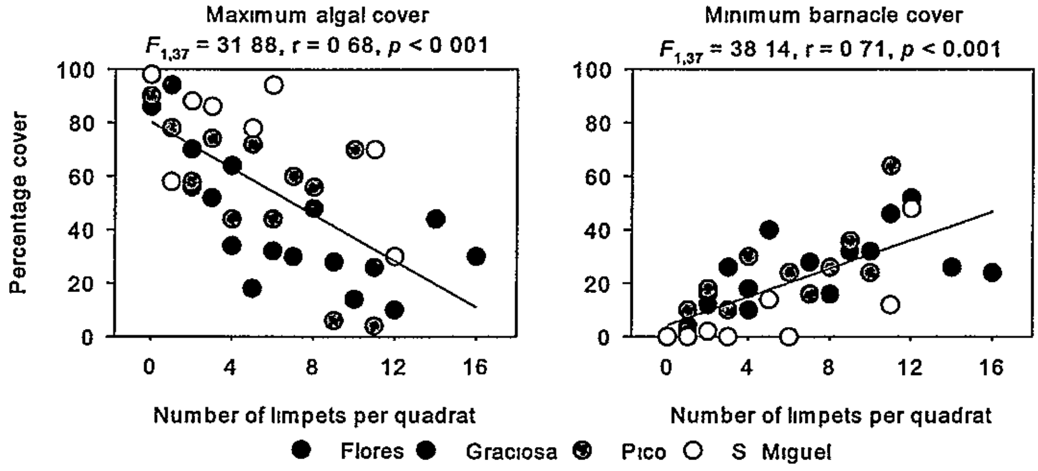

Figure 4.5. Correlations between the abundance of limpets and the maximum and minimum percentage cover of algae and barnacles, respectively

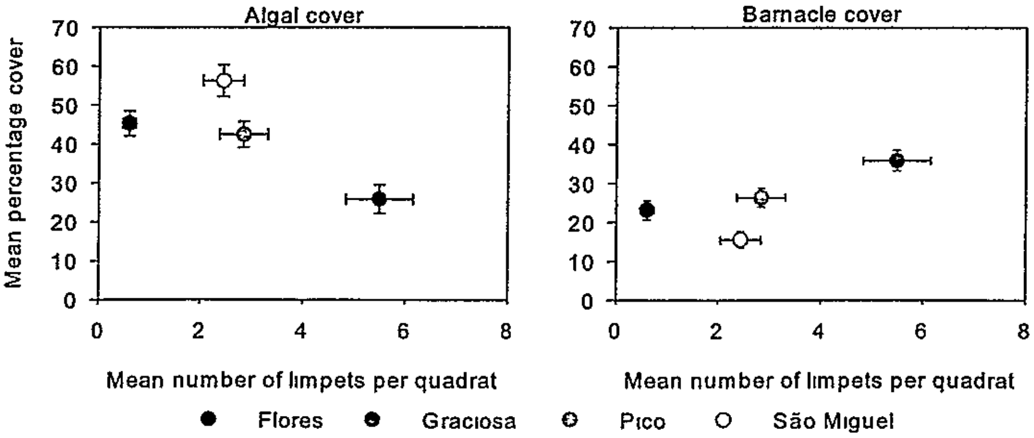

Figure 4.6. Graphical representation of mid-shore assemblage structure of the four islands considered in this study Data correspond to island means and SE's (pooled over 3 locations and 3 sites)

4.5. Discussion

The idea that the sea offers an infinite supply of resources and that humanity could not cause the extinction of marine species is slowly changing (Roberts & Hawkins 1999) and there is growing evidence that, as well as affecting target species, fishing can have a wider influence, through cascading trophic effects (Castilla 1999, Scheffer et al. 2005).

The present study provides a thorough analysis of the abundance of exploited species in a seldom-studied system. The two species of limpets examined, differed greatly in distribution and abundance. *P. candei* occurred on all islands in relatively large numbers, whilst populations of *P. aspera* were small and virtually absent in 3 out of the 4 islands examined. Both species co-occur in the intertidal where their density is maximal at mid shore levels (Hawkins et al. 1990a). Differences in the abundance between the two species could be the result of natural processes such as inter-specific competition (Boaventura et al. 2002a). However, it is unlikely that natural processes alone could have caused the absence of *P. aspera* on 3 islands. Instead, a much more likely explanation is that the low abundance of *P. aspera* is a consequence of intense exploitation. Unfortunately, catch data combines the two species together and it is impossible to determine the fishing effort for each species separately. However, anecdotal evidence suggests that *P. aspera* is harvested in much greater numbers than *P. candei*, probably because the former attains greater maximum sizes. In addition, the biology of *P. aspera* (see Chapter 1) renders it more susceptible to exploitation than *P. candei* (Martins et al. 1987, Roberts & Hawkins 1999), which is likely to amplify the difference in the abundance between the two species.

As hypothesised, the population structure of limpets differed among islands. However, catch data (Table 4.2) failed to provide a comprehensive explanation of such variation These data are based on the log-book records of licensed harvesters. There is, however, much illegal harvesting in these islands (personal observation) and limpets are commonly sold directly to restaurants or on the streets without being declared In addition, as the abundance of larger animals becomes scarcer (see Fig 4 2), harvesters tend to collect smaller animals below the legal size and these are obviously not declared. Hence a large number of animals are not included in official statistics and catch data fails to represent actual rates of exploitation. The number of islanders per coastal perimeter proved a much more reliable index in predicting the variation in the abundance of limpets among islands and especially that of the larger animals Similar indexes (e.g number of fishing boats per island) have been successfully used in other archipelagos (Tuya et al. 2006) suggesting that they can provide adequate information for the management of fisheries in fragmented habitats A similar approach has also been used in mainland coastal areas where the intensity of exploitation was driven by the distance to populated centres (e.g. Rius et al 2006) The drawback of using such correlative approaches is that causality cannot be inferred from results As such, differences in the population structure of limpets among islands cannot be ascribed to exploitation alone since these islands may differ in relation to factors other than fishing intensity (e g competition, productivity, mortality). Hence interpretation of results is made with caution and considering the biology and ecology of the species involved. The use of such indexes and consequent correlative approach may, however, be the only possible way to ascertain the effects of exploitation in areas where suitable control areas (e g no-take marine reserves) are lacking or are not successful (see Chapter 5).

In the present study, the population structure of *P candei* shows clear evidence of intense exploitation Few animals were recorded with shell lengths greater than the minimum legal catch size and there was a clear reduction in the abundance of larger animals across the gradient of exploitation Despite this, limpet numbers seemed to be relatively stable across the archipelago. Martins et al. (1987) argue that the biology of *P. candei* may render this species susceptible to size-exploitation (a reduction in size) but not recruitment-exploitation (a reduction in abundance). However, in the Canary Islands the populations of *P. candei* crashed due to over-exploitation (Côrte-Real et al. 1996, Navarro et al. 2005). This suggests that, even opportunistic species such as *P. candei* may be susceptible to population disruption under intense exploitation. It should be noted that, as an endemic species to the Macaronesian Islands, *P. candei* is self-recruiting and hence more vulnerable to a local reduction in reproductive output. The alarmingly low number of limpets in Graciosa, especially in the smaller size-classes (see Fig. 4.2) may be evidence of such a crash. Graciosa is the smallest (23 km of coastal perimeter) and most northerly island of those in the central group. Since the predominant currents in the Azores are from the NW (Morton et al. 1998) this may mean that Graciosa receives little supply of larvae from the other islands. The low numbers of animals found in Graciosa could therefore be the result of recruitment-exploitation.

Removal of particular species may lead to changes in assemblage composition and structure in a variety of marine environments (e.g. Farrell 1988, Benedetti-Cecchi & Cinelli 1992). These changes can be predicted to a certain extent, depending on the identity of the species lost. Experimental work on the importance of top-down control of algae by intertidal limpets (e.g. Underwood 1984, Hawkins et al. 1992, Coleman et al. 2006, and Chapter 1 and references therein) clearly suggests that patellid exploitation is likely to have a strong impact on community structure. The correlative approach used here showed a clear decrease in algal cover with increasing limpet abundance, which conforms to the wider literature. For instance, in Chile, human exclusion from the rocky intertidal areas resulted in an increase of fissurelid limpets and a concomitant decrease of algae (e.g. Moreno et al. 1984). In addition, there was a positive relationship between the abundance of limpets and barnacle cover Limpets are known to affect the abundance and survival of barnacles directly, by killing or knocking small barnacles off from the substratum (bulldozing), and indirectly, by preventing barnacle overgrowth by algae (e g Denley & Underwood 1979) As such, our results conform to the wider literature indicating the importance of limpets in structuring the rocky intertidal does not differ between insular and continental habitats. However, our study differs from others by providing evidence of the role of humans as top-predators (see Siegfried 1994 for references) at landscape scales. This suggests that fragmented habitats (in general) and islands (in particular) can be good model systems to broaden the generality of other studies (Hewitt et al 2007) although the results should be validated whenever possible, for instance by using suitable control areas (e.g no-take marine reserves)

In the present study, it was not possible to ascertain the specific role of each species (*P candei* or *P aspera*) in controlling algae in the Azores. Patellid species can differ significantly in the effectiveness in which they control macroalgae. For example, Moore et al (2007) showed that *P vulgata* was a more effective grazer than *P depressa* in southwest Britain, although in Portugal both species had similar strengths (Boaventura et al. 2002a) In the Azores, there is no evidence to conclude that the two species of limpets differ in terms of diet and future studies should therefore examine this However, considering the overall scarcity of *P aspera* in the archipelago, it is most likely that *P candei* is, at present, the most important grazer of the Azores rocky intertidal.

The effects of human activities on biological systems are complex (Lindberg et al 1998) and it becomes increasingly difficult to predict the wider effects of exploitation at higher trophic levels Islands commonly support assemblages that are less diverse than those observed in the corresponding continental habitat Over-exploitation could have irreversible impacts such as the local extinction of target species and the subsequent elimination or substantial decrease in the ecosystem functioning provided by the exploited species. In a more extreme scenario, it could lead to the disruption of a system by altering the food chain length.

The present study is one of few providing a thorough characterisation of the population structure of limpets across the Azores. It assessed the current status of these populations providing good background data against which future studies can be compared. Results suggest that differences among islands may likely be related to the islands' history of exploitation although the fact that before and suitable no-take marine reserves data are not available prevents causality to be determined. Our study is of particular interest since the fragmented nature of islands habitats allowed us to examine the role of limpets in structuring the rocky intertidal at landscape scales.

CHAPTER 5

Illegal harvesting affects the success of fishing closure areas

Illegal harvesting affects the success of fishing closure areas

5.1. Abstract

Marine reserves are emerging as tools that can foster the recovery of disturbed ecosystems. In the Azores, intense exploitation of the patellid limpets *Patella candei* and *P. aspera* led to a rapid decline of limpets' populations and the fishery substantially collapsed in 1985. In 1993, legislation was passed to protect limpets and this included the establishment of limpet protected zones (LPZ) and seasonal closures. In the present study, I examined the impact of 13 years of protection on the structure and recovery of exploited species of limpets in the Azores. Results reveal that populations still show clear signs of exploitation including low abundance and reduced size; this was evident both inside and outside LPZ's. Observations showed that illegal harvesting was the most likely reason for the failure of these measures to protect limpet populations thus postponing the recover of the stock.

5.2. Introduction

Globally the number of over-exploited fish and shellfish stocks has increased markedly over the last years (Jackson et al. 2001, Myers & Worm 2003). This has increased the need to protect and conserve fished populations. Classical fishery management has traditionally been done in two forms: management of catch or of effort (Roberts & Polunin 1991). Management of catch is usually achieved by restrictions of gear or catch limits, whereas management of effort can include limitation of the number of vessels or licences and the establishment of closed seasons. These approaches have been successful in many cases leading to increased yelds of exploited species (Ye 1998, Govender et al. 2006, Fernández-Rueda & García-Florez 2007) although they are mainly designed for single species fisheries (Munro & Williams 1985, Roberts & Polunin 1991)

The establishment of no-take marine reserves, areas closed to fishing, has been suggested as a viable alternative with several potential advantages (Roberts & Polunin 1991, Lubchenco 2003) and there is mounting evidence that marine reserves have a diverse range of effects which are generally regarded as positive (Halper & Warner 20002, Halpern 2003, Micheli et al 2004, Guidetti & Sala 2007, Claudet et al. 2008) making marine reserves an important tool in coastal management and conservation. For instance, since all fishing methods are size-selective, most targeting the larger individuals within a stock, fishing pressure will consequently lead to a decrease in average size of target species Cessation of fishing has been shown to increase average size of target species compared to fished areas (Branch 1975a, Bell 1983, McClanahan & Muthiga 1988, Lasiak 1993, Branch & Moreno 1994). Reduced mortality rates within reserves also result in increasing abundances of fished stocks (Bell 1983, Alcala 1988, Halpern 2003, Micheli et al. 2004, Guidetti & Sala 2007) The combined effects of increased abundance and size can benefit adjacent fished areas via emigration of adults and juveniles across borders (spill-over effects) and via increased production and export of pelagic egg and larvae (Gell & Roberts 2003, Kaunda-Arara & Rose 2004, Abesamis & Russ 2005). The effects of marine reserves appear stable and long-lasting (Shears & Babcock 2003) indicating that these can be used as a valuable strategy for the protection and management of fisheries

In the Azores, the fishery of limpets collapsed in 1985 (Martins et al 1987, Santos et al 1990, Hawkins et al. 2000, see Chapter 1 for further description of the history of this fishery). In 1993, legislation was passed to protect this resource Limpet protected zones (LPZ) were created around each island where the collection of animals was permanently banned. In addition to these species-specific marine reserves, a more classical conservation strategy was also established in the remainder of the archipelago with the creation of a seasonal fishing closure between November and May and the establishment of minimum legal catch size of 30 and 50 mm shell length for *Patella candei* and *P. aspera*, respectively. Although much work has been done individually on the success of these two approaches, there has been little work as to how these two distinct approaches compare in regards to fishery management (Röckmann et al. 2007).

In 2006, I established a monitoring programme to assess and compare the effectiveness of the permanent and temporary closures and here report on the first 3 years of data. In addition, I examine the extent to which illegal harvesting determines the success of the established management strategies.

5.3. Materials and methods

5.3.1. Study sites

The present study was done in São Miguel Island, Azores. São Miguel is the most developed island of the archipelago with a human population of c.a. 130,000 in 2007 (SREA – Secretaria Regional de Estatística dos Açores). The main economic activities are dairy and fisheries although tourism is a developing industry. The present study was developed at 4 exposed rocky shores: Caloura, Maia, Lagoa and Fenais-da-Luz. The former two have been LPZ's since 1993 where harvesting of limpets is completely banned. In the remaining two areas (Lagoa and Fenais-da-Luz), limpet harvesting is allowed from June to September although there is a minimum catch size (see Chapter 1) and a daily quota of 1 kg per person. As such, the fished areas Lagoa and Fenais-da-Luz are, in their essence, partial closure areas There are no areas within the Azores where the collection of limpets is entirely unrestricted

The four shores support similar assemblages of animals and plants and, apart from wave action, have similar environmental conditions (e.g. slope, substratum). Although all the 4 shores are exposed to wave-action, swell is more frequent in the northern coast due to the prevailing NE winds (Instituto Hidrográfico, 2006) One LPZ and one fished area were selected on both northern and southern coasts. Hence, the influence of variable exposure was similarly distributed between complete and partial closure areas

5 3 2 Sampling design

To examine the effectiveness of LPZ's in enhancing the yields of limpets, the population structure of the exploited limpet *P candei* was compared between each of the four locations for a period of 3 years Formal comparisons were made from *P candei*, but not *P aspera*, as the latter were rare in the intertidal at São Miguel (see Fig 4.1)

At each shore, two sites were randomly selected at least 30 m apart and all *P candei* were counted and measured (shell length) to the nearest mm in ten 25 × 25 cm quadrats Because variation in wave-action among shores may influence the vertical distribution of animals, sampling was done immediately above the upper limit of the dense cover of turf-forming algae that characterised the lower shore Because fished areas were partial closures (seasonal closure), sampling was done twice in each year towards the end of the closed and open harvesting seasons, respectively As such, if protection was effective, a significant reduction in limpet abundance should be noted by the end of the open season in the seasonal closure areas compared to LPZ's. This would be identified in the analysis by a significant time × protection interaction. Alternatively, effective protection of LPZ's may also be identified by a significant main effect of protection, although this would suggest that the seasonal closure of fished areas was generally ineffective.

Analysis of data used the limpet density and biomass per quadrat. The biomass of each limpet was estimated indirectly using a previously calculated relationship (Appendix B). The total biomass of all animals in each quadrat was then used in the analysis.

Preliminary analyses of data corresponding to the first 2 years of the study revealed no significant effect of LPZ's. Illegal harvesting is known to occur and could affect the interpretation of results. Hence, an attempt to estimate the intensity of illegal harvesting was made in the third year of the study by assessing the number of limpet harvesters per day during each of 10 random sampling events in each of two seasons: closed and open. Anthropogenic activities are highly variable in time and space (Underwood & Kennelly 1990). Sampling was thus standardized to low-tide morning periods and excluded weekends. In addition, each single sampling event had a fixed duration of 2 hours (starting ~1h before low tide). Due to logistical constrains, this approach was restricted to two of the four shores: Caloura (LPZ) and Lagoa (fished area), which are both on the south coast. This causes some problems of pseudo-replication (Hurlbert 1984) and therefore results were interpreted with caution. During the course of this PhD, I also recorded the presence of limpet harvesters on every field-sampling trip. While this data was not collected in a properly structured way (with respect to times of day, season, weather conditions), it provides an indication of patterns of limpet harvesting over a 3-year period.

5 3.3 Data analysis

Data were analysed using Analysis of Variance (ANOVA). Prior to analysis, data were checked for heterogeneity of variances using the Cochran's test and transformations applied where appropriate (Underwood 1997). Mean limpet density and biomass were analysed using a 4-way mixed model ANOVA with time (2 levels open and closed, fixed and orthogonal), protection (2 levels· LPZ and partial closure; fixed and orthogonal), location (2 levels random and nested within protection), site (2 levels random and nested within time, protection and location) and 10 replicates The analyses were done separately for each year to provide a valuable denominator for the terms of interest (Underwood 1997) Limpet population size structure was compared between LPZ's and fished areas using the Kolmogorov-Smirnov test Data from each of the two locations (and hence 4 sites) within each level of protection were combined prior to this analysis

The per day mean number of harvesters in LPZ and fished areas was compared using a 2-way factorial ANOVA with time (2 levels fixed) and location (2 levels fixed) and 10 replicates Data on the frequency of limpet harvesting were analysed using 95% confidence intervals

5.4. Results

5 4.1 Limpet population structure

A total of 2150 *P candei* were counted during the 3 years of the study and these had an average shell length of 12 6 ± 0.08 mm (mean ± 1SE) Despite significant variation in space and time, the interaction protection x time was not significant in any of the 3 years examined (Fig. 5.1, Table 5.1 and 5.2) suggesting no difference between LPZ's and partially fished areas. The main factor protection was also non-significant indicating that LPZ's present no advantage over partial closures.

Analysis of population size structure showed variable results (Fig. 5.2). By the end of the closed season, individuals in fished areas were smaller than in LPZ's in 2007 and 2008 but not in 2006. However, by the end of the open season, differences in the size structure were only evident in 2007 and here, in contrast to the closed season, individuals in fished areas were larger than populations in LPZ's. It should be noted that the total number of sampled animals decreased by the end of the open season in both LPZ's and fished areas and that no specimen was larger than the legal catch size (30 mm shell length). Hence, it would appear that exploitation was occurring at all sites.

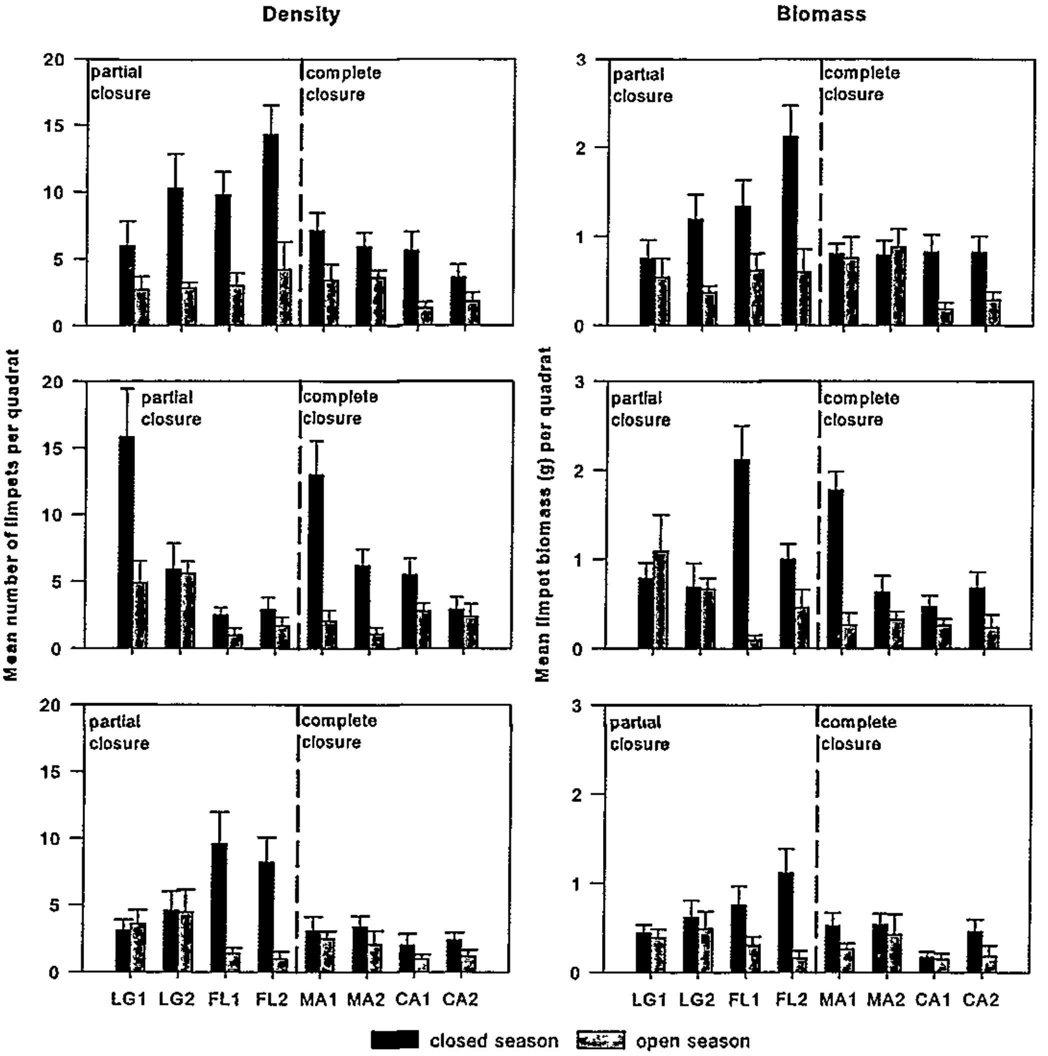

Figure 5.1. *Patella candei* Comparison of the mean density and biomass (+ SE, quadrat size = 625 cm^2) at the end of the open and closed fishing seasons over 3 years inside partial (temporal) closures (Lagoa (LG)) and Fenais-da-Luz (FL)) and complete (permanent) closures (Maia (MA)) and Caloura (CA)).

Table 5.1. 4-way mixed model ANOVA comparing the abundance of *Patella candei* in LPZ's and fished areas during the open and closed harvesting seasons.

		2006		2007		2008	
Source	df	MS	*F*	MS	*F*	MS	*F*
Time = T	1	35.47	34.36*	24.17	6.05	11.81	1.96
Protection = P	1	6.21	1.67	0.18	0.01	7.86	8.37
Location = L (P)	2	3.72	5.78	13.55	5.65*	0.94	6.50*
Site (T × P (L))	8	0.64	0.87	2.40	3.74***	0.14	0.28
T × P	1	3.20	3.10	1.17	0.29	2.62	0.44
T × L (P)	2	1.03	1.61	4.00	1.66	6.02	41.74*
Residual	144	0.74		0.64		0.51	
Transformation		Sq-Rt		Sq-Rt		Sq-Rt	
Cochran's		*C* = 0.17		*C* = 0.16		*C* = 0.15	

Table 5.2. 4-way mixed model ANOVA comparing the biomass of *Patella candei* in LPZ's and fished areas during the open and closed harvesting seasons.

		2006		2007		2008	
Source	df	MS	*F*	MS	*F*	MS	*F*
T	1	1.55	7.30	231.51	3.05	0.51	3.89
P	1	0.29	0.87	24.46	2.48	0.23	3.19
L (P)	2	0.33	6.27*	9.87	0.66	0.07	2.94
Site (T × P (L))	8	0.05	0.97	15.02	2.62*	0.02	0.79
T × P	1	0.28	1.32	0.78	0.01	0.06	0.48
T × L (P)	2	0.21	4.01	75.85	5.05*	0.13	5.39*
Residual	144	0.05		5.74		0.03	
Transformation		Sq-Rt		ArcSin		Sq-Rt	
Cochran's		*C* = 0.13		*C* = 0.17		*C* = 0.16	

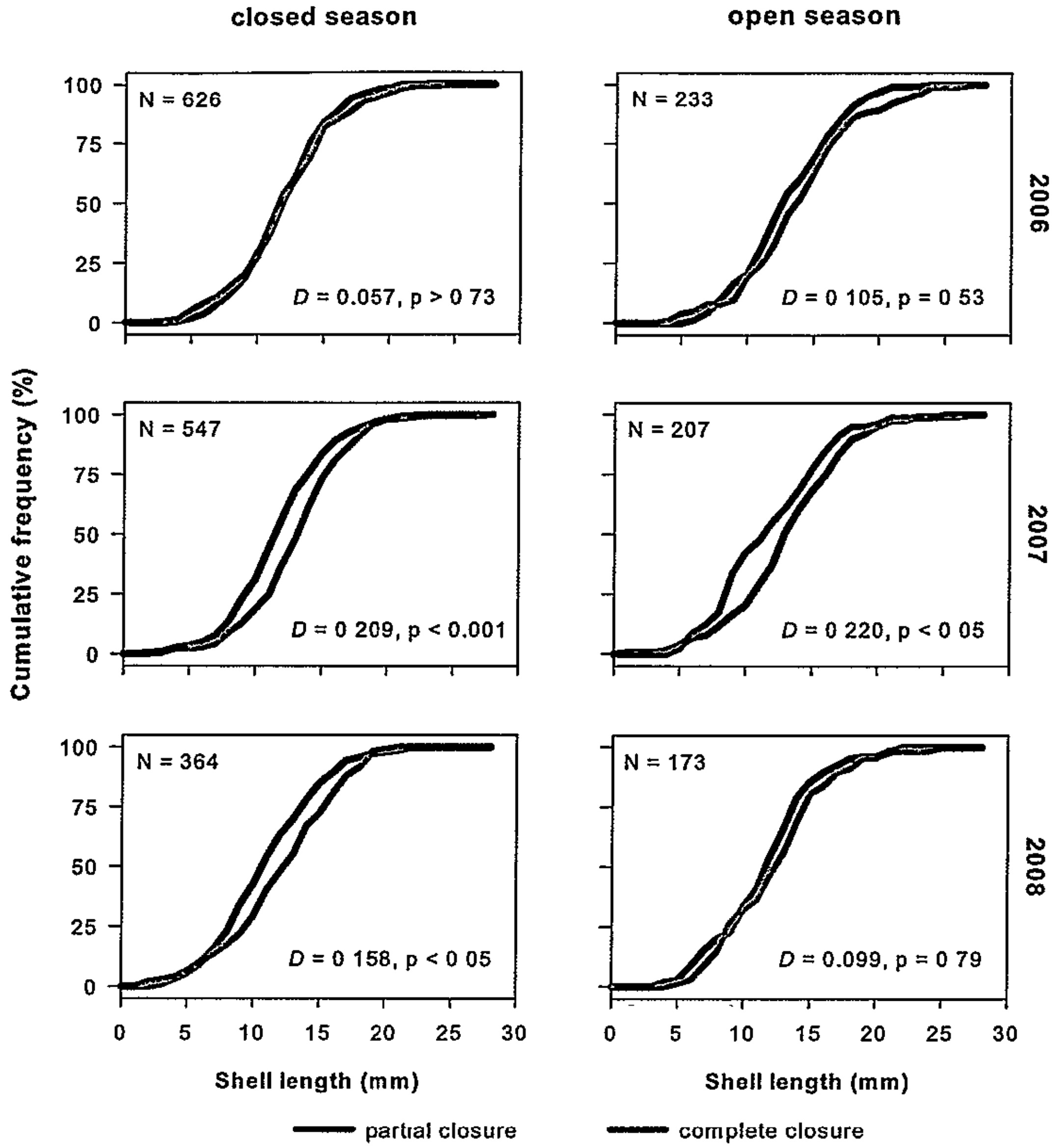

Figure 5.2. *Patella candei* Analysis of the size structure of limpet populations in partial and complete closures. For each level of protection (partial and complete closures) data were pooled between the two corresponding locations The Kolmogorov-Smirnov test (*D*) is shown

5 4 2. Limpet harvesting

Limpet harvesting was observed in both the protected and fished areas although harvesting frequency was greater in the later with a per day mean number of harvesters of 0 7 ± 0 19 (mean ± 1SE) in comparison with the 0 1 ± 0.07 recorded in the LPZ (Fig.

5.3, Table 5.3). The number of harvesters did not show significant variation with season although it tended to be greater during the open season in the fished area.

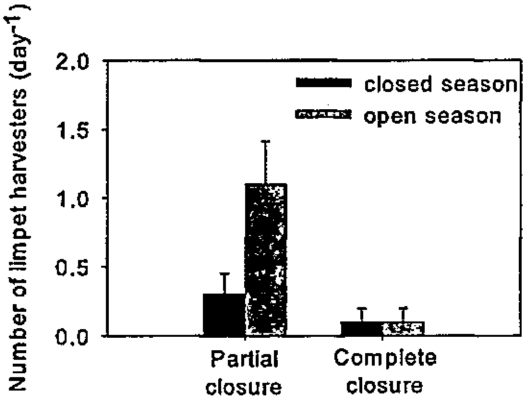

Figure 5.3. Comparison of the mean (+SE) number of people harvesting limpets in 2008 between one partial (temporal, Lagoa) and one complete (LPZ, Caloura) closure areas at the end of the open and closed fishing seasons. Data were collected in a standardised way. See methods for further details.

Table 5.3. 2-way factorial ANOVA comparing number of people harvesting limpets in 2008 between one partial (temporal, Lagoa) and one complete (LPZ, Caloura) closure areas at the end of the open and closed fishing seasons.

Source	df	MS	*F*
Time	1	25.56	3.68
Location	1	75.43	10.87**
T × L	1	25.56	3.68
Residual	36	6.96	
Transformation		ArcSin	
Cochran's		*C* = 0.49	

Data collected over a period of 3-years showed that despite temporal and spatial variability in harvesting frequency, limpets were collected irrespective of site status (LPZ's vs. fished areas) or temporal (open vs. closed season) protection (Fig. 5.4).

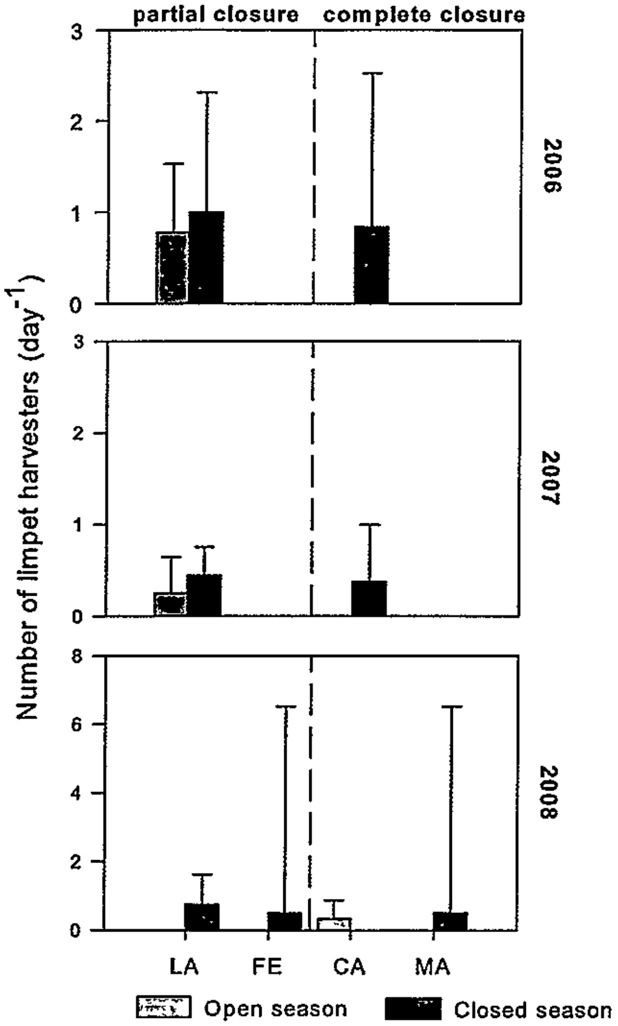

Figure 5.4. Comparison of the mean (+CI) number of people harvesting limpets between partial (temporal) and complete (LPZ) closure areas over 3 years Legend as in Fig. 5 1 Data were collected in a non-standardised way See methods for details

5.5. Discussion

This study showed that 13 years of protection have had little impact on the populations of limpets in the Azores Data show clear signs of size exploitation with no individuals larger than the minimum catch size recorded either in LPZ's or fished areas Comparing to 1988 (Hawkins et al 1990a), at the same location (Caloura) the mean abundance of *P. candei* decreased from ~ 61 to 7.2 m^{-2} (pooled over the 3 years of the present study). Although Martins et al. (1987) argue that the opportunistic life-history of *P. candei* renders it relatively insensitive to recruitment exploitation, populations of *P. candei* have become extinct in all but one of the 9 islands of the Canaries (Núñez et al. 2008). The dramatic decrease in population size over 20 years in the Azores suggests that *P. candei* could also become locally extinct. For example, if the population size decreased below a threshold whereby Allee effects resulted in reproductive or recruitment failure (Miller et al. 2009).

Lack of significant effects of marine reserves have been reported elsewhere. For instance, Parnell et al. (2005) showed no clear benefits from protection in a marine reserve in California 30 years after fishing cessation. Likewise, Denny & Babcock (2004) showed that partial closure in New Zealand was ineffective in protecting the locally exploited stocks of snappers. Illegal harvesting can severely influence the success of conservation strategies (Kritzer 2004, Little et al. 2005, Samoilys et al. 2007, Guidetti et al. 2008), especially in the intertidal where a single collection can be very extensive resulting in long-lasting effects. The increasing perception that no-take marine reserves are areas of biomass accumulation where exploited species occur at larger numbers and attain a larger size may also increase the appeal for poaching (Sethi & Hilborn 2008). Keough & Quinn (2000) found that effective protection of Australian marine reserves required physical barriers and greatly increased enforcement to effectively exclude humans. Guidetti et al. (2008) also showed that the success of marine protected areas along the Italian coast was related to the level of enforcement and that of the 15 marine reserves examined, only 3 had levels of enforcement that were adequate to effectively protect exploited stocks. Illegal harvesting is a worldwide phenomenon and may explain why some marine protected areas, including the ones used here, fail to fulfil their role.

Although variable in space and time, limpet harvesting was recorded on the shore regardless of the level of protection (LPZ vs partial closure) or season (open vs closed) and this was true for all the four locations examined My estimates indicated that LPZ's could receive 37 harvesters per year Although this level of exploitation was much lower than that recorded in the fished area, it could still impact populations. Most of the limpets for sale in the local market are now supplied from Madeira However, recreational harvesting is still a common practice and illegal catches occurs inside LPZ's (personal observation) Clearly, legislation and current levels of enforcement are insufficient at protecting these populations of limpets This would require a much greater level of enforcement, probably including the establishment of physical barriers that limit people access to the shore.

An interesting approach that has had positive results is that of co-management policies (Costello et al 2008). For instance, in Chile the so-called Management and Exploitation Areas for Benthic Resources (MEABR), grant territorial user rights to small-scale fishers who share the management of local resources in well-defined coastal areas (Odendaal et al. 1994, Gelcich et al 2005, 2008) thus promoting the sustainable exploitation of resources This management strategy follows the increasing awareness of the need to increase ownership of conservation areas and of involving all interested parties in the development of new management schemes (Baxter 2001, Thompson et al. 2002) In Chile, the establishment of a network of MEABR's has had positive effects both for the fishermen (by increasing the fishery efficiency) and the resources (including non-target populations) (Gelcich et al 2008) This suggests that the establishment of MAEBR's could provide an interesting option for the management of coastal resources in the Azores

CHAPTER 6

Exploitation-driven community structure in the rocky intertidal: the role of disturbance and limpet grazing on the dominance of turf-forming algae

Exploitation-driven community structure in the rocky intertidal: the role of disturbance and limpet grazing on the dominance of turf-forming algae

6.1. Abstract

In the Azores, intense exploitation of limpets for over 20 years has significantly decreased abundance resulting in changes in assemblages where turf-forming algae have displaced barnacles as the dominant space occupier. Here I used 3 experiments to: (i) examine the balance between algae and grazers at exploited densities of limpets, (ii) examine how this alternate community state, where turf-forming algae are the dominant species, resists to different types and timings of disturbance, and (iii) examine how different densities of limpets mediate space acquisition in patches cleared of turf-forming algae. Compared to areas where limpets were kept at exploitation-driven densities, areas where limpets were experimentally excluded supported a significantly greater, albeit small, increase in the cover of algae whilst barnacle cover tended to be reduced. Simulation of a natural disturbance that removes turf-forming algae was applied in the form of a single and large cleared area (small perimeter-area (PA) ratio) and also as several small areas (large PA ratio) to examine the impact of different strengths of edge effects on turf resistance. Moreover, this experiment was initiated at two dates to examine the influence of temporal variations in species colonisation on the outcome of succession. The cover of turf-forming algae in unmanipulated areas (undisturbed) remained high throughout the experiment and successfully prevented the colonisation and establishment of other biota. In contrast, the disturbed areas were readily colonised by limpets, barnacles and other algae. Although initially limpets recruited at relatively high numbers to disturbed patches, their number soon decreased to densities similar to those in the surrounding area (exploited densities). One year after disturbances, disturbed areas supported two divergent assemblages – one dominated by barnacles and the other where turf-forming algae had regained the space back

resembling undisturbed areas. However, neither the type nor the timing of disturbance apparently influenced the outcome of succession In a third experiment I examined how different and controlled limpet densities mediated space acquisition by turf-forming algae in small areas where these had been removed In the absence of limpets, turf-forming algae rapidly reinvaded the cleared space via lateral vegetative growth. In contrast, where limpets were present, grazing by limpets successfully prevented space reinvasion by turf-forming algae and the colonisation of other macroscopic algae allowing barnacles to recruit Moreover, the space available for colonisation increased linearly with increasing limpet density These results suggest that grazing by *Patella candei* is a key processes in structuring the Azorean intertidal In addition, it indicates that this exploitation-driven community state where turf-forming algae are the dominant space occupier is highly resilient but that changes in the structure of this community toward a barnacle-dominated community are likely in the event of harvesting cessation

6.2. Introduction

Rapid urbanisation over the last century has substantially increased anthropogenic pressure on marine coastal ecosystems Exploitation of living marine resources, pollution, habitat destruction, eutrophication and the introduction of non-native species are examples of the impacts on the structure and functioning of marine systems worldwide (Thompson et al 2002, Airoldi and Beck 2007) In developed regions, such as Europe, these impacts are such that pristine habitats have become restricted to small and isolated localities, such as islands However, even these are not protected from large-scale impacts such as climate change Understanding how natural systems behave under disturbed conditions and the extent to which they are resilient to environmental impacts is crucial if we are to predict the consequences of our actions or foster the recovery of degraded systems.

Utilisation of coastal living resources has been taking place since pre-historic times (Siegfried et al. 1994). Recently, over-exploitation of marine populations has become a global problem that can have dramatic effects at a range of levels from populations through to ecosystems (see Chapter 1 for review). For example, where exploitation targets keystone species it can lead ecosystems to switch to alternate community states (Castilla and Durán 1985, Sala et al. 1998, Castilla 1999, Pinnegar et al. 2000). Two examples are well documented for temperate regions and include the over-fishing of predatory fish, which leads to increased grazing by sea-urchins and the consequent formation of barrens in the central Mediterranean (e.g. Guidetti 2006, Guidetti & Sala 2007); and the overfishing of a predatory gastropod, which leads to the spatial dominance of mussels over barnacles in the rocky intertidal of central Chile (e.g. Castilla & Durán 1985, Moreno et al. 1986). These alternate communities persisted for many years. However, upon the establishment of no-take marine reserves, these communities returned to their original states within a few years.

In the Azores, intense exploitation of patellid limpets has caused dramatic reductions in limpet abundance (Santos et al. 1990, Morton et al. 1998, Hawkins et al. 2000) promoting a shift between animal-dominated to algal-dominated mid shore communities (see Chapter 4). Vertical transects show that the distribution of turf-forming algae now extends further up on shore on islands with the longest history of limpet exploitation history (Fig. 6.1) with algae displacing the barnacle *Chthamalus stellatus* as the dominant space occupier in the upper mid-eulittoral. These changes are most probably related to the reduced limpet grazing pressure, which is known to determine the upper vertical limit of many algal species (Underwood 1980, Hawkins &

Hartnoll 1983, Underwood 1985, Boaventura et al. 2002b) together with direct and indirect interactions, which influence the abundance of algae and barnacles (e.g Van Tamelen 1987). As such, the rocky intertidal of the Azores may present a further example illustrating how human exploitation of key species has led to alternate community states

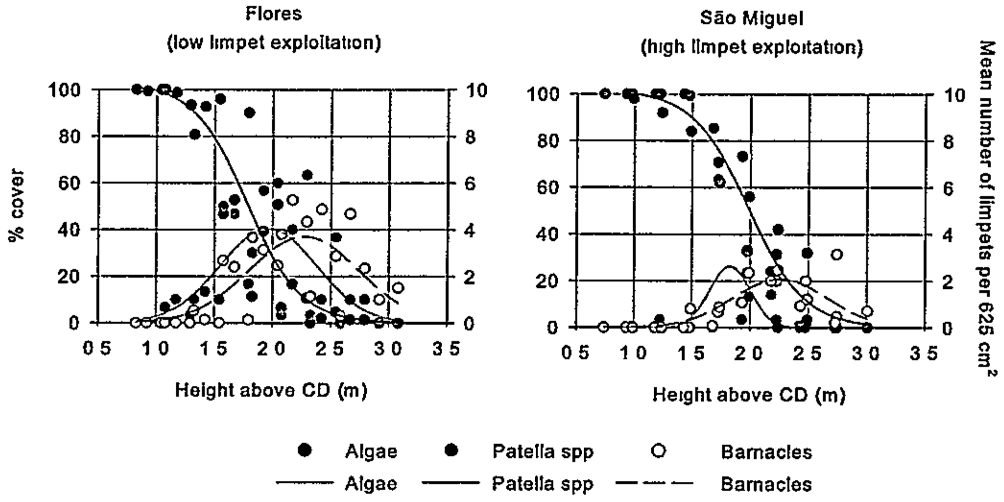

Figure 6.1. Vertical distribution of algae, barnacles and limpets in Flores (least exploited island) and São Miguel (highly exploited island). Data were collected in three vertical transects done at each of 3 locations in each island Note the lower abundance of limpets in São Miguel and the upward extension of algae, which outcompete barnacles becoming the dominant space occupier at mid shore heights.

As a consequence of anthropogenic disturbance coupled with rapid rates of vegetative growth, the cover turf-forming algae is increasing worldwide and has replaced key biota such as canopy-forming algae (e g Airoldi 1998, Benedetti-Cecchi et al 2001b, Connell et al 2008, Mangialajo et al 2008). Turf-forming algae can inhibit the establishment of other algae (Benedetti-Cecchi 2000c) or grazers (Benedetti-Cecchi et al. 1999) and so the dominance of turf-forming algae on the upper mid shore in the Azores may persist in the event of limpet harvesting cessation.

The important role of disturbance in structuring marine benthic communities was highlighted by the pioneering work of Dayton (1971). His work and numerous of subsequent studies (e.g. Sousa 1984) demonstrated that disturbance is a key process in providing new space for colonisation and influencing the outcome of inter-specific competition. Specifically, the size and shape of disturbed patches determines the PA (perimeter - area) ratio and hence influences the extent to which the surrounding community can affect succession in the disturbed patches via edge effects (Airoldi 2003). Generally, it is assumed that large disturbed areas with a small PA ratio facilitate the development of a community that diverges from the surrounding community. In contrast, in small-disturbed areas, strong edge effects will preclude community divergence (Petraitis & Latham 1999, Dudgeon & Petraitis 2001). The type of disturbance, however, is not the only determinant of the outcome of succession in disturbed patches. For instance, work made by Farrell (1991) showed that the presence or absence of recruiting species with strong competitive ability could also affect community development. Moreover, given the temporal variability in species recruitment, the timing of a disturbance can also influence inter-specific competition between recruiting species and thus affect the community structure (e.g. Benedetti-Cecchi 2000c).

In the present study I examined how a reduction in the abundance of *Patella candei* due to intense over-fishing affects the balance between limpets, grazers and barnacles. In addition, I examined the resistance of turf-forming algae, which are now the dominant space occupier of the upper mid shore, to disturbance. Specifically I compared the resistance and persistence of turf-forming algae in disturbed and undisturbed areas as well as the influence of different types of disturbances (leading to disturbed areas that differ in PA ratio) and timing of a disturbance on patterns of succession in disturbed patches The effect of grazing by limpets kept experimentally at different densities in mediating resource (space) acquisition by turf-forming algae in small-disturbed patches was also examined to investigate the ability of the system to recover in the event of limpet harvesting cessation.

6.3. Materials and methods

6.3 1. Study sites

The present study was conducted at mid-shore tidal levels at two locations Lagoa and Caloura. The biotic and environmental conditions of these two shores have already been described in previous chapters (Chapter 2).

6.3 2. Sampling design

6 3 2 1 Grazing by limpets at exploited densities

The effect of limpet exploitation in the balance between limpets, algae and barnacles in the upper mid shore was examined. Twelve 20 × 20 cm areas were marked on each shore above the vertical extent of turf-forming algae zone at random but with the following provisos that the lower side of quadrats were just above the upper extent of turf-forming algae, there was less than 1% cover of erect algae, and more than 50% cover of barnacles. Assemblage structure was similar among locations and treatments at the start of the experiment (Appendix C) The mean number of limpets in all the 12 areas was recorded. Limpets were then removed from 6 randomly selected areas and from the surrounding 50 cm, whereas the remaining 6 areas were left unmanipulated

Treatments were maintained by manual removals as previous experience had shown people interfere with exclusion cages. Removal was achieved fortnightly visits and included the addition of limpets to compensate for any that were lost due to natural mortality or harvesting.

The experiment was set up in November 2007 and ran for one year. During this period, areas were sampled in March, May, August and November (2008). The abundance of algae and sessile animals was estimated by recording the species underneath each of the 45 points in a uniformly distributed grid and later converting these to percentage cover. An arbitrary percentage cover of 0.5 was given to all species that were present but were outside any of the 45 points. Macroalgal species were identified to the lowest taxonomic level achievable in the field (typically species or genus). Mobile animals other than limpets (e.g. littorinids and predatory whelks) were rarely recorded inside marked areas and hence were not included in the analysis.

6.3.2.2. Algal turf persistence and the role of disturbance

To examine the persistence of turf-forming algae and the role of disturbance on its persistence in the upper mid shore twenty-four areas of 25 × 25 cm were marked towards the upper limit of vertical distribution of turf-forming algae (e.g. *Caulacanthus ustulatus*) on each shore in areas where turf-forming algae covered more than 90% of the substratum. Areas were randomly selected and assigned to one of three treatments (n = 8 per treatment). Treatments were similar to those described by Benedetti-Cecchi et al. (1999) and consisted of total biota removal, partial biota removal and an unmanipulated control. In the total removal treatment, the entire area was scraped of all biota until no macrobiota were seen. In the partial treatment, the area was divided in 10 equally sized smaller areas and the biota was removed from 5 randomly selected areas.

This treatment simulated a disturbance of lower intensity and was included to test for the effects of space when provided in the form of several small areas, as opposed to a single and relatively large area The prediction being that edge effects increase with perimeter such that pre-emption of space would be greater in partial removal treatments

Because I was mainly interested in the effects of space pre-emption in limiting the recruitment of organisms, all treatments were surrounded by a buffer zone of dense turf cover to prevent immigration of mobile animals. Natural recruitment of limpets into cleared areas was allowed and their numbers were not controlled The number of limpets was sampled regularly as was colonisation by algae and barnacles Areas available for colonisation differed among treatments. In order to maintain the sampled area equivalent among treatments sampling was done using a 5 × 10 cm sampling quadrat with 10 intersections which was haphazardly laid 3-times in each area so that a total of 30 sampling points corresponding to 150 cm^2 were read in each replicate. These were then converted to percentage cover. Limpet density, not limpet number, was used in the analyses to make the abundance of animals comparable among treatments.

Many marine invertebrates and algae have discrete temporal windows of recruitment and these could affect the outcome of competitive relationships among colonising species Thus, the abovementioned experiment was replicated twice with different starting dates (February and October 2007), to test the hypothesis that the timing of disturbance affects the outcome of succession

6 3.2 3 The role of grazing by limpets in disturbed patches

Over-exploitation of limpets has led to an upward extension of turf-forming algae to the upper mid shore (see Fig 6 1 and Chapter 4). Here I examined the role of grazing by *P. candei* in preventing resource acquisition (space) by turf-forming algae following a disturbance that removes it.

Just below the upper vertical extent of turf-forming algae, areas of approximately 5 × 5 cm were scraped clean. This size of these clearings simulated the size frequently produced by natural disturbances such as mechanical abrasion by cobbles (personal observation). A total of fifteen clearings were prepared on each shore and randomly assigned to one of three treatments (n = 5 per treatment): 0L – no limpet added, 1L – one limpet added, 2L – two limpets added. The 1L and 2L treatments were equivalent to very high densities of limpets (400 m^{-2} and 800 m^{-2}, respectively). Although the density of limpets currently found on these shores was much lower, aggregations of this density do occur in similarly sized natural patches (personal observation). Limpets were transplanted into experimental clearings from nearby areas and ranged between 10 and 15 mm (shell length). Limpets were placed inside clearings so as to mimic natural patterns of distribution (e.g. Farrell 1989). The experiment was established in January 2008 and limpet densities corrected, when necessary, approximately every 2-weeks. The size of clearings was examined prior to the start of the experiment and every 2-months thereafter using a 10 x 10 cm quadrat with 100 subdivisions (1 subdivision = 1 cm^2). Each subdivision was given a score from 0 to 4 (0, 25, 50, 75 and 100 % bare rock cover). Each subdivision was then converted to the corresponding area and summed to calculate the area free of erect algae. Although bare space is not a biological variable per se, it was recorded and used in the analysis since it is directly related to the hypothesis being tested.

6.3.3 Data analysis

Data for all the 3 experiments were analysed using analysis of variance (ANOVA). Generally, a 2-way mixed model ANOVA was used with location (2 levels and random) and treatments (fixed and orthogonal to location) as factors. Variations between analyses were due to differing numbers of levels within treatments and numbers of replicates In all experiments time was not independent between sampling events and thus analyses were made separately for each time. Prior to ANOVA, data were checked for homogeneity of variances using the Cochran's test and transformations applied where necessary (Underwood 1997)

In the third experiment, analysis of the effect of grazing by limpets on space acquisition by turf-forming algae following a disturbance was examined as the temporal variation in the area kept free of algae according to the following formula

$$\mathrm{Log}\frac{A_{tn}}{A_{t0}},$$

where A_{tn} was the area of the clearing at time n and A_{t0} was the area of each clearing prior to the start of the experiment In addition, 95% confidence intervals were calculated for each treatment to examine if variation in the size of clearings on a given date differed from that set at the start of the experiment

6.4. Results

6.4 1. Grazing by limpets at exploited densities

When considering data from all maintenance visits the mean number of limpets in grazed (+G) and ungrazed (– G) treatments was respectively 3.93 ± 0.31 (mean ± SE) and 0.30 ± 0 08 for Lagoa and 1.13 ± 0 21 and 0 04 ± 0 03 for Caloura

Differences in algal cover between treatments increased with time, with algae in the grazer exclusion treatment becoming significantly greater from August 2008 onwards (Fig. 6.2, Table 6.1a). This result was consistent between the two shores examined. Although the extent of algal growth in treatments where limpets had been removed was limited, algae covered approximately 8-10% of space by the end of the experiment representing up to a 6-fold increase compared to grazed areas. Algal colonisation in the absence of grazers (- G) was mostly by fast-growing ephemeral species including *Ulva rigida*, *Polysiphonia* sp. and *Rivularia* sp. and to a smaller extent the turf-forming alga *Gelidium microdon*. Differences in barnacle cover between treatments were only statistically significant in May 2008 (Fig. 6.3, Table 6.1b). Nevertheless, the abundance of barnacles tended to be lower where limpets were excluded.

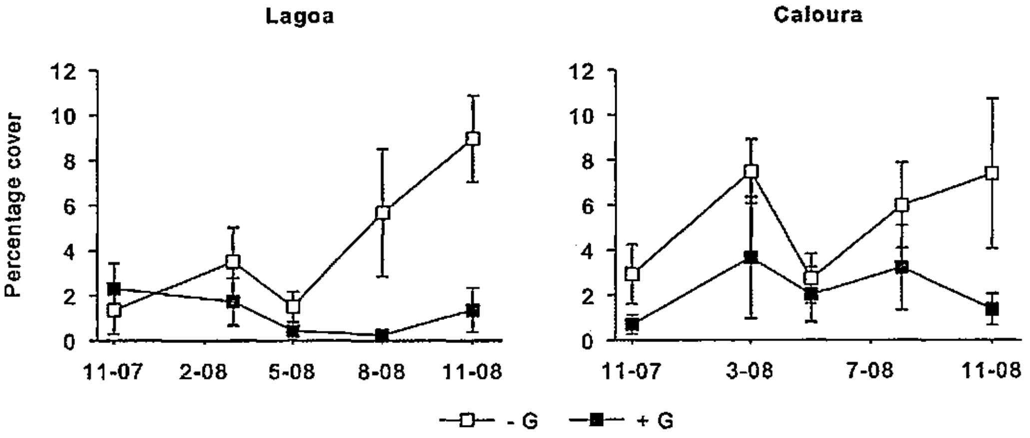

Figure 6.2. The effects of grazing by *Patella candei* on algal cover on the upper mid shore. + G = grazed areas where limpets were kept at exploited densities, - G = ungrazed areas where limpets were manually removed. Standard errors are shown.

Table 6.1. Analysis of the effects of limpet harvesting on the balance between grazers and algae on the upper mid shore. ANOVA comparing the cover of algae (a) and barnacles (b) between treatments grazed (+G) and ungrazed (-G) areas. L = locations (random), T = treatments (fixed and orthogonal to L). For all data, there was no heterogeneity of variances and hence transformation were not applied.

		Nov '07		Mar '08		May '08		Aug '08		Nov '08	
(a) algal cover	df	MS	*F*	MS	*F*	MS	*F*	MS	*F*	MS	*F*
Location = L	1	<0.01	<0.01	52.51	2.73	11.48	2.34	15.68	0.68	4.00	0.17
Treatment = T	1	2.54	0.17	46.76	7.42	4.68	23.21	100.04	4.55*	277.40	12.04**
L × T	1	15.04	2.31	6.3	0.33	0.2	0.04	10.94	0.45a	3.84	1.13a
Residual	20	6.50		19.21		4.9		22.76		24.14	
Pooled	21							22.14		23.1	
Cochran's		*C* = 0.41		*C* = 0.57		*C* = 0.46		*C* = 0.53		*C* = 0.56	
(b) barnacle cover	df	MS	*F*	MS	*F*	MS	*F*	MS	*F*	MS	*F*
Location	1	211.2	2.22	1742.5	15.37***	763.9	5.61*	41.1	0.38	765.0	5.46*
Treatment	1	66.0	2.24	601.0	3.72	1040.2	7.65*	298.2	22.59	2.2	2.2
L × T	1	29.5	0.31	161.7	1.43	91.3	0.67a	13.2	0.12	128.3	0.92
Residual	20	95.1		113.4		138.5		107.5		140.2	
Pooled	21					136.2					
Cochran's		*C* = 0.48		*C* = 0.38		*C* = 0.49		*C* = 0.32		*C* = 0.44	

a – pooled (p > 0.25, Underwood 1997)

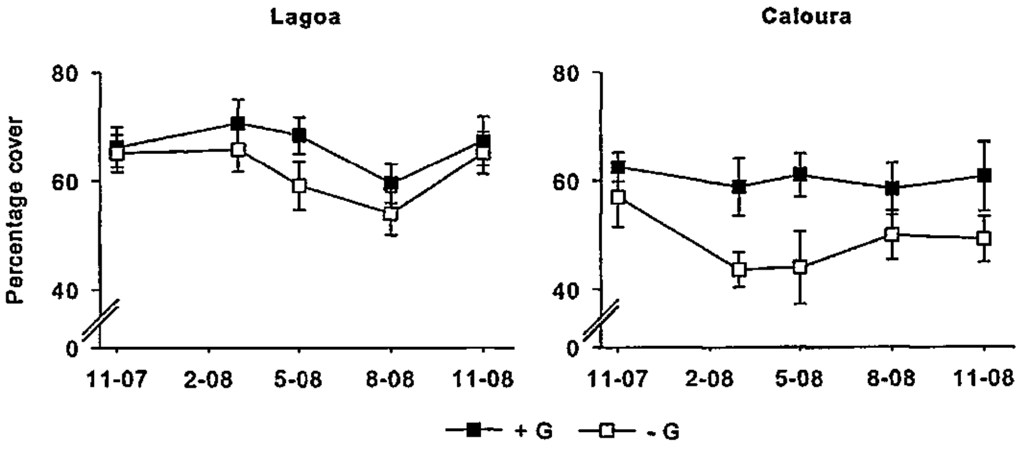

Figure 6.3. The effects of grazing by *Patella candei* on the abundance of barnacles on the upper mid shore. + G = grazed areas where limpets were kept at exploited densities, - G = ungrazed areas where limpets were manually removed. Standard errors are shown.

6.4.2. Algal turf persistence and the role of disturbance

Patterns of succession were variable in time and space. Recruitment of limpets into areas that had been cleared of turf-forming algae to simulate the effects of disturbance by rocks was rapid and appeared to have two peaks: one during late winter (Fig. 6.4 February '07 – Time 1) and one during summer (Fig. 6.4, Time 2). Because the areas that had been cleared of turf-forming algae were made in a way as to be surrounded by a thick cover of turf-forming algae, limpets present in cleared areas were probably the result of settlement from plankton. After initial limpet recruitment, the number of animals tended to decrease and remained at low levels throughout the remainder of the experiment. Statistical analyses showed that there were significant differences in limpet densities between the areas cleared of turf-forming algae and the unmanipulated control, but not among the cleared treatments themselves (Appendix D).

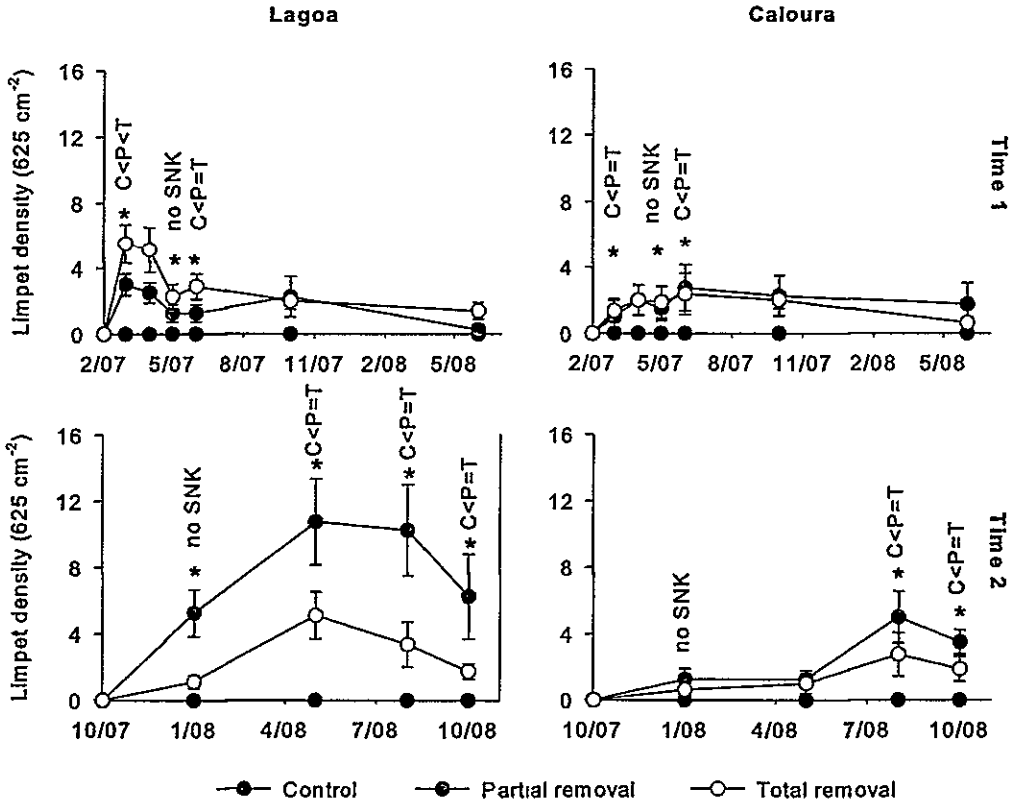

Figure 6.4. Mean (± SE) number of *Patella candei* in areas where turf-forming algae had been removed to examine the role of disturbance shape (C – undisturbed controls, P – partial removal, and T – total removal) and timing of disturbance on organism succession. The outcome of SNK tests done on significant terms (ANOVA) (see Appendix D) is shown. No SNK – although the term of interest was significant, the SNK was not powerful enough to distinguish between the levels of the treatment

Ephemeral green algae (*Ulva* spp.) also rapidly colonised the cleared areas (Fig. 6.5), but were gradually replaced by turf-forming algae, which mostly colonised the space via lateral vegetative growth. With the exception of one site (Lagoa – Time 1), where the cover of algae increased steadily until it was similar to that in the unmanipulated control, algal cover tended to decrease towards the end of the experiment. Statistical analyses showed that, as with limpets, there was generally no consistent difference in cover of erect algae between the two cleared treatments (Appendix D).

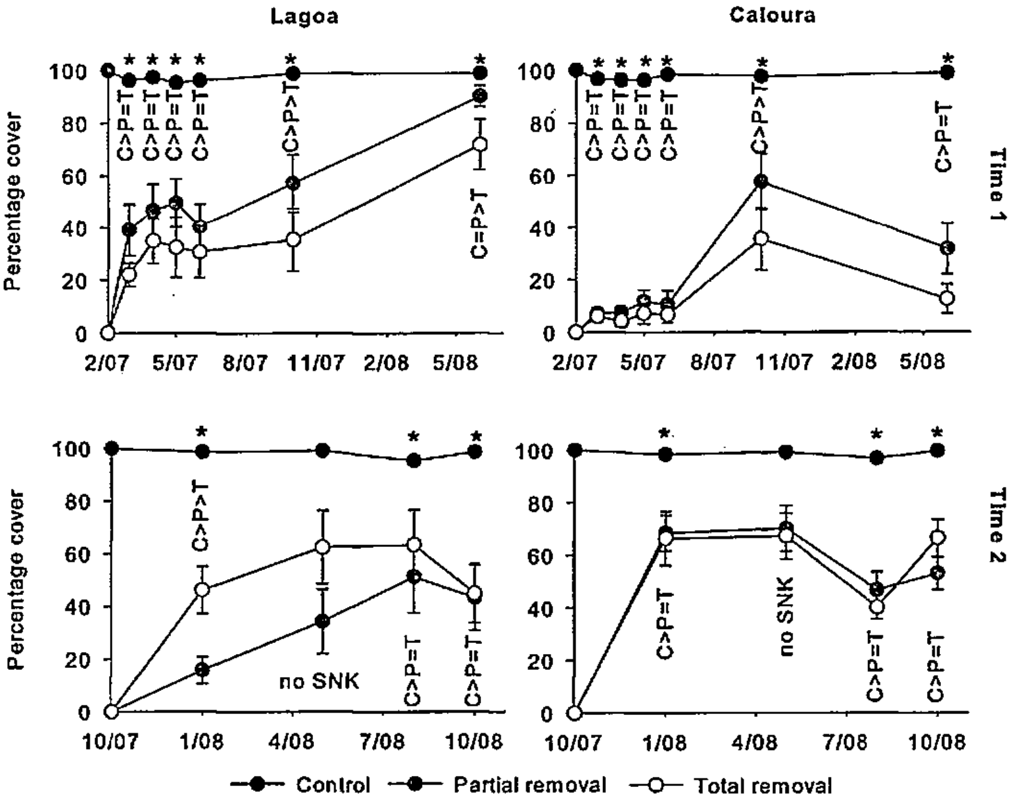

Figure 6.5. Mean (± SE) percentage cover of erect algae in areas where turf-forming algae had been removed to examine the role of disturbance shape (C – undisturbed controls, P – partial removal, and T – total removal) and timing of disturbance on organism succession. SNK analysis as in Fig. 6.4.

Recruitment of barnacles was notable in cleared areas by the end of the summer (Fig 6.6, Appendix D). Barnacle recruitment was, however, highly variable in space and time with contrasting results at each location and starting date. The cover of encrusting algae was also highly variable in time. Following clearing at time 1, encrusting algae were significantly more abundant in cleared areas after 2 months (Fig. 6.7, Appendix D). However, their cover tended to decrease with time thereafter. Following clearing at time 2, the cover of encrusting algae remained relatively low and only increased toward the end of the experiment There were no clear differences in the cover of encrusting algae between cleared treatments

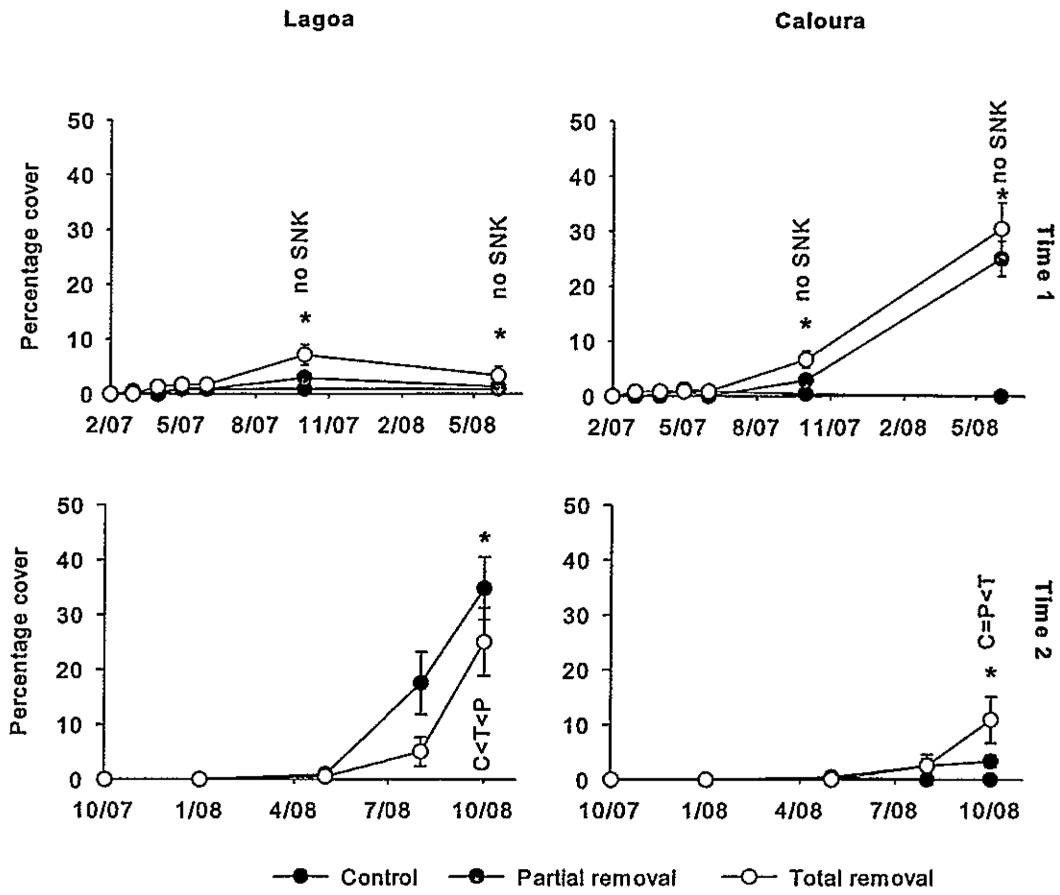

Figure 6.6. Mean (± SE) percentage cover of barnacles in areas where turf-forming algae had been removed to examine the role of disturbance shape (C – undisturbed controls, P – partial removal, and T – total removal) and timing of disturbance on organism succession SNK analysis as in Fig 6.4.

In summary, in this second experiment the cover of turf-forming algae in the unmanipulated control remained high and unchanged through out the experiment and successfully prevented the colonisation and establishment of other biota. In contrast, in areas where turf-forming algae had been removed, following a rapid growth of ephemeral algae, succession led to the development of two divergent assemblages – one leading the monopolisation of space by turf-forming algae and the other by barnacles. This, apparently, was neither related to the shape of the cleared areas or the time at which the experiments started but to differences in the intensity of barnacle recruitment between the two locations.

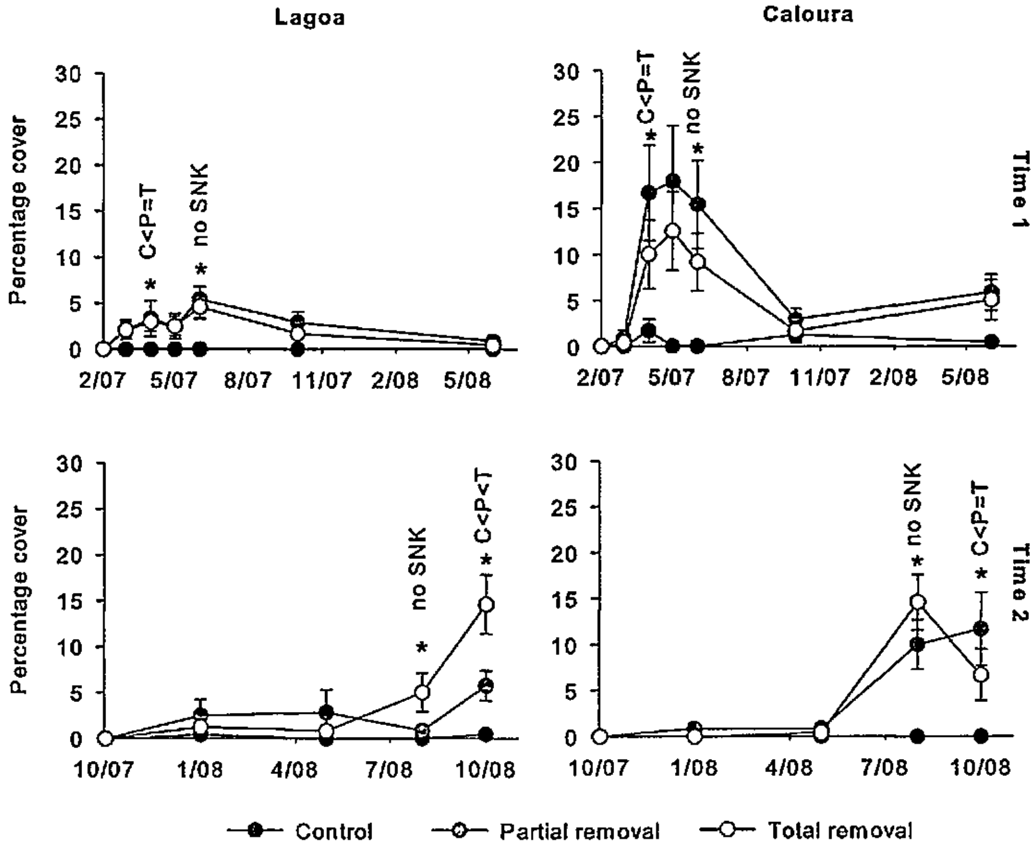

Figure 6.7. Mean (± SE) percentage cover of encrusting algae in areas where turf-forming algae had been removed to examine the role of disturbance shape (C – undisturbed controls, P – partial removal, and T – total removal) and timing of disturbance on organism succession. SNK analysis as in Fig. 6.4.

6.4.3. The role of grazing by limpets in disturbed patches

To test the hypothesis that the grazing by limpets controls the recolonisation of turf-forming algae after disturbances and thus mediating the space available for the colonisation of other algae and animals, limpets were included in areas that had been scraped of turf-forming algae. The mean number of limpets (pooled over sampling times) did not perfectly match the number determined by the respective treatment (0L = no limpet, 1L = 1 limpet, 2L = 2 limpets), but there were clear differences between the three treatments (Lagoa - 0L = 0.0 ± 0 0 (mean ± SE), 1L = 0 8 ± 0.1, 2 L = 1 4 ± 0.2, Caloura - 0L = 0 0 ± 0.0, 1L = 0.8 ± 0 1, 2L = 1 4 ± 0.2)

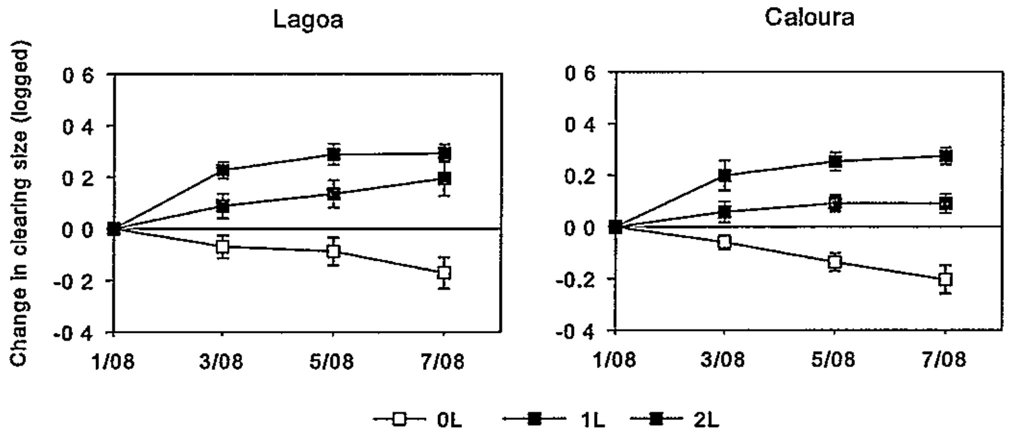

Figure 6.8. The effect of grazing by *Patella candei* on areas cleared of turf-forming algae Data are the change in size of the clearings in relation to initial size (see methods for further details). 0L – no limpets were present, 1L – 1 limpet was added, 2L – 2 limpets were added. Standard errors are shown.

The area kept free of algae changed rapidly and two months after set up (March), significant differences were apparent among treatments (Fig 6 8, Table 6.2) In comparison to the initial period of the experiment, variation in the amount of space available for colonisation, however, was only significant in the treatment corresponding to the highest density (Table 6.3). In the total limpet exclusion treatment (0L), the area that had been scraped of biota decreased in size due to vegetative growth of turf-forming algae In contrast, where grazers were present (1L and 2L) the area of bare rock increased linearly with limpet density Significant differences in the area kept free of algae were evident among the three treatments and remained constant through time Six months after initiation (July), the size of the clearings had changed significantly compared to the initial clearing size (Table 6.3).

Table 6.2. Analysis of the effects of grazing by limpets in areas that had the turf-forming algae removed. ANOVA comparing the mean change in size of cleared areas among the three limpet density treatments: 0L - no limpets were added, 1L - 1 limpet was added and, 2L - 2 limpets were added. Legend as in Table 6.1

		March '08		May '08		July '08	
Source	df	MS	*F*	MS	*F*	MS	*F*
L	1	0.002	0.24	0.015	1.68	0.022	1.79
T	2	0.193	137.69**	0.369	2257.12***	0.576	110.21**
L x T	2	0.001	0.15	<0.001	0.02	0.005	0.43
Residual	24	0.009		0.009		0.012	
Transformation		none		none		none	
Cochran's		*C* = 0.30		*C* = 0.26		*C* = 0.31	
SNK tests (Treatment)							
Among treatments		0L < 1L < 2L		0L < 1L < 2L		0L < 1L < 2L	

There was some die-off of algae during the summer and this meant that by August some of the clearings (irrespective of treatment) had lost their turf-forming algae and no longer presented a barrier to limpets, which were able to leave (or enter) the clearings. Hence, although this experiment had initially been planned to run for one year, it was no longer possible to maintain limpet density and hence the experiment was terminated.

Table 6.3. Change in clearing size due to the grazing of limpets in areas cleared of turf-forming algae. The 95% confidence intervals (CI) for each treatment are given: 0L – no limpets, 1L – 1 limpets, 2L – 2 limpets.

Time	Location	Treatment	Mean	95% CI	Differs from zero?
March	Lagoa	0L	-0.070	-0.155 – 0.016	no
		1L	0.088	-0.005 – 0.181	no
		2L	0.226	0.165 – 0.288	yes
	Caloura	0L	-0.059	-0.116 – -0.003	yes
		1L	0.057	-0.021 – 0.136	yes
		2L	0.199	0.085 – 0.312	yes
May	Lagoa	0L	-0.087	-0.192 – 0.018	no
		1L	0.135	0.032 – 0.238	yes
		2L	0.288	0.209 – 0.368	yes
	Caloura	0L	-0.137	-0.205 – -0.068	yes
		1L	0.091	0.029 – 0.152	yes
		2L	0.252	0.182 – 0.323	yes
July	Lagoa	0L	-0.171	-0.289 – -0.052	yes
		1L	0.194	0.063 – 0.325	yes
		2L	0.292	0.225 – 0.358	yes
	Caloura	0L	-0.204	-0.310 – -0.097	yes
		1L	0.090	0.020 – 0.160	yes
		2L	0.273	0.209 – 0.337	yes

Recruitment of other algae to treatments was negligible (even in the treatments where limpets were not included) However, recruits of *Chthamalus stellatus* could be identified by July suggesting that had the experiment been maintained longer and barnacles would probably have become the dominant space occupier

6.5. Discussion

This study shows that present day levels of grazing by *P. candei* in the Azores, although reduced by harvesting, significantly affected the structure of mid shore communities limiting the upper vertical extent of macroalgae. However, in plots where limpets were excluded in order to quantify their effects, the growth of algae was considerably lower than that recorded in similar exclusion experiments conducted elsewhere. For examples, at locations in mainland Europe, removal of limpets was typically followed by extensive macroalgal growth, notably fucoids in colder temperate regions (British Isles: Hawkins 1981, Boaventura et al. 2002b, Jenkins et al. 2005 Coleman et al. 2006; Northern Atlantic Spain: Arrontes et al. 2004, Coleman et al. 2006) and turf-forming algae in warmer temperate regions (central Portugal: Boaventura et al. 2002b, Coleman et al. 2006). The distribution of macroalgae at mid tidal heights is set by an interaction between physical (e.g. desiccation) and biotic (e.g. herbivory, competition) processes (Underwood 1980, Hawkins and Hartnoll 1985, Underwood 1985, Harley 2003, Thompson et al. 2004). In São Miguel, the response-ratio (natural log of the mean algal cover of control plots divided by the mean algal cover of exclusion plots; in this study -1.79) was within the range of that found in experiments made in the central and southern Portugal and approximately half of that recorded in the North of Spain, South of England and Isle of Man (Coleman et al. 2006). This suggests that the upper vertical limit of algae was close to the physiological tolerance level of algae to emersion stress (temperature, desiccation), which may reduce of algal growth rates. This result also suggests that the increasing cover of turf-forming algae on the upper mid shore in São Miguel (Fig. 6.1) was driven by the reduced number of limpets as a consequence of the heavy of exploitation in São Miguel. At reduced numbers of limpets, the spores of macroalgae that settle on the shore have increased probability of growing to a size that allows them to escape grazing by limpets and thus forming patches that are able to persist through time (Moore et al. 2007)

Below the upper vertical extent of the turf-forming algae, areas that were cleared but ungrazed were rapidly re-invaded by turf-forming algae via lateral vegetative growth, gradually reducing the amount of space that was potentially available for colonisation of other biota However, when present, limpets maintained the space free of turf-forming algae Petraitis & Latham (1999) and Dudgeon & Petraitis (2001) suggest that only large-scale disturbances trigger a shift between alternate assemblages (*Ascophyllum nodosum* vs. filter-feeder dominated assemblages) and that in smaller scale disturbances edge effects might preclude such change This was clearly not the case here as limpets were able to prevent turf-forming algae from re-invading space in relatively small-disturbed areas. These results support Farrell's (1991) model that grazers can mediate the fate of succession In fact, in the present experiment limpets not only maintained the space free of algae but also increased the area of open rock surface. Although it has been believed that *Patella* spp scrape the substratum for biofilms, which may include the spore and germlings of macroalgae, (Hawkins & Hartnoll 1983, Moore et al 2007), there is now evidence that limpets can also graze on well-established patches of mature macroalgae (Davies et al. 2007, 2008) Limpets may also have caused damage to turf-forming algae at the perimeter of the clearances by abrading plants with their shell while feeding on the open rock

Despite the effect of limpets above and below the upper vertical extent limit of turf-forming algae, turf-forming algae were generally very resilient preventing the colonisation of other biota via space pre-emption Colonisation of space in cleared areas (total and half removal treatments) was variable in space and time but generally two divergent successional outcomes were noted towards the end of the experiments: one where the turf-forming algae had re-colonised space that had been cleared and another where, after an initial phase of rapid algal growth, barnacles became the dominant space occupier. There was no evidence that the outcome of succession was affected by differences in the area cleared between the two cleared treatments once more refuting the model that strong edge effects around small disturbed areas will preclude the establishment of assemblages that are divergent from the surrounding community (Petraitis & Latham 1999, Dudgeon & Petraitis 2001). Contrasting explanations of how assemblages react to varying disturbance intensities are common in the literature. For instance, in the Gulf of Maine, USA Dudgeon & Petratis (2001) found recruitment of the densely settling barnacle *Semibalanus balanoides* to be greater in larger patches. In contrast, in the SE Australia, barnacles recruited at greater numbers to smaller patches (Airoldi 2003). Similarly, Benedetti-Cecchi & Cinelli (1993) found significant effects of clearing size on the community recovery following disturbance in the central Mediterranean, whilst Jenkins et al. (1999) found no such effects in the Isle of Man, UK. It thus seems that variation in the response of assemblages to disturbance size is probably specific at any given time to the species present, the pool of potential colonisers and the competitive hierarchies among them.

The timing of disturbance can also have a substantial effect on subsequent succession because of seasonality in reproductive patterns and growth. For instance, Hawkins (1981) showed that different timings of disturbance led to varying sequences of colonisation. Although ultimately the end-point of succession was consistent among treatments with the species with the greatest competitive ability in that system (*Fucus* sp.) eventually becoming dominant, examples exist where multiple end-points are possible and the timing of disturbance event determines the outcome (e.g. Benedetti-Cecchi 2000c). In the present study, the date at which turf removal was made and succession started led to temporal variations in the abundance of taxa, but did not appear to influence the end-point of succession Instead, there was evidence that the successional trajectory were determined by spatial variation in the intensity of barnacle recruitment This was also noted by Hartnoll & Hawkins (1985) who showed that variable patterns of recruitment influence dominance. Given the above, making generalisations and predicting the outcome of disturbances in rocky intertidal assemblages is fraught with difficulties. A number of processes influence the sequence of colonisation and successional end-points such that a deterministic view of succession is increasingly recognised as elusive (Sousa 1984, Pickett & White 1985, Jenkins & Martins in press).

In summary, under conditions of limpet harvesting, the structure of mid-shore communities in the Azorean intertidal where turf-forming algae monopolise much of the space seems highly persistent and resistant to disturbance-induced change There was evidence, however, that grazing by limpets and variable patterns of recruitment can lead to development of divergent assemblages – possibly resembling those prior to the start of limpet harvesting As such, it seems likely that should the harvesting of limpets cease, the community would gradually return to its original state. The creation of no-take marine reserves would allow this hypothesis to be tested (e g. see work by Moreno et al 1984, Castilla & Durán 1985, Durán & Castilla 1989) Unfortunately, current lack of enforcement means that marine protected areas in the Azores are ineffective in protecting the populations of limpets (Chapter 5)

CHAPTER 7

Discussion

Discussion

The main focus of this thesis was to examine the ecology of patellid limpets on oceanic islands, to identify the sources of variation in limpet distribution, and to investigate the population and community level effects of limpet exploitation. I have demonstrated that the Azorean rocky intertidal is a dynamic system and that processes operating at different spatial scales interact to set emergent ecological patterns (Chapter 2). In Chapter 3 I showed that limpet distribution was influenced by small-scale substratum microtopography and in Chapter 4 by large-scale variation in harvesting intensity. I demonstrated that current conservation and management strategies have been ineffective in protecting limpet populations (Chapter 5) and that this has led to cascading community level impacts with important ecological and energetic consequences for the functioning of the Azorean rocky intertidal (Chapter 6).

7.1. Novel findings

The present study focused on the ecology of a seldom-studied species, *Patella candei*, in a seldom-studied habitat, oceanic islands. Despite the value of the limpet fishery to the regional economy and the well-known effect of patellid limpets in structuring the rocky intertidal in the NE Atlantic (e.g. Hawkins & Hartnoll 1983), information on the population status and the potential community level impact of limpet harvesting in the Azorean rocky intertidal was remarkably scant. Here I showed that heavy exploitation has led to dramatic decreases in limpet abundance and that both patellid species show clear signs of over-exploitation. I showed that the harvesting of limpets has resulted in important changes in the structure and functioning of the Azorean rocky intertidal adding to the existing literature that human activities can shape the natural environment. Importantly, I showed that coastal engineering could be modified to provide an additional conservation measure to enhance the local abundance of exploited species

7.2. The consequences of geographic isolation on assemblages

Recruitment of larvae or propagules to the shore is key for the replenishment of marine benthic species (see Caley et al. 1996 for review) For this reason, it is important to understand the degree to which local geography affects species distribution and dynamics. To what extent are marine benthic populations open has remained a central question in ecology and has important ecological and management ramifications (Botsford et al. 2001, Shanks et al. 2003, Bell 2008)

Most marine species have a planktonic stage (Thorson 1950) during which they have the capacity to disperse over long distances. This resulted in the general belief that marine populations are well connected via long-distance dispersal of larvae (or propagules) (Cowen et al 2000). In contrast to this belief, however, there is now mounting evidence that marine benthic populations may not be as open as previously thought and that local larval retention as well as long-distance dispersal is an important determinant of the local dynamics and persistence of marine populations (Swearer et al. 1999, Cowen et al 2000, Patterson & Swearer 2007).

Anecdotal evidence suggests that the relative importance of self-recruitment to the maintenance of local populations increases proportionally with site isolation because it is unlikely that an isolated population could be maintained from a distant source (Sponaugle et al. 2002) This is partially supported by observations showing that loss through larval diffusion and mortality increase with the time that larvae spend in the plankton so that extremely low numbers of larvae may reach and colonise a distant site

(Cowen et al. 2000). The occurrence of endemism is obvious evidence of the importance of self-recruitment. In fact, with increasing isolation the number of endemic species tends to increase (provided that habitats are old enough to allow speciation to occur) (Robertson 2001), whilst diversity generally decreases (see Peach & Cresswell 2007 for examples of forest fragments, Matthews et al. 2005 for wetlands and Long et al. 2009 for islands).

Although the importance of self-recruitment is easy to recognize in the more isolated cases, such as in oceanic islands or seamounts, in less isolated populations the relative role of self-recruitment in maintaining local populations is still not clear. Estimates made by Jones et al. (1999) and Swearer et al. (1999) suggest, however, that larval retention may contribute as much as 60% to local recruitment in a reef fish in the Great Barrier Reef. Whatever the relative contributions of self-recruitment and long-distance dispersal for the maintenance of marine benthic populations, it is clear that isolated populations are more dependent on local production of larvae and that the reduction in the abundance of mature reproductive individuals (e.g. over-fishing, diseases, environmental catastrophes) is more likely to drive the species locally extinct than would be expected in less isolated populations. This suggests that populations in isolated habitats such as oceanic islands are more susceptible to over-fishing than populations in less isolated habitats.

Except for large and slow growing marine mammals and birds, extinction of marine species due to fishing is considered relatively rare and unlikely (Tegner et al. 1996, Carlton et al. 1999, Roberts & Hawkins 1999). This is because the reduction in abundance following over-fishing makes their exploitation no longer economically viable. Nevertheless, examples of marine species on the brink of extinction as a result of over-fishing exist (e.g. Tegner et al. 1996, Núñez et al. 2003). To my knowledge there is no study comparing species susceptibility to exploitation in isolated habitats. My results, however, showed that *P aspera* is virtually extinct in the rocky intertidal and only a few subtidal populations persist (personal observation). In addition, *P candei*, an opportunistic species (Martins et al. 1987), showed dramatic reductions in abundance over 20 years. My results also showed that the population size and the number of juvenile *P candei* was lower than expected in Graciosa in comparison to other islands. This could indicate that populations of *P candei* in Graciosa are experiencing recruitment limitation The small size and geographic location of Graciosa (in relation to the other islands in the group and the predominant direction of oceanic currents) may be an indication that the spatial configuration of islands (or other patchy habitats) may affect the extent to which local populations are connected via larval dispersal to adjacent islands Genetic studies have shown that whilst some marine populations show large genetic homogeneity over large spatial scales (Doherty et al 1995, Shulman & Bermingham 1995), others show clear separation between populations a few km apart (Bell 2008, Miller et al. 2009) How biological traits (e g time that larvae spent in the plankton, type of larval development) interact with the physical environment (e g coastal geomorphology, predominant currents and eddies) to set patterns of larval dispersal and subsequent recruitment warrants further investigation (Aiken et al. 2007, Lagos et al 2008) Examination of the patterns of limpet recruitment at a range of spatial scales coupled with genetic studies could provide important clues on the role of island geography and oceanographic factors on the rates of larval exchange among islands providing valuable information of ecological and management relevance.

7.2.1. Spatial scales of variability

The role of scale has been central in ecology (Fig. 7.1) and the perception that processes operating at different spatial and temporal scales interact to determine emergent patterns in ecological systems is increasingly recognised (e.g. Hewitt et al. 2007). Because different ecological processes generate variability at different spatial (or temporal) scales, examination of patterns across a range of scales is a fundamental step before explanatory models for these patterns can be proposed (Underwood & Chapman 1996, Hewitt et al. 2007).

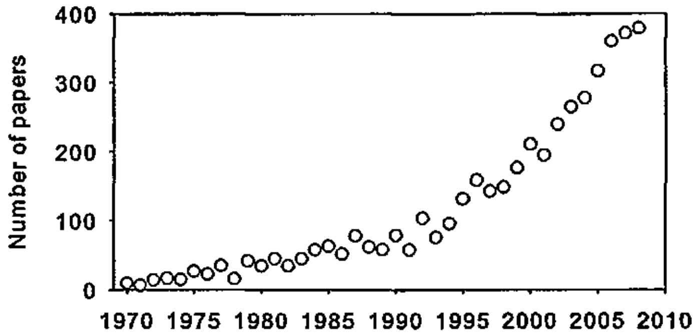

Figure 7.1. Graph showing the increasing trend of ecological studies focusing on the role of scale. Data are the per year number of ecological papers with the word scale in the title. Search was done using ISI Web of Science.

My results showed variation at all the spatial scales examined but for most taxa the highest percentage of the variation explained was associated with the largest (islands) and smallest (quadrats) spatial scales. This is not at all an unusual result in marine systems (e.g. see Fraschetti et al. 2005 for review). However, it does indicate that processes operating at the scale of islands as well at the scale of quadrats (metres apart) are the most important in structuring these populations.

The finding that an important proportion of the variation in population distribution was found at the scale of islands is not surprising given the likely importance of self-recruitment to the maintenance of isolated populations (described above). If population size tracks recruitment levels, recruitment can be identified as the major determinant of adult population size. In contrast, if population size is stable despite fluctuations in recruitment, density-dependent post-settlement mortality is likely to predominate as a regulating factor (reviewed in Caley et al. 1996) Holm (1990), however, showed that density-dependent mortality does not necessarily preclude recruitment regulation in open populations, especially under low levels of larval settlement or weak density-dependent mortality In addition, there is mounting evidence that fluctuations in recruitment interact with density-dependent post-recruitment processes to control adult abundance (Roughgarden et al. 1985, 1988, Menge 1991, Hughes et al. 1999, Menge 2000b) and that the strength of density-dependent mortality changes with time (Jenkins et al 2008).

Although I have not examined patterns of recruitment, finding significant variability in species abundance at the scale of islands suggests that islands could be considered as discrete habitats and relatively independent from each other That is, the geographic location of the island could determine the degree to which self-recruitment or inter-island larval exchange is important in determining local population size. The large-scale variability found at the scale of quadrats also suggests that small-scale processes such as biological competition (e g Underwood 1978, Navarrete & Wieters 2000) and the physical environment (e g Power et al 2001, Underwood 2004) are important and these could alter patterns set during settlement and recruitment stages Therefore, even if patterns of recruitment had been examined, a clear relationship between recruitment and adult population size may not have become apparent It is clear that examination of the patterns of recruitment and adult abundance in a range of species differing in dispersal ability could provide valuable insights into the ecology of Azorean communities

Another interesting outcome of this study was that the relative importance of small-scale processes tended to increase with height on the shore. In other words, small-scale patchiness in organism distribution increased along an increasing gradient of physical harshness. A possible explanation is that the influence of processes operating at larger-spatial scales may be masked by the increased physical harshness (e.g. desiccation) at higher levels on the shore (Underwood and Chapman 2000). For instance, variability in the distribution of the barnacle *Chthamalus stellatus* was significant at the scale of islands at mid tidal levels. On the upper shore, however, there was no significant variation at the scale of islands but the relative importance of small-scale variability increased. Increased physical harshness could have meant that post-recruitment mortality higher on the shore masked patterns of barnacle recruitment. This is a clear indication that processes operating at different spatial scales can interact to determine emergent ecological patterns. For instance, in the western USA replication of small-scale manipulative experiments over large spatial scales revealed interactive effects of processes operating at large-spatial scales (upwelling intensity) in the outcome of small-scale processes (predation or grazing) (Menge et al. 1999, 2002, 2003, 2004, Freidenburg et al. 2007). Such designs, whereby small-scale manipulative studies are replicated over larger spatial scales, provides an important methodological framework to disentangle the role of scale in complex ecological systems (Hewitt et al. 2007).

7.3. Harvesting of intertidal species

7.3.1. Predator-prey interactions in natural systems

The rocky intertidal is a dynamic system where biological (e.g. competition) and physical (e.g. desiccation) factors interact to determine emergent ecological patterns. In natural systems, density-dependent processes tend to promote stability (Katz 1985) For instance, density-dependent predation occurs when the size of a predator population tracks fluctuations in prey abundance and is a common process in terrestrial (e g. Romo et al 2004), freshwater (e.g. Johnson et al. 1995) and marine (e.g Hixon & Carr 1997) systems

In the course of evolution prey have adapted and show a number of behavioural and physiological strategies that help them avoiding predation. For instance, finding refuge in space (e.g Johnson et al. 1998), time (e.g. Sigh et al 2000) and size (e.g. Silva 2008). These strategies help alleviate the risk of local extinction allowing prey populations to persist over time As such, density-dependent predation will preclude over-exploitation (Hockey 1994).

7 3 2 Human predation in the rocky intertidal

Predation by man in the rocky intertidal targets a diverse assemblage of prey including herbivorous and predatory gastropods, bivalves, echinoderms, ascidians, arthropods, polychaetes and algae Unlike other predators, however, predation by humans is facultative, often made in excess of individual needs (Hockey 1994) and is not regulated by the abundance of target species Moreover, man is a tool-using predator, which may help him overcome a number of prey strategies used to alleviate predation risk under natural conditions (see above) The only anti-predator adaptation that may effectively deter human predation is chemo-defence (except perhaps the Japanese who eat Fugu, a poisonous puffer-fish).

7.3.3. Consequences of harvesting of intertidal species

The harvesting of littoral species has been made since pre-historic times. For many years, however, this activity was restricted to the rocky intertidal due to its accessibility. In addition, the rocky intertidal typically supports sessile or slow moving species that are easily hand-collected. This and the fact that the rocky intertidal assemblages are restricted to a small area render intertidal species highly vulnerable to exploitation.

Many exploited rocky intertidal species include primary space occupiers such as mussels and barnacles and primary space creators such as grazing and predatory gastropods. Selective removal of these species may lead to major changes in community structure which persist in the event of continued exploitation. These effects, however, are usually not stable since major changes can occur when exploitation ceases (Moreno et al. 1984, Castilla & Durán 1985, Hockey & Bosman 1986, Oliva & Castilla 1986, Durán & Castilla 1989, Lasiak 1991). Irreversible change in community structure and functioning may require predation-mediated extinction of species.

Size selective removal of larger individual prey often results in the reduction of the most fecund individuals (Dadzie et al. 2007, Harding et al. 2007, LaPlante & Schultz 2007). These may also be those individuals with the lowest natural mortality (Hsieh et al. 2006). This selection, therefore, reduces the reproductive output disproportionally to the numerical fraction of the population that is removed (Hockey 1994). As discussed above, populations in isolated habitats are more vulnerable to reductions in reproductive output. Irreversible change in community structure caused by exploitation-driven extinction is thus more likely to occur in such isolated habitats.

My results concur with the wider literature in that the harvesting of a key grazer has led to changes in the community structure and functioning in the Azorean rocky intertidal. Moreover, this alternate community state was not stable and community changes should also occur if limpet exploitation ceases. I also show, however, that if limpet populations are driven extinct, the alternate community state dominated by turf-forming algal species has the ability to persist via effective space pre-emption, that limits the colonisation of other species, and rapid vegetative growth rates, that allow turf-forming algae to rapidly recover from disturbances (Fig. 7.2). Should limpets go extinct in the Azores, then this may be the first example of an irreversible community-level impact of fishing in the structure and functioning of intertidal communities.

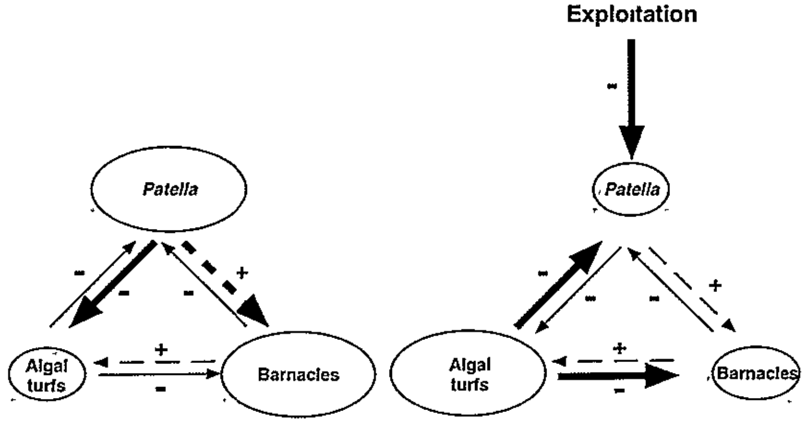

Figure 7.2. Schematic representation of the ecological interactions in Azorean mid shore rocky intertidal and influence of limpet harvesting Continuous and dashed are direct and indirect effects, respectively. Arrow thickness is proportional to the interaction strength Balloon size is proportional to the taxa abundance. The red arrow stands for the negative effect of turf-forming algae on limpet recruitment, which had not been considered by previous models.

The reduction in diversity with increasing habitat isolation (e g. Quinn & Harrison 1988, Shulman & Chase 2007) also suggests that the Azorean rocky intertidal has fewer functionally redundant species that could be able to compensate for the loss of species In the eastern Atlantic the intertidal *Littorina littorea* is considered a less-efficient grazer than patellid limpets (e.g. O'Connor & Crowe 2005). In contrast, in the western Atlantic coasts *L. littorea* is a strong grazer and can significantly reduce the growth of large perennial algae (Norton et al. 1990, Jenkins et al. 2008). The ecological role of *L. striata*, an endemic species to the Macaronesia, is virtually unknown although it can be present in the upper intertidal at high abundances. Future studies should thus examine to what extent could the grazing by *L. striata* compensate the eventual loss of limpets.

7.4. The management of the rocky intertidal

As discussed above, the harvesting of intertidal populations differs from other types of biological interactions in that humans are less regulated by the abundance of the target species and because the reduction of the resource does not influence human populations in the slightest. Thus, unlike "natural" predation, human predation is analogous to a negative one-way biological interaction (e.g. amensalism). Moreover, human exploitation of the intertidal is highly generalist and includes primary producers, filter feeders, grazers and predators. In addition, the harvesting of intertidal species can indirectly disturb many other (e.g. birds), which are not the primary target of the fishery. Figure 7.3 illustrates the complexity of biological interactions and how human predation affects the ecosystem at many levels.

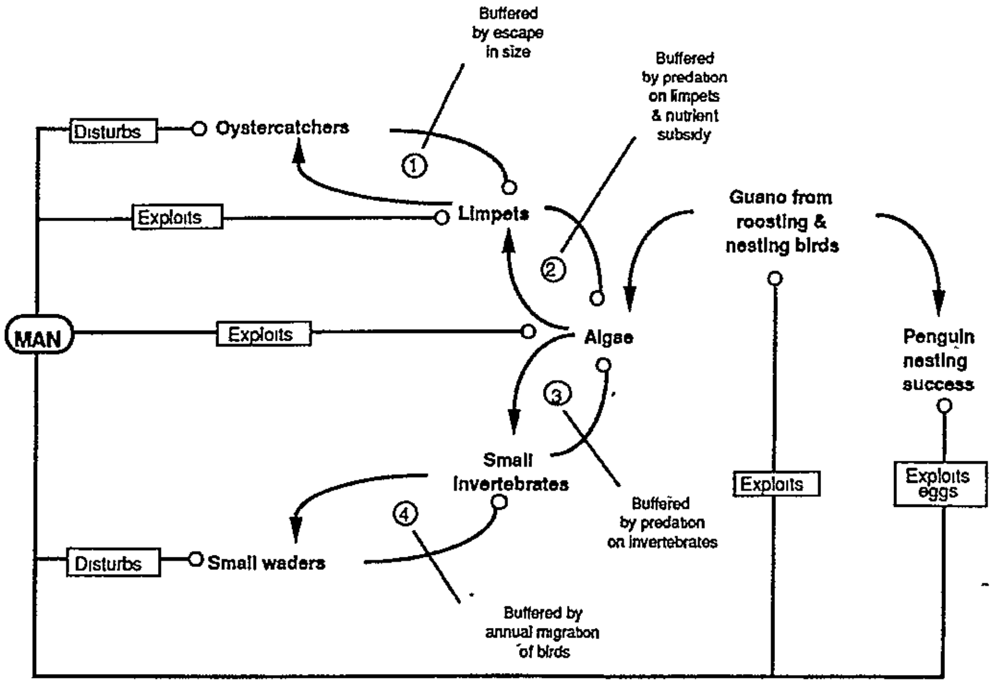

Figure 7.3. Human impact on biological interactions occurring in a rocky intertidal zone on islands off the coast of South Africa The processes which stabilize four of the biological interactions (1 to 4) are shown. Arrows and circles, respectively, indicate the positive or negative nature of the interactions (In: Dye et al 1994)

Thus, the management of natural systems is complex and needs to consider all biological interactions In addition, many species differ in their life-history strategies, which affect their vulnerability to exploitation For instance, *P aspera* is a slow-growing protandrous species, whilst *P candei* is a fast-growing gonochoric species Such differences in biological characteristics between the two patellid species affect their vulnerability to exploitation so that *P aspera* is considered to be more vulnerable to human exploitation (Martins et al 1987) Exploitation of *P aspera* will cause a distortion of the sex ratio and a reduction in reproductive output as the larger female individuals are collected first The result of this inequality between species became quite clear in this study *P aspera* was virtually extinct in the rocky intertidal of all but one of the islands examined, whilst *P. candei*, although showing signs of exploitation (reduced size of individuals), was still relatively common. Dye et al. (1994) has listed a number of biological characteristics that influence the extent to which a species may be more or less vulnerable to human exploitation. This list was subsequently improved by Roberts & Hawkins (1999) who included a few more biological characteristics. I argue that the level of habitat isolation and whether a species is endemic or not should also be included in this list.

7.4.1. The objectives of management

For many years, management of living resources has focused almost entirely on the protection and conservation of individual species. Clear examples of this practice include the fixation of individual quotas and species-specific minimum individual collection sizes or the establishment of single-species areas of conservation where the harvesting of that particular species is restricted, such is example the management of the limpet fishery in the Azores. Yet, all fisheries in the world impact more than one species either directly or indirectly (Botsford et al. 1997). The increased perception that natural systems are intrinsically complex, has led to a recent shift in the aims of management strategies from species to ecosystem levels. Examples include the increasing number of established no-take marine reserves (also called marine sanctuaries or marine protected areas) whereby the collection of living organisms or the destruction of the habitat is prohibited. Within some of these marine reserves, there are even specific areas where the presence of humans is restricted (Keough & Quinn 2000).

Management of living resources must also distinguish between the different types of exploitation (Dye et al. 1994). Profit-making or professional exploitation tends to be species-specific, often uses sophisticated methods of collection and is responsible for removing large amounts of these species. In contrast, artisanal harvesting is usually done for subsistence rather than commercial gain This type of exploitation is generally broad in scope removing several species, but at lower numbers, as a complement to the diet of local human populations. In addition, artisanal fisheries are often well integrated in the local culture As such, the management of intertidal fisheries is a complex science that needs to consider all the relevant biological, economical and social aspects of the fishery (Castilla & Defeo 2005)

Another aspect that needs to be considered in the management of fisheries is the influence of fluctuations in the physical environment on stock abundance Recent studies have shown that large-scale temporal variations in oceanographic conditions and climate can significantly affect the abundance of target populations (e g. Hsieh et al 2005, Pecl & Jackson 2008, Kerr et al 2009) and thus a more holistic science that predicts the effects of future climatic changes on natural populations must be adopted in the management of fisheries

7.4.2 Improving the management and conservation of marine systems

As the number of collapsed fisheries increases worldwide (Botsford et al 1997, Jackson et al 2001, Hilborn et al. 2003, Myers & Worm 2003) there is increasing need for better management and conservation strategies that foster the sustainable exploitation of living resources We clearly need to pass from paper and discussion to the real world That is, we need to have a clear understanding of how the different management strategies influence the structure and functioning of marine ecosystem. For instance, there is accumulating evidence that illegal harvesting can have strong and long lasting impacts on the success of marine reserves (Keough & Quinn 2000, Kritzer 2004, Little et al. 2005, Samoilys et al. 2007, Guidetti et al. 2008). Illegal unreported and unregulated harvesting has even been highlighted as the principal contributing factor for the worldwide collapse of fish stocks (Le Gallic & Cox 2006, Pitcher et al. 2002). This is clearly of relevance in the limpet protected zones in the Azores, whereby substantial levels of illegal harvesting have considerably impacted the recovery of limpet populations. Therefore, we need sampling programmes that reliably assess the efficiency of the different management strategies so that managers can choose the best strategy for each case.

Several changes in the way fisheries are managed could also improve fisheries sustainability: the adoption of a more precautionary approach to fishery management (Garcia 1994); the establishment of management strategies (e.g. closures) well before the collapse of the fisheries occurs (Botsford et al. 1997); and the use of a more spatially variable and explicit management approach. The latter includes the establishment of full no-take marine reserves as well as territorial user rights for fishers.

In contrast to other management options (common property or private-ownership), the implementation of territorial user rights for fisheries management has some benefits. Here property rights on resource allocation are conferred to groups of people and include the right to exclude non-members (Odendaal et al. 1994). These co-operatives tend to be self-sanctioning and self-restraint and are generally thought to reduce resource destruction by illegal harvesting. This type of management started to be implemented in Chile in 1991 where a total of 547 Management and Exploitation Areas for Benthic Resources (MEABR's) have been established (Gelcich et al. 2008). Recent studies have shown that MEABR's could confer benefits to both the participants (by increasing the efficiency of harvesting) and the resources. In fact, compared to open areas, the establishment of MEABR's seems to have benefited both target and non-target populations resulting in an overall increase in biodiversity (Castilla et al 1998, Gelcich et al. 2008).

In the Azores, the relevant authorities must increase enforcement and foster the establishment of full no-take marine reserves Properly enforced marine reserves have been shown to be efficient management tools and are an essential tool for the investigation of fishing impacts. As discussed above, the creation of a network of marine reserves, such as MEABR's, which are spatially interspersed within areas open to the general public, could probably be a valuable strategy for the management and sustainable exploitation of the Azorean coastal resources Efforts should also be made to develop environmental programmes in schools and in the fishery villages to inform the general public and increase their environmental awareness

7.4 3 Pro-active conservation

Although marine protected areas are emerging as prominent management tools, they may not suffice where recruitment over-fishing occurs (Wallace 1999). Stock enhancement from hatchery-reared seeds has been perceived as an alternative strategy to enhance the regeneration process, particularly for the conservation of threatened species (Burton & Tegner 2000, Booth & Cox 2003, Okuzawa et al. 2008) and has been increasingly used for the local enhancement of a number of species such as abalones, crabs, clams and seahorses (Okuzawa et al 2008) Despite the increasing success of this conservation strategy, there is some concern that this measure could have negative impacts such as changing the genetic diversity of wild populations or the introduction of diseases (Bartley et al 2006, Bell et al. 2006) In addition, the hatchery rearing of seed for some species is still in its infancy and for intertidal animals such as limpets may require sophisticated technology to simulate tidal regimes

Another option is to deploy artificial structures that attract and provide protection for the juvenile stages of exploited species. This strategy has proved to be effective in enhancing the local abundance of exploited resources, particularly subtidal species such as rock lobsters (Butler and Herrnkind, 1997; Briones-Fourzán et al., 2007; Herrnkind et al., 2007), fish (Santos and Monteiro, 1997; Leitão et al. 2008) and algae (Choi et al., 2002; Oyamada et al., 2008). In this study I showed that the abundance of intertidal populations could also be enhanced via modifications made to coastal engineering. To date, the few attempts to increase the quality of artificial structures (e.g. breakwaters, seawalls) have been made through taking into consideration the assemblage as a whole (Moschella et al. 2005). However, I showed that such structures could function as important nursery grounds for specific exploited intertidal species by increasing recruitment and reducing juvenile mortality. Furthermore, I also showed that such positive effects on limpet recruitment persisted through time resulting in a local greater population of adult animals one year following the set up of the experiment. The predicted changes in climate and the increasing requirements for alternative green sources of energy production (e.g. windmills) suggests that the number of artificial structures being deployed in coastal areas is likely to increase over the next few years (Thompson et al. 2002). This therefore offers an opportunity for integrated management where both the need to protect our coasts from coastal erosion and energy production is made in ways that foster the recovery of exploited species.

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APPENDICES

Appendix A

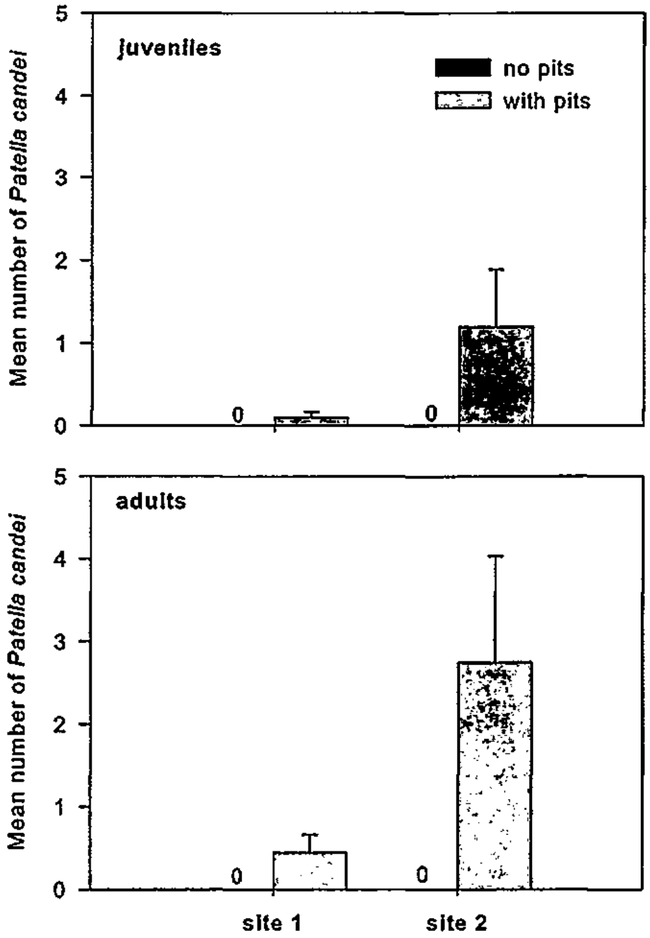

Figure A.1. Mean (+SE) number of *Patella candei* (includes animals that were both inside pits and on open rock) in treatment (including the 4 treatments, n = 20) and control areas (no pits, n = 5). Data were collected 11 months after initial set up. Only 1 recently recruited individual (< 5 cm) was recorded and hence this size-class is not analysed. See chapter 3 for further detail.

Table A1. Asymmetrical ANOVA comparing the abundance of *Patella candei* (includes both animals inside pits and on open rock) between controls (no experimental pits) and treatments (with experimental pits). C = control, T = treatments. Data were collected 11 months after initial set up. Only 1 recently recruited individual (< 5 cm) was recorded and hence this size-class is not analysed. *F*-ratios as in Table 3.3. See chapter 3 for further details.

	6-10 mm			≥ 11 mm	
Source	df	MS	*F*	MS	*F*
Site	1	9.68	3.03	0.17	1.41
Among all	4	31.68	1.15	0.92	1.32
C vs. T	1	3.38	1.40	0.90	20.72
Among T	3	28.3	9.43	0.93	1.01
Site x Among all	4	27.52	6.88	0.70	5.66**
Site × C vs. T	1	2.42	2.42	0.04	0.35
Site × Among T	3	25.1	8.37	0.92	7.42***
Residual	40	127.6		0.12	
Transformation		none		$x^{0.1}$	
Cochran's test		*C* = 0.92**		*C* = 0.30	

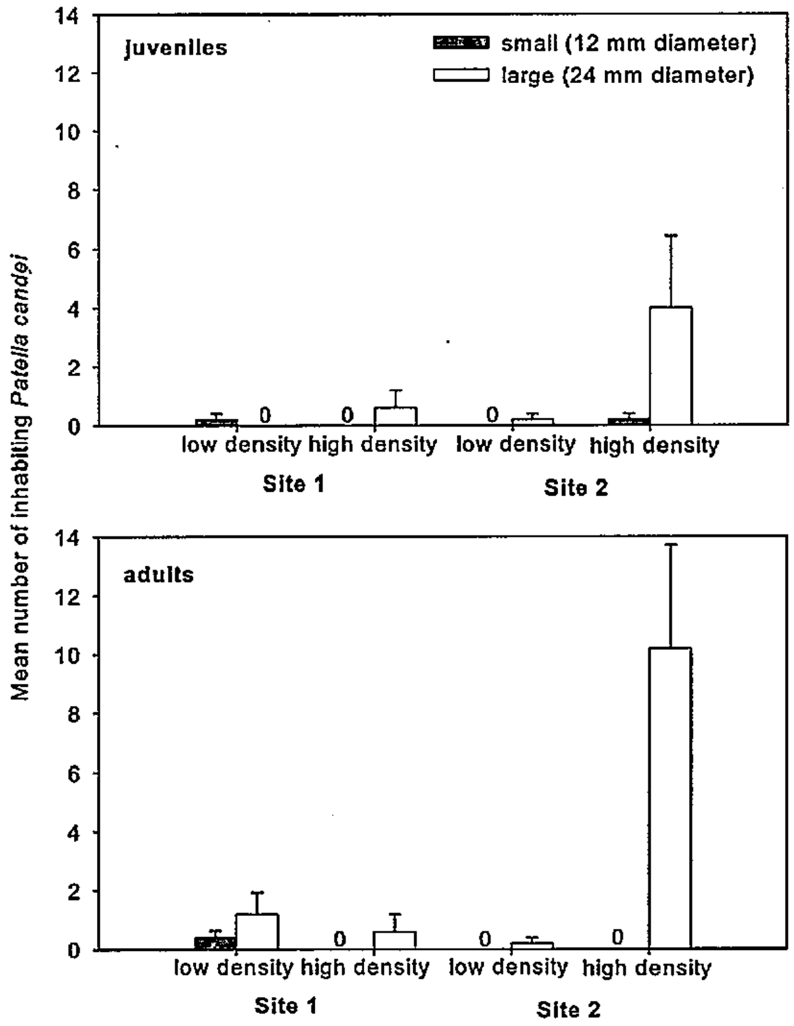

Figure A.2. Mean (+SE, N = 5) number of *Patella candei* (only animals inhabiting pits) in each of the 4 treatments. Data were collected 11-months after initial set up. Only 1 recently recruited individual (< 5 cm) was recorded and hence this size-class is not analysed. See chapter 3 for further detail.

Table A2. ANOVA examining the effect of pit density and size on the number of *Patella candei* inhabiting experimental pits. Data were collected 11-months after initial set up. Only 1 recently recruited individual (< 5 cm) was recorded and hence this size-class is not analysed. *F*-ratios as in Table 3.4. See chapter 3 for further detail.

		6-10 mm		≥ 11 mm	
Source	df	MS	*F*	MS	*F*
Site = S	1	0.334	2.10	0.02	0.11
Pit Size = PS	1	0.334	1.00	1.35	2.26
Pit Density = PD	1	0.293	1.00	0.01	0.01
S × PS	1	0.334	2.10	0.60	3.32
S × PD	1	0.293	1.84	1.27	7.03*
PS × PD	1	0.293	35.15	0.54	2.22
S × PS × PD	1	0.008	0.05	0.24	1.35
Residual	30	0.159		0.18	
Transformation		$x^{0.1}$		$x^{0.1}$	
Cochrans' test		$C = 0.33$		$C = 0.26$	

Appendix B

Table B1. Morphometric data for 75 individuals of *Patella candei*. Limpets were dehydrated over 48h at 60°C prior to measurements.

	Weight (g)	Shell length (mm)	Shell height (mm)
1	0.638	21.7	5.3
2	0.481	20.3	5.1
3	0.597	23.0	5.5
4	0.938	26.9	6.3
5	1.604	30.2	6.8
6	1.250	31.2	7.1
7	0.642	22.7	5.8
8	0.564	23.5	5.5
9	0.542	23.8	5.4
10	1.571	32.9	7.9
11	0.645	22.2	5.9
12	0.744	21.9	6.6
13	0.801	20.9	7.5
14	0.473	21.6	5.4
15	0.630	23.0	5.5
16	0.450	21.3	4.9
17	0.678	23.0	6.0
18	0.581	19.4	5.3
19	0.631	22.0	4.9
20	0.575	21.0	5.7
21	0.421	18.0	4.6
22	0.262	19.0	3.8
23	0.485	20.1	5.4
24	0.697	21.4	7.0
25	0.502	20.6	6.5
26	0.289	15.9	5.2
27	0.630	23.6	5.7

Table A1. (Continuation)

	Weight (g)	Shell length (mm)	Shell height (mm)
28	0.314	16.9	5.3
29	0.370	17.5	5.0
30	0.408	19.1	5.5
31	0.362	18.4	4.7
32	0.381	18.2	5.2
33	0.222	15.0	3.7
34	0.377	18.1	4.2
35	0.329	17.4	4.8
36	0.319	17.1	4.3
37	0.274	16.3	5.0
38	0.365	18.5	4.1
39	0.324	16.8	4.7
40	0.235	16.3	3.7
41	0.210	13.3	3.7
42	0.346	17.1	5.2
43	0.267	15.6	5.2
44	0.191	15.3	3.9
45	0.230	14.5	4.2
46	0.230	15.2	4.2
47	0.197	14.7	4.5
48	0.267	16.2	4.7
49	0.187	14.3	3.4
50	0.217	14.9	3.3
51	0.211	16.9	3.7
52	0.206	15.2	3.9
53	0.220	14.4	3.9
54	0.196	15.0	4.0
55	0.083	10.9	3.1
56	0.034	9.3	2.0
57	0.037	8.1	2.2
58	0.031	6.8	2.2

Table A1. (Continuation)

	Weight (g)	Shell length (mm)	Shell height (mm)
59	0.075	10.7	2.7
60	0.089	11.3	2.6
61	0.089	12.1	2.7
62	0.080	11.0	2.7
63	0.205	15.5	4.1
64	0.112	11.5	3.0
65	0.152	13.6	3.6
66	0.166	15.3	3.3
67	0.140	15.3	3.4
68	0.106	13.1	3.3
69	0.058	9.5	2.5
70	0.118	13.3	3.4
71	0.097	12.6	2.8
72	0.092	12.2	3.3
73	0.072	11.0	2.9
74	0.052	9.1	2.2
75	0.018	6.3	1.7

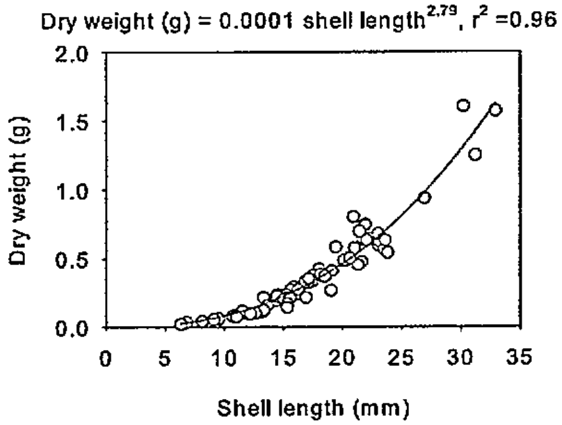

Figure B1. *Patella candei.* Shell length-biomass relationship based on 75 individuals (see data above).

Appendix C

Analysis of community structure of experimental areas (chapter 6) before the initiation of the experiment.

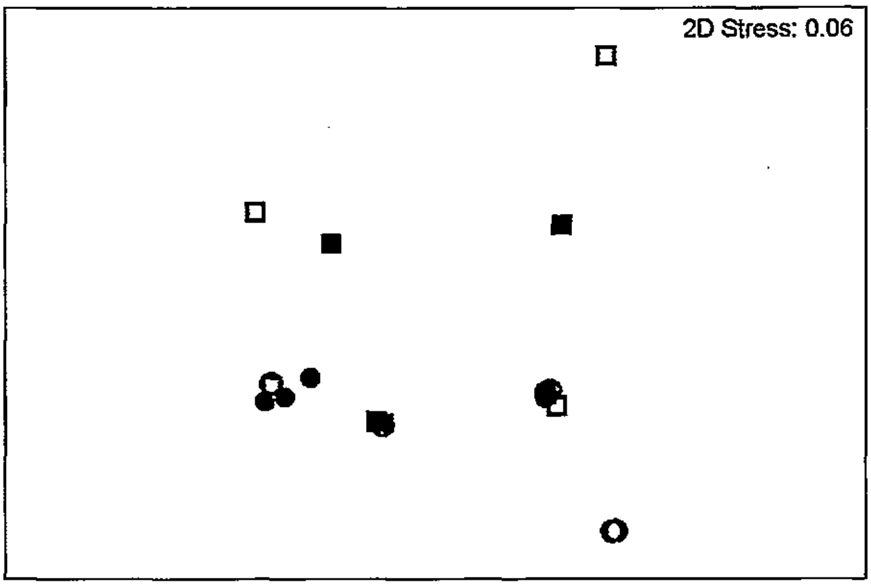

Figure C.1. MDS comparing the community structure of selected areas prior to the start of the experiment. Quadrats = Caloura, Circles = Lagoa, open symbols = limpet removal, dark symbols = limpets unmanipulated.

Table C1. PERMANOVA comparing the community structure of experimental areas randomly sorted into treatments: Quadrats = Caloura, Circles = Lagoa, open symbols = limpet removal, dark symbols = limpets unmanipulated. Data were 4th root transformed and analysed using the Bray-Curtis dissimilarity index. Note that the assemblages were similar among locations and treatments.

Source	df	MS	*F*	p	Uniq. Perm.	p(MC)
Location (L)	1	580.56	2.87	0.087	9958	0.079
Treatment (T)	1	123.45	0.48	0.506	3	0.627
L × T	1	258.23	1.28	0.294	9961	0.292
Residual	20	4050.8				

Appendix D

Table D1. Summary of results of the Analysis of Variance on the density of *Patella candei* in areas that were cleared of turf-forming algae. Treatments were C – unmanipulated control, P – partial removal of turf-forming algae (50%) and, T – total removal of turf-forming algae (100%) (see Chapter 6 for further details). Only relevant terms of ANOVA are shown and the result of SNK tests.

Month	Time 1 Significant term	SNK	Month	Time 2 Significant term	SNK
March '07	L × T	Lagoa: C<P<T	January '08	L × T	n.p.
		Caloura: C<P =T	May '08	L × T	Lagoa: C<P=T
					Caloura:C=P =T
April '07	n.s.		August '08	T	C< P=T
May '07	T	n.p.	October '08	T	C<P=T
June '07	T	C<P=T			
October '07	n.s.				
June '08	n.s				

n.p. SNK not possible

n.s. Relevant terms not significant

Table D2. Summary of results of the Analysis of Variance on the cover of upright algae in areas that were cleared of turf-forming algae. Legend as in Table B1.

Month	Time 1 Significant term	SNK	Month	Time 2 Significant term	SNK
March '07	T	C>P=T	January '08	L × T	Lagoa: C>T>P
April '07	T	C>P=T			Caloura: C>P=T
May '07	T	C>P=T	May '08	n.s.	
June '07	T	C>P=T	August '08	T	C>P=T
October '07	T	C>P>T	October '08	T	C>P=T
June '08	L × T	Lagoa: C=P>T			
		Caloura: C>P=T			

Table D3. Summary of results of the Analysis of Variance on the cover of barnacles in areas that were cleared of turf-forming algae Legend as in Table B1.

	Time 1			Time 2	
Month	Significant term	SNK	Month	Significant term	SNK
March '07	n s		January '08	n s	
April '07	n s.		May '08	n s	
May '07	n s		August '08	n s	
June '07	n s		October '08	L × T	Lagoa C<T<P
October '07	T	n p			Caloura C=P<T
June '08	L x T	n p			

Table D4. Summary of results of the Analysis of Variance on the cover of encrusting algae in areas that were cleared of turf-forming algae Legend as in Table B1.

Time 1			Time 2		
Month	Significant term	SNK	Month	Significant term	SNK
March '07	n s		January '08	n s.	
April '07	T	C<P=T	May '08	n s	
May '07	n s		August '08	L × T	n p
June '07	T	n p	October '08	L × T	Lagoa C<P<T
October '07	n s				Caloura C<P=T
June '08	n s				