Hierarchical spatial structure and levels of resolution of intertidal grazing and their consequences on predictability and stability at small scales

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Abstract

The aim of this research was to assess three hierarchical aspects of alga-grazer interactions in intertidal communities on a small scale: spatial heterogeneity, grazing effects and spatial stability in grazing effects.

First, using semivariograms and cross-semivariograms I observed hierarchical spatial patterns in most algal groups and in grazers. However, these patterns varied with the level on the shore and between shores, suggesting that either human exploitation or wave exposure can be a source of variability.

Second, grazing effects were studied using manipulative experiments at different levels on the shore. These revealed significant effects of grazing on the low shore and in tidal pools. Additionally, using a transect of grazer exclusions across the shore, I observed unexpected hierarchical patchiness in the strength of grazing, rather than zonation in its effects. This patchiness varied in time due to different biotic and abiotic factors.

In a separate experiment, the effect of mesograzers effects were studied in the upper eulittoral zone under four conditions: burnt open rock (BOR), burnt pools (Bpool), non-burnt open rock (NBOR) and non-burnt pools (NBpool). Additionally, I tested spatial stability in the effects of grazing in consecutive years, using the same plots. I observed great spatial variability in the effects of grazing, but this variability was spatially stable in Bpools and NBOR, meaning deterministic and significant grazing effects in consecutive years on the same plots. Both the significance in grazing effects and spatial stability depended on the level of resolution (species, functional, biomass) at which the algal assemblage was evaluated, suggesting hierarchical variability.

In order to be able to predict spatial variability in the effects of grazers in the upper eulittoral zone using biotic and abiotic micro- and macrofactors, a conceptual model was proposed, based on data from several multiple-regressions. This linked the interactions among three elements: idiosyncratic heterogeneity, micro and macrofactors. This suggests that spatial variability can be a product of these factors, while spatial stability can be caused by the same or different combinations of factors.

In conclusion, grazing and other ecological phenomena must be studied hierarchically, not only through spatiotemporal scales, but also at different levels of resolution, as these also influence our perception of patterns.

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GENERAL INTRODUCTION

“The polemic aspects of ecology and evolution are perhaps to be expected as consequences of a loss of patience with complexity”

L.S. Slobodkin 1986

I. The context for grazing effects and their variability along the coast of South Africa

Food webs on the intertidal rocky shores contain variable numbers of trophic levels. Alga-grazer interactions, herbivory and/or grazing effects include two trophic levels, the basal, represented by primary producers (algae), and primary consumers represented by herbivores (or grazers). The consequences of this interaction have been widely studied in terms of the effects of herbivores on the distribution and succession of algal species (Hawkins and Hartnoll 1983, Foster 1992).

These grazer effects can facilitate or inhibit the algal succession process, grazers either feeding on propagules of generalist algae or feeding on late succession algal groups (Sousa and Connell 1992). It has also been reported that grazing can have an effect on the spatial distribution of algae, decreasing or enhancing the variability in algal distribution. This variability can be understood in both temporal and spatial contexts (Benedetti-Cecchi et al. 2005). The variability in importance of grazing effects, seen as a type of predation (Menge and Branch 2001), has been explained by models of community regulation (Menge and Sutherland 1987). Variability in predation and grazing effects have been explained by gradients of wave exposure and desiccation (Hawkins and Hartnoll 1983, Lubchenco 1986, Menge and Olson 1990). However, gradients of nutrient concentrations and oceanographic conditions can also influence the variability in grazing effects at scales of kilometres (Bustamante et al. 1995ab, Menge et al. 1997).

Two models of community regulation have been described: top-down and bottom-up regulation. Top-down models refer to situations where the abundance of lower trophic levels (e.g. primary producers) is determined directly or indirectly by higher trophic levels, for example through grazing or predation (Menge and Sutherland 1987, Menge 1992, Menge 2000). For example, predators can control grazing effects by the reducing numbers of grazers, indirectly increasing the algal population at the same time (Menge and Branch 2001). Bottom-up models refer to direct or indirect dependence on nutrients on the variation in abundances at lower trophic levels such as primary producers (Menge et al. 1997). For example, an extra supply of nutrients will increase algal growth rate, allowing then to escape in size from grazers. Variability of physical or physiological stress can also exert bottom-up control, in the same way as nutrients do, increasing or decreasing algal growth rates (Menge and Olson 1990, Menge 1992).

The two models/approaches are inextricable linked and it has been demonstrated that even when bottom-up factors are strong, strong top-down control is also observed (Gripenberg and Roslin 2007, Freidenburg et al 2007). Examples are reported by: (i) Menge et al. (1997), who studied two sites at which upwelling occurs, however they exhibited differences in community structure and trophic interactions. These differences were not explained by physical factors such as upwelling intensity, wave exposure, water flow or air temperature, but by an extra supply of phytoplankton from the northern site to the south site, attributed to the interaction among offshore currents, winds and continental shelf bathymetry. At the southern site, grazing, predation and recruitment were stronger. (ii) On the east coast of New Zealand water column productivity is low due to absence of upwelling, while on the west coast, upwelling events lead to high productivity. Upwelling events increase algal biomass and consequently grazing effects are enhanced on the west coast of New Zealand (Menge et al. 1999, Menge 2000). (iii) Similar examples have been demonstrated for the coast of South Africa by Bosman and Hockey (1986). These authors report the influence of guano from faeces of bird colonies of South African islands that increases the nutrients supply, enhancing primary productivity and algal biomass of the islands and consequently increasing limpet densities. However, an interesting point was that birds producing the guano also prey on limpets, thus simultaneously reducing the grazing effect. (iv) Another South African example was given by Bustamante et al. (1995). These authors observed that the coast of South Africa presents a gradient of epilithic primary productivity decreasing from the west coast to the east coast, and associated with nutrient availability and phytoplankton productivity. Biomass of grazers and filter feeders is strongly correlated to this gradient of primary productivity. However, macroalgal productivity did not change between east and west, but was lower at the south coast. Despite the stronger grazing effect of the limpets *Scutellastra granatina* and *S. argenvillei* (over 200 ind per m^2) on epilithic and macroalgal communities on the west coast, their energetic requirements are not fully supported by benthic productivity. The deficiency is subsidised by drifting pieces of kelps that are caught by both limpet species. At the same time, these limpets have the most profound effect on algal abundance on the west coast (Eekhout et al. 1992, Bustamante et al. 1995ab, Bustamante and Branch 1996). Therefore, bottom-up factors (nutrients) support grazers (from both subtidal and intertidal environments), but at the same time, grazers exhibit strong top-down control on the benthic macroalgal community creating macroalgal barrens on the low shore of the west coast.

These studies suggest that ecological systems receiving strong nutrient input (strong bottom-up supply) will exhibit strong top-down interactions too. Differences between oligotrophic and eutrophic systems support this relationship between bottom-up and top-down forces. Lotze et al. (2001) reported that eutrophic systems in the Baltic Sea support more grazers than the oligotrophic north west Atlantic system. The eutrophic system seems to be dominated by perennial algae with antiherbivore defences, providing evidence of strong grazing impacts on the evolution of the alga-grazer interaction. In contrast, oligotrophic systems are dominated by annual opportunistic algae and these will be more susceptible to grazing, though in these systems the grazer effect is weak in comparison to eutrophic systems.

The west coast of South Africa exhibits high primary productivity, therefore it should show stronger grazing effects on the low shore than on east coast, where upwelling is rare. In addition, Branch et al. (1992), in an attempt to explain the evolution of gardening in limpets, suggested that the relative proportions of three main algal functional groups can reflect the grazing intensity and subsequently the level of eutrophication of the system. For example, foliose algae dominate in areas with low grazing intensity, while encrusting coralline algae will dominate areas with high grazing intensity, this agrees with the views of Steneck and Dethier (1994). But at intermediate grazing intensities, red turfs and brown and red encrusting corallines are present, as well as gardening limpets. Bustamante et al. (1995b) assessed the proportions of foliose, encrusting corallines and turfs across the whole intertidal around South Africa. They reported the domination of corallines over turf and foliose algae on the east coast, while on the west coast foliose algae are dominant over the encrusting corallines. This scenario suggests a contradiction. On one hand ecological models of community regulation would predict that areas with low nutrient levels would have weaker trophic interactions, enhancing the dominance of opportunistic foliose algae, but the presence of encrusting corallines in the east coast suggests strong grazing effects. This phenomenon can be explained by the fact that, on the west coast, grazing effects are extremely strong on the low shore, while on the east coast, grazing effect are homogenously distributed among zones. In addition, the west coast is considered to be cold temperate, while the north-east part of the coast is semi-tropical (Brown and Jarman 1978). Semi-tropical warm conditions tend to exhibit more encrusting algal groups than cold temperate areas (Menge 1991). Dye (1993, 1995) reported strong grazing effects on the low shore of the east coast, resulting in the dominance of encrusting algae. The south coast is also dominated by encrusting algae, but at lower abundances than on the east coast (Bustamante et al. 1995). This suggests grazing effects are weaker than on the east coast. Grazing effects of limpets on the south coast have been studied on the low and mid shore with a focus on particular species: the limpet *Cymbula oculus* feeding on *Gelidium pristoides* (Carter and Anderson 1991) and the grazing effect of the limpet *Scutellastra longicosta* feeding on *Ralfsia verrucosa* (McQuaid and Froneman 1993). These studies reported weak and strong grazing effects respectively, but the effect of the whole grazer community on the algal assemblages is difficult to extrapolate. Whittington-Jones (1997) excluded the whole grazer community experimentally and reported weak grazing effects in a short term (six week) experiment. These studies have been carried out using different experimental designs at different spatial and temporal scales, therefore the results are not conclusive and a reassessment of grazing effects in the different zones using one single experimental design is required. Therefore, the main objective of this thesis is to re-assess the importance of small scale grazing effects across the shore on the south coast of South Africa.

II. Consequences of grazing effects among zones: differences in spatial patchiness

A known consequence of grazing is variability in the spatial and temporal distribution of algae (Lubchenco and Gaines 1981, Benedetti-Cecchi 2001). The variability in algal spatial distribution is represented by patches of different sizes in specific areas in the intertidal. Patchiness has been defined as the spatial variability in the distribution of any organism (Dayton 1971, Paine and Levin 1981, Rossi et al. 1992, Underwood and Chapman 1996). Two of the sources of spatial variability generating patchiness are disturbance and environmental stress (Levin and Paine 1981, Steneck and Dethier 1994, Wu and Loucks 1995). Stresses include desiccation and wave exposure gradients (Hawkins and Hartnoll 1983, Underwood and Jernakoff 1984, Lubchenco 1986, Benedetti-Cecchi 2001, Jenkins and Hartnoll 2001), these two gradients induce spatial patchiness through modifications of grazing effects at small scales. Also, the combination of stresses and differences in algal recruitment can induce variation in grazing intensity, allowing algae to escape from grazers (Hawkins and Hartnoll 1983, Menge and Sutherland 1987, Underwood and Chapman 1996). Underwood and Jernakoff (1984) described situations when algae can escape in size from grazing under benign conditions such as the lower part of the intertidal, during cooler seasons or in tidal pools. Williams et al. (2000) working on the high shore of Hong Kong, showed that areas near grazer refuges show strongly reduced amounts of algae compared to areas further from grazer refuges. They concluded that spatial heterogeneity of the substratum can drive variability in grazing intensity through the topographic variability in the distribution of benign and harsh areas. Benedetti-Cecchi (2000) modelled scenarios that explain algal spatial distribution. He stated that the effect of algal spatial variability depends on: (1) the intensity of the grazing effect represented by the ‘mean’ effect, (2) the ‘variance’ of the mean grazing effect and (3) the residual variability (sources of algal variability caused by biotic and abiotic factors, but independent of those caused by grazers). He predicted and described scenarios with either abundant or sparse algae, either strong or weak mean grazing, and with either large or small variance. These scenarios predict: no grazing effects on the spatial distribution of algae when grazing has a smaller variance than the algal residual variance, but only when the algal abundance is large. However, grazers will diminish algal spatial variance in environments with sparse algae. Abundant and sparse algae can be represented by the low shore and high shore, or by high and low productivity systems, respectively. In addition, and more importantly, an increase and/or decrease in algal spatial variance implies an increase or decrease in the level of algal patchiness (Benedetti-Cecchi 2000, 2003).

At different levels of rocky shores (or in different zones) the balance of wave exposure and desiccation changes, as do the rates of post-settlement of algae and the importance of topography, so that algal residual variance will differ inducing different types of patchiness (Underwood 1985). From this point of view the ‘residual variability’ tends to increase with the gradient of desiccation or any stress gradient (Underwood 1980, Underwood and Jernakoff 1984, Benedetti-Cecchi 2000, 2003). At the same time, the mean grazing effect tends to vary due to changes in grazer movement due to differences in foraging patterns and food availability in different zones (Chapman 1995, Williams and Morrit 1995, Chapman and Underwood 1996, Underwood and Chapman 1996, Burrows and Hawkins 1998, Aguilera and Navarrete 2007). Because the balance between growth algal rate and grazing rate changes from low to high shore, I would expect not only different intensities of grazing effects, but also different levels of patchiness in different zones. This hypothesis has not been studied in South Africa. This is based on the fact that different grazer assemblages and algae inhabit different parts on the shore.

The only quantification of levels of patchiness on the south coast of South Africa has been done for the mussel *Perna perna*, their recruits and for the alga *Gelidium pristoides* (Erlandsson and McQuaid 2004, Erlandsson et al. 2005). These authors investigated the distributions of these species at several sites and reported patchiness on scales 10s of meters on the low shore within one site. In addition, the causes of algal patchiness are different from those affecting the spatial patchiness of grazers, therefore it is necessary to distinguish between patchiness in grazing effects and causes that act separately on alga and grazers.

Common conditions can induce algal and grazer patchiness, especially when the conditions are benign. Under such conditions, both grazers and algae can recruit and survive in benign areas such as tidal pools and shaded areas (see example given by Williams et al. 2000). For this reason in this thesis I will refer to grazing effects as the degree of spatial reduction of algal biomass or abundance in specific areas, this is estimated by contrasting areas where grazers have been excluded with non-grazer exclusion areas (Underwood 1985, Coleman et al. 2006, Atalah et al. 2007). This estimation can be expressed numerically using effect sizes (Osenberg et al. 1997). In this context, the ‘mean’ of this effect size gives the strength of the grazing effects and the variance represents the patchiness of grazing effects.

III. Grazing effects and the problem of scale

Algal patchiness can be caused by factors operating at different scales. Patches can vary in size, and their detection is dependent on the scales used (Wiens 1989, Levin 1992, Wu and Loucks 1995), because grazing can induce different sizes of patches according to the scale of interaction with the alga. These interactions vary according to the size, density and degree of mobility of the grazer. The minimal scale of interaction between benthic grazers (limpets) and algae can vary from cm to meters, the scale at which patches can be found (Branch 1981, Denny et al 1985, Branch et al. 1992, Johnson et al. 1997, 1998). Then, if the scale of observation is increased, grazing effects can depend on patches created through variation in wave exposure (Menge and Olson 1990, Jenkins and Hartnoll 2001) or desiccation (Underwood and Jernakoff 1984) at scales of meters to 10s of meters, within a specific geographical location. At this scale, physical disturbances can modify the intensity of grazing effects, generating random patches of different sizes (Dayton 1971). Finally, at scales of kilometres, it is possible to recognize changes in the intensity of grazing effects related to biogeographical conditions as mentioned above: the existence of upwelling on the South African west coast and the New Zealand west coast, or the effects of coastal morphology such as headlands (Broitman and Kinlan 2006, Blanchett et al. 2006).

Thus, one can expect to find different sizes of patches using different scales or ‘grains’ of observation which describe the different processes generating spatial and temporal patchiness of grazing effects.

At this point, it is important to discuss the concepts of spatial and temporal patterns. The spatial or temporal distribution of any variable studied can be random (non dependent on distance or time), or dependent on distance or time (Legendre 1993). It has been observed that any change in the scale of observation produces a change in the variance, often large scales have smaller variance than small scales (Levin 1992). Estimations of changes in variability at different lags (or two equidistant points) makes it possible to detect different patches (Legendre 1993, Kostylev et al. 2005).

Grazing effects have often been studied using experimental exclusions contrasted to open areas distributed randomly in a zone or among zones, within a site and among sites (Boaventura et al. 2002, Coleman et al. 2006). Often these comparisons give a clear estimation of grazing effect variability at specific scales that are dependent on the area of grazer exclusion. In order to complement this design, it is possible to use different sizes of fences, mixed as is usual in a block design (Underwood 1997) or to complement the experiment design at one scale using estimations of spatial variance at different (equidistant points) or lags along a transect as is used in correlation analysis. This can be used to find breakpoints where the relationship between variance and distance changes. This corresponds to a change from one type of patch to another. In this way, it is possible to estimate sizes of patches for both algae and grazers at different lags or scales.

In addition to estimating the effect of grazing in each zone at one site on the south coast of South Africa, I estimated the spatial pattern of algae and grazers in every zone at two sites separated by 25 km.

IV. Grazing patchiness to hierarchy theory: generating variability in grazing effects

Research done on spatial patterning of variables often reports patchiness at different scales, commonly nested patches i.e. smaller patches within larger patches (Legendre 1993, Li and Reynolds 1994, Hewitt et al. 1997, Thrush et al. 1997a,b). Therefore a hierarchical structure of patchiness can be noticed with factors operating at large and small scales, which I refer to in this thesis as 'macrofactors' and 'microfactors', respectively. The factors causing variability at microscales are assumed to produce random spatial patterns (at scales of cm), making the system unpredictable (Levin 1992). Therefore, the common wisdom in ecology tends to deal with small factors in terms of averages and uses them to explain patchiness at larger scales while avoiding the estimation of variability induced at small scales which can be great and influenced by e.g. 'weak indirect effects', 'substratum complexity' and 'stochastic disturbance' (see Rand and Wilson 1995, Berlow 1999, Marquet et al. 2005). The systematic avoidance of small scale processes using the average could be appropriate: i. if the factors causing variability operate linearly when the process is scaled-up and ii. if the relationship between the average and the variance is linear at different scales. These relationships are often not linear (Hewitt et al. 1997, Benedetti-Cecchi 2003) and the variability induced by indirect effects, disturbance and complexity are not insignificant (Berlow 1999, Menge and Branch 2001). The idea that processes observed at scales that are too small will be dominated by stochastic effects (Rand and Wilson 1995), has precluded attempts to study the hierarchical structure and dynamics induced at such small scales (Rand and Wilson 1995, Lawrie and McQuaid 2001). Grazing effects on rocky shores have been generally studied at single scales; few studies have design that extend across scales (Menge et al.

2005). This thesis examines the hierarchical structure of the variability in grazing effects across small scales. One method to quantify this hierarchy at small scales is to use fractal geometry (Mandelbrot 1977). This type of geometry allows one to quantify how many times a shape can be self divided, in a hierarchical way, into smaller parts that resemble the larger parts (Mandelbrot 1977). This type of approach has been used successfully in terrestrial (Burrough 1981) freshwater (Cooper et al. 1997) and marine ecosystems (Kostylev and Erlandsson 2001), and describes spatial patterns as random, patchy or trend-like (Kostylev and Erlandsson 2001).

It is worthwhile to mention that algal patches can comprise different species that may, or may not share ecological features such as similar growth rates, resistance to disturbance and herbivory. If these features are shared, the species can be classified in functional groups (Littler and Littler 1980, Steneck and Watling 1982, Steneck and Dethier 1994, Padilla and Allen 2000). However, a simple algal patch can comprise species belonging to different functional algal groups. Therefore the balance between grazing resistant and non-resistant species produces variation in the outcome of grazing. Thus grazing effects can be understood as a hierarchy affecting specific levels (or particular algae), functional levels, or total algal biomass. The same can occur for grazers. It is possible to make categories varying from specialized to generalist grazers. Thus we can deal with single species of grazers that affect particular algae, functional groups of grazers categorized according to their feeding system (Steneck and Watling 1982) or size, or simply the total grazer community.

At this point it seems that grazing effects vary within a hierarchical framework linked to the level of resolution of the observations (O’Neill et al. 1986, Rahel 1990, Levin 1992, Thrush et al. 1997ab), where resolution refers to the level of detail of the description of an algal assemblage, and can vary from ‘coarse’ to ‘specific’. ‘Coarse’ refers to a level that involves a group of components in the observed process, whereas the specific level considers only individual components (Rahel 1990). Indeed, our perception of nature is profoundly influenced by three aspects of scale. i. Spatio-temporal scales where one pattern/process can emerge at small/short-term scales and completely different ones at large/long-term scales (Wiens 1989). ii. Taxonomic levels of resolution, which have been used to detect effects of disturbance on ecosystems. Generally higher taxonomic levels (family, order) offer better explanations of disturbance processes than specific levels (genus, species) (Thompson and Townsend 2000, Hansson et al. 2004), though there may be consistency between taxonomic levels at some spatio-temporal scales and levels of perturbation (Chapman 1998, Olsgard et al. 1998). iii. Functional-species versus species-identity situations, when functional groups of species (coarser level) offer different interpretations of ecosystem functioning and trophic interactions from species (finer level) (Steneck and Watling 1982, Steneck and Dethier 1994). These three examples show that explanations based on hierarchical levels will affect the predictability of the phenomenon studied, which is the basic principle of hierarchy theory (O’Neill et al. 1986, Wu and Loucks 1995), in this specific case, the outcome of grazing. This theory was conceived to understand hierarchical organization in any ecological process: how ordered structures emerge hierarchically in any ecological phenomenon, and why stratified ecological processes exhibit more stability at higher/coarser levels of organizations than at lower/finer/specific levels (O’Neill et al. 1986, Wu and Loucks 1995). This theory assumes that coarser levels will be more stable in time and in space than finer levels. For example, small spatial scales exhibit higher variability, and low spatial and temporal stability (Benedetti-Cecchi 2001, Lawrie and McQuaid 2001). However, it seems higher levels of organization such as guilds or functional groups are also more stable and enduring than their components individual species (O'Neill et al. 1986, Steneck and Dethier 1994).

For this reason, grazing effects were assessed in this thesis at different levels of resolution in terms of both functional groups and species, when possible.

V. Stability and persistence of mosaics: persistence of grazing effects

Apart from the debate on whether the mosaics of organisms are organized or randomly distributed, it is interesting to assess if grazing effects are spatially persistent after perturbation, and to know the factors that influence stability after disturbances. Recent perspectives in ecology consider communities to be in stages of non-equilibrium or instability (O'Neill 2001). However, stable ecological patterns such as ubiquitous zonation patterns persist in rocky shores (Southward 1975, Branch and Branch 1981). These patterns can be observed on any rocky shore or sandy beach, and after any perturbation, these patterns return their initial states suggesting some sort of resilience and stability (Castilla 1988, Wai and Williams 2006b, Erlandsson et al. 2006). Resilience refers to the rapidity with which a system returns to a previous equilibrium after disturbance (Pimm 1984). This resilience has been object of studies testing the existence of 'stable states' (Bertness et al. 2002, 2004, Petraitis and Dudgeon 2005). These authors observed that mussel beds dominate exposed habitats and macroalgal stands dominate sheltered sites in the Gulf of Maine (Petraitis and Dudgeon 2005). These authors hypothesized that these could be alternative stable states in intermediate exposure systems, depending on the size of the disturbance.

These authors, while discussing the existence or non-existence of stable states, indirectly mention some mechanisms which are responsible for returning a specific system to its original state, including temporal variability of predation/grazing. Bertness et al. (2002, 2004) conclude that predation/grazing delays return to the original state whether dominated by *Ascophyllum nodosum*, or mussels. However, if the size of the disturbance is large enough, the community starts a divergent successional pathway (Petraitis and Dudgeon 2005).

Other studies were conducted to analyze the persistence of bare space on San Juan island (Washington, USA) (Navarrete and Berlow 2006). These authors suggest an 'equilibrium state' of sparse barnacle beds (*Semibalanus cariosus*) which dominated 25% of the space, while the rest of the space is bare rock. This pattern is stabilized or maintained by predators and grazers, which optimally operate at certain spatial scales, that maintain the level of bare rock. In hypothetical cases, if disturbance causes an increase in the bare rock, the system returns to the same pattern during the next barnacle recruitment event due to the inability of predators to cover larger areas than their own optimal spatial scale of predation. If recruitment is high and recruits cover all the bare rock, predation returns the system to the original level of bare rock. Interestingly these authors observed that predation is deterministic in specific areas of the shore and not uniform, otherwise the system would be devoid of barnacle beds (Berlow and Navarrete 1997). On the Isle of Man, a degree of resilience has been reported in the interactions among fucoids, limpets and barnacles. For example, Burrows and Hawkins (1998) concluded that on homogenous substrata, the spatial patterns of the fucoid-limpet-barnacle system is not deterministic, because this is an emergent property of the interactions among components of the system that can occur in any position, while in heterogeneous substrata it can be deterministic due to differences between harsh and benign microsites. In this sense the interactions are restricted to certain specific positions. Although disturbance can play an important role in creating more free space, limpets seem to play an important role returning the system to its original state (Burrows and Hawkins 1998). Spatial patterns within this systems can change in time as a consequence of this dynamic patchiness.

The last two examples are found in different geographic regions on the mid shore, while one system seems to be static or deterministic (San Juan Island) in its spatial pattern and the other kinetic (Isle of Man), both exhibit a certain resilience to perturbation and therefore some stability. Stasis means that an ecological phenomenon only occurs at specific/determined positions on a rocky shore, while kinesis implies that the phenomenon can occurs at different positions.

The hypothesis, that grazing effects can be spatially stable has not been tested on South African coasts and must fulfill two conditions to be supported: i. statis/determinism within an area and ii. consistently significant grazing effects before and after a perturbation. This was tested in the upper eulittoral zone at one site on the south coast of South Africa in tidal pools and open rock habitats.

VI. Hypotheses and structure of the thesis

The general goal of the present study is to assess the effect of intertidal grazers on the algal community on the south coast of South Africa. The oligotrophic conditions of this region suggest that there won't be significant grazing effects on the algal community, however the spatial structure of functional groups suggests the contrary, high impact of grazers on the algal community. The second, third and fourth chapter investigate grazing effects on the algal community using different methodologies in an attempt to bridge observational and experimental evidence, this is assessed at different levels on the shore.

VII. Specific hypotheses:

(i) Variability in the intensity of the effects of grazing induce different algal spatial patterns at different levels on the shore. This hypothesis is studied using geostatistical tools such as semivariograms and cross-semivariograms in the second chapter.

(ii) The effects of grazing on the algal community vary among zones of the intertidal due to the change in the balance of variability in the intensity of grazing and changes in the residual spatial variability of algae among zones. This might be induced by an increase in the desiccation gradient towards to the land. These specific hypotheses are assessed in the third chapter using two experiments: (a) different types of grazing exclusions were set at different levels0

on the shore and (b) a transect of` grazer exclusion was set across the shore.

(iii) There is a degree of determinism of grazing effects represented as consistence in the intensities of grazing at specific positions within a shore in time. Additionally, it is hypothesized that the spatial persistence of the effects of grazers will vary according to the level of resolution at which the study is conducted. These hypotheses were studied in the fourth chapter.

(iv) Grazing is an ecological process that can be defined hierarchically, therefore it is hypothesized that the predictability of its intensity and variance will change at different levels of resolution, and this will be represented as changes predictors variables at each level. This hypothesis is assessed in the fifth chapter and a model is proposed. This chapter includes multiple regression analyses to explain the variation in grazing effects as a function of a number of environmental factors operating at large and small spatial scales.

The sixth chapter places the experimental results in the context of hierarchical theory.

CHAPTER II

THE EFFECTS OF GRAZING ON SPATIAL PATTERNS

INTRODUCTION

Geometry and arithmetic have generally been used in the study of order in nature. It was formerly supposed that geometry was the study of the nature of the space where animals and plants live (Russell 1953). Many important spatial shapes in nature are either irregular or fragmented and therefore, cannot easily be described using Euclidean geometry. Non-Euclidean, and especially Fractal geometry, provides a simple description of many natural forms through a property called self-similarity. Self-similarity describes objects that can be fragmented into smaller and smaller pieces each of which resembles the whole object; closely analogous to building a square out of similar smaller squares (Hastings and Sugihara 1993). Therefore, a perfect fractal is a complex form which is divided into infinite copies of itself (Mandelbrot 1977, Feder 1988).

It is well known that species in landscapes exhibit great variability at different scales. Fractal geometry has been used to describe spatial patterns in the distribution of animals and plants (Hastings and Sugihara 1993, Underwood and Chapman 1996). From this point of view, fractal geometry helps determine whether spatial distributions of organisms follow some degree of order or pattern (Peitgen et al.1992, Hasting and Sugihara 1993).

Most natural ecological phenomena display geographical patchiness, exhibited at all spatial scales, from microscales (centimetres) to macroscales (continental scales, kilometers) (Levin 1992, Legendre 1993). The distribution of flora and fauna in both terrestrial and marine ecosystems is viewed as a mosaic of patches of different kinds and sizes, and the spacing of those patches is an important characteristic of an ecosystem. When these mosaics exhibit a certain level of predictability, allowing them to be described quantitatively, they can be described as spatial patterns (Dale 2000). To explain these spatial patterns, it is necessary to use the concepts of spatial variability and spatial heterogeneity (Legendre 1993, Cooper et al. 1997). Variability is represented by the "variance" indicating changes in the value of a variable around the average (Erlandsson et al. 2005). Because variance is very sensitive to the size of the sampling unit (grain size) and the distance (lag) between samples, it is necessary to combine measures of variance and scale (Levin 1992). When both 'grain size' and 'lag' are increased, their variances theoretically exhibit divergent behaviours: on one hand the variance decreases as the grain increases in size (scale) (Levin 1992), while an increase in the distance (scale) between samples (increased lags) induces the contrary effects on the variance (Rossi et al. 1992, Underwood and Chapman 1996). Here, I study grazing effects in terms of the variability represented by the lag. Therefore, 'spatial heterogeneity' combines variance and scale (represented as lag), indicating the structure in the variability across different scales (Legendre 1993, Kostylev and Erlandsson 2001, Erlandsson et al. 2005).

Concepts of spatial pattern and spatial heterogeneity can be similarly understood, however spatial heterogeneity must be interpreted in this study as the level of dependency of one variable on different spatial scales (Legendre 1993, Erlandsson et al. 2005).

Different statistical tools are used to examine spatial heterogeneity, and are reviewed by Legendre (1993), Underwood and Chapman (1996), Cooper et al. (1997), and Kostylev and Erlandsson (2001), who suggest the use of 'semivariograms' and other spectral analyses. Semivariograms describe the changes in magnitude of the variance between pairs of samples separated by different distances or lags (Underwood and Chapman 1996). It is worth noting that one 'lag' represent only one scale, and that semivariogram analysis describes the variances across a spectrum of increasing lags (Underwood and Chapman 1996, Dale 2000, Kostylev and Erlandsson 2001). In this way, any change in the relationship between variance and lag represents a breakpoint between one scaling region and another. Therefore, semivariograms can describe the behaviour of spatial variability at different scales through the fractal dimension of the variance (in this particular case semivariance, half of variance, see Dale 2000). The fractal dimension of the semivariance describes how many times the variance can be subdivided by itself. In that way three behaviours of the variability can be observed and described by the fractal dimension: (1) persistent in the form of a trend or gradient, when the relationship between variance and lags continuously increases or decreases with increasing size of the lag. (2) anti-persistent behaviour, in which the variance is dependent only at certain lags and not others, (3) random distribution of the variance, when the variance is not dependent at any lag (Cooper et al. 1997, Erlandsson et al. 2005). Semivariograms plot variability as a continuous function of the lag (distance between samples), and the fractal dimension can be used to quantify this spatial heterogeneity and the strength of spatial dependence in measured variables (Cooper et al. 1997, Kostylev and Erlandsson 2001, Erlandsson and McQuaid 2004, Erlandsson et al. 2005).

Theoretical and empirical work in limnic, terrestrial and marine systems has shown that spatial heterogeneity is a functional property of ecosystems, representing the complexity necessary to allow the coexistence among species (Dale 1990, Palmer 1992, Underwood and Chapman 1996, Cooper et al. 1997, Kostylev et al. 2005). Often studies of spatial pattern in ecology examine particular species and their relationship to topographic complexity, which is one of the main sources of variability in the distribution of species.

However, few studies have examined interactions: (1) between different species, e.g. Broitman and Kinlan (2006) found a positive relationship between kelp and phytoplankton biomass at large regional scales (>150 to 200 km), but a negative one at their definition of mesoscales (<50 km); (2) between variability in topography and different species, i.e. Erlandsson et al. (2005) found positive and negative relationships between variability in topography and the distribution of mussels (depending on rock slope or depressions), and negative relationships between mussels and the red algae, *Gelidium pristoides*, at small scales (10s of meters).

A secondary source of variability which induces aggregation and patchiness can be recognized in ecological interactions such as trophic and predator-prey interactions. Kareiva (1987), in an experiment between a ladybird (*Coccinella* sp.) and its prey, an aphid (*Uroleucon* sp.), demonstrated that the degree of patchiness of the habitat affects the aggregation and survivorship of the prey.

The spatial structure of seaweeds has scarcely been assessed at different scales especially at small scales of cm to 10s of meters. Broitman and Kinlan (2006) found that the distribution of kelps in the west coast of North America is driven at large scales (100s of kilometres) by continental geomorphology, which influences near shore oceanography and along-shore variation through upwelling systems (Menge et al. 1997). In addition, they found that at scales varying among 10s to 100s of meters, the availability of rock substratum plays one of the principal roles as a source of variability in a kelp forest. On the Isle of Man (UK), Johnson et al. (1997) found that patch structures of limpets and algae at all sites were correlated between 0.1 and 2 meters. On the south coast of South Africa, *Gelidium pristoides* is the only alga analysed at different spatial scales and does not exhibit spatial structure at small scales (10s to 100s of centimetres), but does at larger, within-shore scales (10s of meters) if this is induced by spatial structure in topography (Erlandsson et al. 2005).

Grazing in marine systems exhibits variability from small scales (Underwood 1980, Underwood and Jernakoff 1984, Williams 1993, Underwood and Chapman 1996, Benedetti-Cecchi 2000) to continental scales (Bustamante et al. 1995ab, Coleman et al. 2006, Freidenburg et al. 2007). In this context, a hierarchy of factors operates at different scales, determining the community structure and grazing effects on rocky shores. Large scale processes (at continental scales) can modulate the intensity of local processes, and they can affect processes occurring at micro-scales (Menge et al. 1997). For example, coastal geomorphology can influence oceanographic processes such as upwelling, and therefore the abundance and diversity of species (Bustamante et al. 1995b, Menge 1992, Menge et al. 1997, Broitman and Kinlan 2006). Local factors such as wave exposure will modulate the interaction strength among species, affecting abundance and diversity of the species (Hartnoll and Hawkins 1983, McQuaid and Branch 1985, Jenkins and Hartnoll 2001). Finally, small-scale variability, created by random distribution and microhabitat complexity, affects the strength of ecological interactions and the distribution and abundance of species. Indeed, it is interesting to note that small scale variability is considered to be large, governed by stochastic process, and unpredictable in terms of the grain size (e.g. Lawrie and McQuaid 2001). In contrast, in terms of lag (distance between samples), spatial structure and order is expected. However, few studies have tried to understand small-scale spatial structure from centimeters to meters (e.g. Underwood and

Chapman 1996, Johnson et al. 1997, Kostylev and Erlandsson 2001, Erlandsson and McQuaid 2004).

It is interesting to notice that spatial pattern can change from site to site and time to time. This was observed by Erlandsson et al. (2005) who studied the spatial structure of mussel beds. These authors found changes in the heterogeneity of mussel beds at different levels within a zone, and at the same site in consecutive years. They found differences also in the spatial structure of the alga *G. pristoides* within a zone (Erlandsson and McQuaid 2004). Using cross-correlative techniques such as cross-semivariograms, these authors found indirect evidence for competitive interactions between *G. pristoides* and mussels in most sites and zones (Erlandsson and McQuaid 2004). From this point of view, the spatial distribution and structure of grazing effects are dependent on the spatial structures of algae and grazers. Following the results of the following chapter, grazing effects vary among zones, being important on the low shore (Bustamante et al. 1995), but less important on the mid shore and high shore under conditions of recovery after perturbation. It is possible that patchiness and spatial structure of the same algal groups, such as Ulvales, encrusting corallines and corticated algae are different at different levels of the shore. Areas where patches of algae and grazers converge are hypothesized to be the places where grazing effects occur (Johnson et al. 1997, 1998). In these patches, grazers can reduce the probability of foliose algal recruitment, or enhance it as a positive interaction with encrusting algae (Branch et al. 1992).

This chapter aims to study spatial patterns of algae and grazers using semivariograms, and to understand how and at which scale these patterns are related, using cross-semivariograms. The relationships extracted from the cross-semivariograms allow us to understand the possible influence of grazers on particular algae. The analyses were carried out in terms of functional algal groups and grazer density and biomass. It was assumed that either the presence of algae and grazers or the presence of algae and the absence of grazers at specific scales imply positive or negative relationships respectively between grazers and algae. Therefore, co-occurrence of grazers and algae at the same scale indicates a positive effect, such as a limpet-alga mutualism e.g. *Scutellastra cochlear* and encrusting coralline or *S. longicosta* and *Ralfsia verrucosa* (Branch et al. 1992, Bustamante et al. 1995). In contrast, a negative relationship can indicate that grazers are consuming algae.

In order to simplify the analysis I categorized algae in functional groups (Steneck and Watling 1982, Steneck and Dethier 1994). Grazers could have been grouped in functional groups according to their feeding apparatus or diet, but this was not necessary because grazers on the low shore have the same diet e.g. *Scutellastra* spp feed on encrusting non coralline (*Ralfsia* spp., reported by Branch et al. (1992), McQuaid and Froneman (1993)), foliose algae, corticated algae and encrusting corallines. Additionally, these grazers all exhibit docoglossan type of radula (Steneck and Watling 1982). On the mid shore, grazers such as *Cymbula oculus, Oxystele* spp. and *Siphonaria* spp. Exhibit different radula types but converge in their diets (Whittington-Jones 1997). The same has been reported on the high shore, *Nodilittorina africana* and *N. knysnaensis* have the same radulae and feed on the same microalgal community (Kaehler and Froneman 2002). Therefore, categorizing grazers into functional groups was considered unnecessary as, within zones, the grazers have similar effects on the same algal functional groups. It is more important then to quantify them in terms of density and biomass to understand the effects on the algal assemblage.

MATERIALS AND METHODS

I. Site

Grazers and seaweeds were sampled on two sandstone shores, Old Woman's River mouth (33º28'57'', 27º09'09'') and Hamburg (33º17'56'', 27º28'46''). Three levels on the shore were assessed at each site using a 15 meter transect in April 2006. These three zones were recognized by the following algae and grazers: a low zone characterized by the corticated alga *Hypnea spicifera*, red turfs and the grazer *Scutellastra cochlear*; a mid zone characterised by the alga *Gelidium pristoides* and the limpet *Cymbula oculus*; and a high shore defined by the presence of littorinid grazers (Branch and Branch 1981, McQuaid and Branch 1985). These transects were sampled using contiguous quadrats of 0.25 x 0.25 m, which allowed a sample size of 60 quadrats per transect with a minimum lag of 0.25 m, defined as the distance between centers of two adjacent quadrats. During March/April 2006 digital photographs for cover and field measurements were taken on the shores. Percent cover of algae was estimated from the digital photographs using the program Image Tool 3.0 and the abundances and lengths of the grazers were assessed *in situ*, through direct counting and using a vernier callipers. Due to the great abundance of littorinids, opercular diameter and biomass were estimated in the laboratory from a sub-sample of littorinids taken from an area of 5 cm^2 within each quadrat of 0.25 m x 0.25.

I categorized the algal species into functional groups in each zone. On the low shore the functional groups consisted of foliose algae (mainly *Ulva* spp) called Ulvales in this chapter, red turfs, corticated algae (*Hypnea spicifera*), encrusting corallines (*Leptophytum* spp and *Spongites yendoi*), erect articulated coralline (*Corallina* spp, *Cheilosporum* spp, *Arthrocardia* spp) and non-coralline encrusting algae (*Ralfsia verrucosa*). On the mid shore, the assemblage was simpler; the algae comprised corticated algae (*Gelidium pristoides*), foliose algae (*Ulva* spp) and non-coralline encrusting spp. (mainly *Hildenbrandia rubra*). On the high shore, it was not possible to find macroalgal species; therefore the spatial structure analysis was restricted to the grazers, mostly the littorinids *Nodilittorina africana* and *N. knysnaensis*. The grazers were incorporated into the analysis in terms of abundance (the pooled number of grazers per quadrat) and biomass of grazers. All these conversions were possible through the estimations of size/dry biomass equations done by McQuaid et al. (1985). The grazers on the low shore comprised the limpet species *Scutellastra tabularis*, *S. barbara*, *S. longicosta*, and *S. cochlear*. In the mid zone, the limpets *Cymbula oculus*, *Siphonaria capensis*, *S. serrata*, *S. concinna*, and the winkles *Oxystele tigrina* and *O. tabularis* occurred. The urchin *Parechinus angulosus* and the sea star *Patiriella exigua* were found on the low and mid shore at low abundances. On the high shore, the littorinids *Nodilittorina africana* and *N. knysnaensis* were common with few of the mesograzers found on for the mid shore.

II. Data analysis

The statistical technique used was derived from Erlandsson and McQuaid (2004) and Erlandsson et al. (2005):

To determine the spatial variability in the distribution of seaweeds and grazers, I used semivariogram analysis. The semivariance ($Y_{(h)}$) was estimated using the equation:

$$Y_{(h)} = 1 / (2N_{(h)}) \sum_{i=1}^{N-h} (Z_{i+h} - Z_i)^2 \qquad (1)$$

where N is the total number of data points; $N_{(h)}$ is the number of pairs of data points separated by the distance or lag h; Z_i and Z_{i+h} are the values of the studied variable at points $_i$ and $_{i+h}$. The Fractal scaling analysis was used to estimate heterogeneity of spatial distributions over the range of scales. The fractal dimension (D) was calculated from the logarithmic semivariogram (log-log plot of semivariance and scale), using the equation:

$$D = (4 - m)/2 \qquad (2)$$

where m is the absolute slope of the regression between semivariance and spatial scale. D is the fractal dimension which is a non-integer measure of heterogeneity. Values of D between 1 and 1.5 indicate a gradient behaviour of the variability with the scale, while values from 1.5 to 1.97 indicate patchy distribution of the variance with the scale. Finally, values between 1.97 and 2.00 indicate independence of the variance from the scale (Erlandsson et al. 2005).

Lags (h) up to half of the transect length were included in the regression analysis of the semivariogram. In order to make the analysis statistically robust, the minimal sample size used to analyze the variance at different lags was 30 (Underwood 1997). In this way Semivariances do not represent variation between all data points at lags larger than half of the transect length, because at each successively larger scale, the number of comparisons decreases by one (from 59 pairs of combinations at lag 0.25 m to 30 pairs at lag 7.5 m) (Erlandsson and McQuaid 2004, Erlandsson et al. 2005).

In order to describe relationships between two variables across different spatial scales (from 0.25 to 7.5 m lags), I used cross-semivariogram analysis. The cross-semivariance was estimated by the equation:

$$Y_{(h)} = 1 / (2N_{(h)}) \sum_{i=1}^{N-h} (X_{i+h} - X_i)(Z_{i+h} - Z_i) \quad (3)$$

where N is the total number of data points; N(h) is the number of pairs of data points separated by the distance or lag h; X_i and X_{i+h}, and Z_i and Z_{i+h} are the values of two different variables at points $_i$ and $_{i+h}$ (Erlandsson and McQuaid 2004, Erlandsson et al 2005).

A positive or a negative cross-semivariance value at a certain lag indicates a positive or a negative relationship respectively at that scale. A cross-semivariance value approaching zero indicates no relationship between variables at that scale. To test whether cross-semivariance values were significantly different from 0, the distributions of pairs of variables along each transect were randomized 1000 times and cross-semivariance was calculated at each scale for each random permutation. Each randomized value was compared with the appropriately observed cross-semivariance value. Then I calculated the probability of each observed cross-semivariance value being higher (positive relationship) or lower (negative relationship) than by chance alone, and applied an alpha level of 0.05. The analyses were carried out using Matlab 7.0.1.

II.1. Detection of multiple scaling regions

Different fractal dimensions can be estimated within each scaling region, and to detect these scaling regions three conditions need to be achieved (Kostylev and Erlandsson 2001):

i. Detection of scaling breaks using residual analysis: once the differences between observed data points and the fitted regression line were estimated and plotted, it was necessary to recognize the maximum positive or negative residual value with the opposite sign from the first residual value on the chart. The largest residual value with the opposite sign to the first residual value could represent the breakpoint between two scaling regions. Once the potential breakpoints are distinguished, step ii is carried out. The following residuals are re-examined, but this time the residuals are calculated excluding the valid scaling region detected in the previous ‘residual analysis’. The same procedure is repeated at the range of scales following the scaling breaks found.

ii. For each potential scaling region found in the residual analysis, a linear regression was conducted and a significant slope was the second condition used to distinguish that scaling region.

iii. This condition stated that in order for contiguous scaling regions to be considered different, they must exhibit a significant difference in slopes. Therefore I compared slopes using the multiple comparison of slopes test (Sokal and Rohlf 1995).

RESULTS

I. Low shore

I.1. Spatial structure of algal functional groups

Spatial patterns of algal functional groups differed between the two sites. At Old Woman's River, four out of six algal groups exhibited spatial dependence, while Hamburg was characterised by spatially independent patterns related to randomness (fractal dimensions: 1.97-2.00) in the distribution of algal functional groups (Table 2.1 and Fig. 2.1- 2.6).

I.2. Spatial structure of grazers

The grazers were analysed using the total density and the biomass of the species observed. Neither parameter showed spatial dependence at either site, instead, exhibiting high fractal dimensions and random patterns (Table 2.2).

Table 2.1. Linear regression analysis of logarithmic semivariograms, and the fractal dimension (D) for different spatial scales of distribution of functional algal groups at the two sites (A. Old Womans River and B. Hamburg) on the low shore. * = P < 0.01, ** P < 0.001, *** P < 0.0001 and NS = non-significant.

A. Low Shore. Old Womans River

Transect	**Scale (m)**	**Slope**	**SE**	R^2	**t (df)**	**D**	**Spatial pattern**
Red turf	0.25-7.5	0.15	0.045	0.25	3.26(28)*	1.95	dependent
Corticated	0.25-7.5	0.16	0.03	0.45	5.04(28)***	1.92	dependent
Ulvales	0.25-7.5	0.11	0.043	0.16	2.57(28)*	1.94	dependent
Erect coralline	0.25-7.5	0.05	0.046	0.03	0.98(28)NS	1.97	independent/random
Encrusting coralline	0.25-7.5	0.08	0.027	0.22	3.03(28)*	1.96	dependent
Encrusting non-coralline	0.25-7.5	0.02	0.035	0.01	0.62(28)NS	1.98	independent/random
Significant multiple scaling regions							
Red turf	0.25-2.75	0.39	0.05	0.85	7.75(9)**	1.8	Patchy
	3.00-7.5	-0.41	0.18	0.46	-3.78(17)**	1.8	Patchy
Encrusting coralline	0.25-1.25	0.39	0.09	0.97	10.96(3)*	1.8	Patchy
	1.5-7.5	0.11	0.04	0.23	2.65(23)*	1.94	Patchy

B. Low Shore. Hamburg

Transect	**Scale (m)**	**Slope**	**SE**	R^2	**t (df)**	**D**	**Spatial pattern**
Red turf	0.25-7.5	0.03	0.04	0.03	0.9(28)NS	1.98	independent/random
Corticated	0.25-7.5	0.00	0.03	0.00	0.06(28)NS	1.99	independent/random
Ulvales	absent						
Erect coralline	0.25-7.5	0.06	0.04	0.06	1.39(28)NS	1.97	independent/random
Encrusting coralline	0.25-7.5	0.02	0.03	0.02	0.68(28)NS	1.99	independent/random
Encrusting non-coralline	0.25-7.5	-0.1	0.06	0.09	-1.66(28)NS	1.96	independent/random

Table 2.2. Linear regression analysis of logarithmic semivariograms, and the fractal dimension (D) for different spatial scales of distribution of grazer density and biomass on the low shore of the two sites (A. Old Womans River and B. Hamburg). NS = non-significant.

A. Low shore, Old Woman's River

Transect	Scale (m)	Slope	SE	R^2	t (df)	D	Spatial pattern
Grazer density	0.25-7.5	-0.00	0.03	0.00	0.04(28)NS	1.99	independent/random
Grazer biomass	0.25-7.5	0.01	0.03	0.00	0.41(28)NS	1.99	independent/random

B. Low shore, Hamburg

Transect	Scale (m)	Slope	SE	R^2	t (df)	D	Spatial pattern
Grazer density	0.25-7.5	-0.02	0.04	0.03	-0.87(28)NS	1.98	independent/random
Grazer biomass	0.25-7.5	0.06	0.03	0.13	2.03(28)NS	1.97	independent/random

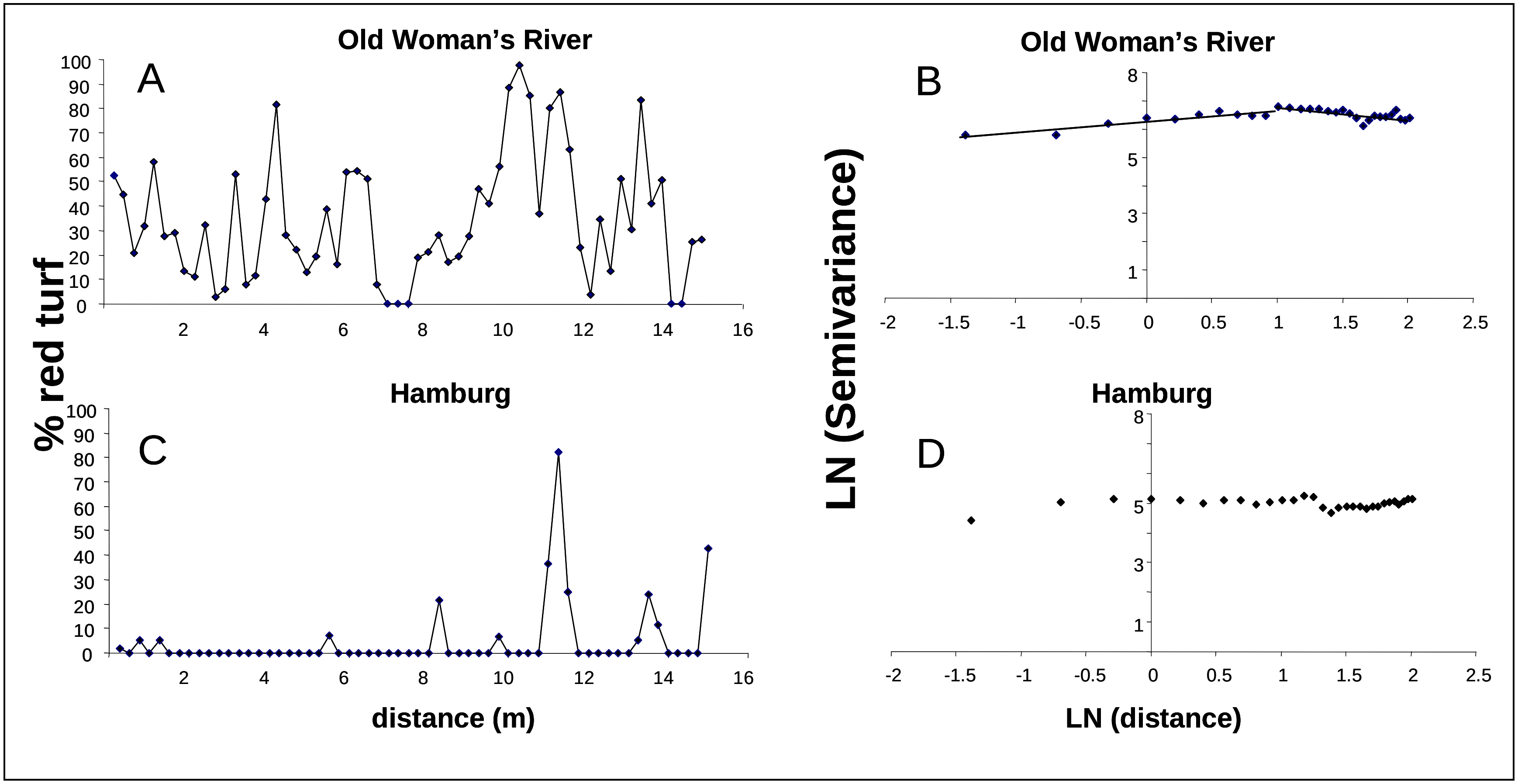

Figure 2.1. Distribution of red turfs in the low shore of the two sites studied: A. Old Woman's River and C. Hamburg. B and D. Semivariograms, where the solid lines indicate significant slopes showing scaling regions at $p < 0.01$, at Old Woman's River (B) and Hamburg (D).

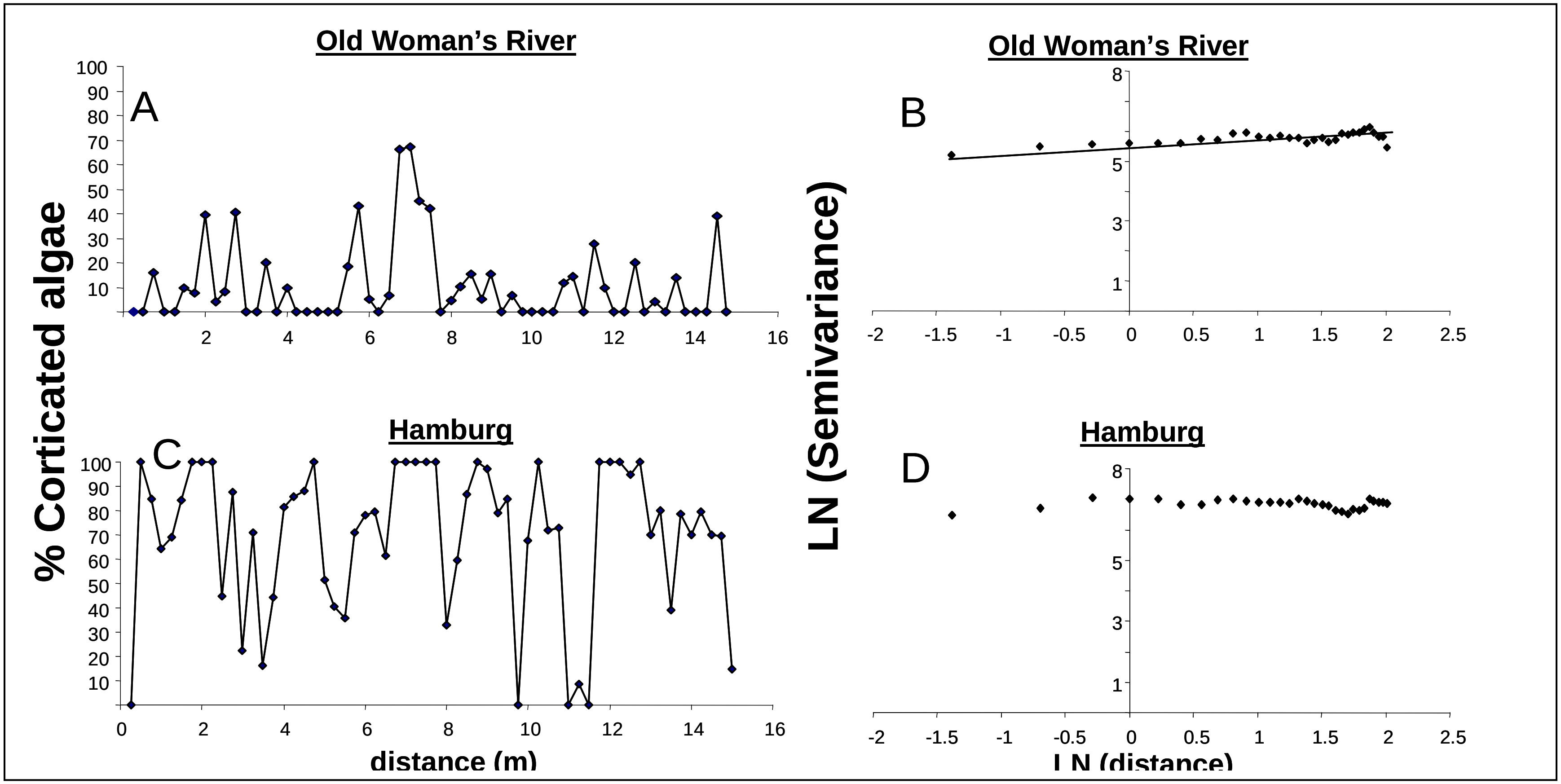

Figure 2.2. A and C. Distribution of corticated algae (mainly *Hypnea spicifera*) on the low shore of the two sites studied, Old Woman's River and Hamburg. B and D. Semivariograms, where the solid line indicates significant slopes showing scaling regions at $p < 0.01$.

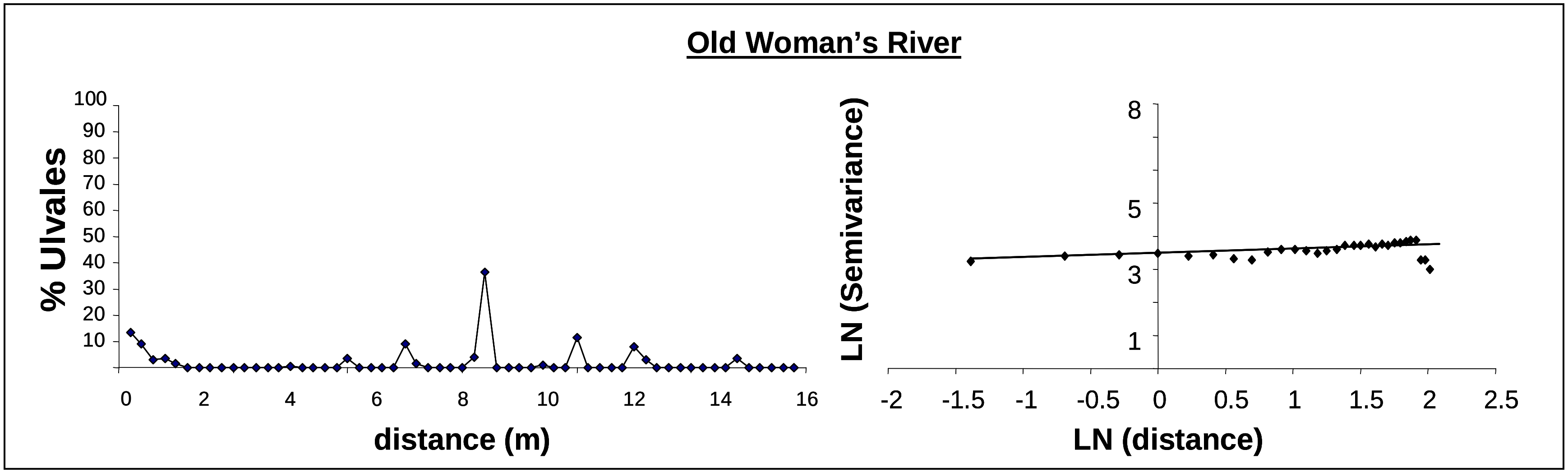

Figure 2.3. Distribution of Ulvales on the low shore of Old Woman's River. No Ulvales spp were detected in the Hamburg transect; second plate, semivariogram, where the solid line indicates significant slopes showing scaling regions at $p < 0.01$.

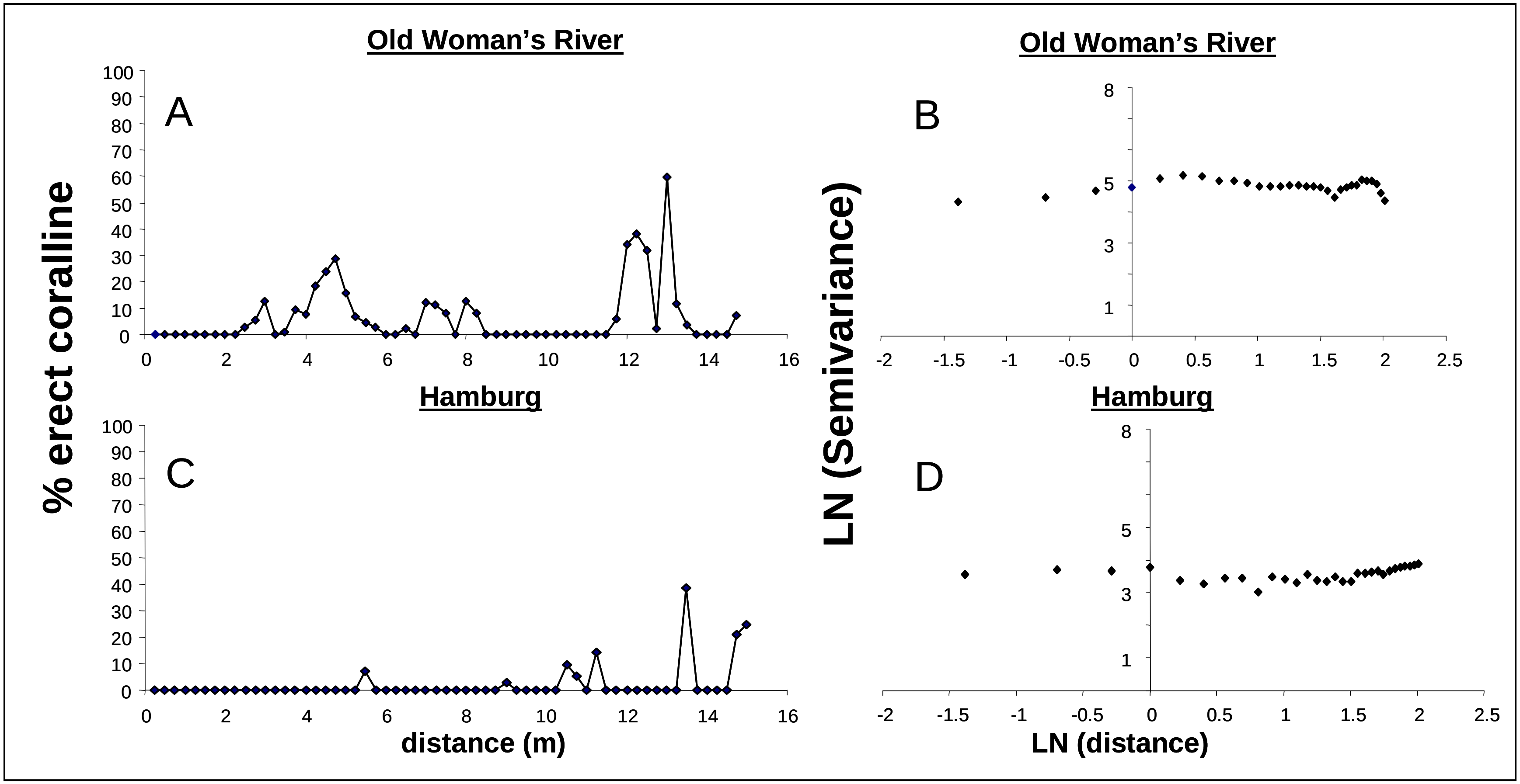

Figure 2.4. A and C. Distribution of erect coralline algae on the low shore of the two sites studied, Old Woman's River and Hamburg. B and D. Semivariograms, where there were no scaling regions.

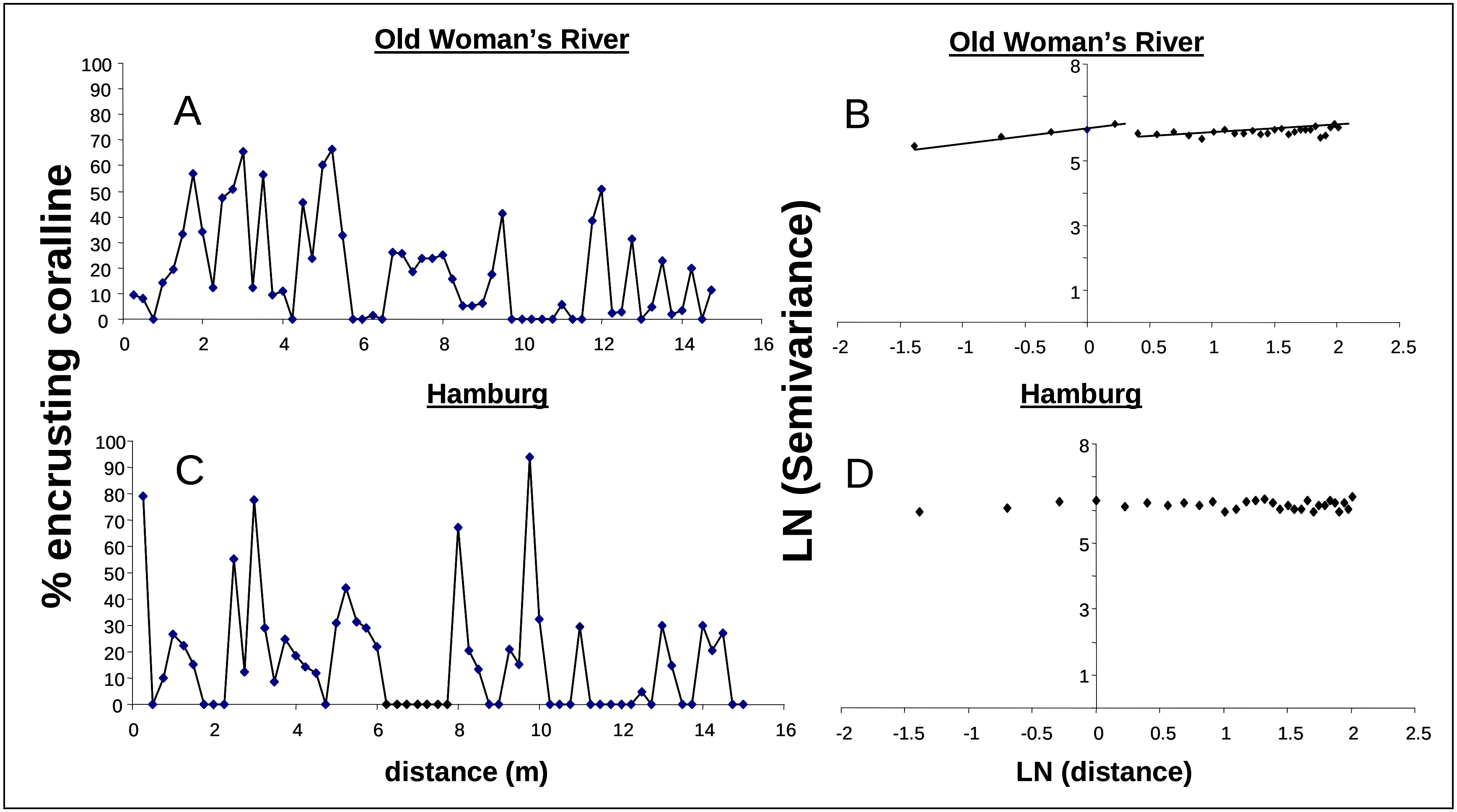

Figure 2.5. A and C. Distribution of encrusting coralline algae on the low shore of the two sites studied, Old Woman's River and Hamburg. B and D. Semivariograms, where the solid line indicates significant slopes showing scaling regions at $p < 0.01$.

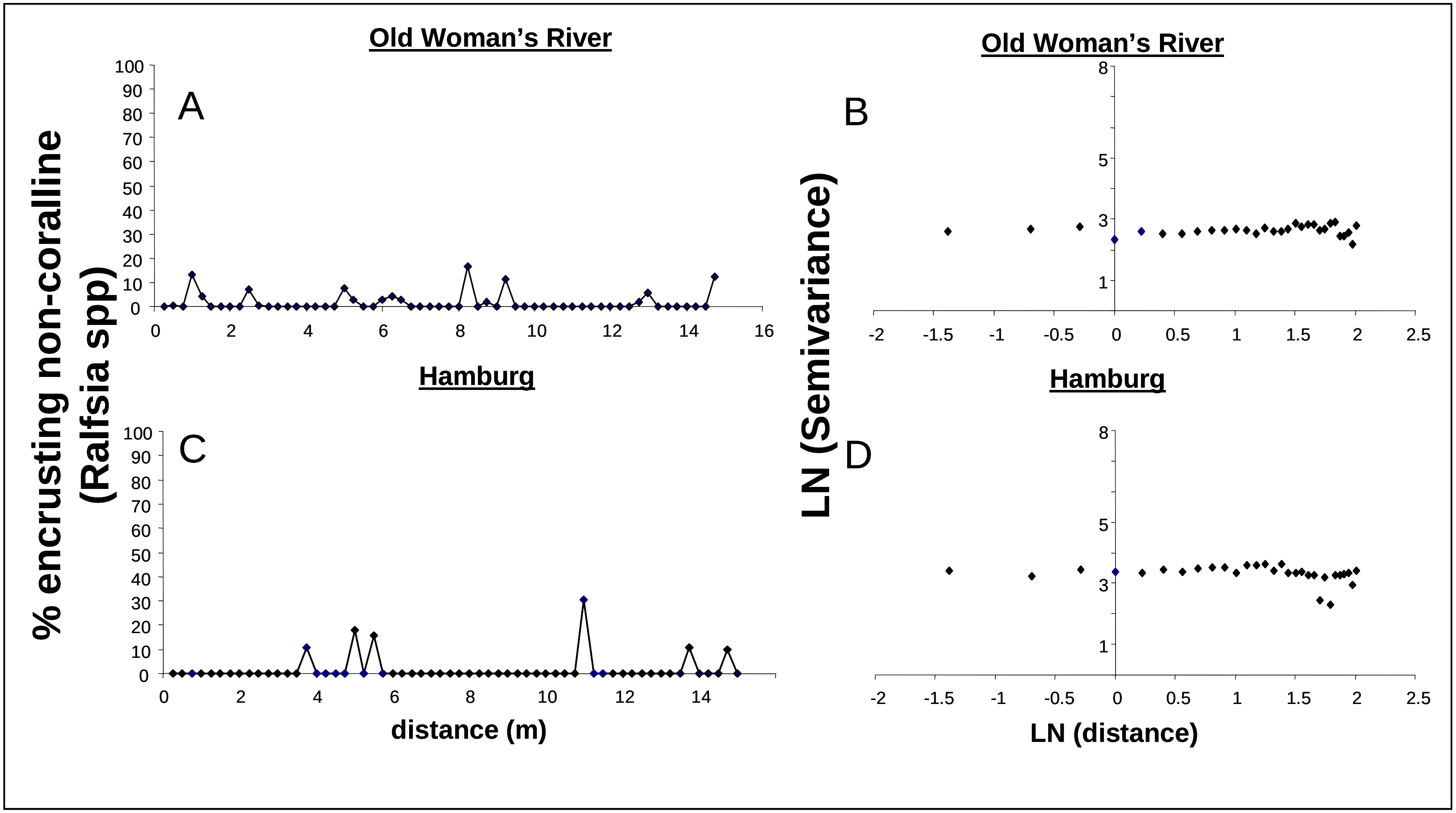

Figure 2.6. A and C. Distribution of encrusting non-coralline algae on the low shore of the two sites studied, Old Woman's River and Hamburg. B and D. Semivariograms, where there were no scaling regions.

I.3. Relationship between the spatial variability of algal groups and grazers on low shore

The cross-semivariograms showed three types of relationships: positive, negative and neutral. There was no significant relationship between red turf cover and the density of grazers at Old Woman's River, but there was a significant positive relationship at Hamburg at most scales (Table 2.3 and Fig. 2.7). In contrast, red turf and biomass of grazers exhibited a significant negative relationship at most scales from 1.00 to 7.5 meters at Old Woman's River, but a non-significant relationship at Hamburg (Table 2.3 and Fig. 2.7).

Corticated algae and density of grazers mainly showed significant relationship at Old Woman's River, while at Hamburg this relationship was negative and significant at all scales (Table 2.3 and Fig. 2.8). In terms of biomass of grazers, corticated algae showed no relationship at Old Woman's River but negative relationships (significant at 1-2 m, 3.78-4.25 m and 5.75-7 m scales) at Hamburg (Table 2.3 and Fig. 2.8).

The Ulvales algal group exhibited a significant negative relationship with both density of grazers and biomass of grazers at many small scales at Old Woman's River (Table 2.3 and Fig. 2.9). At Hamburg, the algal group of Ulvales was absent.

The erect corallines showed significant negative relationships with density at many scales from 1.5 to 7 meters and mainly no relationship with biomass of grazers at Old Woman's River (Table 2.3 and Fig. 2.10). The relationships were also mainly non-significant between grazer density or biomass and erect corallines at Hamburg (Table 2.3 and Fig. 2.10).

Encrusting coralline algae and density of grazers showed significant positive relationships with grazer density at some scales from 0.75 to 6.75 m at Old Woman's River, but no relationship with grazer biomass (Table 2.3 and Fig. 2.11). At Hamburg, again positive relationships were detected from 1 to 6.75 m (only significant at three scales) with density of grazers. For biomass of grazers, significant positive relationships were detected at ca 0.5-1m, 3.5-4 m and 6-7.5 m scales (Table 2.3 and Fig. 2.11).

Encrusting non-coralline algae showed no significant relationship with density of grazers, but a significant positive relationship was found with biomass of grazers at Old Woman's River (Table 2.3 and Fig. 2.12). At Hamburg no relationship was found between density of grazers and encrusting non-coralline algae. Here, this algal group exhibited a significant negative relationship with grazer biomass at some scales, although mainly there was no relationship (Table 2.3 and Fig. 2.12).

Table 2.3 Cross-semivariogram synthesis. General relationships between functional algal groups and grazers, in terms of either density or biomass examined using cross-semivariograms at different scales.

Variables	**Old Woman's River Low Shore General relationship**		**Hamburg Low Shore General relationship**	
	density	**biomass**	**density**	**biomass**
Red turfs vs grazers	none	negative	positive	none
Corticated vs grazers	none/negative	none	negative	negative
Ulvales vs grazers	negative	negative/none	absent	absent
Erect corallines vs grazers	negative	none/negative	none/negative	none/negative
Encrusting corallines vs grazers	positive	none	positive/none	positive
Encrusting non-coralline vs grazers	none	positive	none	none/negative

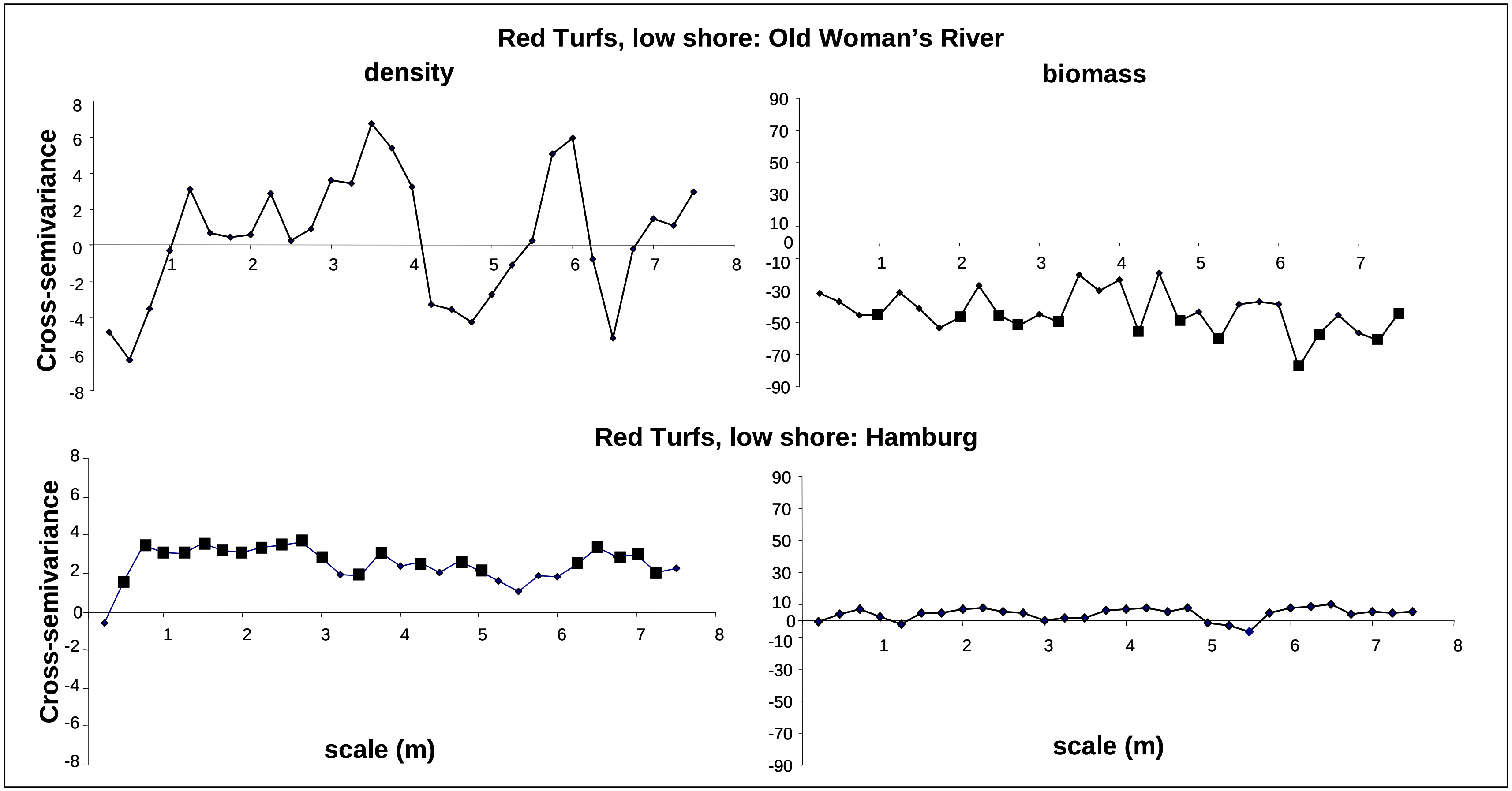

Figure 2.7. The relationship between red algal turfs and grazers in terms of grazer density and biomass, using cross-semivariograms for both sites: Old Woman's River and Hamburg. Black squares represent either positive or negative significant relationships.

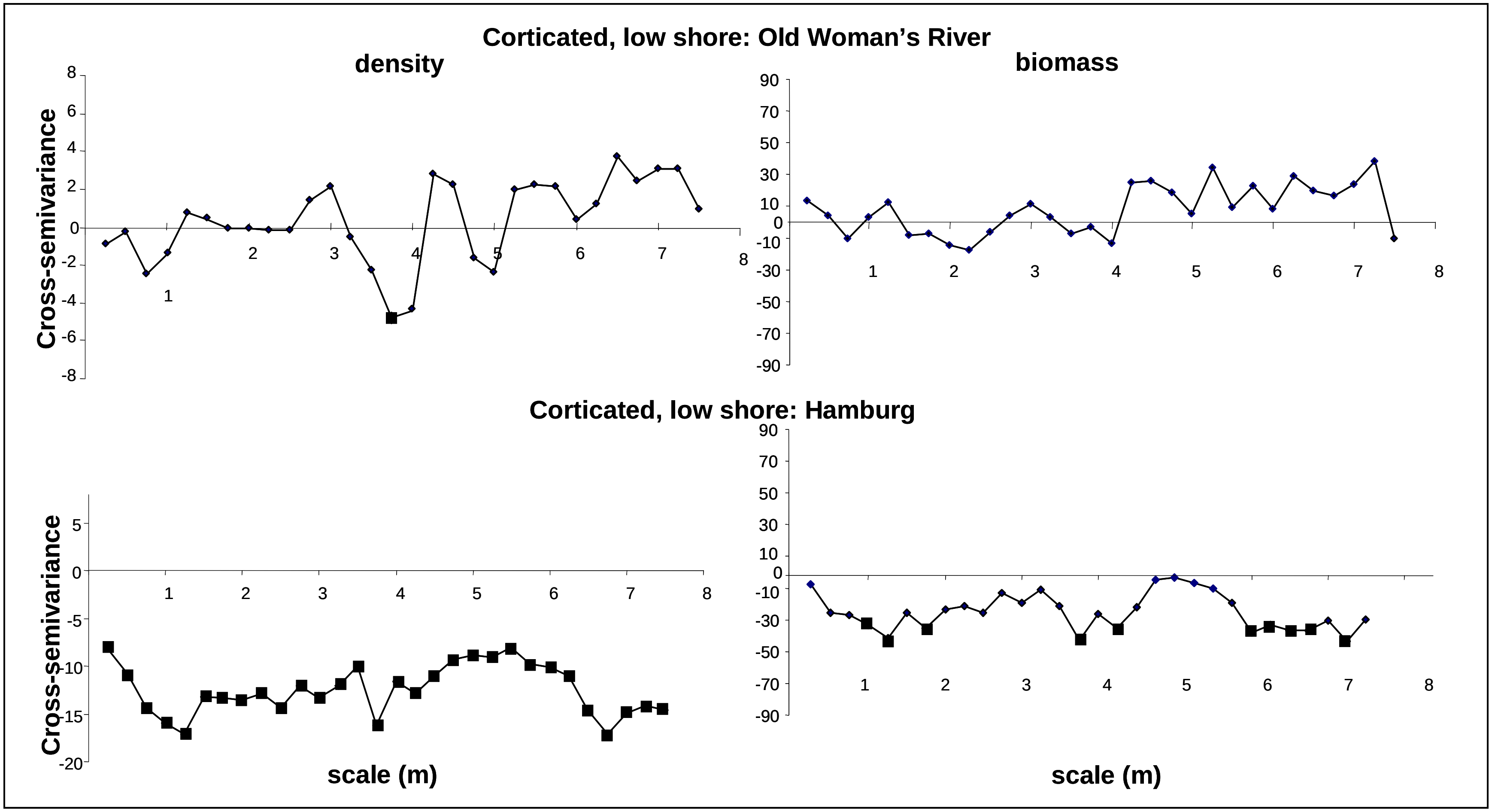

Figure 2.8. The relationship between corticated algae and grazers in terms of grazer density and biomass, using cross-semivariograms for both sites: Old Woman's River and Hamburg. Black squares represent either positive or negative significant relationships.

Figure 2.9. The relationship between Ulvales and grazers in terms of grazer density and biomass, using cross-semivariograms for Old Woman's River. Black squares represent either positive or negative significant relationships.

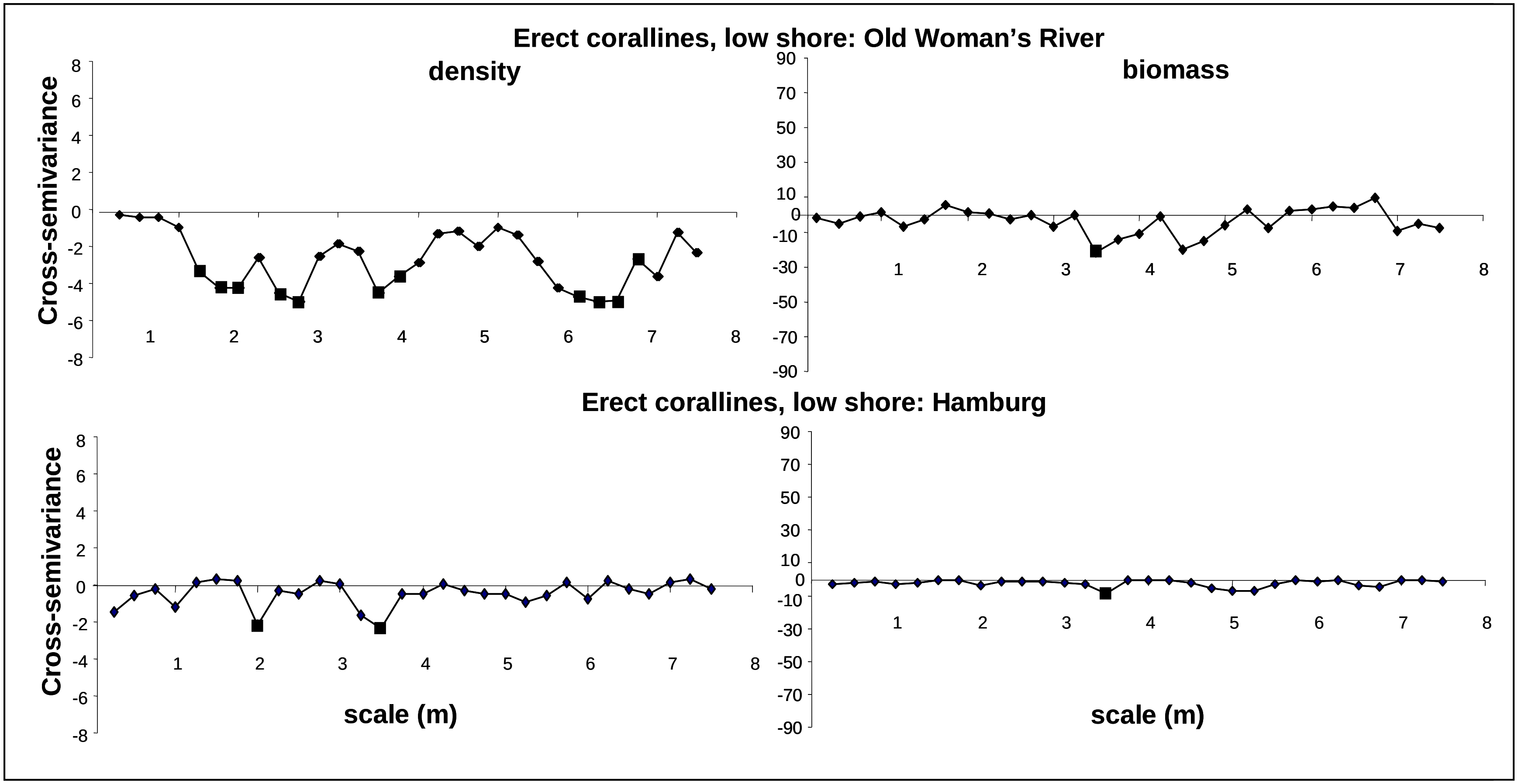

Figure 2.10. The relationship between erect corallines and grazers in terms of grazer density and biomass, using cross-semivariograms for both sites: Old Woman's River and Hamburg. Black squares represent either positive or negative significant relationships.

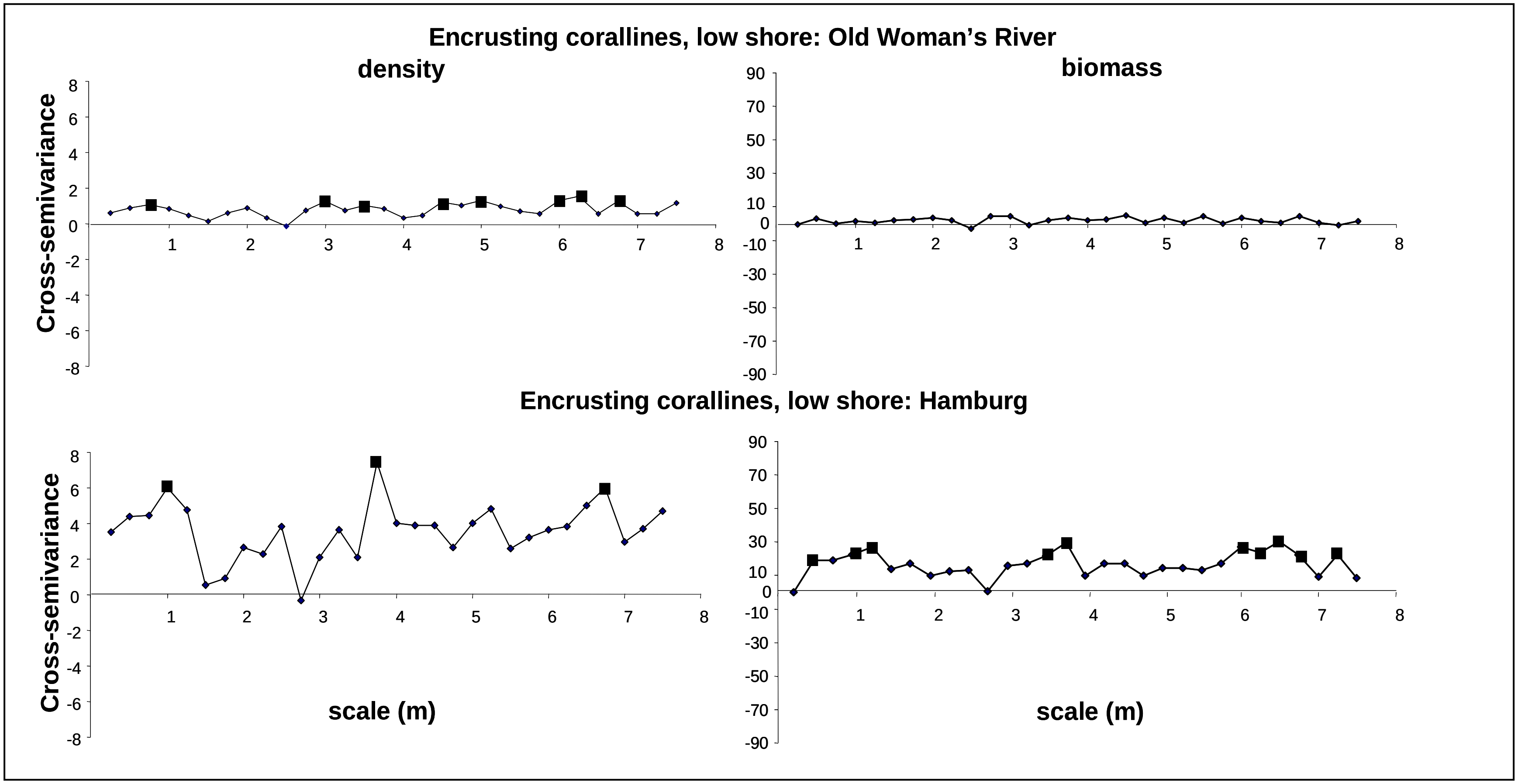

Figure 2.11. The relationship between encrusting corallines and grazers in terms of grazer density and biomass, using cross-semivariograms for both sites: Old Woman's River and Hamburg. Black squares represent either positive or negative significant relationships.

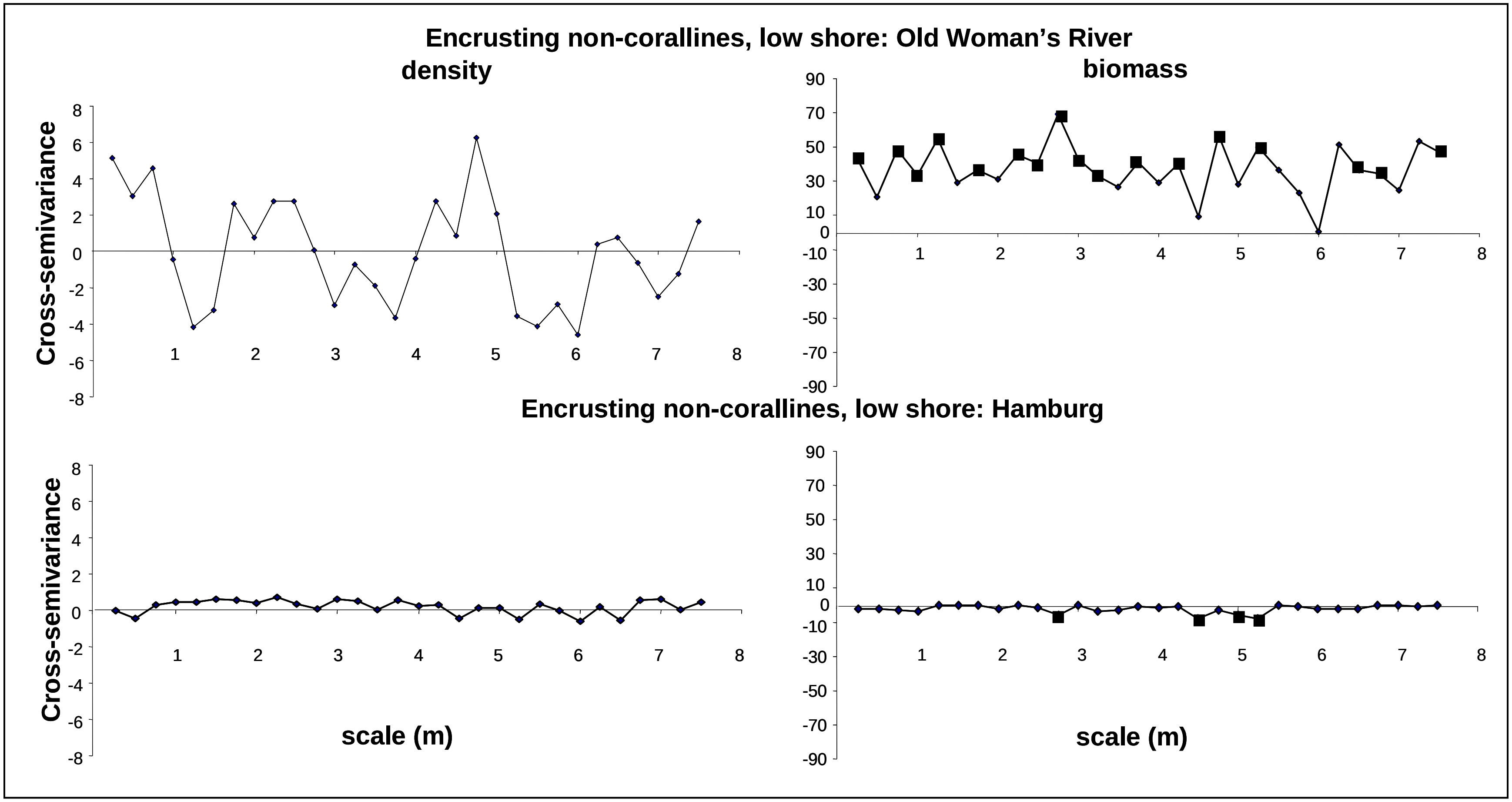

Figure 2.12. The relationship between encrusting non-corallines and grazers in terms of grazer density and biomass, using cross-semivariograms for both sites: Old Woman's River and Hamburg. Black squares represent either positive or negative significant relationships.

II. Mid Shore

II.1. Spatial structure of algae

Spatial dependence was found in one out of five algal groups at Old Woman's River, while no algal groups exhibited spatial structure at Hamburg (Table 2.4).

The only algal group exhibiting spatial structure at Old Woman's River was the corticated algae, represented by *Gelidium pristoides*. This alga exhibited two scaling regions (0.25-1.75 m and 2.00-7.5 m), both indicating patchy distributions with fractal dimensions of 1.7 and 1.88, respectively (Table 2.4 and Fig. 2.13). Figures 2.14-2.17, show the spatial distribution of the algal groups: Ulvales, encrusting non-corallines, erect corallines and encrusting corallines, respectively. The erect coralline group, was restricted to an area where there was a small shallow pool at Old Woman's River, and encrusting corallines were not observed at Hamburg.

II.2. Spatial structure of grazers

The spatial structure, (i.e. spatial dependence), of grazers was only significant in terms of biomass at Old Woman's River (Table 2.5 and Fig. 2.18, 2.19). Here it was possible to detect two scaling region between 0.25-4.25 meters and between 4.5-7.5 meters with fractal dimensions of 1.96 and 1.72, respectively. Both fractal dimensions indicate patchiness (Table 2.5 and Fig. 2.19). As with the algae, grazers at Hamburg did not exhibit spatial structure (Table 2.5 and Fig. 2.18, 2.19).

Table 2.4. Linear regression analysis of logarithmic semivariograms, and the fractal dimension (D) for different spatial scales of distribution of functional algal groups at the two sites on the Mid shore. * = P < 0.01, ** P < 0.001, *** P < 0.0001 and NS = non-significant.

Mid shore, Old Woman's River **Transect**	**Scale (m)**	**Slope**	**SE**	**R^2**	**t (df)**	**D**	**Spatial pattern**
Corticated	0.25-7.5	0.16	0.03	0.5	5.35(28)***	1.91	dependent
Ulvales	0.25-7-5	0.05	0.04	0.05	1.27(28)NS	1.97	independent/random
Encrusting non-coralline	0.25-7.5	0.05	0.03	0.06	1.37(28)NS	1.98	independent/random
Erect coralline	0.25-7.5	0.09	0.17	0.13	2.04(28)NS	1.95	independent/random
Encrusting coralline	0.25-7.5	-0.06	0.03	0.13	-2.1(28)NS	1.97	independent/random
Significant multiple scaling regions							
Corticated	0.25-1.75	0.45	0.04	0.96	10.9(5)***	1.77	Patchy
	2.00-7.5	0.22	0.06	0.40	3.7(21)*	1.88	Patchy

Mid shore, Hamburg **Transect**	**Scale (m)**	**Slope**	**SE**	**R^2**	**t (df)**	**D**	**Spatial pattern**
Corticated (*G. pristoides*)	0.25-7.5	0.05	0.18	0.07	1.48(28)NS	1.97	independent/random
Ulvales	0.25-7.5	0.06	0.03	0.09	1.71(28)NS	1.97	independent/random
Encrusting non-coralline	0.25-7.5	0.09	0.03	0.04	1.1(28)NS	1.98	independent/random
Erect corallines	0.25-7.5	0.02	0.06	0.003	0.27(28)NS	1.99	independent/random

Table 2.5. Linear regression analysis of logarithmic semivariograms, and the fractal dimension (D) for different spatial scales of distribution of density and biomass of grazers in the two sites on the Mid shore. * = P < 0.01, ** P < 0.001, *** P < 0.0001 and NS = non-significant.

Grazers, Old Womans River	**Scale (m)**	**Slope**	**SE**	***R*²**	**t (df)**	**D**	**Spatial pattern**
Density	0.25-7.5	0.02	0.03	0.02	0.67(28)NS	1.98	independent/random
Biomass	0.25-7.5	0.11	0.04	0.23	2.89(28)**	1.94	dependent
Significant multiple scaling regions							
Biomass	0.25-4.25	0.48	0.05	0.82	8.8(15)***	1.96	Patchy
	4.5-7.5	0.56	0.09	0.76	6.34(11)**	1.72	Patchy

Grazers, Hamburg	**Scale (m)**	**Slope**	**SE**	***R*²**	**t (df)**	**D**	**Spatial pattern**
Density	0.25-7.5	-0.005	0.03	0.00	-0.16(28)NS	1.99	independent/random
Biomass	0.25-7.5	0.02	0.03	0.01	0.6(28)NS	1.99	independent/random

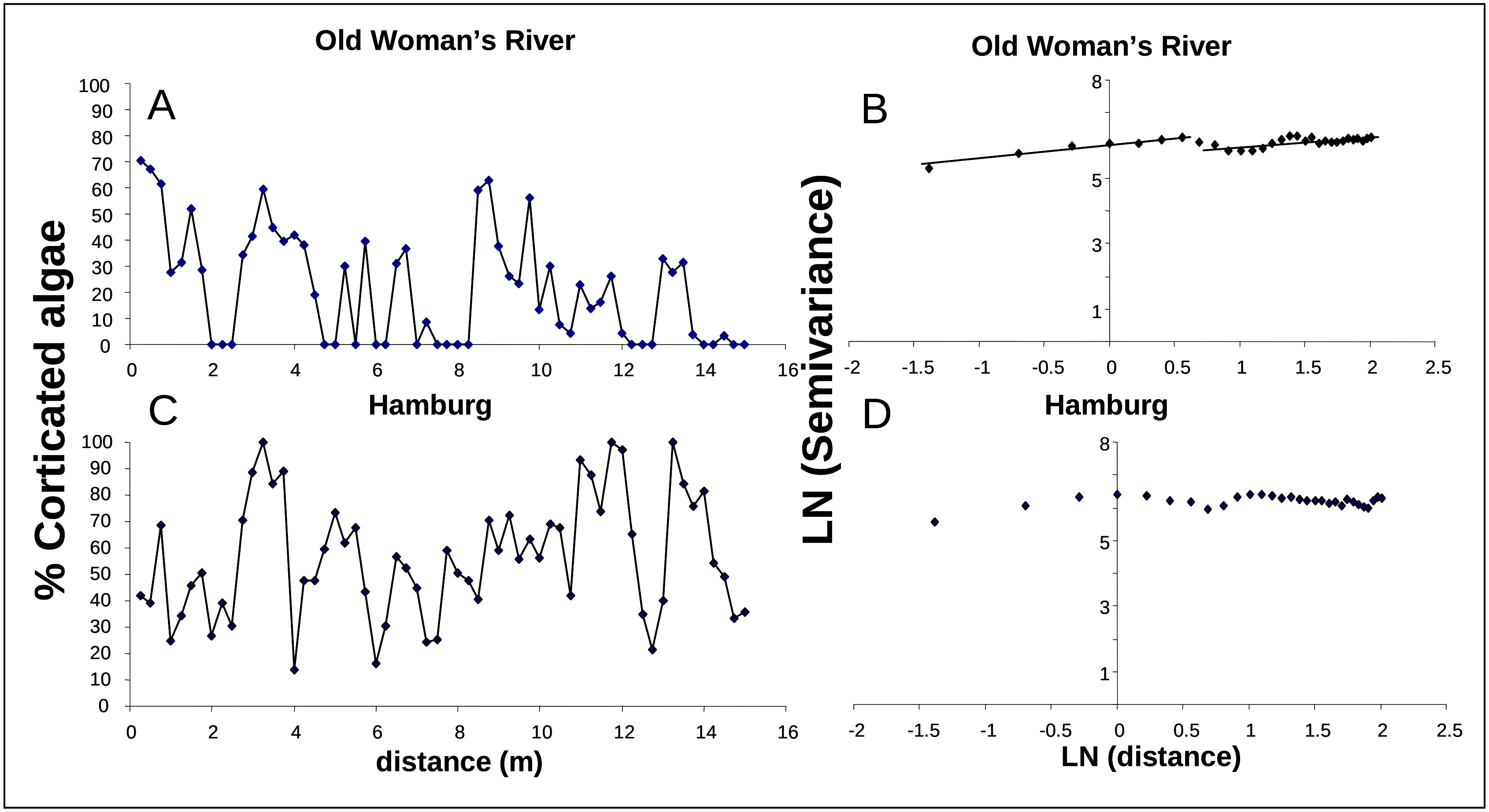

Figure 2.13. A and C. Distribution of corticated algae on the mid shore of the two sites studied, Old Woman's River and Hamburg. B and D. Semivariograms, where the solid line indicates significant slopes showing scaling regions at $p < 0.01$.

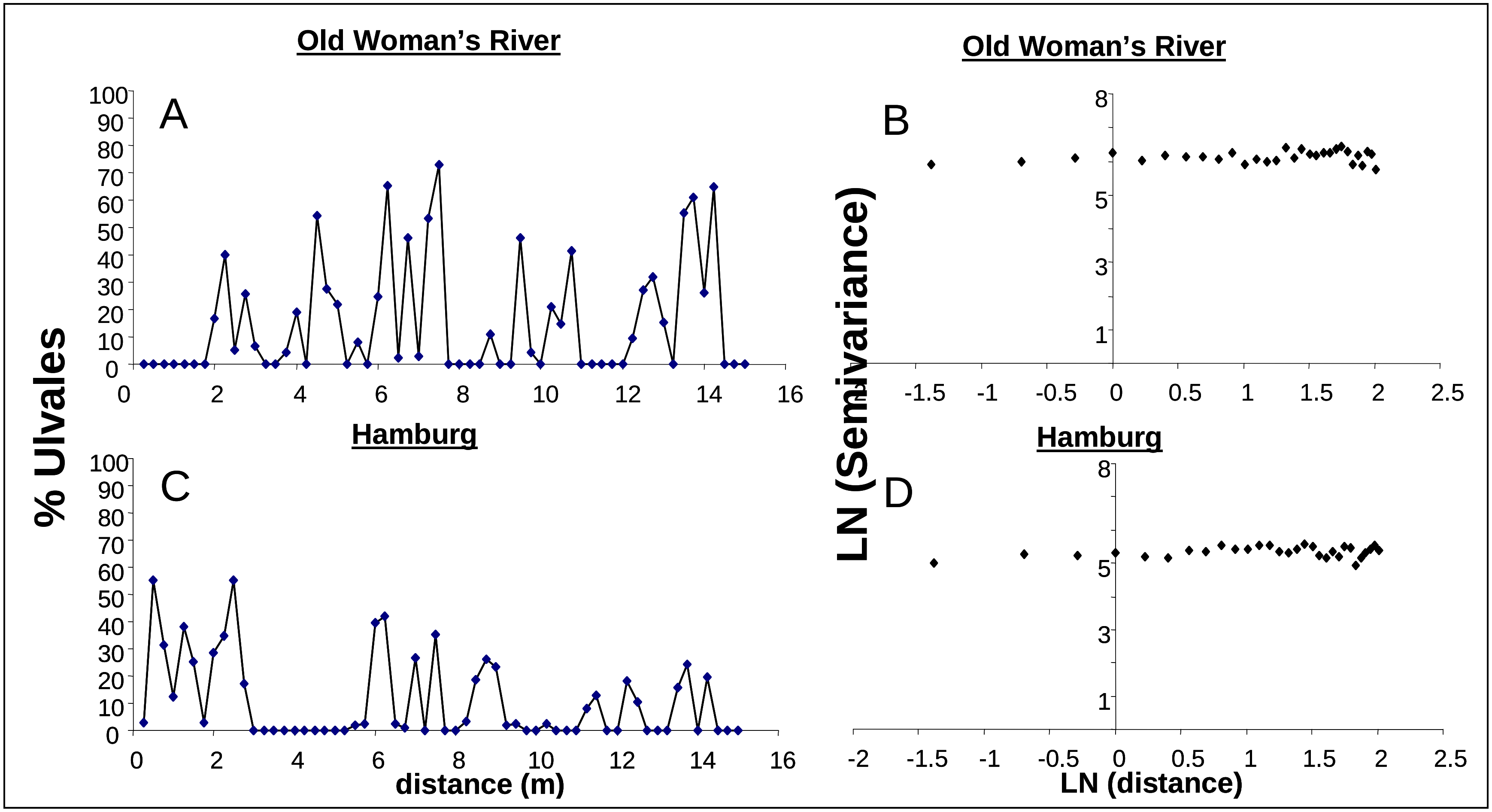

Figure 2.14. A and C. Distribution of Ulvales in the mid shore of the two sites studied, Old Woman's River and Hamburg. B and D. Semivariograms, where there were no scaling regions.

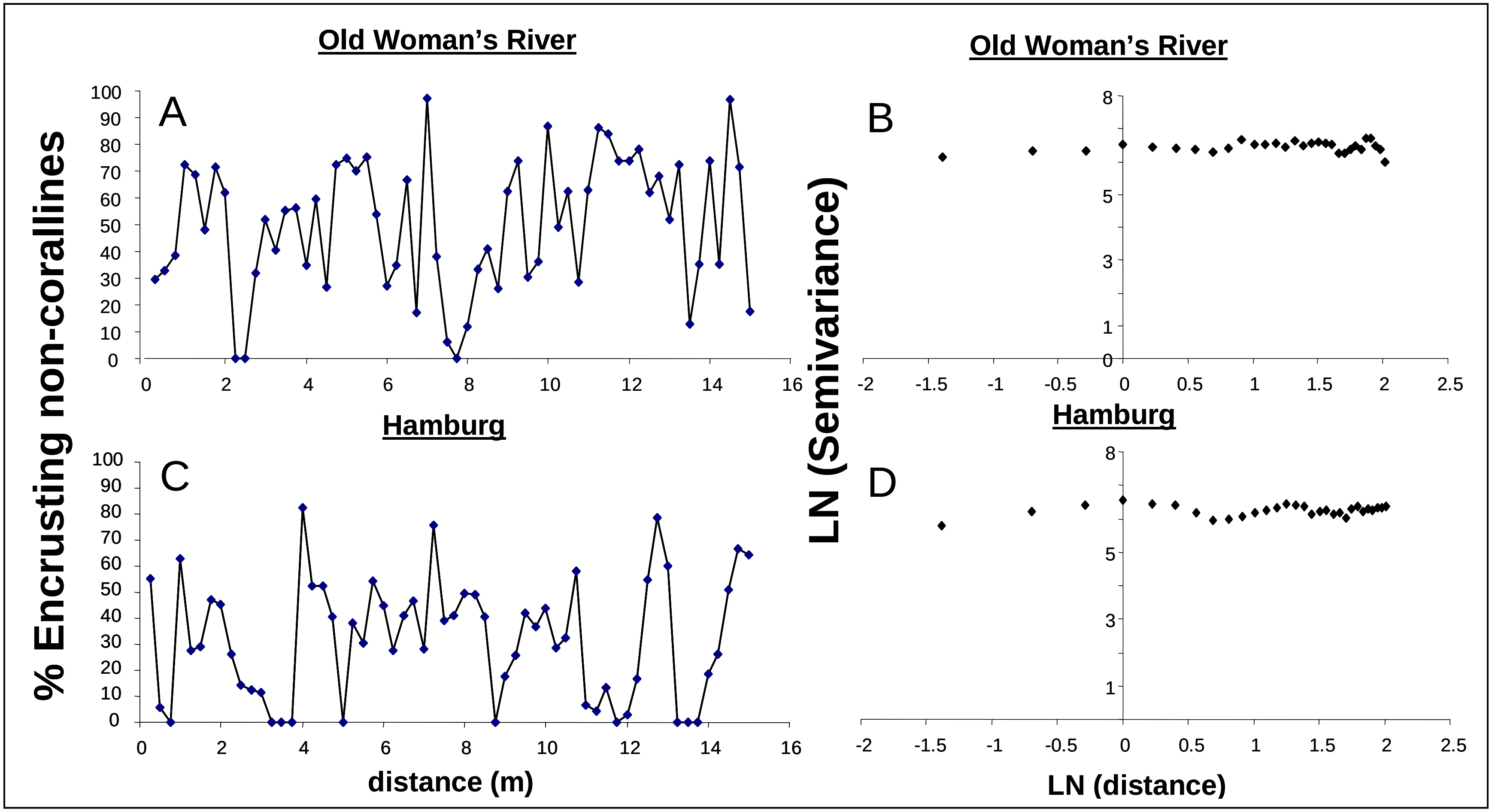

Figure 2.15. A and C. Distribution of encrusting non-coralline algae on the mid shore of the two sites studied, Old Woman's River and Hamburg. B and D. Semivariograms, where there were no scaling regions at $p < 0.01$.

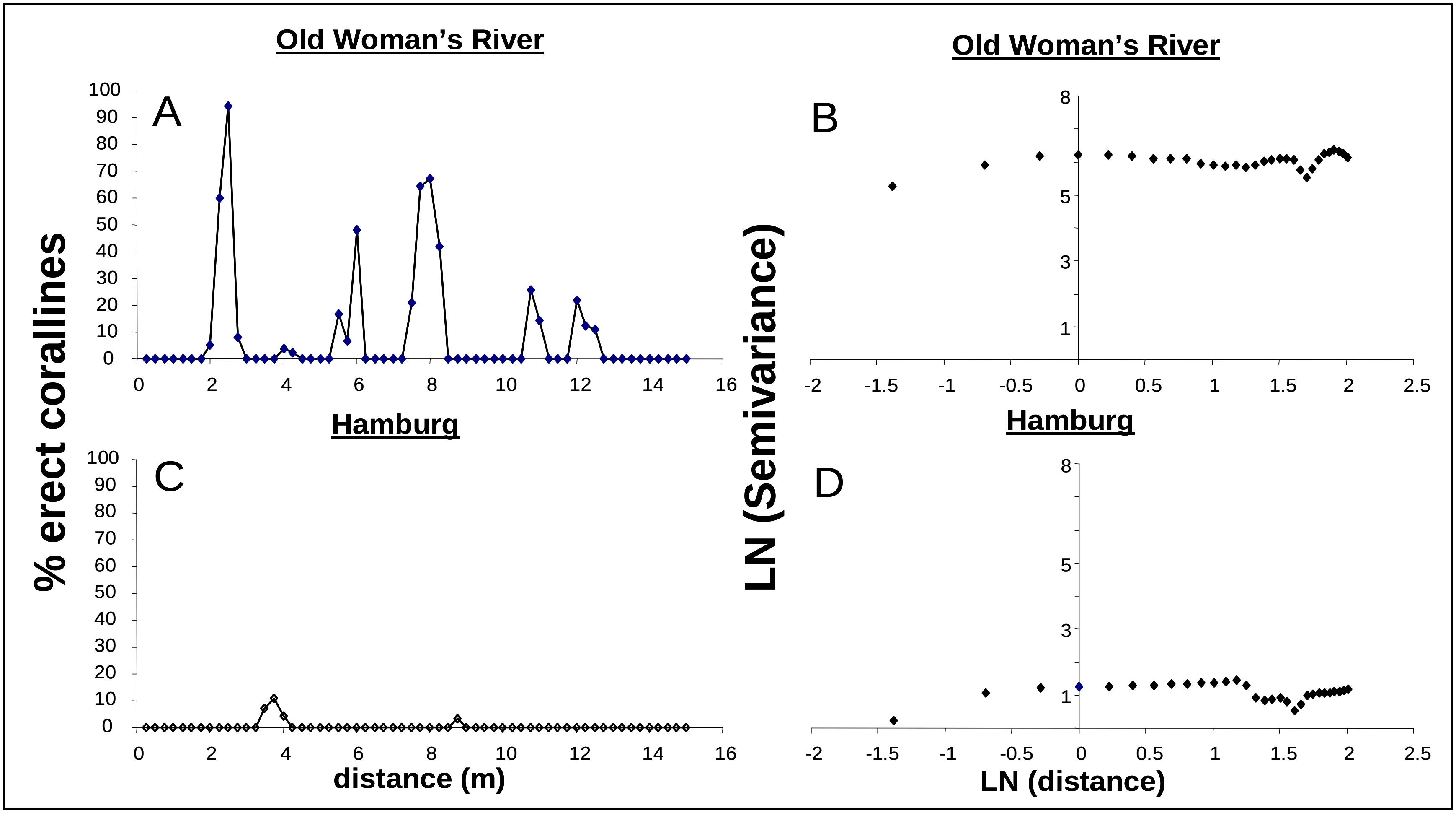

Figure 2.16. A and C. Distribution of erect coralline algae on the mid shore of the two sites studied, Old Woman's River and Hamburg. B and D. Semivariograms, where there were no scaling regions at $p < 0.01$.

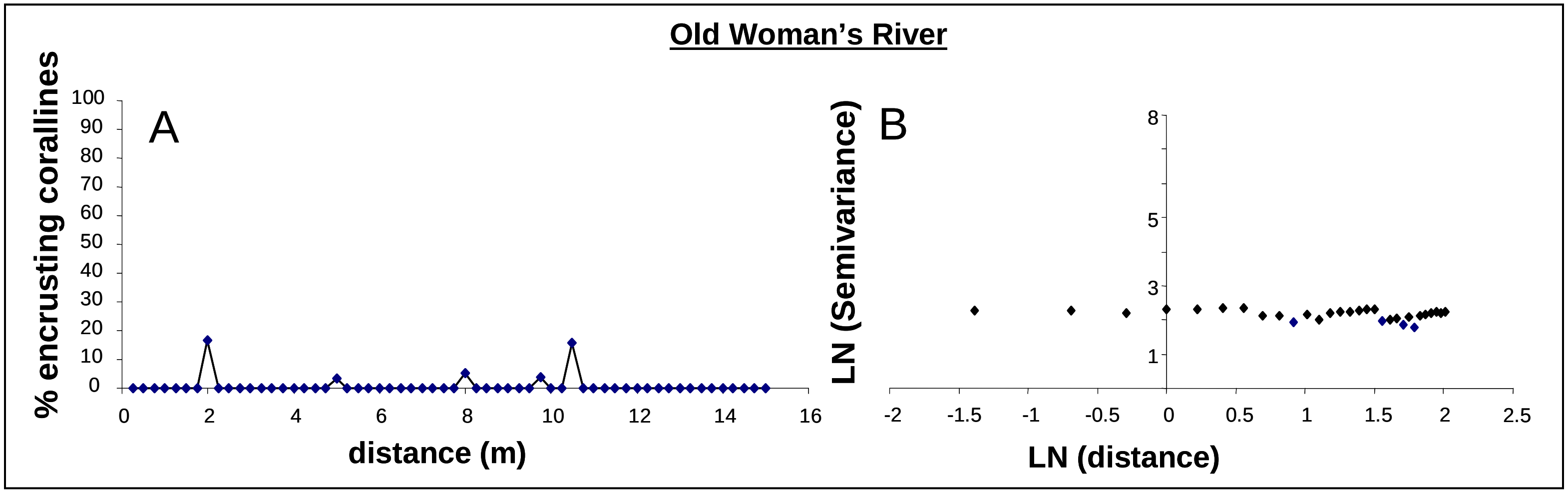

Figure 2.17. A. Distribution of encrusting coralline algae on the mid shore of the Old Woman's River. B. Semivariogram, where there were no scaling regions at $p < 0.01$.

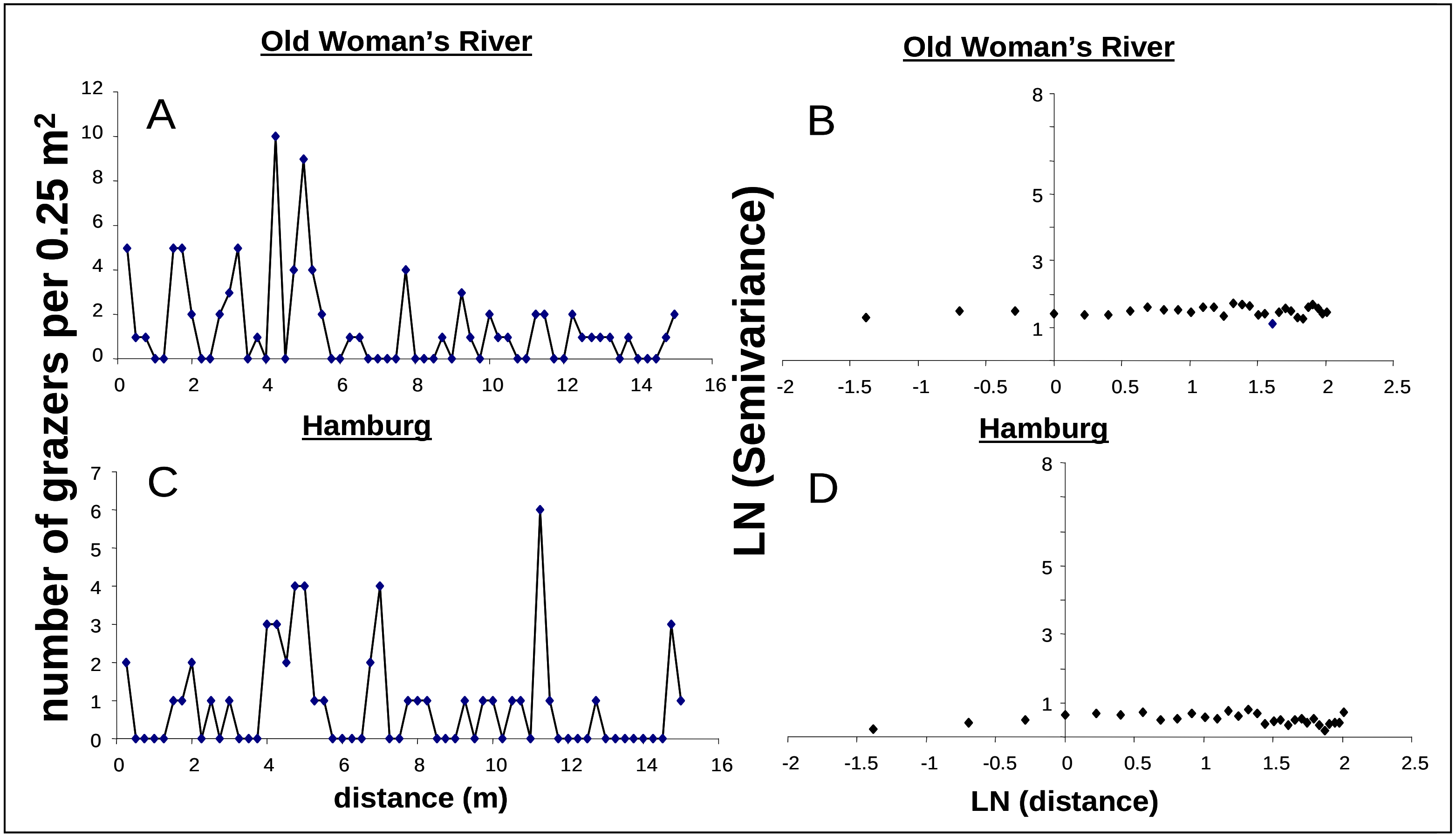

Figure 2.18. A and C. Distribution of density of grazers on the mid shore of the two sites studied, Old Woman's River and Hamburg. B and D. Semivariograms, where there were no scaling regions at $p < 0.01$.

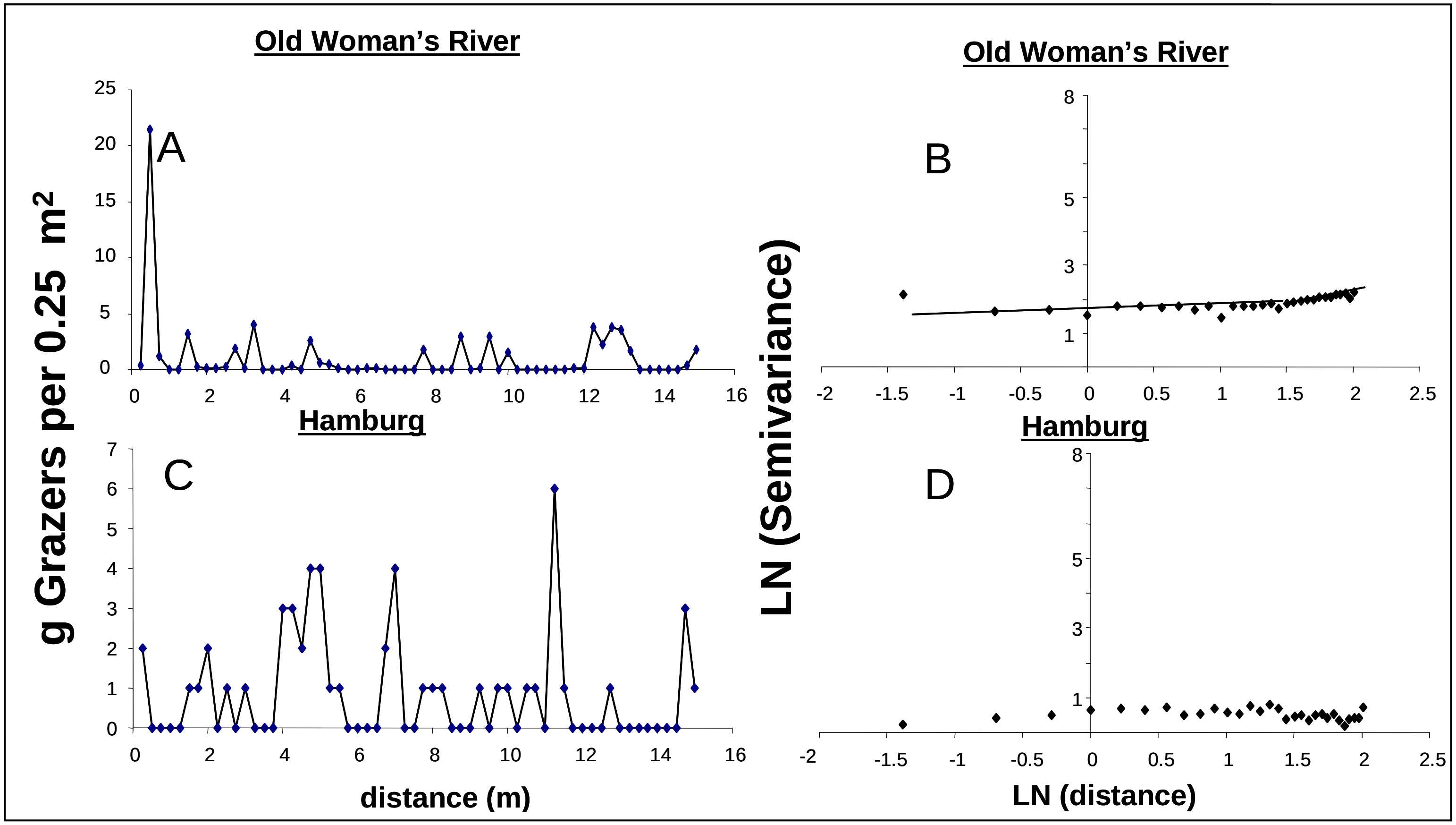

Figure 2.19. A and C. Distribution of biomass of grazers on the mid shore of the two sites studied, Old Woman's River and Hamburg. B and D. Semivariograms, where solid line indicates significant slopes at $P < 0.01$.

II.3. Relationship between the spatial variability of algal groups and grazers on the midshore

The corticated alga *Gelidium pristoides* exhibited no significant relationship with density of grazers, but a significant positive relationship with grazer biomass at many scales (especially larger ones) at Old Woman's River (Table 2.6 and Fig. 2.20). At Hamburg, significant negative relationships were detected at scales between 6.25 and 7 m with both density and biomass, with no significant relationship at other scales (Table 2.6 and Fig. 2.20).

The functional group of Ulvales was negatively related to density of grazers (significant at some scales) but mainly showed no relationship with grazer biomass, at either Old Woman's River or Hamburg (Table 2.6 and Fig. 2.21).

The encrusting non-coralline group was represented mainly by *Hildenbrandia rubra* and occasionally by *Ralfsia expansa*. There was a significant positive relationship with the density of grazers at scales between 1 and 5 m, but no relationships with the biomass of grazers at Old Woman's River (Table 2.6 and Fig. 2.22). At Hamburg, a significant positive relationship with density of grazers was found at 6.25 to 7 m and with biomass of grazers at most scales (Table 2.6 and Fig. 2.22).

The erect coralline algae showed a significant negative relationship with density of grazers between 0.75 and 3 m scale and with biomass of grazers at a few scales at Old Woman's River (Table 2.6 and Fig. 2.23). At Hamburg, there were mainly no relationships between erect coralline algae and density or biomass of grazers, with significant negative relationships at a few scales (Table 2.6 and Fig. 2.23).

With two minor exceptions, the encrusting corallines showed no relationships with the density or biomass of grazers at Old Woman's River (Table 2.6 and Fig. 2.24).

Table 2.6. Cross-semivariogram synthesis. General relationships between functional algal groups and grazers, either in terms of density or biomass, using cross-semivariograms at different scales on the mid shore.

Variables	**Old Woman's River Mid Shore General relationship**		**Hamburg Mid Shore General relationship**	
	Grazer density	**biomass**	**density**	**biomass**
Corticated vs grazers	none	positive	none/negative	none/negative
Ulvales vs grazers	negative	none/negative	negative	negative/none
Encrusting non-coralline vs grazers	positive	none	positive/none	positive
Erect coralline vs grazers	negative	negative/none	none/negative	none/negative
Encrusting coralline vs grazers	none	none/negative	absent	absent

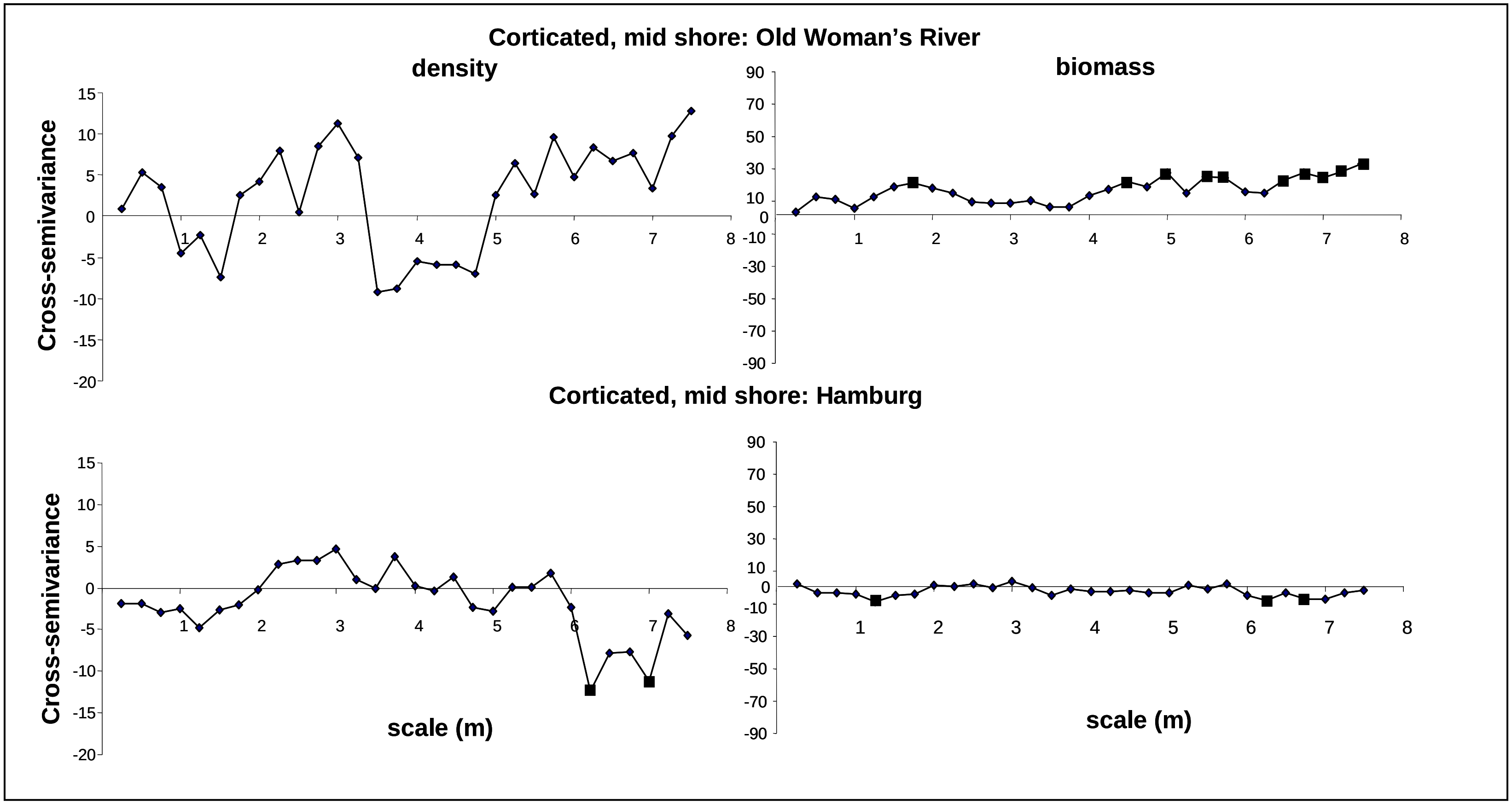

Figure 2.20. The relationship between encrusting corticated algae and grazers in terms of grazer density and biomass, using cross-semivariograms for both sites: Old Woman's River and Hamburg. Black squares represent either positive or negative significant relationships.

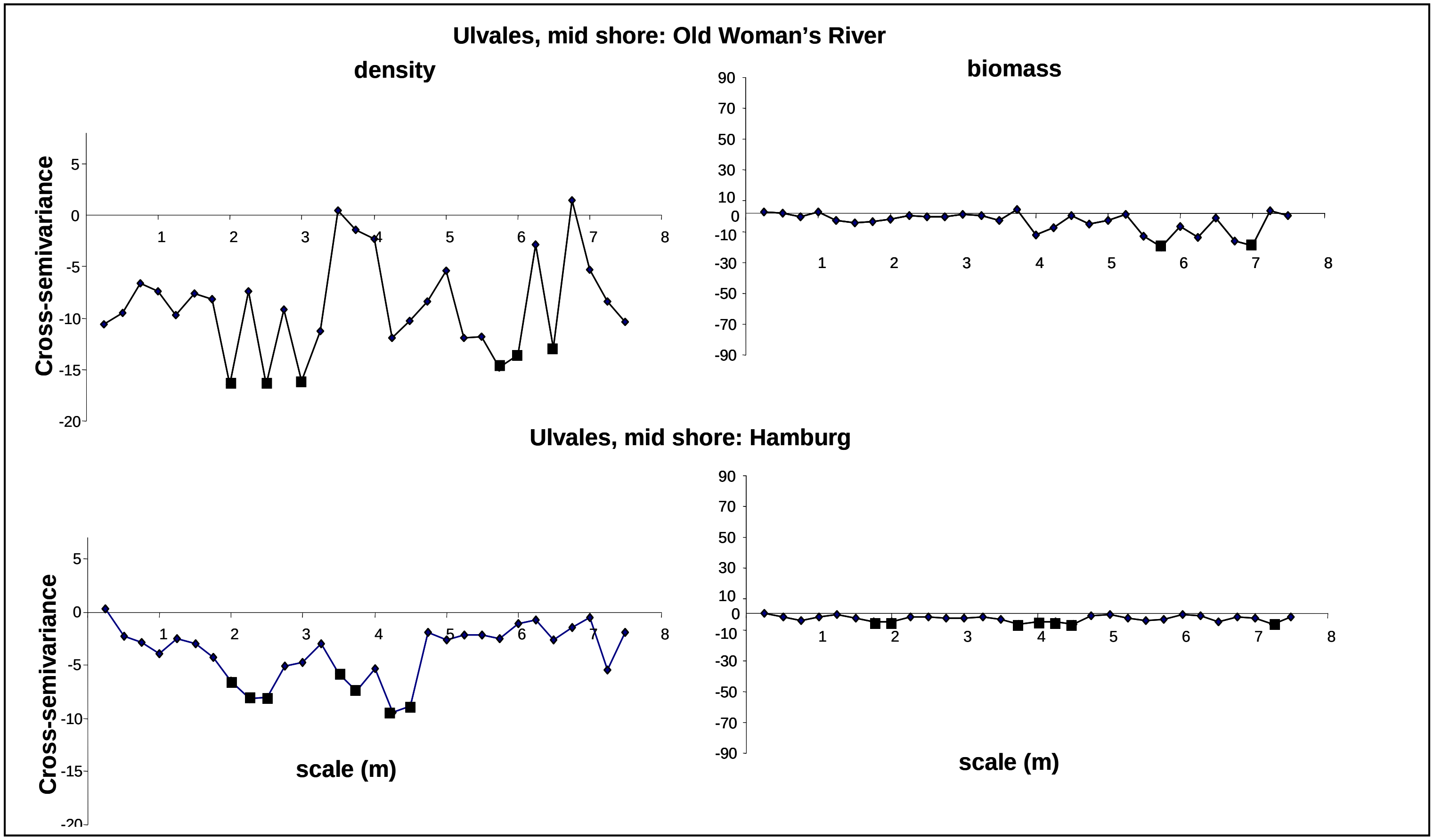

Figure 2.21. The relationship between Ulvales algal group and grazers in terms of density and biomass, using cross-semivariograms for both sites: Old Woman's River and Hamburg. Black squares represent either positive or negative significant relationships.

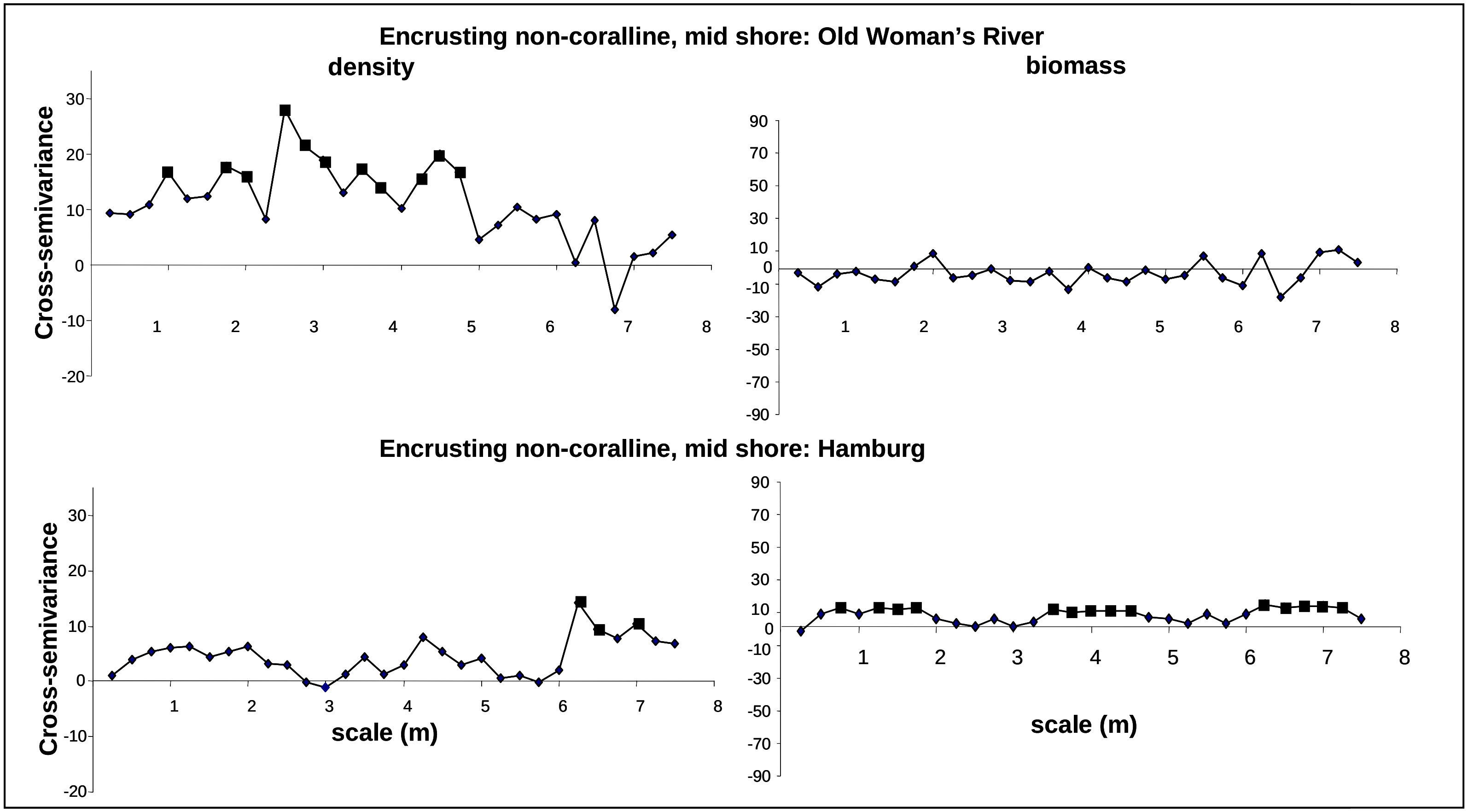

Figure 2.22. The relationship between encrusting non-corallines and grazers in terms of density and biomass, using cross-semivariograms for both sites: Old Woman's River and Hamburg. Black squares represent either positive or negative significant relationships.

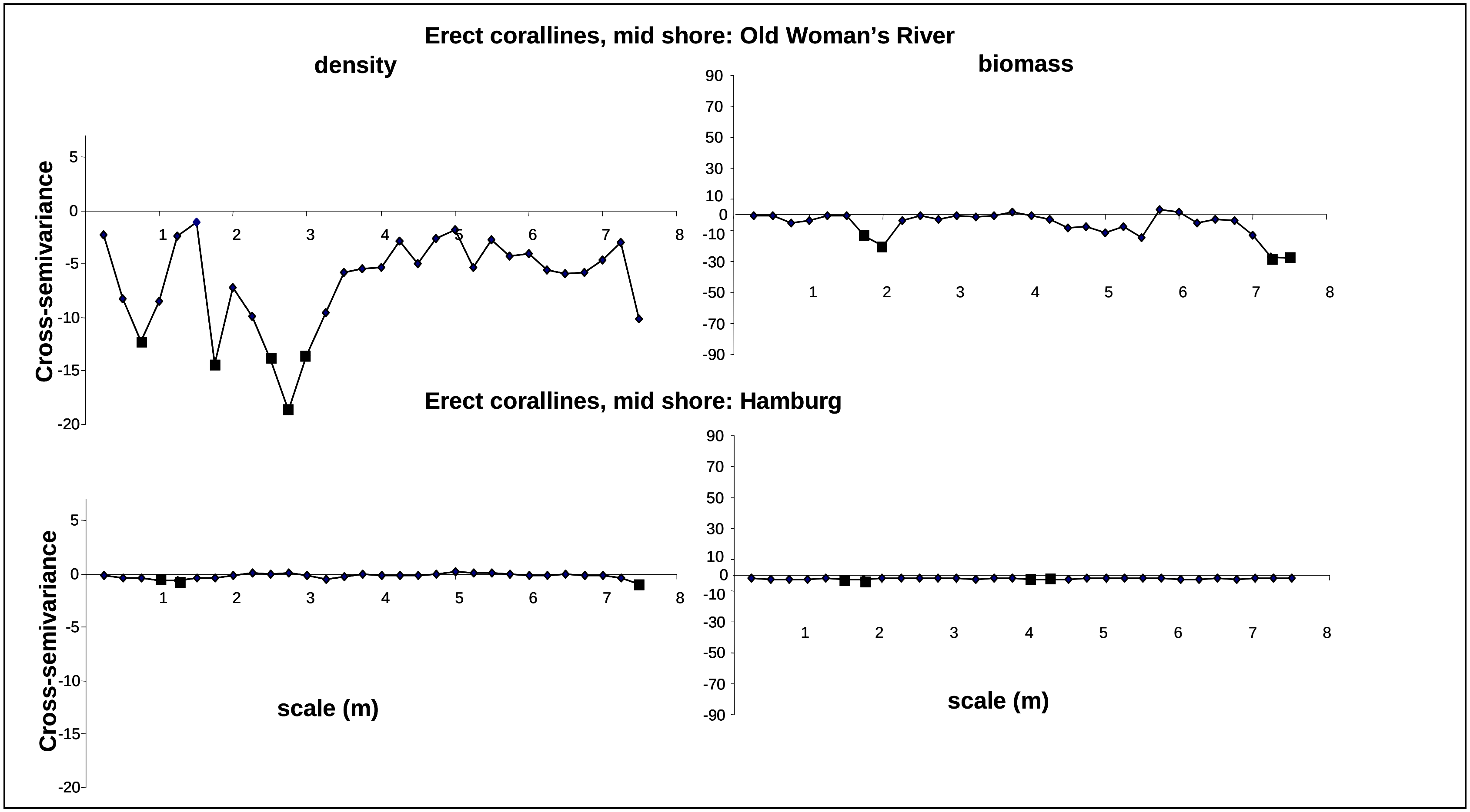

Figure 2.23. The relationship between erect corallines and grazers in terms of density and biomass, using cross-semivariograms for both sites: Old Woman's River and Hamburg. Black squares represent either positive or negative significant relationships.

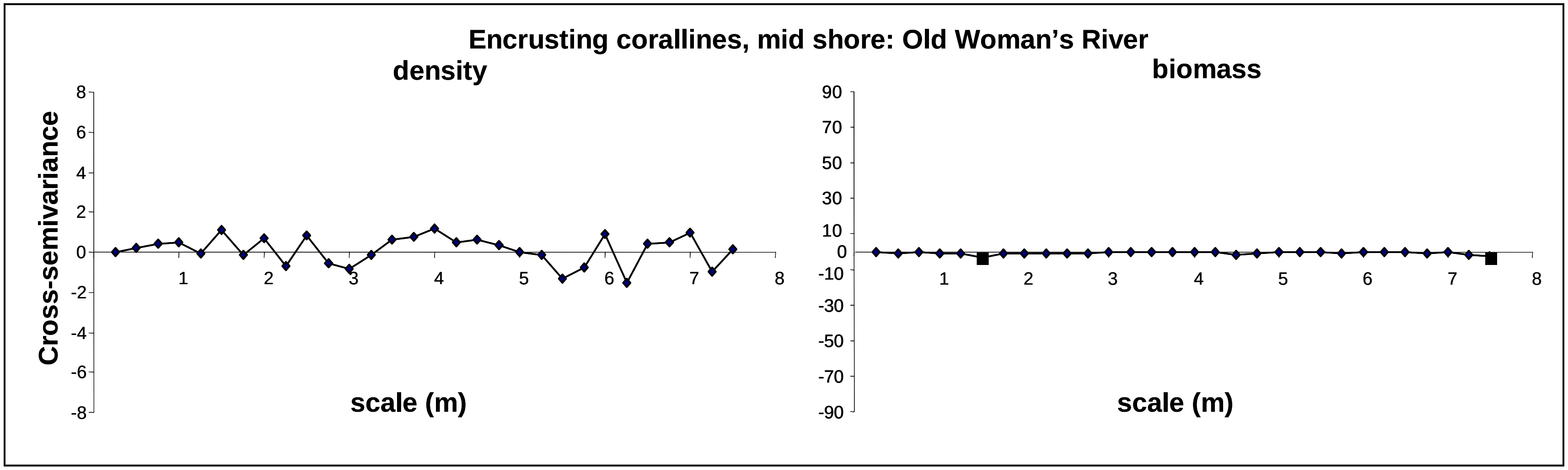

Figure 2.24. The relationship between encrusting corallines and grazers in terms of density and biomass, using cross-semivariograms at Old Woman’s River. Black squares represent either positive or negative significant relationships.

III. High shore

Macroalgae were completely absent in both transects at each site, so the analysis was restricted to the spatial structure of grazers.

Despite the fact that both transects were sampled in the higher part of the intertidal zone, the sites differed in species composition. At Hamburg the assemblage comprised only littorinids (*Nodilittorina africana* and *N. knysnaensis*), but at Old Woman's River there were both mesograzers *Siphonaria capensis*, *S. concinna*, *S. serrata*, *Helcion pectunculus* and littorinids.

III.1. Spatial structure of grazers

The only case of spatial structure was for littorinid density at Old Woman's. They showed one patchy scaling region along the whole transect 0.25-7.5 m (Table 2.7, Figs. 2.25 and 2.26).

Spatial structure of mesograzers did not exhibit spatial dependence (Table 2.7 and Fig. 2.27), nor did littorinids at Hamburg (Table 2.7 and Fig. 2.28).

Table 2.7. Linear regression analysis of logarithmic semivariograms, and the fractal dimension (D) for different spatial scales of distribution of grazers using different levels of resolution: total grazer, mesograzers and littorinids on the high shore of the two sites. * = P < 0.025, ** P < 0.001, *** P < 0.0001 and NS = non-significant.

A. High shore Old Woman's River

1.Littorinids

Transect	**Scale (m)**	**Slope**	**SE**	**R^2**	**t (df=28)**	**D**	**Spatial pattern**
Density	0.25-7.5	0.27	0.04	0.6	6.5***	1.86	dependent
Biomass	0.25-7.5	0.3	0.04	0.62	6.8***	1.87	dependent

2. Mesograzers

Transect	**Scale (m)**	**Slope**	**SE**	**R^2**	**t (28)**	**D**	**Spatial pattern**
Density	0.25-7.5	0.1	0.05	0.13	2.09(28)NS	1.94	independent/random
Biomass	0.25-7.5	0.09	0.05	0.1	1.77(28)NS	1.95	independent/random

B. High shore Hamburg

1.Littorinids

Transect	**Scale (m)**	**Slope**	**SE**	**R^2**	**t (28)**	**D**	**Spatial pattern**
Density	0.25-7.5	0.00	0.02	0.0	0.09(28)NS	1.99	independent/random
Biomass	0.25-7.5	0.00	0.03	0.0	0.19(28)NS	1.99	independent/random

Mesograzers were not observed along this transect.

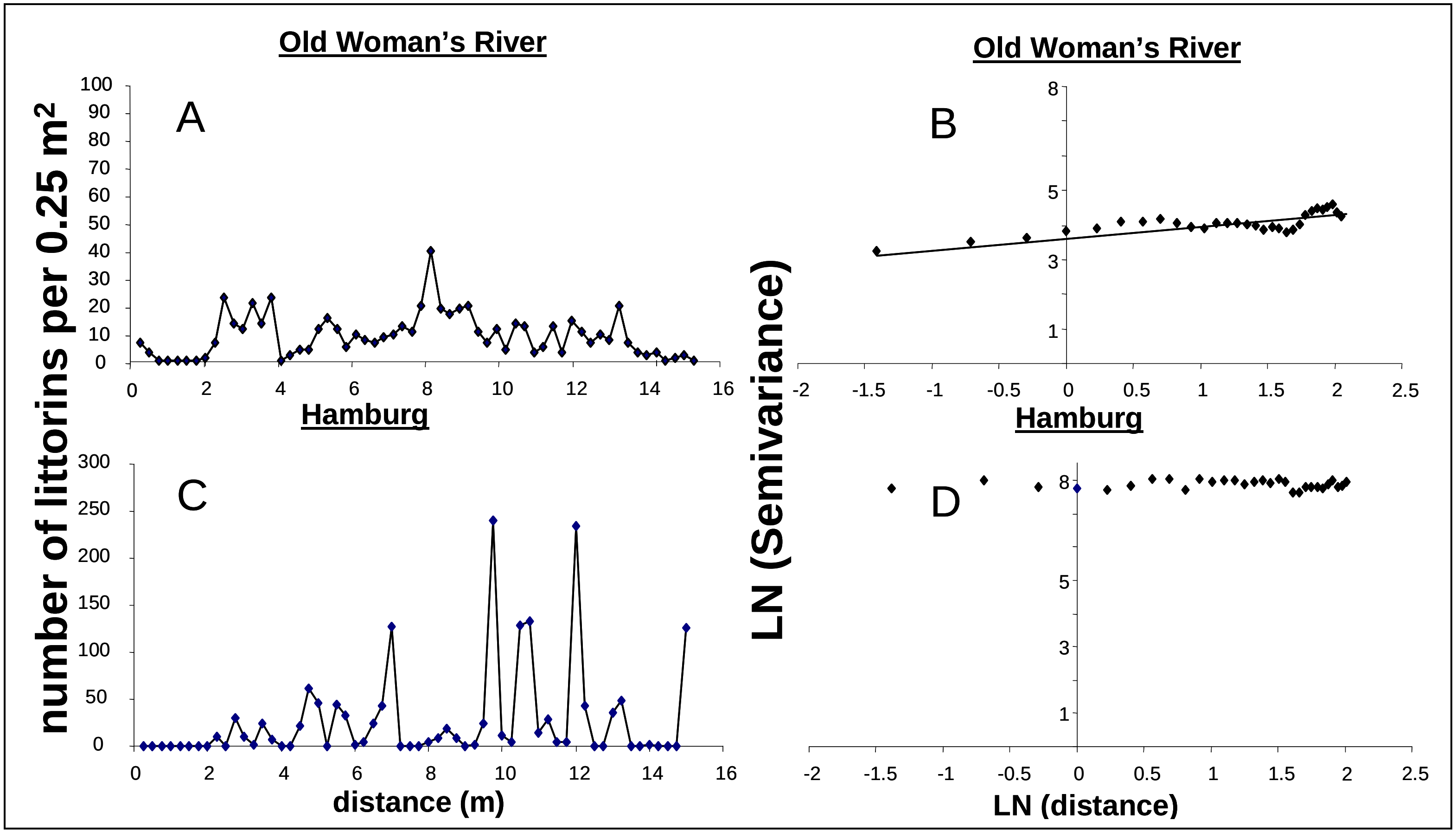

Fig 2.25. A and C. Distribution of the total density of littorinids on the high shore of Old Woman's River and on Hamburg. B and D. Semivariograms showing the variability at different scales. Solid line indicates significant scaling region detected using linear regression at P < 0.05.

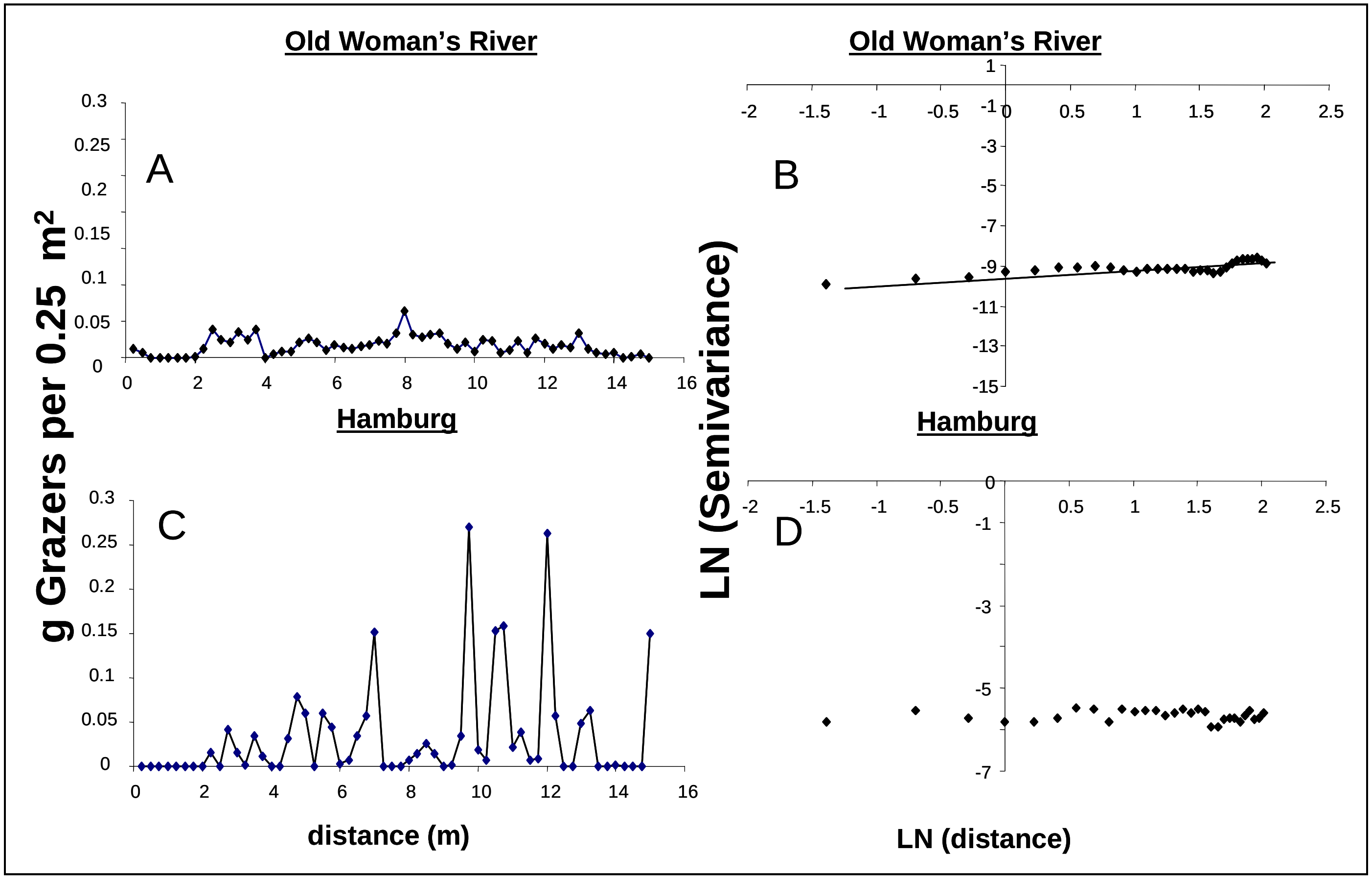

Figure 2.26. A and C. Distribution of the biomass of grazers including mesograzers and littorinids on the high shore of Old Woman's River and including only littorinids in Hamburg. B and D. Semivariograms showing the variability at different scales. Solid line indicates significant scaling region detected using linear regression at $P < 0.05$.

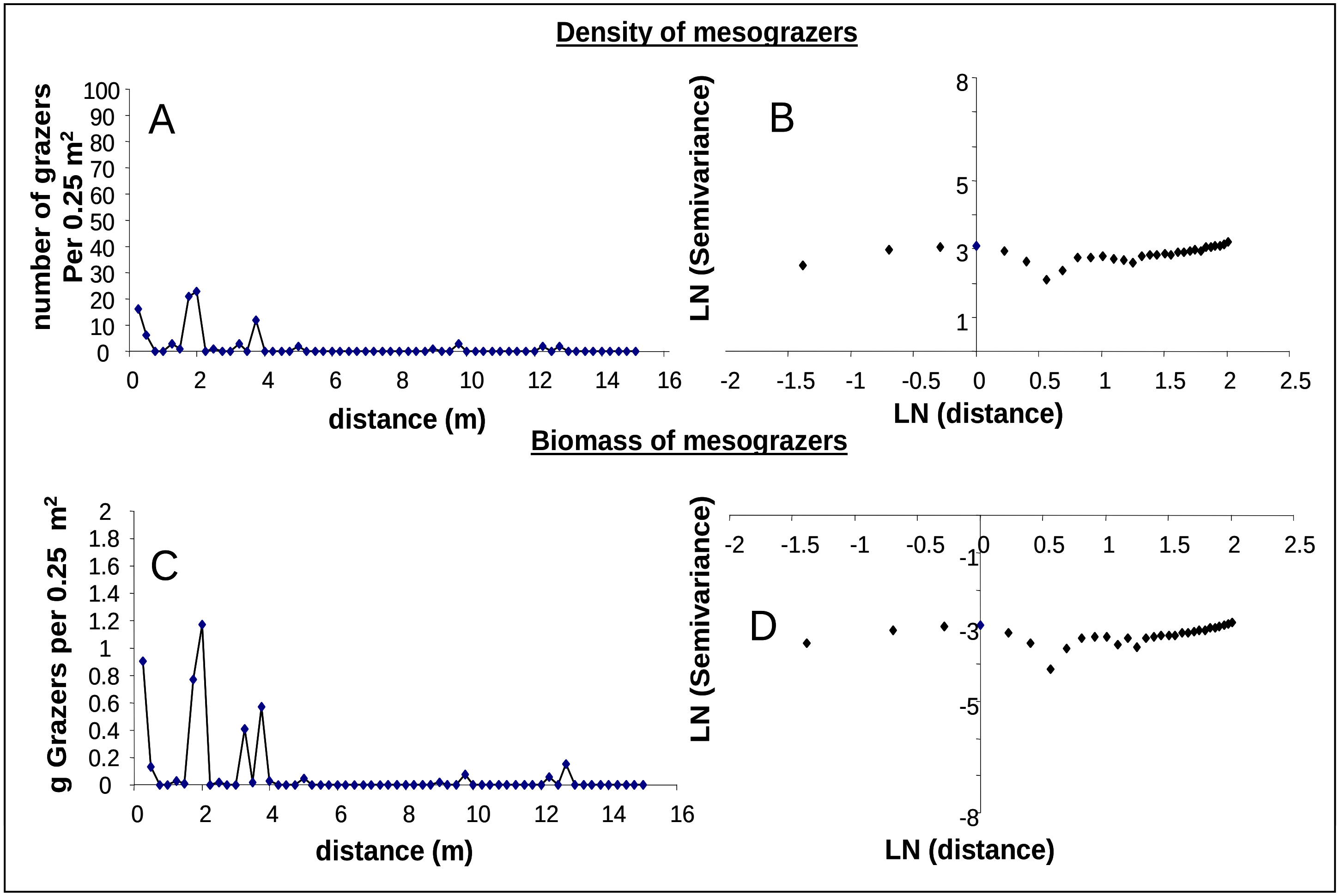

Figure 2.27. A and C. Distribution of the biomass of mesograzers in the high shore of Old Woman's River and in Hamburg. B and D. Semivariograms showing the variability at different scales. Significant Scaling region were not observed.

IV. Comparisons of density and biomass of grazers between sites

The density of grazers was higher at Old Woman's River than at Hamburg for the low shore, but the opposite trend was found on the high shore (Table 2.8). Conversely, the biomass of grazers was higher at Old Woman's River than Hamburg, on the low and the high shore (Table 2.8). These trends reflect the fact that grazers are smaller at Hamburg and smaller in number than Old Woman's River on the low shore, while there were more and smaller grazers on the high shore.

Table 2.8. A. Comparison of sites and zones in terms of total density of grazers using 2-factor Permanova and B, comparison of sites and zones in terms of total biomass of grazers using 2-factor Permanova.

A. Comparison for density

Source	df	SS	MS	F	P(perm)	P(MC)
Site	1	41394.5	41394.5	16.4	0.001	0.0010
Zone	2	144329.7	72164.8	28.6	0.001	0.0010
Site x Zone	2	14536.8	7268.4	2.88	0.0220	0.033
Residual	354	892243.0	2520.5			
Total	359	1092504.2				

Post hoc test

Site	Hamburg > Old Woman's River
Zone	High > Mid > Low
Site x Zone	Low shore: Old Woman's River > Hamburg Mid shore: Hamburg = Old Woman's River High shore: Hamburg > Old Woman's River

B. Comparison for biomass:

Source	df	SS	MS	F	P(perm)	P(MC)
Site	1	35615.2	35615.2	12.7	0.0002	0.0002
Zone	2	190854.2	95427.1	34.0	0.0002	0.0002
Site x Zone	2	14371.2	7185.6	2.5	0.02200	
Residual	354	992422.4	2803.4			
Total	359	1233263.1				

Post hoc test

Site	Old Woman's River > Hamburg
Zone	Low > Mid > High
Site x Zone	Low shore: Old Woman's > Hamburg Mid shore: Old Woman's = Hamburg High shore: Old Woman's > Hamburg

DISCUSSION

I. Technique

The results show for first time the use of geostatistical tool (semivariograms and cross-semivariograms) to detect relationship between different algal functional groups and grazers at small scales. The results coincided with those obtained in the chapter III using fence exclusion experiments: grazers influence distribution of algae on the low shore, but not on the mid shore or high shore. Using semivariograms, I could detect the spatial structure of the variability of algae and grazers, and, using cross-semivariograms, how the spatial variability of grazers and algae is positively and negatively correlated at certain scales.

Using cross-semivariograms it was possible to quantify and confirm relationships reported in the literature such as negative relationships between some functional groups and positive relationships between others, for example encrusting corallines and grazers.

High spatial organization was found for both algae and grazers at Old Woman's River but not Hamburg. This spatial organization was represented as a hierarchical structure of spatial scales in the functional groups of red turfs and encrusting corallines.

Grazers exhibited random patterns on the low shore of both sites, plus both other levels on the shore in Hamburg, but not on the mid and high shore of Old Woman's River.

Despite the fact that grazers and some algal groups were randomly distributed, spatial relationships were found between algal functional groups and grazers using cross-semivariograms.

Pooling grazers from low to high shore, there were more grazers at Hamburg than Old Woman's River, but there were larger numbers of grazers and greater biomass at Old

Woman's River on the low shore. On the mid shore, grazer density and biomass were similar between shores.

Finally, there are differences in human access and the usage of the sites. Hamburg has free access to the rocky shore and heavy harvesting has been reported on mussels, limpets and abalone, while Old Woman's River has restricted access, and the exploitation of marine invertebrates is considerably lower (Rius et al. 2006). Nevertheless, I observed in few opportunities the legal-organized collection of *Gelidium pristoides* in Old Woman's River.

II. Spatial structure at different levels on the shore

II.1. Low shore

The results of this study indicate that different spatial patterns exist in the distribution of algae and their grazers on the low shore at the two sites. Old Woman's River showed spatial structure for algae but not for grazers, while Hamburg exhibited random spatial patterns for both algae and grazers. Spatial dependence at scales from 0.25-7.5 meters was present in four out of six algal functional groups at Old Woman's River. Two of them, red turfs and encrusting corallines, exhibited two scaling regions, the rest exhibited a single scaling region (Table 2.1).

Red turfs exhibited two scaling regions, a positive one at smaller scales (0.25-2.75 m) nested in a negative one observed at larger scales (3.00 to 7.5 m). Both scaling regions are considered small scales. The first scaling region can be a consequence of direct interaction between species either between red turfs and grazers or as competition among algae, as this type of interaction often occurs at scales of a few centimeters. The other, larger scale exhibited a negative slope, indicating that as the lag increases, the variability among samples decreased. This could indicate either that algal dispersion in this group tends to homogenize cover at lags from 3-7.5 m or that the cover of the algae showed decreased variability among lags due to a homogenizing effect of grazing. The cross-semivariogram between red turfs and grazer biomass showed a negative relationship between 1-7.5 m indicating that grazers reduced variability of red turfs. At Old Woman's River red turfs dominated the substratum indicating benign conditions for this algal group. Negative scaling regions can be found in benign microhabitats where the variable studied shows low spatial variability (Erlandsson et al. 2005, Kostylev et al. 2005). This could help to explain the negative scaling region at Old Woman's River: red turfs tend to dominate the low shore, but they are disrupted by grazers at small scales. Finally, random spatial structure of red turfs was found at Hamburg. However, cross-semivariograms showed a positive relationship between red turfs and grazers at all scales. This could indicate that grazers promote the spatial variability of this functional group, while at Old Woman's River grazers decreased the variability (Fig. 2.1). At Hamburg, the substratum is dominated by encrusting corallines, which inhibit colonization by other algal groups under grazing conditions (Keats et al. 1994, 1997) however red turfs grow only in small pits where there are no encrusting corallines such as the edges of home scars of the limpet *Scutellastra cochlear*. In synthesis, the different results from cross-semivariograms between sites are presumably a consequence of benign conditions for red turfs at Old Woman's River, which promote more abundance and therefore more spatial homogeneity. At Hamburg however, the analyses suggest the creation of patches of red turfs by grazers. At this location the substrata is dominated by encrusting corallines and

S. cochlear, but in the limpets scars it is possible observe some red turfs, suggesting a positive effect between limpets on red turfs. This positive interaction was reported by Plaganyi and Branch (2000) on the west coast of South Africa where some algal gardens comprised some red turfs filaments.

The second algal group exhibiting a hierarchy of scaling regions was encrusting corallines, again only at Old Woman's River. This functional group is associated with strong grazing at exposed sites in the west coast of South Africa (Branch et al. 1992). A smaller scaling region (0.25-1.25 m) was detected, nested in a larger positive scaling region (1.5-7.5 m). Again this could be related to the small scale of individual grazing interactions with the encrusting algae, promoting cover at scales of (0.25 to 1.25 m), but at larger scales another relationship was observed, that could be related to the foraging ranges of grazers at scales of (1.5 to 7.5 meters). Although, the mobility of the limpets on the low shore is not large, other grazer such as *Turbo sarmaticus* (Gastropoda) and sea urchins can move longer distances, feeding on large amount of algae, and creating grazing barrens on the shores of these coasts (Foster and Hodgson 1998, Foster et al. 1999).

Besides these explanations, it is still necessary to study the causes of generation of hierarchical spatial scales or multi-scale behaviour. Multiple scaling behaviour seem to be related to different factors operating at different scales (see chapter V).

It is possible that differences are explained by wave exposure, in this way Old Woman's River seems to have features of wave protected site while Hamburg those ones of an exposed site. Branch et al. (1992) and Bustamante et al. (1995ab) noted that the abundance of *S. cochlear* with barrens of encrusting algae is higher at exposed sites on the east coast of South Africa. The major species observed on the low shore of Hamburg was *Scutellastra cochlear* while there were several species at Old Woman's River (*S. cochlear*, *S. tabularis*, *S. Barbara*. All these limpet species exhibit gardening behaviour). However, differences in wave action were not calculated between sites. In addition the differences in diversity and abundance of limpets on the low shore can be explained by human exploitation, for example, some of these limpet species such as *S. tabularis, S. barbara*, *S. longicosta* are known to be collected by people (Eekhout et al. 1992), while *S. cochlear* is not (V. Nakin and C.D. McQuaid unpublished data). In this sense, if larger sizes of gardening limpets are constantly removed by human collectors, (as at Hamburg), their ability to protect gardens will decrease, decreasing the biodiversity of other algal groups (non encrusting coralline and red turf) and increasing the population of *S. cochlear*. This could explain the switch from the domination of red turfs to encrusting algae at Hamburg. This is confirmed by reports of free access to rocky shores at Hamburg, here is observed close distances to rural areas and several collectors, while at Old Woman's river the distance to rural areas is longer and the access is much more restricted (Rius et al. 2006).

Cross-semivariograms between encrusting coralline algae and biomass and density of grazers showed no relation and positive relationships at different scales, at both sites (Fig. 2.11). Often these relationships were significant at small (0.5 to 1.0) and at large scales (6 to 7 meters), indicating that grazers promoted the variability of encrusting algae at these scales.

Although topography is an important source of spatial variability for these species, I tried to minimize this effect by choosing two sites with similar slopes, complexity of the rock surface (flat platforms) and rock type (sandstone).

The relationship between other of algal functional groups and grazers described using cross-semivariograms showed results consistent with the literature at both sites. Corticated algae, Ulvales and erect corallines were often negatively related to grazers. At Old Woman's River a single negative relationship was found at 3.75 m with the density of grazers, while at Hamburg density and biomass were negatively related to density and biomass of grazers. This suggests that the effect of grazers on the corticated alga *Hypnea spicifera* is stronger at Hamburg than Old Woman's River. The Ulvales are recognized to be susceptible to grazing and this was tested at this site in the previous chapter. Their softness and simple monolayer structure make them susceptible to most grazers (Steneck and Dethier 1994). The functional group of Ulvales was absent along the transect at Hamburg. Interestingly, it was observed in the previous chapter that after a disturbance (i.e. as removal of biomass by Sousa (2001)) the first algal group to recruit in an empty substratum is *Ulva* spp. Therefore the presence of *Ulva* spp. on the low shore of Old Woman's River suggests disturbance events that release space. This was often observed after severe storms or after clearings in experimental manipulations. At the same time I observed areas inhabited by single territorial limpets with substratum covered by non-coralline algae for several weeks, until the limpets were removed by an unknown agent. This could be wave action or predation by Oystercatchers, which feed on limpets on the low and mid shore (S. Kohler, unpublished data). These areas were rapidly re-colonized by *Ulva* spp. The domination of encrusting corallines at Hamburg can be longer term and more stable as this groups were resistant to disturbance, and can inhibit overgrowth by other algal groups, especially Ulvales (Keats et al. 1994,1997, Pueschel and Keats 1997). Encrusting corallines were often positively related to grazers, confirming the fact that grazers cannot remove them and reflecting the consequences of strong grazing effects (Branch et al. 1992). Grazers facilitate the survivorship of encrusting algae by protecting these groups from opportunistic algae and epiphytes. Similar mechanisms have been described for gardens of encrusting non-coralline algae (Eekhout et al. 1992, Branch et al. 1992, McQuaid and Froneman 1993, Plaganyi and Branch 2000). However, the relationship between encrusting non-corallines and grazer biomass differed between sites. This is related to the absence from Hamburg of gardening limpets that promote the alga *Ralfsia expansa*, such as *S. longicosta*, S. *tabularis* and *S. barbara* (Table 2.3). The cross-semivariograms showed results consistent with this observation, first at Old Woman's river biomass of grazers increases the spatial variability of encrusting non-corallines, and second, at Hamburg the relationship is mainly neutral, with few scales showing a reduction of non-encrusting corallines (Fig. 2.12).

II.2. Mid Shore

Spatial structure of one algal functional group on the mid shore was found at Old Woman's River, but not at Hamburg. At both sites the density and biomass of grazers was similar, but there were striking differences in abundance of the commercially exploited algae *Gelidium pristoides*.

Corticated algae represented by *G. pristoides* at Old Woman's River showed heterogeneous structure at two different scales. This group was represented by *Gelidium* *pristoides* which exhibited two levels of patchiness (two nested scaling regions): one at very small scales (0.25 to 1.75 m) nested in another of 2 to 7.5 m. Cross-semivariograms showed only positive relationships between corticated algae and biomass of grazers mainly at scales above 4.5-7.5 meters at Old Woman's river. The opposite relationship (negative relationship) was observed at Hamburg using cross-semivariograms in terms of grazer density and biomass. Positive cross-semivariograms indicate that grazers increased the spatial variability of algae. Benedetti-Cecchi (2000) explained these algal increases when the variability of grazing effects is higher than residual variability affecting algae, independent of the strength of the grazing effect. In this context, *G. pristoides* on the mid shore of Old Woman's River, its residual variability can be explained and increased by the organized commercial algal collection observed at Old Woman's river. This algal spatial variability was represented as patchy distribution, similar to the grazer biomass spatial distribution. Therefore, positive cross-semivariogram indicated that grazers and algae are co-occurring at the same lags. In addition, the latter argument can be explained because the *G. pristoides* sporelings can survive harvesting recruiting on the shells of some limpets (Carter and Anderson 1991, Whittington-Jones 1997). At Hamburg, negative cross-correlations suggested grazers and *G. pristoides* do not co-occur in the same places, therefore when the variability of *G. pristoides* increases in some places, the variability of the grazers decreases. The other functional groups (Ulvales, erect corallines and encrusting corallines) were randomly distributed along the transect at Old Woman's River and Hamburg. At both sites, negative relationships were found with density and biomass of grazers (Broitman et al. 2001). Encrusting non-corallines represented by *Hildenbrandia rubra* were positively related to grazers at both sites. Grazers would increase the survival of this group; keeping by its surface clean of opportunistic algae and competitors and by preventing overgrazing by non-territorial grazers (McQuaid and Froneman 1993). Similar relationships were observed between grazers and non-encrusting corallines in Australia by Underwood (1980), Hong Kong by Kaehler and Williams (1998), and on the west coast of South Africa by Madikiza (2005).

II.3. High shore

Differences between sites in terms of density and biomass were found. Although transects were set on the highest part of the shore, there were more grazers at Hamburg, but the biomass was greater at Old Woman's river (Table 2.8). Mesograzers were observed at Old Woman's River, but not at Hamburg. In addition differences in spatial structure were found. Patchiness of littorinids were found at Old Woman's River while random patterns were found at Hamburg. The patchy spatial patterns observed at Old Woman's River can be variable according to foraging behaviour, therefore, it is possible that spatial patterns of grazers change day to day and between tides. For example, littorinids on the Australian coast have been studied in order to understand the mechanisms that control their aggregation patterns; despite these efforts no conclusive results have been discovered (Chapman 1995, Underwood and Chapman 1996). The sampling here was carried out on two consecutive days, but not information about temporal changes of the littorinids spatial patterns have been studied. Among the factor inducing variability in spatial pattern in littorinids are crevice availability and microalgal patchiness. The relationship of these factors deserved to be studied in future research.

McQuaid (1981) found that bigger sizes of littorinids are more tolerant to wave action suggesting, a third feature that can imply higher wave exposure at Hamburg. The presence/ of mesograzers on the high shore at Old Woman's River seems to be a consequence of crevices and shallow and small tidal pools, while no shallow tidal pools occurred on the Hamburg transect consequently no mesograzers were found.

III. Conclusions

Different zones and/or levels on the shore can exhibit different level of patchiness, but this varied between sites. Old Woman's River exhibited spatial structure in algal functional groups mainly on the low shore, and in grazers on the mid and high shore, while Hamburg was dominated by random spatial patterns. It seems that differences between sites can be primarily driven by the degree of wave exposure of the shore and human exploitation on marine grazers.

The algal functional group most commonly observed to show spatial structure on the low and mid shore were corticated algae.

The biotic structure of Hamburg exhibits signs of exposure, the low shore dominated by the limpet *Scutellastra cochlear* and encrusting corallines, and supports larger littorinids.

The level of exploitation of low shore species could be a source of variability not studied using this type of geostatistical tools. In summary, two conjectures are proposed from these results: sites can exhibit less wave exposure patchiness and low human exploitation, can exhibit more spatial structure than more exposed sites with high human exploitation. However, both factors human exploitation and level of waver exposure need to be separated and analyzed in futures studies, in order to predict how the spatial heterogeneity can change when is the ecosystem are commercially harvested and how this varies as function of the exposure (Branch and Odendaal 2003, Nielsen and Navarrete 2004).

Because the samples were taken *in situ* without any manipulations, the patterns found are a consequence of historical natural effects occurring at both sites, including competence, recruitment, predation and disturbance. This implies that these spatial patterns can vary in time, as has been reported for mussel beds by Erlandsson et al. (2005). Cross-semivariograms exhibited negative or positive relationships with algae and grazers, which may or may not imply grazing effects on the spatial distribution of the algae. This is indirect evidence of grazing effects, based at the positions where algae and grazers are sampled and at the same time dependent on the spatial scale. Testing the effect of grazing using experimental exclusion confirms this results (see Chapter III).

Finally, this study comprised a single quantification of the spatial heterogeneity at two sites at small scales, here most of the analysis from semivariograms and cross-semivariograms showed a tendency to randomness or chaos in the distribution of algae and grazers under certain conditions (exploitation or exposure). Despite this, significant results show a level of order in the organization of algae and grazers, mostly in patchy spatial patterns. This finding threatens the common intuition of extremely chaos/randomness in ecological process (such as grazing) at small scales.

CHAPTER III

EFFECTS OF GRAZERS ALONG AND ACROSS THE SHORE UNDER EARLY SUCCESION

INTRODUCTION

Grazing effects are recognized as an important factor structuring algal communities on rocky shores in the northern hemisphere, including the temperate north east Pacific (Dayton 1971, Foster 1992, Menge et al. 2005), the north east Atlantic (Coleman et al. 2006), the north west Atlantic (Lubchenco 1986, Menge and Branch 2001), and the Mediterranean (Benedetti-Cecchi 2000, Benedetti-Cecchi et al. 2000). On the temperate reefs of the southern hemisphere, there are also strong effects of grazing as has been shown on the coast of Chile on the mid shore at different latitudes (Jara and Moreno 1984, Nielsen and Navarrete 2004, Aguilera and Navarrete 2007) and in Australia on the low, mid shore and tidal pools (Underwood 1980, Underwood and Jernakoff 1984). Finally, grazers are also important in tropical regions such as Panama (Menge et al. 1986) and Hong-Kong, (Williams 1993, 1994). This shows that grazing effects are important ecological process worldwide, however the zonation of grazing effects and their spatial structure across the shore have not been analyzed using a transect across the shore. Often grazing effects are analyzed with experimental exclusions at different levels along the shore leading to hypothetical predictions for those places where grazers are not excluded. In order fully to understand grazing, it is necessary combine exclusions along and across the shore.

Different species of grazers and algal groups in different zones across the shore can exhibit variability in grazer effects. The broad patterns of zonation scheme in south coast of South Africa includes four zones. From the bottom to the top of the shore, these are: 1. The cochlear zone, inhabited by the limpet *Scutellastra cochlear* and encrusting algae. Below the cochlear zone the sublittoral fringe, characterized by inhabited by the alga

Hypnea spicifera and in places the kelp *Ecklonia radiata*. 2. The lower balanoid zone is inhabited by urchins, mussels (the lower part *Perna perna* and in the upper part *Mytilus galloprovincialis*), abalone, limpets (*Scutellastra longicosta*, *S. barbara*, *S. granularis*), some winkles (*Oxystele sinensis*) and red algal turfs, and in its upper part it is possible to find the limpet *Cymbula oculus* and the alga *Gelidium pristoides*. 3. The upper balanoid zone biota also comprises several winkles (*Oxystele tigrina*, *O. tabularis*), limpets (*Helcion spp*), barnacles (*Chthamalus* spp) and several siphonarid limpets and the algae *Ulva rigida* and *Porphyra capensis*. 4. The supralittoral fringe, also known as littorinid zone, is characterized by two species of periwinkles: *Nodilittorina africana* and *N. knysnaensis* (Branch and Branch 1981).

These differences in the patterns of distribution of grazers suggest differences in grazing pressure on macroalgae. First in the cochlear zone, where enormous densities (200 ind.m^2) of these limpets only allows the survival of encrusting coralline algae plus red algal turfs that forms limpets gardens (Branch et al. 1992, Bustamante et al. 1995a). Second, studies done on the south coast in the low balanoid zone have shown strong spatial effects on algae by the limpets *Scutellastra longicosta* and *Cymbula oculus* (McQuaid and Froneman, 1993). Third, in between the lower and upper balanoid zone Whittington-Jones (1997) found weak overall grazing effects. Forth, in the supralittoral zone, strong grazing effects on the epilithic algal community were found by Kaehler and Froneman (2002). There are no reports on grazing in the supralittoral tidal pools of South Africa (Huggett and Griffiths 1986). These pools are inhabited by high densities of the limpet *Siphonaria capensis* and other herbivores such as winkles like *Oxystele* spp (Hodgson 1999), but their role in the spatial distribution of algal distribution has not been analyzed. So far no study has assessed the effects of grazing across the shore using one experimental design simultaneously at different levels on the south coast of South Africa, nor has the patchiness of grazing effects across the shore been examined.

The distribution of algae and grazers across the shore is partly explained by a gradient of desiccation from the bottom to the top of the shore, this gradient of desiccation is directly due to an emersion gradient caused by the tidal cycle (Southward 1975, Menge and Branch 2001), but this gradient does not completely explain the distribution of organisms, biotic interactions have great influence too (Underwood 1978, 1980). At the same time, wave action can operate in an inverse way to the gradient of desiccation (McQuaid 1982). On the low shore, large waves forces can affect the attachment of grazer species and modify trophic interactions: stronger waves have consequences on the mobility of grazers and therefore in their foraging behaviour (Hawkins and Hartnoll 1983, Branch et al. 1992, Foster 1992, Menge and Branch 2001). Primary productivity and the availability of nutrients for algae is however greater on the low shore. Grazers do not necessarily have to move long distances for feeding, for example *Scutellastra cochlear* does not move off its home scar (Branch et al. 1992), a few meters up on the shore *S. longicosta* does not move off its garden (McQuaid and Froneman 1993). On the mid shore, it seems that wave effects and desiccation are less stressful for grazers; therefore intertidal ecologists often test grazing effects on the mid shore, since it easier to predict grazing effects there than either at the bottom or at the top of the shore. This is probably also explained by the notion that the biotic force dominating the low shore is competition, while on the high shore physical factors are the crucial forces structuring algal community (e.g. Jara and Moreno 1984, Williams 1993, 1994, Benedetti-Cecchi 2000, Benedetti-Cecchi et al.

2000, Nielsen and Navarrete 2004, Coleman et al 2006). In contrast, on the high shore grazers are not strongly affected by waves during the most of the tidal cycle, however food availability is low and they have to forage over relatively long distances to get sufficient food to survive (McQuaid 1981, 1982, Chapman and Underwood 1996). Additionally, on the high shore, it can be thought unlikely to find grazing effects, but it has been reported that grazing by littorinids and limpets on the microalgal community represented by cyanobacteria, lichens and also macroalgal spores and propagules can be important (Cubit 1984, Mak and Williams 1999, Kaehler and Froneman 2002).

Several reviews of the role of grazing indicate that it has importance in determining both the composition and the spatial distribution of algal assemblages between the mid and the high shore, because the harsh physical conditions make algae more susceptible to grazers than in conditions where rapid growth (high primary productivity on the low shore) exceeds the ability of grazers to consume them (Hawkins and Hartnoll 1983, Foster 1992 and Fig. 3.1).

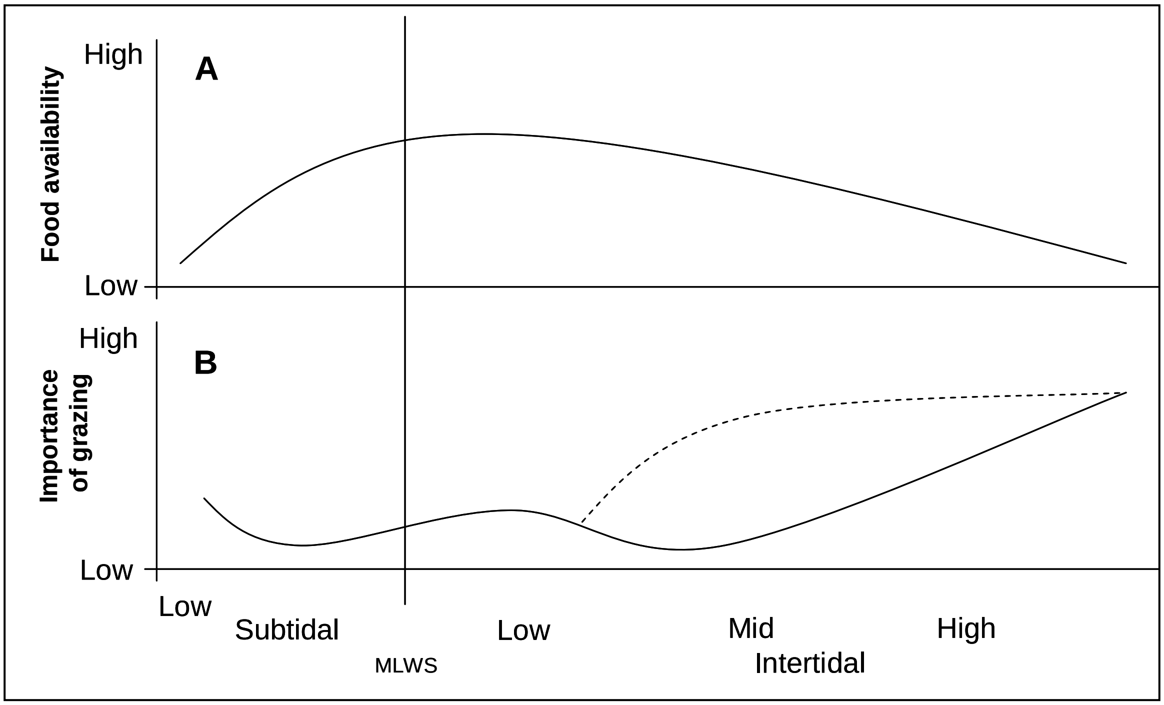

Figure 3.1. Scheme which synthesizes the effects of grazing across the shore, based from Hawkins and Hartnoll (1983) description, but taken from (Foster 1992). A. Availability of food (algae availability), B. Importance of grazing across the shore. Dashed line indicates how the slope changes when desiccation increases. MLWS: mean low water springs, the average of the lowest levels reached by the tide on each fortnightly set of tides.

The scheme of Hawkins and Hartnoll (1983) describes the effect of the distance from MLWS (mean low water springs) on the importance of grazing effect. As we move up from the MLWS, the elevation increases and the grazer impact increases until a certain point, where the importance of grazer effects diminishes again. The combination of both distance from the sea and elevation of the substratum can influence the strength and effects of grazing. It is possible to find areas near MWLS that exhibit high elevation where grazing effects can be strong, and conversely areas far from MWLS where the elevation is low, creating areas of high primary productivity, such as depression/platforms of variable size, or tidal pools, where grazing effects may or may not be important. These sources of variability can affect the total grazing effect across the shore. This variability of grazing effects can emerge like patches, gradients or random distribution of grazing effects across the shore, however these spatial patterns in grazing effects have not been studied across the shore.

Grazing effects across the shore can also vary because the type of grazer changes (Branch and Branch 1981, McQuaid 1982, Madikiza 2005). On the south coast of South Africa, grazers on the low shore consume macroalgae and are also able to feed on the epilithic community. These grazers include *Scutellastra* spp. and *Cymbula* spp.; generally these limpets are larger than 3 cm in shell length and are termed macrograzers. There are also grazers that live on the low shore which only feed on the epilithic algal community and soft filaments of foliose algae such us *Ulva* spp and red algal turf filaments. V. Nakin (unpublished data) examined the gut content of low shore macrograzers such as *Scutellastra* spp. and found spores, propagules and filaments of green and red algae, furthermore Whittington-Jones (1997) examined the gut content of the grazers: *Oxystele tabularis* and *O. tigrina* and *Siphonaria* spp. on the mid shore and he also found spores and propagules of and filamentous green algae. The grazers examined by Whittington-Jones (1997) were smaller (average size 1.5- 2.0 cm) and are referred in this thesis as mesograzers. On the high shore it is possible to find littorinids which are classified as epilithic grazers (feeding only on microalgae and spores), (McQuaid 1996).

Therefore, grazers can have effects on the spatial pattern of algal settlement, influencing algal succession and the spatial patterns observed on the shore (Hawkins and Hartnoll, 1983, McQuaid 1996, Johnson et al. 1997, Burrows and Hawkins 1998). Additionally, macroalgal grazers (macrograzers) could have consequences on spatial patterns of the late stages of succession of algae. If complexity of habitat exists across the shore with areas that combine variable elevation and variable distances from the sea (MLWS), I would expect areas where the distribution of different types of grazers overlap, therefore the spatial pattern of algal settlement would be driven by different grazers. In addition, physical factors could also have consequences on algal settlement or early grazing effects by providing a range of areas with variability in primary productivity, and influencing the effects of grazing. Since environmental conditions can change at different temporal scales such as seasonality and daily fluctuations in desiccation, the susceptibility of algae to grazers can change and this can be reflected as change in the spatial pattern of grazing effects. These changes in the spatial pattern in time have been reported for recruitment of mussels in the south coast of South Africa (Erlandsson and McQuaid 2004, Erlandsson et al. 2005). For these reasons, temporal change in the spatial pattern of grazing effects across the shore was investigated using a transect of exclusions.

Two general hypotheses are studied in the present chapter:

(i) Different sizes of grazer induce different effects on the algal community. This effect will change according to the position from MLWS and between habitats such tidal pools on the high shore. The objective was separate the grazers into micrograzers and meso and macrograzers using different types of exclusions at different levels in the intertidal.

(ii) Grazing intensity varies spatially across the shore exhibiting spatial structure which is a consequence of the interactive effects of biotic and abiotic factors. Similarly, it is hypothesized that this spatial structure changes in time in response to changes in these factors. In order to assess these hypothesis my objective was to understand the spatial structure of grazing intensity as effect sizes on the main algal group across the shore. The second objective was to examine the co-variation between the spatial structure of grazing (represented as effect sizes) and the spatial structure of biotic and abiotic factors. In order to determine this it is necessary to know the spatial structure of physical (elevation and water movement) and biotic (density of macro, meso and micrograzers) factors across the shore.

MATERIALS AND METHODS

I. Study site

Experiments were conducted at Old Woman's River (33º45'S, 27º15'E) on the south coast of South Africa. This platform was chosen because the low substratum heterogeneity (the shore is mainly flat rocks), makes it suitable for grazing manipulations. Two experimental designs were used to detect grazing effects at different levels of the shore, first a randomized block design set on the low, mid, high shore and in high shore tidal pools and second, a transect of blocks, running from the bottom of the shore (MLWS) to the supralittoral zone.

Several algal species occurred across the shore, but most were too rare to allow robust statistical analysis. For this reason, algae were categorized into three functional groups: i. green foliose algae, represented only by *Ulva rigida* and other Ulvales, ii. red foliose algae represented by *Porphyra capensis*, and finally, iii. red turfs, represented by *Pterosiphonia cloiophylla*, *Polysiphonia spp*, *Ceramium spp*, *Callithamnion stuposum*.

II. Experiment 1: Randomized block design at different levels on the shore

This experiment aimed to separate the effects of different sizes of grazers, i.e. macrograzers, mesograzers and micrograzers. Macrograzers included snails, limpets and sea urchins, exhibiting sizes over 3 cm, while mesograzers were snails and limpets exhibiting sizes between 1 to 2 cm. Micrograzers were represented mainly by littorinid snails and juveniles of mesograzers smaller than 1 cm.

The experimental design corresponded to a randomized block design comprising four treatments: total exclusion of grazers (ET), excluding macro, meso and micrograzers; exclusion treatment (T) excluding only meso and macrograzers; procedural control (Pc) to detect any artefacts of fences; and control (C), open areas with free access to any grazers. The total exclusion (ET) consisted in fenced areas of 0.25 m x 0.25 m, surrounded by an antifouling paint strip (5 cm wide) outside of the fence to prevent micrograzers for attempting to get into the fenced area. The exclusion treatment (T) consisted only of a fenced area (without paint), allowing access to micrograzers. This paint has been successfully used in previous experiments by Dye (1993) and Kaehler and Froneman (2002) who did not report additional artefacts. The procedural control involved two partial cages anchored in opposite corners of a square, potentially limiting access to any grazer, and controls (C) were areas marked using four screws at the four corner of a square with free access to any grazer. The blocks were randomly distributed in every zone, the replication was 10 blocks in each zone/habitat. In addition, nine shallow tidal pools (area average 2 m^2 and 5 cm deep) on the high shore were used to assess grazing effects. The substratum where the treatments were set was previously scraped and cleared using a butane/propane torch to remove the existing algal community. The minimum and maximum distance among blocks ranged from one to ten meters, respectively. The distance among treatments was around 15 cm.

The experiment was replicated in each of three levels on the shore plus in high shore tidal pools. Shore levels were recognized by the following algae and grazers: 1) the low shore, characterized by the corticated alga *Hypnea spicifera*, red turfs and the grazers *Scutellastra cochlear, S. tabularis* and *S. barbara*. This zone varied between approximately 0 to 8 m from MLWS and 0 to 0.45 m above chart datum (Personal observation). It is worth noting that the MLWS is practically impossible to distinguish at a determined site, however I defined it as a fixed point based on several field observations of fauna and flora during spring tides. I assumed this fixed point corresponded to MLWS and 0 m above chart datum (C.D.). 2) The mid shore was characterised by the alga *Gelidium pristoides* and the limpet *Cymbula oculus*. This extended for 8 to 25 m from MLWS and 0.6 to 0.85 m above C.D.. 3) The high shore defined by the presence of littorinid grazers, and corresponded to the supralittoral fringe. This zone was recognized between 25 to 55 m from MLWS and 1.2 to 1.8 m above C.D.. In addition, blocks were set in the nine available tidal pools that lay within the high shore. The experiment was initiated on 12th of February 2005 and ended on 6th of March 2006. The concentration of chlorophyll *a* was measured for every experimental unit and cover of algae was calculated using digital photographs from which cover was estimated using the program Image tool 3.0.

Three rock chips (approximately 1 cm^2 each) were collected using a chisel from each experimental unit (468 chips per sample/date) and transported immediately to the laboratory, where they were individually submerged in 8 ml of 80% methanol for 24 hours in darkness. At the beginning of the experiment, the rock chips collected from the treatments on the low, mid shore and in tidal pools were not covered by macroalgae. After a few weeks the treatments were covered by macroalgae and consequently the chlorophyll *a* extracted included macroalgae as well as microalgae. On the open rock of the high shore there were episodic appearances of macroalgae, but most of the time the chips bore no macroalgae. The samples were taken initially at monthly intervals and finally at one and half month intervals. The concentration of chlorophyll *a* was estimated using a spectrophotometer (SHIMADZU UV-1201) following the formula:

$$[\text{Chl-}a] = (\text{A.V.}13)/\ \text{a.d}$$

Where A = absorbance at 665 nm – absorbance at 750 nm, V = volume of solvent, 13 = spectrophotometric constant, a = area of the chip (cm^2, measured for each chip individually by image analysis 3.0), and d = cell path length (cm). The concentration of chlorophyll *a* was expressed in µg. cm^{-2}. This method was successfully used by Bustamante et al. (1995b) and Jenkins et al. (2001).

Additionally physical factors were estimated for each block, the horizontal distance from the fixed pointed representing MLWS was measured, the elevation of the substratum was measured using a dumpy level at each block, and relative water movement was estimated from weight loss of cement balls during three spring tides. These cements balls were left for 48 hrs to determine the amount of erosion due to water movement. The cement balls were dried and weighed before being anchored to the shore and again 48 hrs later. Prior to each weighing, they were left to dry for 12 hrs in an oven at 60º C. In December 2005 the density of macro, meso and micrograzer was estimated using a quadrat of 1 m^2 set in each block.

III. Experiment 2: Grazing effect across the shore using a transect

A transect of cages in a block design was used to detect grazing effects across the shore. Each block comprised three treatments as described in experiment 1: i. Total exclusion

(ET), ii. Procedural control, and iii. control areas. This experimental design involved blocks from the MLWS to the upper limit of the supralittoral zone, a total 54 blocks. The length of the transect was 54 m covering the entire intertidal zone. The blocks were separated by 1 m (measured between centers of blocks). Before applying treatments, the substratum was scraped and cleared using a butane/propane torch to remove the existing algal community.

The elevation, distance from the MLWS and water movement were recorded at every block as I described above.

The experiment was started on the 1st July of 2005 and finished on 15th June 2006. During this period, four recordings of algal cover and physical factors were made.

IV. Statistical analyses

IV.1. Experiment 1: Randomized block design at different levels on the shore

Abiotic and biotic factors were individually compared among levels on the shore using 1-way ANOVA tests or t-tests, depending on the number of elements to be compared.

For the first level of resolution (concentration of chlorophyll *a*) a 2-way RM-ANOVA was used, where the fixed factors were zone (4 levels: low, mid, high shore and high tidal pools) and treatment (4 levels: total exclusion, exclusion, procedural control and control).

Functional groups were analyzed using 1-way RM-ANOVA for each functional group in each zone. Where more than one group of functional algal species was recognized, Bonferroni correction was used. When the assumptions of homocedasticity and normality were violated in a few cases, the data were transformed (Underwood 1997).

IV.2. Experiment 2: Grazing effect across the shore using a transect

Relationships among physical factors and biotic factors (density of grazers) were assessed using Spearman correlation tests.

To assess the grazing effect (treatment effect) along the transect, analysis of covariance (ANCOVA) was used with several covariables: distance from the sea, elevation, water movement, macrograzer density, mesograzer density and micrograzer density. Because the assumption of parallelism among treatment slopes was violated, RM-ANOVA test was used to complement and confirm this analysis of treatment effects. To assess the contribution of the factors to the overall grazing effect, multiple regressions were used to complement the results of ANCOVA. In order to test grazing effects in the multiple regression, the total algal abundance in the exclusion treatment (ET) and in the control treatment were convert to effect sizes, using the formula:

ES = Ln (% algal cover of Control / % algal cover of Exclusion treatment).

The effect size describes the strength of the grazing effect, and is represented by negative to positive values (Osenberg et al. 1997, Coleman et al. 2006). Negative values indicate strong effects of grazers on algal abundance, and positive values indicate that grazers have weak effects and facilitate algal abundance. For example, McQuaid and Froneman (1993) found the territorial limpet *Scutellastra longicosta* has strong positive effects on abundance of the encrusting alga *Ralfsia verrucosa* by preventing destructive grazing by non-territorial grazers.

Values of the effect size were used as a dependent variable and contrasted with the independent variables: elevation, water movement, distance from the sea, density of macro, meso, and micrograzers. Since the effect size described grazing effects inversely (negative values mean stronger grazing effects through the reduction of algal abundance and positive values indicate that grazing effects enhance the algal abundance somehow e.g. McQuaid and Froneman (1993)), a positive relationship between effect size and any independent variable represents a reduction in the grazing effect and *vice versa*.

IV.2.a. Heterogeneity and dependent scaling regions of grazing across the shore

In order to describe the spatial pattern of abiotic and biotic factors, the spatial pattern of *Ulva rigida* in the exclusion treatments and the spatial pattern of the strength of grazing effects across the shore, the heterogeneity in terms of the fractal dimension was calculated:

$$D = (4- m)/2$$

Where D, represents the fractal dimension, or the degree of partitioning in similar pieces of a variable along a transect (Mandelbrot 1977). This in ecological terms varies from 1 to 2, where values closer to 1 indicates a trend-like distribution and values close to 2 indicate a patchy distribution. The term ‘*m*’ represents the slope in the regression between the natural logarithm of the semivariance and the natural logarithm of the distance.

The semivariance is a measure of the dispersion of the data at different scales, calculated as:

$$Y_{(h)} = 1 / (2N_{(h)}) \sum_{i=1}^{N-h} (Z_{i+h} - Z_i)^2$$

where N is the total number of data points; $N_{(h)}$ is the number of pairs of data points separated by the distance or lag h; Z_i and Z_{i+h} are the values of the studied variable at points $_i$ and $_{i+h}$. 27 lags were included in the transect, therefore the variation in the number of pairs of lags varied between 53 pairs at lag 1 m to 27 at lag 27 m. A number of 27 replicates was considered a sufficient sample size for a robust analysis.

To detect scaling regions, 3 steps were done as I described in the chapter II. Cross-semivariance analysis was used to examine the relationship between every independent variable (abiotic and biotic factor) and the strength of grazing effects, expressed as effect size. The cross-semivariance was calculated as:

$$Y_{(h)} = 1 / (2N_{(h)}) \sum_{i=1}^{N-h} (X_{i+h} - X_i)(Z_{i+h} - Z_i)$$

where N is the total number of data points; N(h) is the number of pairs of data points separated by the distance or lag h; X_i and X_{i+h}, and Z_i and Z_{i+h} are the values of two different variables at points $_i$ and $_{i+h}$. 27 lags were also included in the analysis, to be consistent with semivariance analysis. n = 27 was considered appropriated to set the length of the analysis of the transect.

Relationships were determined as positive, negative or no relationship as described in chapter II (Erlandsson and McQuaid 2004). These relationships were interpreted in the same way as those obtained in the multiple-regressions: a positive relationship indicated a reduction in the grazing effect (since effect sizes must be interpreted in an inverse way), while a negative relationship indicated a positive effect on the grazing.

RESULTS

I. Experiment 1: experiments among zones

I.1. Variability of abiotic and biotic factors among levels on the shore

Physical factors represented by ‘distance from the sea’, ‘elevation of substratum’ and ‘water movement’ differed significantly among levels on the shore (Table 3.1), as did biotic factors such as density of grazers. Macrograzers were present only on the low and mid shore where they exhibited similar densities (Table 3.1). Although densities did not differ, species composition did: on the low shore *Scutellastra cochlear*, *S. barbara*, *S. tabularis* and very few *Cymbula oculus* were observed, while on the mid shore, only *C. oculus* was present. Macrograzers were absent on the high shore and tidal pools. Although, mesograzers were equally abundant on the low and mid shore, the densities were significantly greater in tidal pools. No mesograzers were observed on the high shore (Table 3.1). Micrograzers were observed only on the high shore and tidal pools and were more abundant in open rock than tidal pools habitats (Table 3.1).

Table 3.1. Average ± SD of physical factors in different zones. < or > = represents the result of SNK tests showing the direction of differences. * means $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$ and NS non significant. 0 means organisms not present.

Factor	**zones**						
	Low		**Mid**		**High**		**Tidal pools**
		(1-way ANOVA or t-test)					
Distance from Sea from MLWS (m)	6.3 ± 2.2	<	28.3 ± 2.8	<	50.9 ± 1.3	<	56.1 ± 2.1
			$F_{3,34}$ = 1051.5***				
Elevation above Chart datum (m)	0.5 ± 0.2	<	0.8 ± 0.1	<	1.7 ± 0.2	>	0.9 ± 0.54
			$F_{3,34}$ = 89.07***				
Water movement (g)	10.4 ± 0.6	>	6.6 ± 0.6	=	6.2 ± 0.9	=	5.7 ± 1.2
			$F_{3,34}$ = 62.2***				
No. macrograzers (n°.m^{-2})	3.6 ± 1.3	=	2.2 ± 3.2		0		0
		t_{17} = 1.2NS					
No. mesograzers (n°.m^{-2})	0.7 ± 0.6	<	12.4 ± 10.3		0	<	45.8 ± 51.0
			$F_{2,25}$ = 5.7**				
No. micrograzers (n°.m^{-2})	0		0		173.6 ± 105.9	>	45.9 ± 48.7
						t_{17} = -3.3**	

I.2. Grazing effects at the level of algal biomass, represented by concentration of chlorophyll *a*

RM-ANOVA showed a significant effect of ‘Level of the shore’, ‘Treatments’, ‘Level of the shore*Treatment’, ‘time’, and the interaction ‘Time*Level of the shore*Treatment’. An overall grazing effect ‘treatment’ was found on the whole shore, and on the low shore and in tidal pools, while the mid shore and high shore were not significantly affected by grazers.

No differences between total exclusion and exclusion were found. Temporal variability in the concentration of chlorophyll *a* was found with broadly more chlorophyll *a* in the winter months (May, June, July and August), however this pattern was not very clear and a spring month (November) was also similar to those in winter (Table 3.2 and Fig. 3.2).

Table 3.2. RM-ANOVA on the coarsest level of resolution: concentration of chlorophyll *a* at each level on the shore during 2005. The level of significance was α = 0.05. * means P < 0.05, ** P < 0.01,* P < 0.001 and NS non-significant. Data transformed using Ln (x + 1) to achieve homogeneity.**

	DF	MS	F
Level of the shore (LS)	**3**	**388.3**	**384.02*****
Treatment (Treat)	**3**	**11.03**	**10.9*****
Level of the shore*Treat	**9**	**2.66**	**2.6****
Error	**136**	**1.01**	
Time	**7**	**12.66**	**36.6*****
Time*LS	**21**	**4.35**	**12.6*****
Time*Treat	**21**	**0.31**	**0.9NS**
Time*level of the shore*Treat	**63**	**0.56**	**1.62*****
Error	**952**	**0.34**	
Cochran test P < 0.05			
Post hoc SNK test			

Level of the shore: Low = Mid > Tidal pools > High

Overall treatment: TE = E > Pc = C

Level of the shore*Treatment: Low shore: TE = E > Pc = C

Mid & High shore: NS

Tidal Pools: TE = E > Pc = C

Time: August 05 = May 05 > June 05 = April 05 = Nov >Jan 06 = March 06 > March 05

Time*LS: Low shore: Mar05 = Apr05 = May05 = June05 = Aug05 = Nov05 > Jan06 = Mar06

Jun05 = May05 > April 05 &Nov05 & Jan06 & Mar06

Mid shore: August 05 > May 05 = June 05 = Nov 05 > March 05 = Jan 06 = March 06

High shore: NS

Tidal pools: April 05 = May 05 =Aug 05 = Nov 05 > June 05 = Mar 06 > Mar 05

Time*LS*Treatment: No logical groups represented always a trend where the exclusion treatments in some dates were higher in percent of cover than procedural control and controls in other sampling dates and zones. These results are difficult to represent graphically.

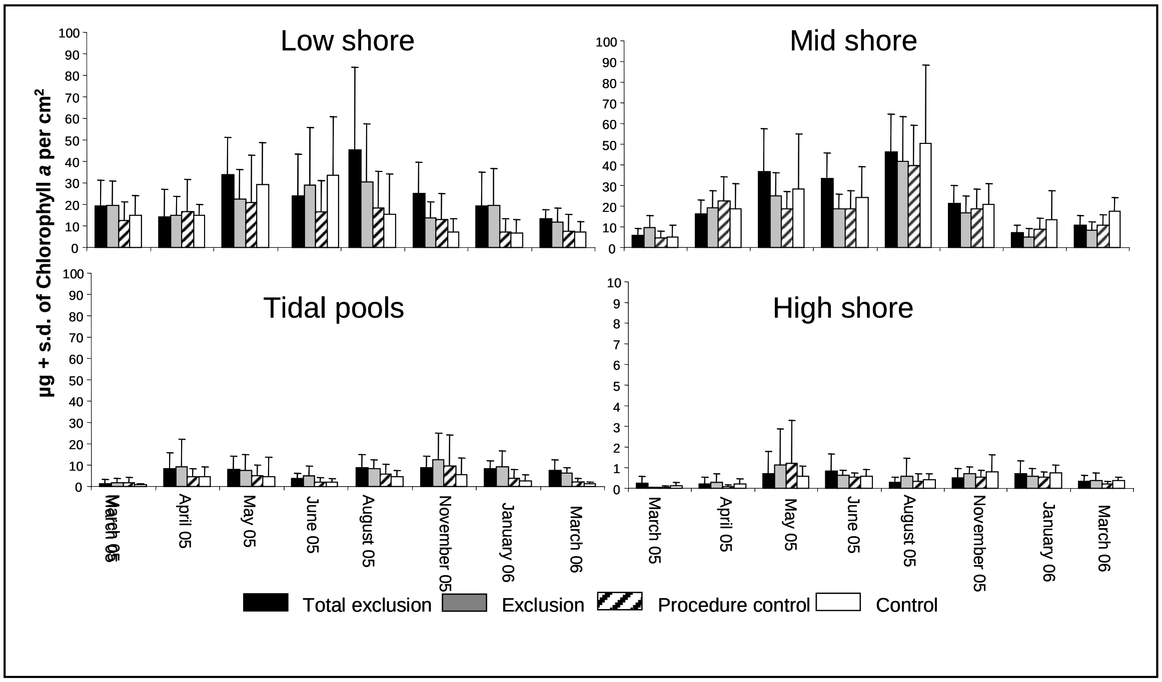

Figure 3.2. Mean + Sd. Temporal variability in the concentration of chlorophyll *a* in the treatments and at different levels on the shore. Notice a change in the scale of 'y-axis' on the high shore plate.

I.3. Grazing effect at the level of algal functional groups

1.3.a. Low shore

Two functional groups were recognized on the low shore, green foliose algae, and red turfs (see methods for genus names and species). The green alga *Ulva rigida* was affected by grazers, but there were no differences among the effects of macro, meso and micro grazers producing effects on the low shore, because there were no differences between total exclusion and simple exclusion (Table 3.3). There was significant temporal variation in the cover of *U. rigida*, with greater cover during the first than the later months. Red turfs were not affected by grazers. Their cover increased with time, the last sampling dates (March and January 2006) exhibiting greater cover (Table 3.3 and Fig. 3.3).

Table 3.3. RM-ANOVA of functional groups of algae, on the low shore during 2005. The data were arcsin(square root (x+1)) transformed to achieve homogeneity and normality. * means P < 0.025, ** P < 0.001, *** P < 0.0001 and NS non-significant. †One sampling date for red turf was removed to run ANOVA because there was no algal recruitment.

	Foliose (*Ulva rigida)*			**Red turfs**		
Factors	**DF**	**MS**	**F**	**DF**	**MS**	**F**
Treatment	**3**	**2.89**	**6.9****	**3**	**0.27**	**0.83NS**
Error	**32**	**0.42**		**32**	**0.32**	
Time	**8**	**3.74**	**30.9*****	**7†**	**2.54**	**27.52*****
Time*Treat	**24**	**0.12**	**1.37NS**	**21**	**0.19**	**2NS**
Error	**256**	**0.121**		**224**	**0.094**	
Cochran C test	**P > 0.05**			**P > 0.05**		
Treatment	**ET=T>Pc=C**			**NS**		
Time	**Mar05=Apr05=May05>Mar06>Jun05=Aug05=Sep05=Nov05=Jan06**			**Mar06>Jan06>Jun05=Aug05=Sep05=Nov05>May05=Mar05**		
Time*Treat	**NS**			**NS**		

ET: total exclusion, T: exclusion for macro and mesograzers, Pc: procedural control, C: control treatment or open areas.

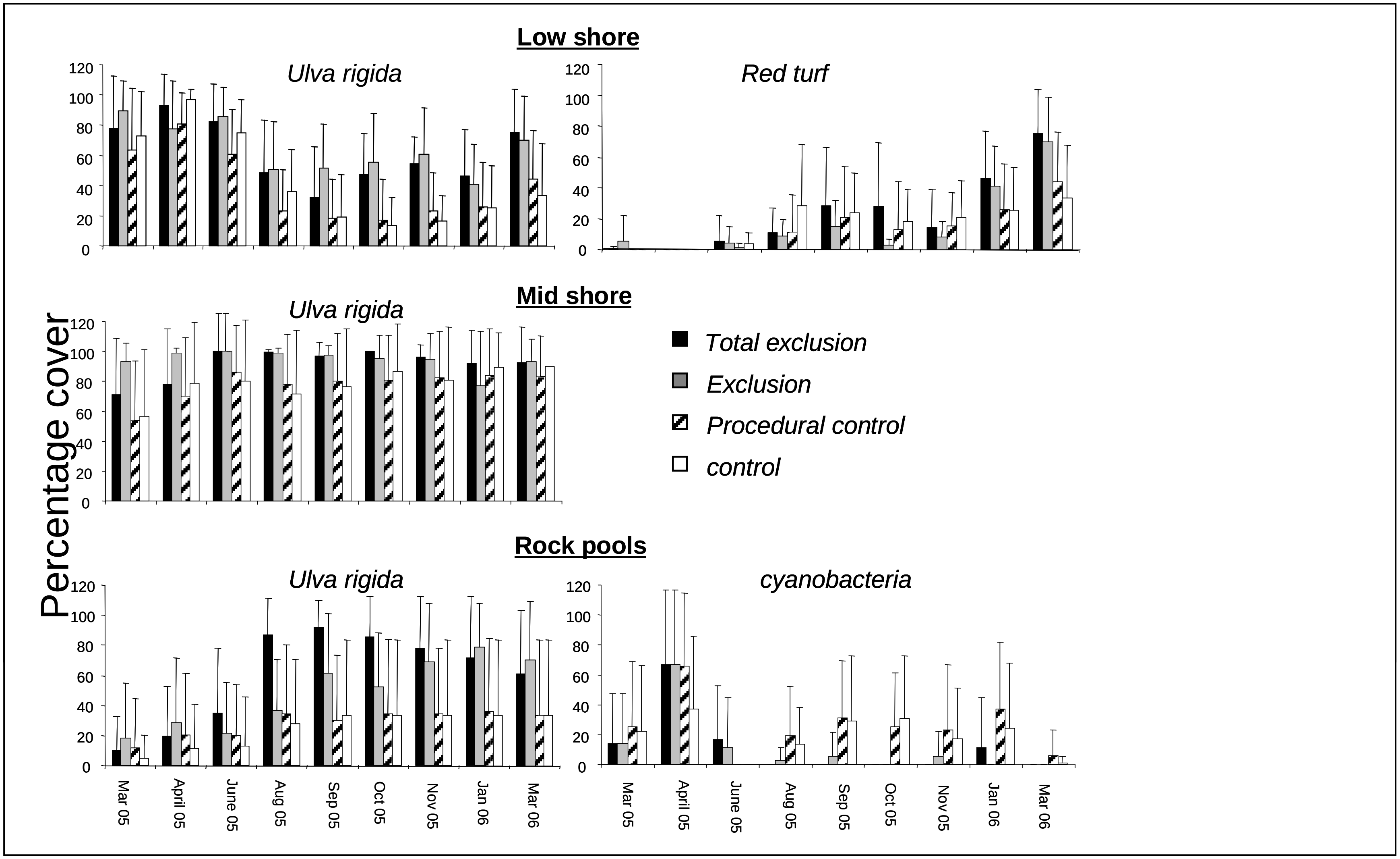

Figure 3.3. Mean + Sd. Temporal variability of cover of the main algal groups observed during the experiment in every zone.

1.3.b. Mid shore

Ulva rigida was the only algal species observed and was not affected by grazing, with minimal temporal variability in cover. The lowest cover was at the beginning of the experiment (Table 3.4 and Fig. 3.3).

Table 3.4. RM-ANOVA to detect grazing effects on the functional algal groups on the mid shore. Only *Ulva rigida* was observed in the experimental treatments. The data were arcsin(square root (x+1)) transformed to achieve homogeneity and normality. * means P < 0.025, ** P < 0.001 and *** P < 0.0001 and NS non-significant differences.

	Foliose (*Ulva rigida)*		
Factors	**DF**	**MS**	**F**
Treatment	**3**	**1.85**	**2.12NS**
Error	**36**	**0.88**	
Time	**8**	**0.48**	**5.32*****
Time*Treat	**24**	**0.12**	**1.3NS**
Error	**288**	**0.09**	
Cochran C test	**P > 0.05**		
Treatment	**NS**		
Time	**Apr05=May05=Jun05=Aug05=Sep05=Nov05=Jan06=Mar06>Mar05**		
Time*Treat	**NS**		

1.3.c. High shore and tidal pools

On the high shore, no macroalgae were observed to recruit in any of the experimental treatments at any time, nor was cyanobacteria cover quantifiable from photographs.

In tidal pools on the high shore, *Ulva rigida* was the dominant species in this habitat, though a black film of cyanobacteria and blue green algae was observed in the treatments.

Macroalgae *Endarachne* sp and *Colpomenia sinuosa* were sporadically observed in tidal pools, but these algae disappeared rapidly (within 2 weeks) and their cover was always lower than 5%.

The dominant foliose alga *Ulva rigida* was affected by grazers. In addition, there was a slight variation in the cover of *U. rigida* once it settled, with March of 2005 exhibiting lower cover than the rest of the sampling dates (Table 3.5).

The another conspicuous algal group was a black film comprising cyanobacteria species such as *Gleocapsa* spp., *Aphanocapsa* spp., *Chroococus* spp. among other blue green groups which could not be identified. This functional group was not affected by grazers, and exhibited a peak in cover in April 2005 (Table 3.5 and Fig. 3.3).

Table 3.5. RM-ANOVA to detect grazing effects on the main algal groups on the high shore tidal pools. Only *Ulva rigida* and cyanobacteria films were observed in the experimental treatments. The data were arcsin (square root (x+1)) transformed to achieve homogeneity and normality. * means P < 0.025, ** P < 0.001, *** P < 0.0001 and NS non-significant.

	Foliose (*Ulva rigida)*			**Cyanobacteria**		
Factors	**DF**	**MS**	**F**	**DF**	**MS**	**F**
Treatment	**3**	**5.35**	**3.66***	**3**	**0.97**	**1.51NS**
Error	**32**	**0.46**		**32**	**0.64**	
Time	**8**	**2.65**	**12.22*****	**8**	**2.41**	**13.14*****
Time*Treat	**24**	**0.33**	**1.21NS**	**24**	**0.25**	**1.36NS**
Error	**256**	**0.22**		**256**	**0.18**	
Cochran C test	**P > 0.05**			**P > 0.05**		
Treatment	**ET=T>Pc=C**			**NS**		
Time	**the rest of sampling dates were similar>Mar05**			**Apr05>the rest of sampling dates were similar**		
Time*Treat	**NS**			**NS**		

II. Experiment 2. Grazing effects across the shore

II.1 Relationships among physical and biological factors

Three different functional groups of algae were recognized along the transect: red turf was located at the lower part of the transect (elevation: below 0 meters from C.D. to 0.51 m above C.D., water movement 10.7 ± 1.1 g/day and distance from sea: below 0 to 5 m above MLWS); foliose green algae was represented by *Ulva rigida* (elevation: below 0 to 1.21 meters above C.D., entire range of water movement and distance from sea: below 0 to 43 meters). Red foliose algae represented by *Porphyra capensis*. This alga was found at elevations: 0.63 to 1.21 meters above C.D., at water movement of 93 ± 75.5 g/day, and distance from sea between 24 and 43 meters from MLWS.

Macrograzers were found below 0 to 0.84 meters above C.D., coinciding with the ranges of *U. rigida* and red turf. Mesograzers were found between 0 to 1.43 m above C.D. and 0 to 50 meters from MLWS, but the highest abundances were at 43 meters from MLWS, and an average of 1.04 ± 0.2 above C.D.. The range of mesograzers overlapped *U. rigida* and *P. capensis*. Micrograzers were found from 44 to 54 m from MLWS.

The factors analyzed along the transect were correlated among themselves in order to understand the relationships among factors (distance from the sea, elevation of substratum and water movement), and their relationships with macro, meso and micrograzers). The relationships observed were highly significant in most cases. These relationships showed the anticipated positive relationships between: distance from the sea and elevation and micrograzers (which inhabit the higher part of the shore). Distance from the sea was negatively correlated with water movement and macrograzers (Table 3.6). No relationship was found between mesograzers and distance from the sea, elevation or water movement (Table 3.6). Negative relationships were found between macrograzers and mesograzers, between macrograzers and micrograzers, and finally between meso and micrograzers (Table 3.6).

Table 3.6. Correlation among the factors across the shore, results from Spearman correlations. N = 54 in all cases.

Correlations	R^2	t	P
Dist. from sea v/s Macrograzers	0.53	-7.6	0.00001
Dist. from sea v/s Mesograzers	0.04	1.4	0.16
Dist. from sea v/s Micrograzers	0.37	5.5	0.00001
Dist. from sea v/s Water movement	0.59	-8.8	0.00001
Dist. from sea v/s Elevation	0.74	12.3	0.00001
Macrograzers v/s Mesograzers	0.13	-2.8	0.006
Macrograzers v/s Micrograzers	0.08	-2.2	0.03
Macrograzers v/s Water movement	0.37	5.6	0.00001
Macrograzers v/s Elevation	0.42	-6.12	0.00001
Mesograzers v/s Micrograzers	0.1	-2.37	0.02
Mesograzers v/s Water movement	0.07	-2.0	0.06
Mesograzers v/s Elevation	0.1	0.76	0.44
Micrograzers v/s Water movement	0.13	-2.73	0.0002
Micrograzers v/s Elevation	0.22	3.9	0.0002
Water movement v/s Elevation	0.3	-4.8	0.00001

II.2. Grazing effects across the shore: effects on different algal functional groups

ANCOVA and RM-ANOVA were used together to confirm each others results about grazing effects. No grazing effect was detected using ANCOVA or RM-ANOVA for red turf (Tables 3.7 and 3.8). Additionally, the covariate elevation was significant during September and October of 2005 and during May 2006.

Grazing effects were detected only for *Ulva rigida* using ANCOVA on all four sampling dates (Table 3.8 and 3.9). RM-ANOVA for *U. rigida* detected grazing effects too, specifically in October 2005 and January 2006 through the interaction between Time and Treatment. RM-ANOVA also showed the maximum cover of *U. rigida* was reached in January 2006. The covariate distance from the sea was significant for September and October of 2005.

No grazing effect was detected for *Porphyra capensis* using ANCOVA or RM-ANOVA, (Tables 3.8 and 3.10).

II.3. Factors affecting grazing effects: multiple regression approach

Different physical factors fluctuated in time, affecting grazing effects on red turf, *Ulva rigida* and *Porphyra capensis*, because grazing effects were represented using the effect size, the positive and negative relationships between effect size and any factor must be interpreted in an inverse way.

In order to detect which factors contributed to the variability of grazing effects on algal functional groups along the transect, multiple regressions were done. Elevation was important for grazing effects on red turf during January 2006 (Table 3.11) and mesograzers increased the grazing effect on *U. rig*ida during October 2005 (Table 3.12).

Table 3.7. Analysis of covariance during the 4 sampling dates on the transect for red turfs. Bonferroni correction was used to avoid dependence due to time and algal groups (4 dates and 3 algal groups: α = 0.05/7=0.007). * means P < 0.007, ** P < 0.001, *** P < 0.0001 and NS non-significant.

	6th September 2005			8th October 2005			6th January 06			21th May 06		
	DF	MS	F	DF	MS	F	DF	MS	F	DF	MS	F
Dist. from Sea	1	0.007	0.39NS	1	0.004	0.61NS	1	0.005	0.5NS	1	0.001	0.54NS
Macrograzers	1	0.02	1.08NS	1	0.04	4.94NS	1	0.002	0.2NS	1	0.08	3.62NS
Mesograzers	1	0.04	2.33NS	1	0.02	2.8NS	1	0.02	0.97NS	1	0.03	1.6NS
Micrograzers	1	0.002	0.13NS	1	0.0004	0.06NS	1	0.0004	0.04NS	1	0.003	0.16NS
Water movement	1	0.003	0.19NS	1	0.01	1.62NS	1	0.001	0.11NS	1	0.004	0.2NS
Elevation	1	0.24	12.5**	1	0.09	13.2**	1	0.069	6.4NS	1	0.26	11.4**
Treatment	2	0.01	0.71NS	2	0.009	1.22NS	2	0.012	1.19NS	2	0.01	0.61NS
Error	153	0.02		153	0.0073		153	0.01		153	0.02	
Cochran C test:	P > 0.05			P > 0.05			P > 0.05			P > 0.05		
Post Hoc Test												
Treatment:	NS			NS			NS			NS		

Table 3.8. RM-ANOVA on the transect for the foliose algal groups represented by Red turfs, *Ulva rigida* and *Porphyra capensis*. The data were arcsin (square root (x+1)) transformed to achieve homogeneity and normality. * means P < 0.025, ** P < 0.001, *** P < 0.0001 and NS non-significant.

	Red Turf			**Foliose (*Ulva rigida)***			***Porphyra capensis***		
Factors	**DF**	**MS**	**F**	**DF**	**MS**	**F**	**DF**	**MS**	**F**
Treatment	**2**	**0.02**	**0.59NS**	**2**	**16.2**	**16.9*** **	**2**	**0.01**	**0.59NS**
Error	**159**	**0.04**		**159**	**0.96**		**159**	**0.02**	
Time	**3**	**0.02**	**2.06NS**	**3**	**2.18**	**19.4*** **	**2[†]**	**0.07**	**6.4** **
Time*Treat	**6**	**0.00**	**0.79NS**	**6**	**0.43**	**3.9** **	**4**	**0.00**	**0.25NS**
Error	**477**	**0.01**		**477**	**0.11**		**318**	**0.01**	
Cochran C test	**P > 0.05**			**P > 0.05**			**P > 0.05**		
Treatment	**NS**			**T>Pc=C**			**NS**		
Time	**NS**			**Jan06>Oct05>Sept05=May06**			**Sept05>Oct05>Jan06[†]**		
Time*Treat	**NS**			**Sept05: NS** **Oct05: T > Pc =C** **Jan06:T > Pc =C** **May06: NS**			**NS**		

[†] There was no cover during May 06, therefore this sample was omitted

Table 3.9. Analysis of covariance during the 4 sampling dates on the transect for the alga *Ulva rigida*. Bonferroni correction was used to avoid dependence in time and algal groups (4 samples and 3 algal groups: $\alpha = 0.05/7 = 0.007$). * means $P < 0.007$, ** $P < 0.001$, *** $P < 0.0001$ and NS non-significant.

	6th September 2005			**8th October 2005**			**6th January 06**			**21st May 06**		
	DF	**MS**	**F**	**DF**	**MS**	**F**	**DF**	**MS**	**F**	**DF**	**MS**	**F**
Dist. from Sea	**1**	**2.84**	**15.55*** ***	**1**	**2.06**	**8.8***	**1**	**0.75**	**3.7NS**	**1**	**0.03**	**0.14NS**
Macrograzers	**1**	**0.13**	**0.73NS**	**1**	**0.51**	**2.2NS**	**1**	**0.59**	**2.9NS**	**1**	**0.29**	**1.38NS**
Mesograzers	**1**	**0.29**	**1.6NS**	**1**	**0.22**	**0.93NS**	**1**	**0.43**	**2.2NS**	**1**	**0.6**	**2.88NS**
Micrograzers	**1**	**0.07**	**0.38NS**	**1**	**0.05**	**0.23NS**	**1**	**0.41**	**2.0NS**	**1**	**0.2**	**0.95NS**
Water movement	**1**	**0.01**	**0.09NS**	**1**	**0.03**	**0.12NS**	**1**	**0.11**	**0.6NS**	**1**	**0.32**	**1.55NS**
Elevation	**1**	**0.11**	**0.63NS**	**1**	**0.00**	**0.11NS**	**1**	**0.79**	**3.9NS**	**1**	**0.85**	**4.05NS**
Treatment	**2**	**3.25**	**17.8*****	**2**	**6.8**	**29.2*****	**2**	**6.13**	**30.5*****	**2**	**1.45**	**6.1****
Error	**153**	**0.18**		**153**	**0.23**		**153**	**0.2**		**153**	**0.24**	
Cochran C test: P > 0.05				**Cochran C test: P > 0.05**			**Cochran C test: P > 0.05**			**Cochran C test: P > 0.05**		
Post Hoc Test												
Treatment: T > Pc =C				**T > Pc =C**			**T > Pc =C**			**T > Pc =C**		

Table 3.10. Analysis of covariance during the four temporal 4 sampling dates on the transect for the alga *Porphyra capensis*. Bonferroni correction was used to avoid dependence in time and algal groups (4 samples and 3 algal groups: α = 0.05/7=0.007). * means P < 0.007, ** P < 0.001, *** P < 0.0001 and NS non-significant.

	6th September 2005			8th October 2005			6th January 06			21st May 06		
	DF	MS	F	DF	MS	F	DF	MS	F	DF	MS	F
Dist. from Sea	1	0.001	0.07NS	1	0.005	0.41NS	1	0.007	1.23NS	no cover		
Macrograzers	1	0.02	0.84NS	1	0.02	1.42NS	1	0.000	0.00NS			
Mesograzers	1	0.11	5.8NS	1	0.001	0.09NS	1	0.001	0.23NS			
Micrograzers	1	0.03	1.7NS	1	0.03	2.8NS	1	0.000	0.02NS			
Water movement	1	0.02	0.9NS	1	0.00	0.006NS	1	0.01	2.33NS			
Elevation	1	0.004	0.25NS	1	0.00	0.09NS	1	0.00	0.00NS			
Treatment	2	0.012	0.65NS	2	0.00	0.03NS	2	0.00	0.58NS			
Error	153	0.02		153	0.01		153	0.005				
Cochran C test:	P > 0.05			P > 0.05			P > 0.05					
Post Hoc Test												
Treatment:	NS			NS			NS					

Table 3.11. Multiple regressions between effect size for grazing effects on red turfs and the abiotic and biotic factors. Bonferroni correction was used to avoid dependence in time and algal groups (4 samples and 3 algal groups: $\alpha = 0.05/7=0.007$). * means $P < 0.007$, ** $P < 0.001$, *** $P < 0.0001$ and NS non-significant. Values are in percentages of contribution to grazing effect. Effects were either positive (+) or negative (-).

Independent variables	**dependent variable**			
	6th September 2005	**8th October 2005**	**6th January 06**	**21st May 06**
Distance from Sea	**ns**	**ns**	**ns**	**ns**
Macrograzers	**ns**	**ns**	**ns**	**ns**
Mesograzers	**ns**	**ns**	**ns**	**ns**
Micrograzers	**ns**	**ns**	**ns**	**ns**
Water movement	**ns**	**ns**	**ns**	**ns**
Elevation	**ns**	**ns**	**(-)16**	**ns**
ANOVA summary				
Source			**$F_{1,52} = 11.6$**	**.**
Regression MS	**.**	**.**	**4.64**	**.**
Residual MS	**.**	**.**	**0.4**	**.**
P	**.**	**.**	**<0.001**	**.**
Multiple R^2	**.**	**.**	**0.16**	**.**

Table 3.12. Multiple regressions between effect size for grazing effects on *Ulva rigida* and the abiotic and biotic factors. Bonferroni correction was used to avoid dependence in time and algal groups (4 samples and 3 algal groups: $\alpha = 0.05/7=0.007$). * means $P < 0.007$, ** $P < 0.001$, *** $P < 0.0001$ and NS non-significant. Values are in percentages of contribution to grazing effect. Effects were either positive (+) or negative (-).

Independent variables	**dependent variable**			
	6th September 2005	**8th October 2005**	**6th January 06**	**21st May 06**
Distance from Sea	**ns**	**ns**	**ns**	**ns**
Macrograzers	**ns**	**ns**	**ns**	**ns**
Mesograzers	**ns**	**(-)25**	**ns**	**ns**
Micrograzers	**ns**	**ns**	**ns**	**ns**
Water movement	**ns**	**ns**	**ns**	**ns**
Elevation	**ns**	**ns**	**ns**	**ns**
ANOVA summary				
Source		$F_{1,52} = 17.3$	**.**	**.**
Regression MS	**.**	**56.1**	**.**	**.**
Residual MS	**.**	**3.24**	**.**	**.**
P	**.**	**<0.001**	**.**	**.**
Multiple R^2	**.**	**0.25**	**.**	**.**

Table 3.13. Multiple regressions between effect size for grazing effects on *Porphyra capensis* and the abiotic and biotic factors. Bonferroni correction was used to avoid dependence in time and algal groups (4 samples and 3 algal groups: α = 0.05/7=0.007). * means P < 0.007, ** P < 0.001, *** P < 0.0001 and NS non-significant. Values are in percentages of contribution to grazing effect. Effects were either positive (+) or negative (-).

Independent variables	dependent variable			
	6t hSeptember 2005	8th October 2005	6th January 06	21st May 06
Distance from Sea	ns	ns	ns	ns
Macrograzers	ns	ns	ns	ns
Mesograzers	ns	ns	ns	ns
Micrograzers	ns	ns	ns	ns
Water movement	ns	ns	ns	ns
Elevation	ns	ns	ns	ns
ANOVA summary				
Source				
Regression MS	.	.	.	.
Residual MS	.	.	.	.
P	.	.	.	.
Multiple R^2	.	.	.	.

II.4. Spatial structure of *Ulva rigida* in the exclusion treatments

The only alga analyzed in terms of spatial structure across the shore was *Ulva rigida*, because this was the only one exhibiting grazing effects, additionally the other algal groups exhibited replication too low to allow a robust analysis. The spatial structure of *Ulva rigida* in areas exhibited significant heterogeneity with two scaling region in September 2005, three scaling regions in October 2005, two scaling regions in January 2006 and one scaling region at the end of the experiment in May 2005 (Table 3.14 and Fig. 3.4). Most of the scaling regions exhibited fractal dimensions that suggest patchy distribution ($1.5 < D < 1.97$) of this alga across the shore. In September 2005 at scales between 11 to 27 m there was a trend-like distribution of this alga, with a fractal dimension of $D = 1.45$. All the semivariograms indicated that variability between blocks increased as the distance between lags increased (Table 3.14 and Fig. 3.4).

II.5. Spatial structure of physical and biotic factors along the transect

Elevation showed high heterogeneity, represented by three positive scaling regions. Two of these scaling regions exhibited patchy spatial patterns represented by fractal dimensions of 1.75 and 1.57 (Table 3.15). Only one scaling region showed a trend-like spatial pattern, with a value for the fractal dimension of $D = 1.01$.

Water movement showed two positive scaling regions with fractal dimension of 1.74 and 1.45 denoting a patchy and trend-like spatial pattern, respectively.

Each of the three grazer classes exhibited a single positive scaling region, with a fractal dimension indicating patchy distribution. For Macrograzers D was 1.78, while meso and micrograzers each had a fractal dimension of $D = 1.74$ (Table 3.15 and Fig. 3.5).

Grazing effects represented as effect sizes on *Ulva rigida* exhibited different spatial patterns with time: there was one positive spatial scale during September and October 2005, two spatial scales (one positive and one negative) in January 2006, and finally a random pattern during May 2006 (Table 3.15 and Fig. 3.6).

Table 3.14 Regression exponents of the double logarithmic semivariograms, and fractal dimensions (D) for the different spatial scales of % of cover of *Ulva rigida* in the exclusion treatments at different times. * means P < 0.01, ** < 0.001, *** P < 0.0001 and NS non significant.

Transect	Scale (m)	Slope	SE	R^2	t (df=25)	D	Spatial pattern
% Ulva in Exclusions September 2005	**1.00-54.0**	**0.53**	**0.05**	**0.81**	**10.35*****	**1.73**	**dependent**
% Ulva in exclusions October 2005	**1.00-54.0**	**0.65**	**0.03**	**0.95**	**21.2*****	**1.67**	**dependent**
% Ulva in exclusions January 2006	**1.00-54.0**	**0.67**	**0.03**	**0.94**	**19.7*****	**1.67**	**dependent**
% Ulva in exclusions May 2006	**1.00-54.0**	**0.17**	**0.04**	**0.46**	**4.6*****	**1.91**	**dependent**
Significant multiple scaling regions							
Ulva September 2005	**1.00-10.00**	**0.21**	**0.04**	**0.75**	**4.96(8)****	**1.90**	**Patchy**
	11.0-27.00	**1.1**	**0.09**	**0.90**	**12.2(15)*****	**1.45**	**Trend**
Ulva October 2005	**1.00-5.00**	**0.24**	**0.03**	**0.94**	**7.2(3)****	**1.88**	**Patchy**
	6.00-13.00	**0.92**	**0.06**	**0.97**	**14.7(6)*****	**1.54**	**Patchy**
	14.0-27.00	**0.62**	**0.05**	**0.92**	**12.4(12)*****	**1.69**	**Patchy**
Ulva January 2006	**1.00-13.00**	**0.64**	**0.08**	**0.86**	**8.34(11)*****	**1.68**	**Patchy**
	14.0-27.00	**0.41**	**0.05**	**0.84**	**7.9(12)*****	**1.80**	**Patchy**

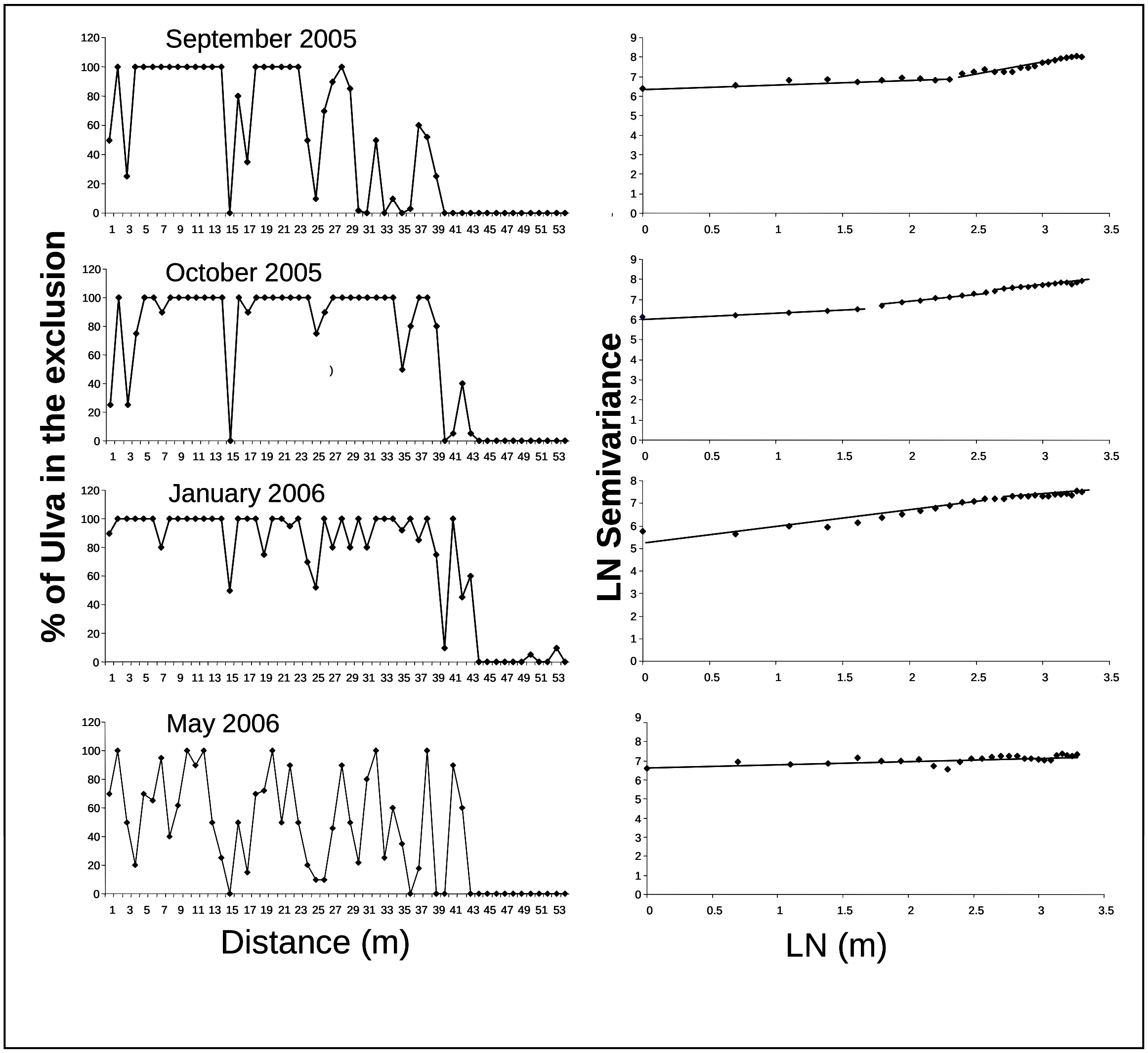

Figure 3.4. Percentage of cover in the exclusion treatment across the shore and in the second column the semivariogram. The regression lines indicate significant scaling regions.

Table 3.15. Regression exponents of the double logarithm semivariograms, and fractal dimension (D) for the different spatial scales in the physical factors (elevation, water movement), and the biotic factors (density of macro, meso, micorgrazers), and the effect of grazing represented by the effect size (ER) for *Ulva rigida* at different sampling dates.

Transect	Scale (m)	Slope	SE	R^2	t (df=25)	D	Spatial pattern
Factors							
Elevation	1.00-54.0	0.65	0.05	0.88	14.06***	1.67	dependent
Water movement	1.00-54.0	0.59	0.04	0.89	13.95***	1.74	dependent
Density macrograzers	1.00-54.0	0.44	0.06	0.73	7.8***	1.78	dependent
Density mesograzers	1.00-54.0	0.52	0.03	0.92	16.89***	1.74	dependent
Density micrograzers	1.00-54.0	0.53	0.04	0.88	13.81***	1.74	dependent
ER Ulva September 2005	1.00-54.0	0.22	0.03	0.67	7.23***	1.89	dependent
ER Ulva October 2005	1.00-54.0	0.26	0.04	0.74	5.6***	1.87	dependent
ER Ulva January 2006	1.00-54.0	0.01	0.06	0.00	0.22NS	1.98	dependent
ER Ulva May 2006	1.00-54.0	-0.00	0.03	0.00	-0.019NS	1.99†	independent
Significant multiple scaling regions							
Elevation	1.00-17.0	0.49	0.03	0.93	15.34(15)***	1.75	Patchy
	18.0-23.0	2.49	0.09	0.99	20.4(4)***	1.01	Trend
	24.0-27.0	0.84	0.17	0.98	10.4(2)***	1.57	Patchy
Water movement	1.00-8.00	0.39	0.04	0.87	10.3(15)**	1.80	Patchy
	9.00-27.0	1.08	0.16	0.83	6.83(8)***	1.45	Trend
†ER Ulva January 2006	1.00-10.0	0.4	0.04	0.93	10.7(8)***	1.79	Patchy
	11.0-27.0	-0.75	0.13	0.69	-5.83(15)***	1.63	Patchy

† scaling regions detected

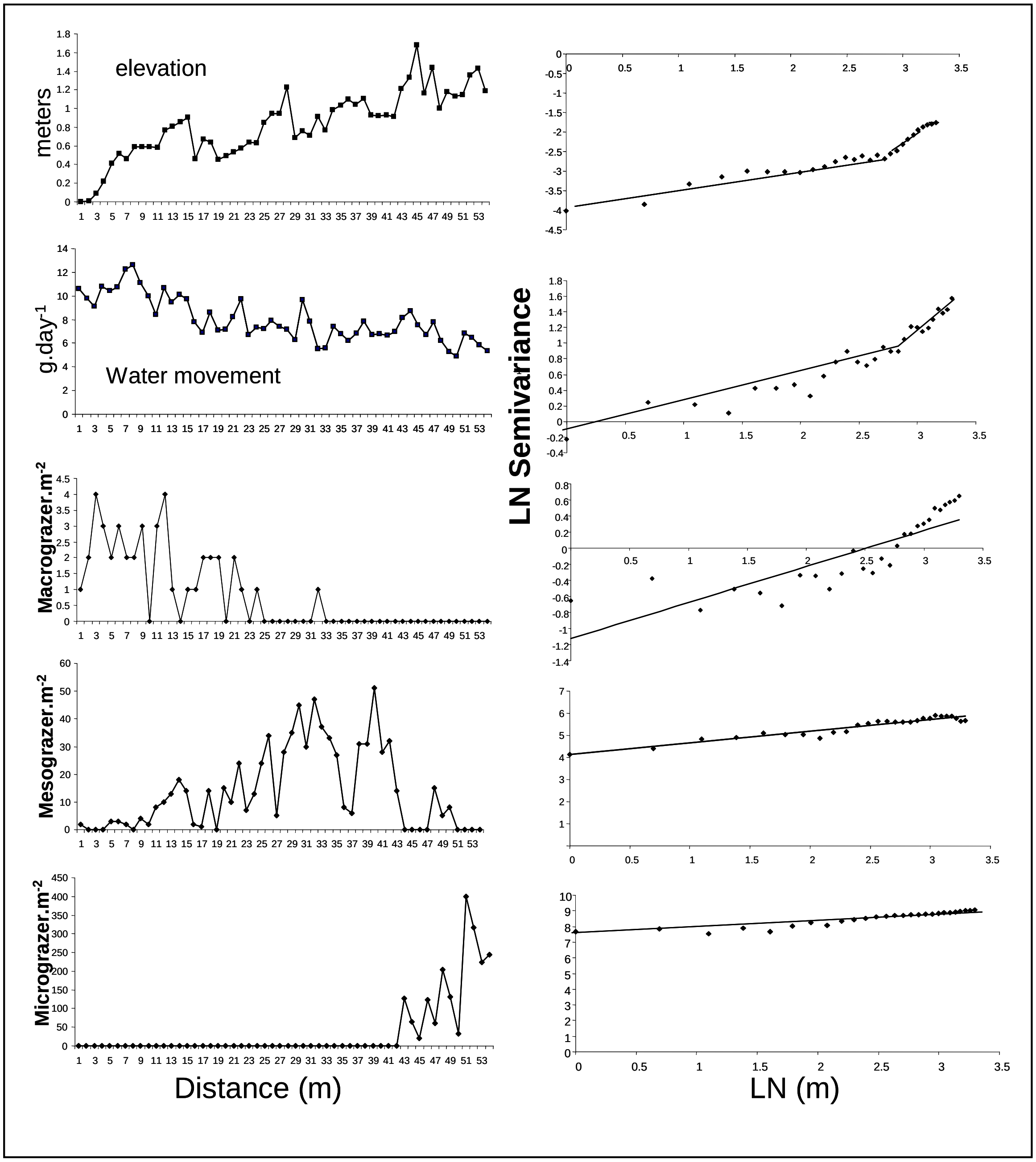

Figure 3.5. Distribution of differences in elevation from C.D., water movement, density of macro, meso and micrograzers. The second column shows the semivariograms. Regression lines indicates significant scaling regions.

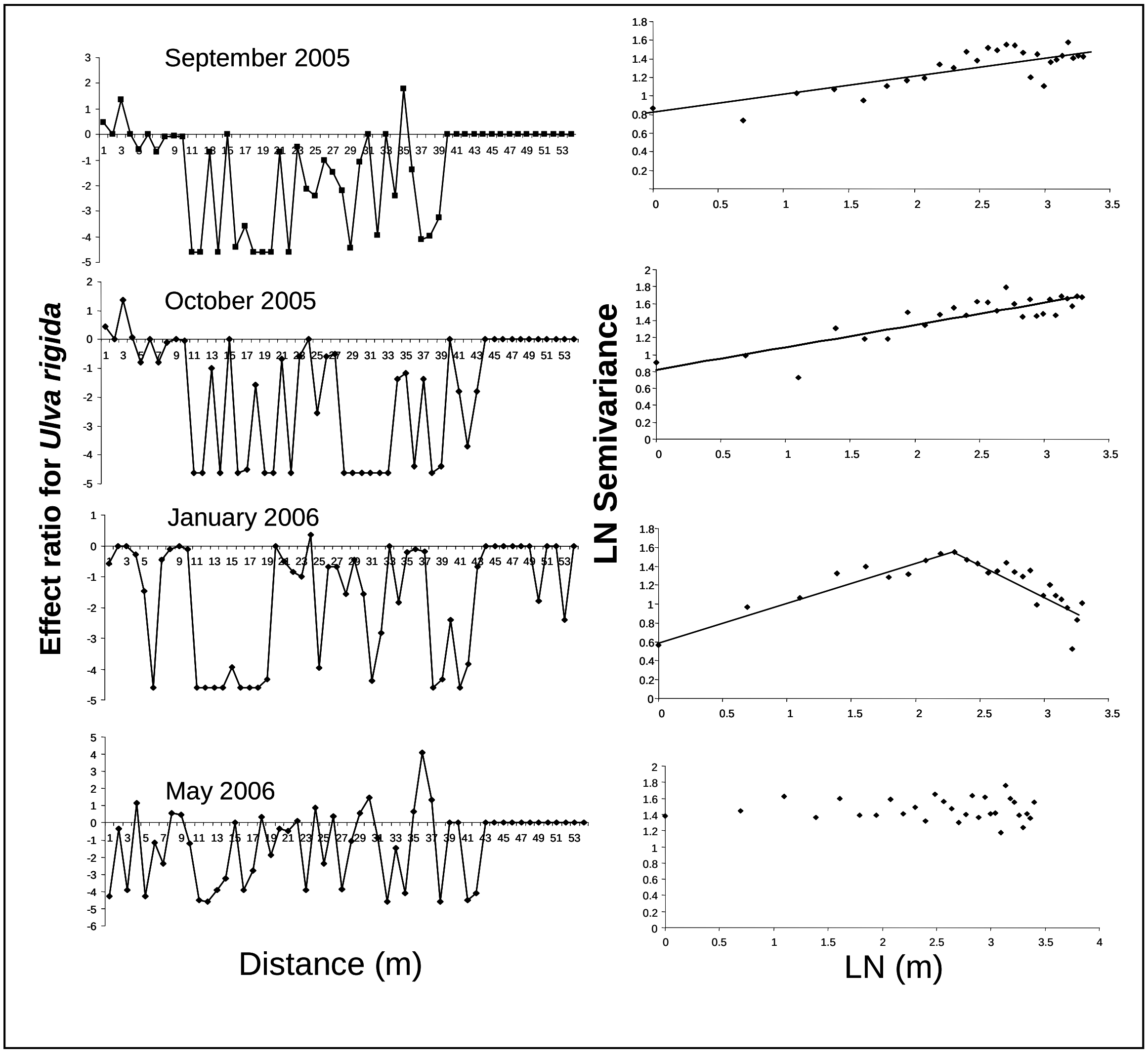

Figure 3.6. Distribution of effect sizes for *Ulva rigida* during four temporal samplings. The second column represents the semivariograms. The regression lines indicate significant scaling regions.

II.6. Factors affecting effects of grazing for *Ulva rigida*, analysed using cross-semivariograms

Different physical factors affected grazing effects on *Ulva rigida* represented by the effect size at different times. In September 2005, elevation and micrograzers decreased the level of grazing, while mesograzers increased it (Table 3.16 and Fig. 3.7). In October 2005, water movement, macrograzers and micrograzers diminished the grazing effect on *Ulva rigida*, though again mesograzers increased it, though across in a wider range of scales than in September (Table 3.16 and Fig. 3.7). In January 2006, micrograzers decreased the grazing effect and mesograzers increased it (Table 3.16 and Fig. 3.8). In May 2006, only macrograzers increased the grazing effect (Table 3.15 and Fig. 3.8).

Table 3.16. Summary of the general relationships between physical and biotic factors (elevation, water movement, density of macro, meso and micrograzers) and effect size for *Ulva rigida*.

Variables	**September 2005 relationship**	**October 2005 relationship**	**January 2006 relationship**	**May 2006 relationship**
Effect size v/s Elevation	**positive**	**no relationship**	**no relationship**	**no relationship**
Effect size v/s Water movement	**no relationship**	**positive**	**no relationship**	**no relationship**
Effect size v/s Macrograzers	**no relationship**	**positive**	**no relationship**	**negative**
Effect size v/s Mesograzers	**negative**	**negative**	**negative**	**no relationship**
Effect size v/s Micrograzers	**positive**	**positive**	**positive**	**no relationship**

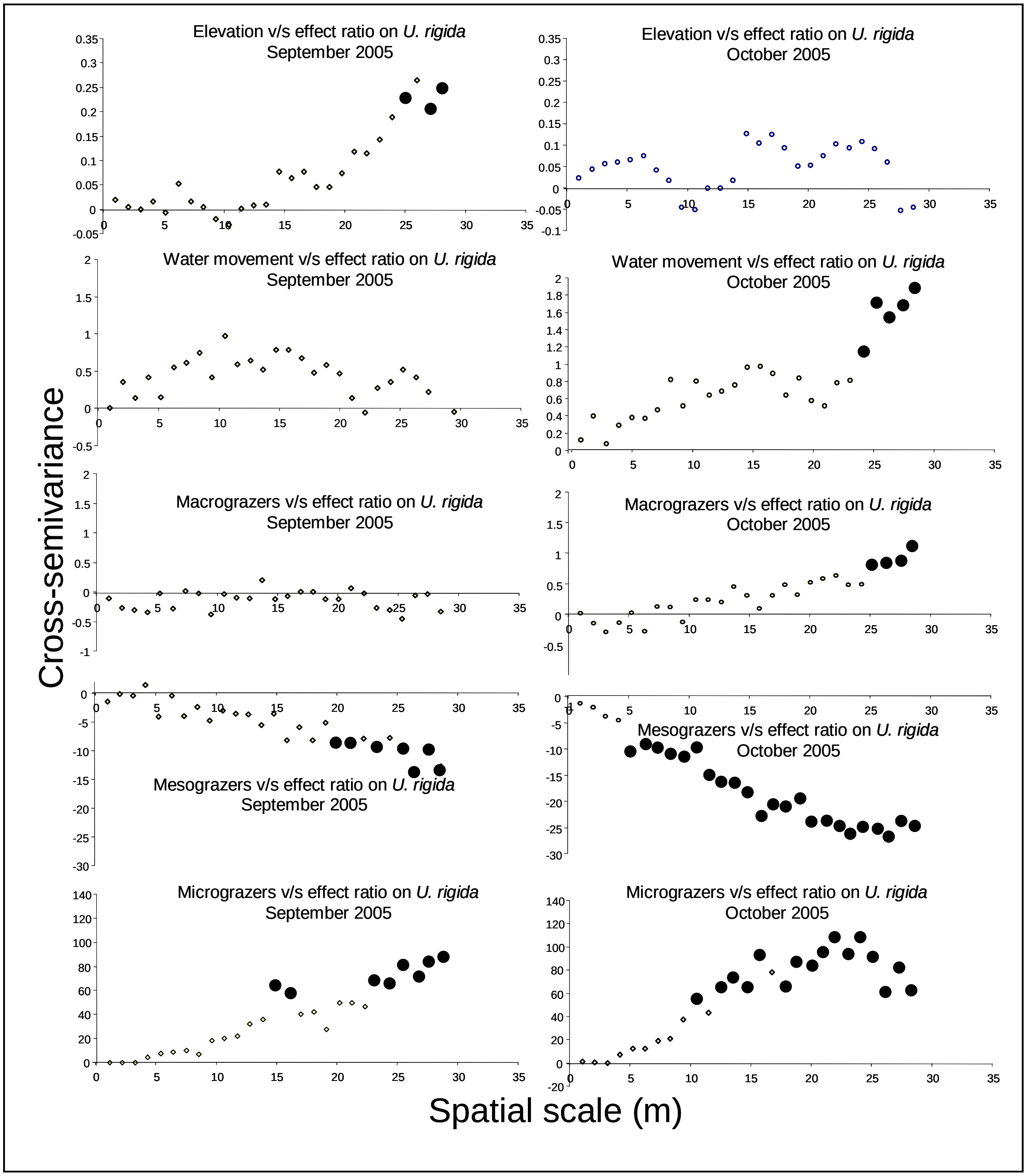

Figure 3.7. Cross-semivariograms of the relationships between effect size and physical factors (elevation and water movement), density of macro, meso, and micrograzers for 2005. Large dots indicate significant relationship at each lag. Non-significant relationships are shown in open small dots.

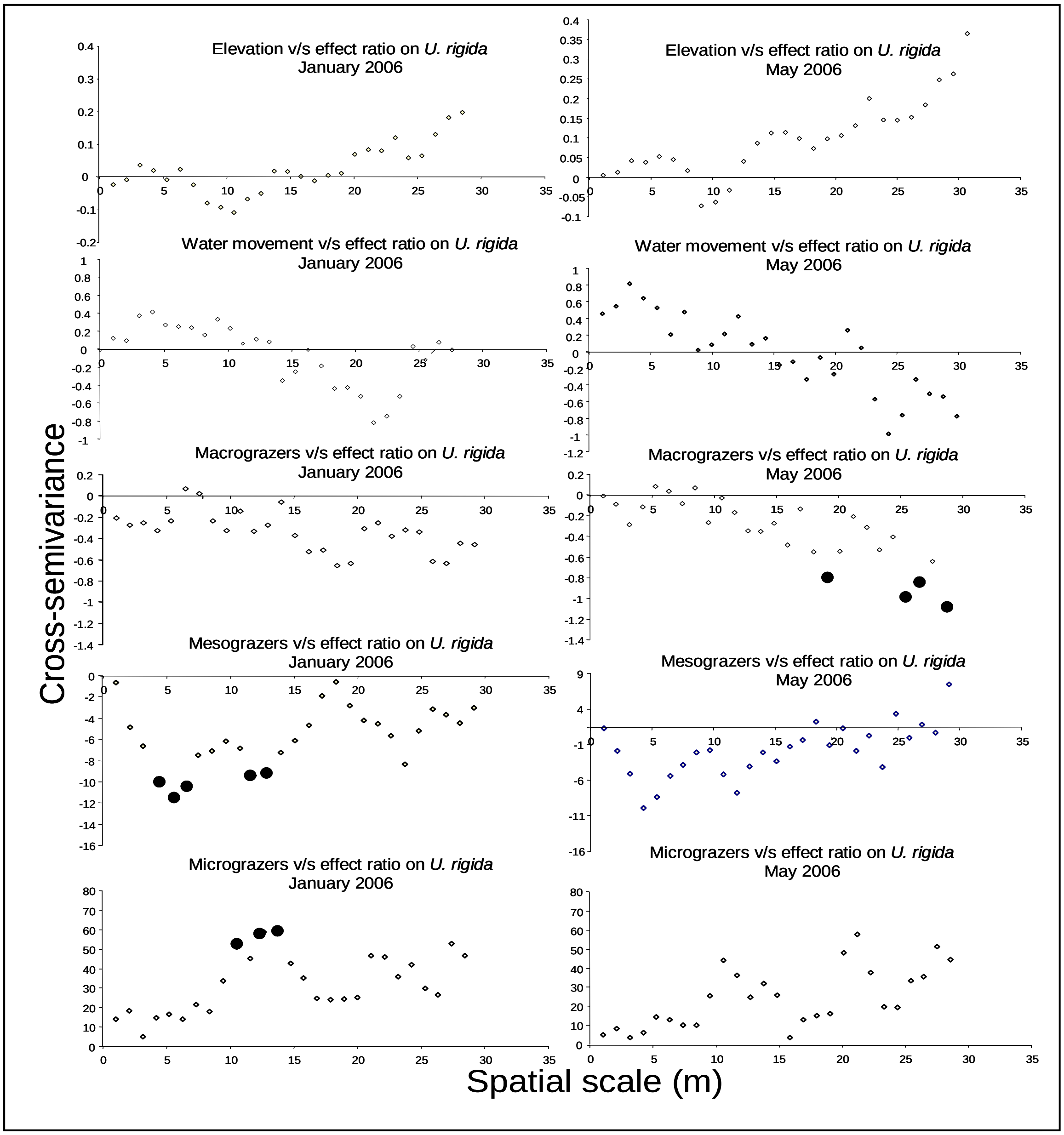

Figure 3.8. Cross-semivariograms of the relationships between effect size and physical factors (elevation and water movement), density of macro, meso, and micrograzers for 2006. Large dots indicate significant relationship at each lag. Non-significant relationships are shown in open small dots.

DISCUSSION

First, no significant differences were found between open and procedural controls, indicating that there was no introduction of artifacts due to the paint or the fences.

Grazing effects were examined across the shore using two types of experimental designs, which complement each other. Throughout a one year period, this study assessed the effects of grazing and the spatial structure of early algal succession during recovery from sterilization (complete removal of algal assemblages), across all zones of the rocky shore.

The experiment 1 comprised two types of exclusion treatments and two types of controls to determine which sizes of grazers contributed most to the algal distribution at different levels of the shore: total exclusion, which barred the entrance of any benthic grazers and simple exclusion, which permitted access to micrograzers only. The total exclusion and exclusion treatment never differed significantly form one another, but both differed significantly from the controls, in terms of both chlorophyll *a* and percentage of algal cover. This suggests that micrograzers do not play an important role in structuring algal communities across the shore examined within a year, even on the high shore as was reported by Kaehler and Froneman (2002) working on the same shore a few years before to the present study. The algal community at that level of the shore was represented by cyanobacteria, and grazers were represented by the littorinids *Nodilittorina africana* and *N. knysnaensis.* This could imply inter-annual variability in environmental conditions which could influence the proliferation of microalgae/macroalgae as it has been reported in fresh water systems by Kjeldsen et al. (1996). Similar results have been demonstrated for marine invertebrates when stochastic climatic processes can induce variability in their recruitment (Navarrete et al. 2002).

It is worth noting that the only grazers present on the high shore were littorinids, while juveniles of grazers and macrograzers co-occurred on the low and mid shore. Therefore the experimental design at different levels of the shore could have been reduced to only otal exclusion, procedural control and control, leaving out the exclusion treatments. However, to be consistent both in the field and with the balance in replication of the statistical analysis for chlorophyll *a*, I decided to work with the full experimental design.

Grazing effects were evident using both types of exclusion treatments and open and procedural controls across the shore in terms of concentration of chlorophyll *a* and algal cover across the shore, and specifically on the low shore and in tidal pools. Interestingly, the low shore is dominated by macrograzers, while mesograzers were found in minimal numbers and micrograzers were completely absent (Table 3.1). Macrograzers appeared to decrease the algal biomass (represented as chlorophyll *a*) and the cover of green foliose algae represented by *Ulva rigida*. In contrast, red turfs were not affected by macrograzers, specifically limpets of the genus *Scutellastra* spp.. In chapter II, however, red turfs were found to be dominant on this shore level at late successional stages after small-scale grazer disruptions. Red turfs did not exhibit differences in cover between exclusion treatments and controls in conditions of recovery (experiments starting with clear substrata), likely due to their late and/or slow recruitment which did not allow them to compete with *U. rigida* during the period of the study. Similarly, Boaventura et al. (2002), using grazer exclusion fences did not detect grazing effects on red turf after more than a year from the start of their experiment. Similar temporal problem has been reported by Aguilera and Navarrete (2007) working with *Mazzaella laminarioides* in the coasts of Chile. Nonetheless, that these macrograzers were able to decrease algal biomass and cover of *U. rigida* supports the study by McQuaid and Froneman (1993), which describes strong grazing effects on the low shore on the south coast of South Africa, related to the limpet *Cymbula oculus*.

On the mid shore, macrograzers and mesograzers were numerically dominant, but they did not affect the algal assemblages during the study period in terms of algal biomass and functional algal groups. Only *Ulva rigida* re-colonized each treatment in every block (including controls), and it exhibited low variability over time. The mid shore can be considered the most vulnerable to grazing for two reasons: i. wave action is weaker than on the low shore allowing mobility of grazers, and ii. desiccation stress is harsher than on the low shore weakening algal growth. The combination of low wave action and higher desiccation is likely to increase the importance of grazing (Hawkins and Hartnoll 1983, Foster 1992). My study however, high spatial variability represented as bare rock in some areas and areas with patches containing algal cover of around 100% despite the presence of two or three individuals of the macrograzer limpet *Cymbula oculus*. Whittington-Jones (1997) reported similar results at the same site. The mid shore can also be considered a mixed zone, combining benign and harsh conditions from low and high shore respectively, so that variability in the spatial variability of grazing effects is expected. This can be explained by spatial variability in primary productivity, which can have consequences for the spatial foraging of grazers. For example, microsites with low primary productivity will exhibit bare rock, because the settlement and growth of micro- and macroalgae is diminished by physical factors, such as increased desiccation in areas where the substratum is elevated. In these types of site, grazers might forage for longer periods and in larger areas in order to acquire the necessary amount of food to survive. In microsites with high primary productivity, settlement and growth of micro- and macroalgae is faster, therefore grazers do not have to search for food items over larger distances and their foraging ranges will be shorter. Under this last scenario, the substratum can exhibit large amounts of algae and the presence of grazers.

In addition on the mid shore, even in exclusion plots, *U. rigida* did not grow large and foliose as it did on the low shore or in tidal pools, and instead grew like short grass. Whittington-Jones (1997) suggested swimming grazers like amphipods were able to enter the exclusions treatments and feed on the algal tips, keeping the plants short.

Grazer effects were strong in tidal pools on the high shore and two dominant algal groups were observed re-colonizing the blocks: *Ulva rigida* and species of cyanobacteria. The grazer community was mainly represented by the limpet *Siphonaria capensis* and a number of winkles (*Oxystele* spp.) (Huggett and Griffiths 1986). The limpets and winkles significantly reduced the amount of chlorophyll *a* and the percent cover of *U. rigida* in the open areas compared to exclusion areas.

In conclusion the shore studied is dominated by *Ulva rigida*, which is strongly affected by macrograzers on the low shore and by mesograzers in shallow tidal pools. This was corroborated by the transect experiment, where mesograzers were found to affect *U. rigida* across most of the experimental transect. Therefore *U. rigida* is not restricted to any particular level on the shore. The experimental transect showed high spatial variability and unclear zonation in mesograzer effects on *U. rigida*. For example, the greatest densities of mesograzers were found between 27 to 43 m from MLWS and above 0.8-1.2 m above C.D. (Fig. 3.5). This zone corresponds to the upper part of the mid shore (upper balanoid zone as Branch and Branch 1981), and exhibited stronger grazing effects which deserve further attention (see chapters IV and V). Red turfs and *Porphyra capensis* were not found to be significantly affected by grazers using the transect across the shore (but see chapter IV).

I. Spatial structure of grazing effects across the shore

Spatial structure of the shore was investigated to describe how the variability in physical factors and densities of grazers induces patchiness in grazer effects across the shore. This study assessed the spatial structure of grazing effects across the shore using semivariograms for the first time, and their possible causes using cross-semivariograms (but see Johnson et al. 1997, 1998). These spatial procedures allowed the identification of patch distributions, gradients and random distribution of grazing effects across the shore. I found that physical factors such as elevation of the substratum, water movement and grazer densities exhibited high heterogeneity. These particular heterogeneities in abiotic factors could have influenced variation in the quality of microsites at small scales, which consequently affects algae and grazers abundances, plus the strength and spatial patterns of grazing effects. The effect of grazers in terms of effect sizes across the shore showed high heterogeneity too, but surprisingly this heterogeneity changed over time. This could be due to two components which can cause variation in grazing effects over time: firstly, temporal variation in densities of grazers across the shore and secondly, variation in algal settlement and growth across the shore. Changes in the spatial patterns of grazing effects have been explained by seasonal migration of grazers to different levels of the shore. For example, *Cellana grata* moves downward in hot months (summer) on the rocky shores of Hong Kong (Williams and Morrit 1995). It has been observed that on the south-west coast of South Africa there is a constant migration of grazers (such as *Oxystele variegata*) from low to upper shore as they reach adult size (McQuaid 1982). Such movement of grazers through zones and the changes of algal abundance across the shore could cause variability in the spatial structure of grazing effects. Similarly, seasonal changes in algal distribution across the shore have been reported by McQuaid (1985).

The analysis of the spatial patterns of *Ulva rigida* across the shore that were not influenced by grazers (in exclusion treatments) was characterized by two scaling regions between September 2005 and January 2006, while one scaling region was observed at the end of the experiment. This can be explained by *U. rigida* changing its distribution and biomass across the shore, because it extends its distribution higher up the shore in cold months and retreats down shore in hot months (McQuaid 1985).

II. Relationship between grazing effect and physical and biotic factors

The contribution of physical factors to grazing effects was tested using the variability across the shore represented by the effect size on *Ulva rigida*, examined cross-semivariograms. Mesograzers were found to be responsible for the majority of increased grazing effects on all sampling dates, with the exception of May 2006. However, with time, mesograzers interacted with other factors and grazers. The physical factors exerted a strong influence on grazing effects in the first sample dates, although by the end of the experiment only the effects of macrograzer density significantly influenced grazing effects (Table 3.16). In contrast, multiple regressions detected that the only significant contribution to the variability of grazing effects for *U. rigida* in October 2005 was the density of mesograzers, while the rest of the factors were not significant. This disparity can be explained by the limited linear behaviour of the independent and dependent variables in the multiple-regressions. When this assumption is not fulfilled, multiple-regression does not show significant dependency, even though the results can be dependent in a non-linear way (Sokal and Rohlf 1995). Despite the divergence between statistical methods, both methods pointed out the importance of mesograzers as the main cause of variability in grazing effects across the shore, suggesting mesograzers are the crucial factor structuring the algal spatial patterns across the shore.

It is worth noting that elevation and micrograzers are positively correlated, therefore micrograzers are restricted to the top of the shore where the abiotic conditions limit the proliferation of macroalgae (Kaehler and Froneman 2002). This probably caused the negative spatial relationship (inversely interpreted from cross-semivariograms) between micrograzers and grazing effects during September, October and January (Fig. 3.7 and 3.8). Similarly, but at the opposite extreme (low shore) the variability in macrograzers decreased the variability in grazing effects in October. Also macrograzers and water movement were positively correlated (Table 3.6), suggesting that where there is high water movement (low and mid shore) there is high primary productivity and wave action and these decrease the effects of grazers. Finally, at the end of the experiment, mesograzers were no longer the main predictor of grazing effects, instead macrograzers were the principal one. This suggests first that at different times of year different types for grazers are responsible for algal spatial structure at different levels on the shore. This change in the importance of grazers could have been caused by the increase in primary productivity under winter conditions (May 2006) which make the algae less susceptible to mesograzers, but not to macrograzers. However, this is highly speculative and more experiments are necessary to test the effects of grazers.

III. Conclusions

Overall, grazing effects seem to be important on this shore based on the transect experiment, but especially on the low shore and in tidal pools based on the horizontal exclusion experiment. This is in contrast to the model of Hawkins and Hartnoll (1983), which describes weak grazing effects on the low shore. This is understandable on exposed shores where the density of *Scutellastra cochlear* are exceptionally high, but this is not the case of sheltered shores or those like the study site where limpet densities are not especially high (Bustamante and Branch 1996). In the present study I did not observe high density of *S. cochlear* what suggests more protected conditions, however grzing was found strong. Tidal pools are strongly affected by grazers and this agrees with work in other parts of the world; including the Oregon coast (Nielsen 2001, 2003), Maine (Lubchenco 1982), Nova Scotia (Metaxas and Scheibling 1993), the Mediterranean coast (Benedetti-Cecchi and Cinelli 1995, Benedetti-Cecchi et al. 2005), and in tropical pools of the Hong-Kong coasts (Wai and Williams 2006ab).

The transect experiment allowed the assessment of variability in grazing effects across the shore as represented by effect sizes and agreed with the Hawkins and Hartnoll (1983) scheme of variation of grazing effects across the shore. Nevertheless, I report a non-monotonic increase in the strength of grazing effects with the distance from the sea, the strength of which was weak until 9 m from MLWS, and then strong until 43 m from MLWS. This range of grazing effects exhibited high variability. This distribution of grazing effects across the shore exhibited spatial heterogeneity represented by a high fractal dimension, and I suggest it may be explained by heterogeneity found in abiotic and biotic factors, which interact and modify the heterogeneity of grazing effects over time.

In consequence, the conclusions from the two experiments differ since the results from one can not be extrapolated from one to another; however, the experiments answer partially different questions, making them complementary. This divergence between experiments was caused partly, because in the first experiment the treatments were randomly and horizontally allocated in three intertidal zones, restricting the findings to those zones without considering intermediate areas between them. The first experiment is the classical approach used in most experiment in ecology on which most intertidal ecological theory is based, while the vertical transect could be a powerful tool to understand ecological processes more fully, given enough replication. Many advantages are exist in using a transect of grazer exclusions: (i) the assessments of grazing effects in intermediate areas between intertidal zones, (ii) the assessment of the total grazing impact across the shore, and the study of changes of (iii) spatial patterns on time, and the relationship between grazing effects and physical factors. The results from the transect experiment were consistent with the literature regarding the position of macrograzers, and micrograzers at opposite ends of the intertidal gradient, while others features were new such as the spatial structure of mesograzers, micrograzers, macrograzers, green foliose algae and more importantly, the structure of the strength of grazing effects. Finally, it is accepted that the relationship found between grazing strength and distance from the sea can be variable depending on the specific spatial structure of the topography across the shore. In the present work I assumed that the relationship between grazing and distance from MLWS is perfectly valid only in the present experimental area of the transect (54 x 1 m). This was as an attempt to explore a new experimental design and the possibility of describing for first time the vertical spatial structure of grazing across the shore using the relationship between semivariance and distance, rather than being an attempt to generalize the spatial structure in the intertidal of the south coast of South Africa.

CHAPTER IV

EFFECTS OF RESOLUTION, AND SPATIAL STABILITY IN GRAZING EFFECTS IN THE UPPER EULITTORAL ZONE

INTRODUCTION

The upper part of the intertidal rocky shore is affected by several physical stresses associated with desiccation which test the physiological response of marine invertebrates and algae. However, many of these organisms thrive in these harsh habitats, while others can only inhabit the high shore for brief periods of time, when environmental conditions are more benign (Cubit 1984).

The upper part of the shore is commonly called the ‘Supralittoral fringe’ or ‘Littorinid zone’ and is characterized by a large number of littorinid spp. There, strong grazing effects of littorinids on the epilithic microalgal community have been reported from several coastal sites around the world: on the coasts of Oregon by Castenholz (1961) and Cubit (1984), Hong-Kong by Mak and Williams (1999), and on the south coast of South Africa by Kaehler and Froneman (2002).

Below the Littorinid zone lies the mid shore, comprising two parts, the lower balanoid zone (mid eulittoral zone) and the upper balanoid zone (upper eulittoral fringe). The emersion time is shorter in these zones than in the Littorinid zone, thus the physical stresses are reduced and primary productivity potentially increases (Steneck and Dethier 1994). As a result stronger significant ecological interactions such as grazing are expected to be the main regulators of community structure in these zones (Menge and Sutherland 1987).

The lower eulittoral zone seems to lack significant grazing effects on macroalgae on the south coast of South Africa, despite the presence of the macrograzers *Cymbula oculus* and *Scutellastra longicosta* and various mesograzers (Whittington-Jones 1997, Carter and Anderson 2001). In contrast, the upper eulittoral zone lacks macrograzers, but supports high densities of mesograzers, which seem to exhibit grazing effects on foliose opportunistic algae (see chapter III). Evidence of a strong grazing effect in the upper eulittoral zone has also been reported on the west coast of South Africa by Madikiza (2005), with no such effects previously reported for the upper eulittoral zone on the east and south coasts of South Africa. Hawkins and Hartnoll (1983) suggest that grazing effects could be very important in the upper eulittoral zone, however it was not possible to find any studies of grazers in the upper eulittoral zone. This study investigates the hypothesis that grazing is important in affecting the epilithic and macroalgal community in the upper eulittoral zone at one site on the south coast of South Africa.

In the upper intertidal zone of the south coast it is possible to recognize two habitats: ‘open rock’ and ‘tidal pools’. These habitats are expected to have different physical conditions, and therefore species assemblages. In addition, more intense biological interactions such as grazing and competition are expected in tidal pools than on open rocks, as has been reported by Metaxas and Scheibling (1993) and Nielsen (2001, 2003) in the northern hemisphere. On the south coast of South Africa this zone is characterized by several types of mesograzers, defined as those individuals with a body length of over two centimeters such as siphonarid limpets and winkles (Branch and Branch 1981, Huggett and Griffiths 1986, Hodgson 1999). Hodgson (1999) pointed out that the most abundant grazers in this zone are siphonarid limpets, which can have a strong grazing effect on the epilithic algal community, and can influence macroalgal distribution by grazing on their early stages. This suggests that foliose algae can grow in areas where these grazers can be excluded. In open rock habitats non-coralline encrusting algae are common (personal observation). They exhibit slower growth rates and are less susceptibility to desiccation stresses than foliose algae (Steneck and Dethier 1994). At the same time they can compete with foliose algae for space (Madikiza 2005). This author reported that the encrusting non-coralline *Hildenbrandia lecalanieri* dominates open rock habitats in the lower and upper eulittoral zone of the west coast of South Africa, and inhibits the settlement of foliose opportunistic algae. Madikiza (2005) concluded that both grazing and *H. lecalanieri* inhibit recruitment of foliose algae. At the present upper eulittoral zone site, patches of encrusting non-coralline alga alternate with bare rock.

In addition, Hodgson (1999) reports the presence of abundant siphonarid limpets in tidal pools, with positive interactions between siphonarids and encrusting coralline algae, where siphonarids would enhance the cover of encrusting corallines by keeping them clean of foliose algae and epiphytes. Encrusting corallines can also have a negative effect on foliose opportunistic algae; by shedding superficial layers or other mechanisms of inhibiting the settlement of foliose algae (Pueschel 1988; Keats et al. 1994, 1997, Hodgson 1999).

Hodgson (1999), Madikiza (2005) and I (see chapter III) suggest strong grazing effects in this zone based on empirical and theoretical evidence (Hawkins and Hartnoll 1983). In addition, grazing can mediate indirect interactions between algal groups and control the settlement of foliose algae. To understand fully the direct and indirect effects of grazing in this zone, treatments with substrata sterilized of encrusting and epilithic algae were compared to non-sterilized ones. This allows an understanding of the effect of the initial conditions on the outcome of grazing.

Authors differ broadly about the term disturbance, but generally they referred to damage that result in the loss of biomass in organisms, caused by physical or biotic agents

(Steneck and Dethier 1994, Sousa 2001). As grazing removes algal biomass it is considered as a biotic type of disturbance (Sousa 2001). Grazing can either affect a whole assemblage of algae or specific algal groups, depending on its strength. Therefore the effects of grazing can be examined at different levels of resolution, from more specific to more general within a hierarchy where the specific levels are contained in the general levels. This is according to the theory that every phenomenon in ecology can be hierarchic (O'Neill et al. 1986). This relationship between the hierarchy in the resolution of the algal community and the strength of any disturbance (such as grazing) has been proposed in the hierarchic-response-stress hypothesis (Olsgard et al. 1998). This hypothesis was based on by the fact that the effect of disturbance can have homogeneous or heterogeneous effects on the components or species of the community depending on its strength. A heterogeneous effect (caused by weak disturbances) refers to differential effects of any disturbance on some species or genera, but not others. However if the disturbance is strong, it is predicted to have a significant effect on most of the species of the community, therefore a propagation of this effect will be evident at higher levels of resolution e.g. family, order, etc. Grazing effects can also be different among species, due to factors such as cellular complexity, morphological and chemical composition, which can deter or attract grazers (Duffy and Hay 2001, Van Alstyne et al. 2001, Díaz et al. 2006). The categorization of algal groups by their different susceptibilities to grazing has led to the concept of algal functional groups (Littler and Littler 1980, Steneck and Dethier 1994). These authors classified species according to their levels of primary productivity and resistance to grazing. The classification of species into functional groups brings simplification to the system and consequently allows predictions about when, where and which functional groups will be susceptible to grazers, according to the combination of the levels of primary productivity and disturbance potential (Steneck and Dethier 1994). For example, habitats combining high primary productivity and low disturbance will allow the dominance of leathery macrophytes such as kelps (weakly stress-tolerant, but strong competitors), while habitats combining low disturbance and low primary productivity potential will allow the domination of encrusting algae (stress-tolerant, but weak competitors). The foliose algal group is predicted to dominate habitats with intermediate levels of primary productivity and disturbance potential. Foliose algae are defined by Steneck and Dethier (1994) as macroalgae formed by simple sheets one or two cells thick, which leaves them very susceptible to be grazed. The domination of specific combinations of levels of primary productivity potential and disturbance by a functional group does not exclude the presence of other functional groups in low amounts (Steneck and Dethier 1994). The effects of grazing on whole algal communities and assemblages have been studied at coarser levels, which include a measure of the amount of biomass of the whole algal assemblage estimated as the concentration of chlorophyll *a*. This approach has been used in pelagic systems (Kiørboe et al. 1985, Bernard and Froneman 2005) and in intertidal systems, especially in the littorinid zone, to estimate grazing effects on the epilithic microalgal community (Mak and Williams 1999, Kaehler and Froneman 2002). Knowing the effects of grazing among different levels of resolution it is possible get an integrated estimation of its strength, by evaluating whether it is significant at every level. A lack of concordance among levels of resolution can be explained by antagonistic effects between functional groups, such as encrusting versus foliose algae (Steneck and Dethier 1994, Atalah et al. 2007). This antagonistic effect can produce a non-significant effect of grazing at the most coarse level of resolution, as happens at the higher levels of taxonomic of resolution when species or genera have an opposite effect (Chapman 1998).

It is worth noting that I refer to 'levels of resolution' and not to 'taxonomic levels of resolution', because taxonomic resolution requires a common descendent among species before a higher taxon is recognized. The present analysis does not mean to reflect a phylogenetic relationship. Therefore, the third aim of this chapter is to investigate algal grazing across levels of resolution, in order to get a better understanding of how mesograzers affect the different components of the upper eulittoral algal assemblage.

Sources of variation in the spatial distribution of assemblages are disturbance, recruitment rate, predation and availability of substratum (Sousa 2001, Menge and Branch 2001, Menge et al. 2005). These sources of variability can interact with physical factors such topography, creating patches comprising several species of algae at different stages of succession (Sousa 2001). The distribution of patches has drawn the attention of ecologists, who have developed tools to distinguish random from non-random spatial and temporal patterns (Shaffer and Kot 1986, Menge et al. 2005, see chapter II and III). The following step in ecology is to understand under which conditions these spatial patterns change in time; or to determine the factors that induce community stability or persistence (Connell and Sousa 1983, Berlow 1997, Navarrete and Berlow 2006). Persistence is understood as the level of invariance of a target variable over time (Pimm 1984), although it is well understood that persistence can vary with the scale of resolution (O'Neill et al. 1986, Wu and Loucks 1995, Navarrete and Berlow 2006). In addition, there is another complexity pointed out by Steneck and Dethier (1994), which is related to the level of resolution of the species. These authors mentioned that at coarser levels of resolution, specifically functional groups rather than species, persistence can be more easily detected. This occurs because, although the identity of the species can vary over time, the proportions of those comprising functional groups may not vary (Steneck and Dethier 1994). On rocky shores it is possible to observe that the spatial pattern of assemblages seem to be static through time, though under certain condition they are dynamic. Menge et al. (2005) studied the dynamics of macrophyte mosaics of turf forming marine macroalgae and surfgrass (*Phyllospadix scouleri*). These authors found dynamism in terms of disturbance, species position and species displacement as the level of wave exposure increase. Menge et al. (2005) concluded that there is high dynamism in the spatial pattern of macrophytes mosaics. The same conclusion was reached by Johnson et al. (1997) and Burrows and Hawkins (1998). These authors described a dynamic system on the mid shore governed by disturbance-competition-grazing interactions among barnacles-fucoids-grazers, where the spatial pattern of patchiness of these components varied with cycles of 5-6 years. It would seem that there is a decrease in the strength of disturbance events (e.g. sand inundation, ice scour, log damage) from the high shore to the low shore. At the same time the availability of benign space decreases with the elevation of the substratum, being restricted to small benign microsites (Sousa 2001). On the high shore, organisms are restricted to areas where conditions are more appropriate for survival, such as microhabitats formed by crevices and tidal pools (Chapman 1995). These microhabitats create isolated patches of assemblages surrounded by harsher areas containing only a few microalgae and in some areas grazers. For these reasons, I hypothesise that the mosaic of patches can be more spatiotemporally dynamic on the low shore (Menge et al. 2005) and mid shore (Burrows and Hawkins 1998) than on the high shore. It is worth noting that these ideas of increasing stability or persistence in the spatial patterns refer to small spatial scales, varying from 10s of centimeters to 10s of meters. Therefore the fourth aim of this chapter is to study the persistence in terms of spatial stability of grazing effects in the upper eulittoral zone.

At the same time, it is necessary to consider the level of resolution at which the spatial stability of an ecological interaction is assessed. For example, algal biomass may not vary over time, but the species comprising this biomass may vary. Spatial stability is expected to be found more at coarser levels than at specific levels as indicated in the model of Steneck and Dethier (1994). In this study, I examined the spatial stability of grazing effects after disturbance during two consecutive years and at three levels of resolution.

In synthesis, the goals of this study are: (1) to describe the grazer assemblage in the upper eulittoral zone in both “open rock” and “tidal pools” habitats and its spatial and temporal variation, (2) to determine if the effects of grazers change according to the type of manipulation of substratum at the beginning of the experiment (presence/absence of epilithic algal community) in both habitats, (3) to determine how the level of resolution of the algal assemblage changes our perception of grazing effects and finally, (4) to determine if there is persistence or stability in grazing effects between two years.

I. Integrative hypothesis approach

The assessment of the goals was carried out by integrating the results of multiple analyses, as is done with the integration of hypotheses from several post-hoc tests in a single analysis.

The central goal of this chapter is the recognition and detection of spatial stability of grazing effects through levels of resolution in different habitats. Therefore, an experimental manipulation was done in two habitats which allows the detection of grazing effects through differences in algal abundances among treatments (greater algal abundance in exclusions than control treatments implies grazing effects). The experimental set up was repeated in time in order to assess the spatial stability of grazing effects. In order to do this, two conditions need to be fulfilled: i. persistence of the significance of grazing effects in different habitats. This was studied by re-starting the experiment in the same blocks in two consecutive years using a physical disturbance (burn and scrape the substratum). ii. Spatial specificity or determinism of grazing. This was indicated by the magnitude of grazing being specific to the same blocks after a disturbance and after the same amount of time, between years.

Additionally the experimental set up allowed the study of the effects of a disturbance (burning of substratum) on the significance of grazing effects and its relationship to the stability among levels of resolution.

Instead of carrying out a single analysis to test the comparison of grazing effects between years, manipulations, and habitats, several repeated-measures analyses were carried out. The reasons which required fragmentation of the analysis into several analyses carried out separately for different years were: i. asynchrony in the sampling time between years. ii. Dependence of temporal data taken from experimental treatments. iii. Grazing effects through levels of resolution vary from multivariate to univariate, from the finest level of resolution to the coarsest. iv. The number of analyses was reduced through the combination of ‘disturbance and habitat’ in each year (2004 and 2005), because during the second year, one combination of habitat and disturbance could not be repeated.

Ecological theory does not prohibit the assessment of hypotheses using several simple approaches and analyses rather than a single analysis which includes all the hypotheses together (Underwood com. pers.). Each analysis addressed the hypothesis on the significance of grazing effects at a specific level of resolution, condition and year. Here, level of resolution varied in three categories: species, functional groups and algal biomass. Combinations of habitats and disturbance were termed ‘condition’ and they fell into four categories: ‘burnt open rock’, ‘non-burnt open rock’, ‘burnt tidal pool’ and ‘non-burnt tidal pool’. Finally, the factor year contained two categories: 2004 and 2005.

Additionally, in order to detect specificity and determinism in grazing effects, several correlation analyses were carried out among these blocks between years. This addressed the hypothesis that there is correspondence in the magnitude of grazing effects at specific microsites.

MATERIALS AND METHODS

I. Site

The experiment was carried out from the 1st March 2004 until the 28th February 2005 and repeated from 18th April 2005 until the 6th May 2006 on the south-east coast of South Africa. The shore chosen was a flat sandstone platform at Old Woman's River (33°S45' 27°S10') with minimal substratum heterogeneity. This shore takes the form of a gently sloping platform of sandstone. On the low shore, a few permanent pools of up to one meter in depth are present (area > 4 m^2), but on the high shore pools are shallower and smaller, with dimensions of up to ten meters in length and four meters in width but only a few centimeters deep. These shallow pools generally support a high density of *Siphonaria* spp. All the tidal pools used in this study were approximately 1.5 m^2 and 5 cm deep (Huggett and Griffiths 1986).

The upper eulittoral zone contains a high abundance of mesograzers (size approximately 2 cm) and micrograzers (< 1 cm). The mesograzer group is represented by limpets, snails and sea stars, while the micrograzers comprise littorinids and juvenile mesograzers. There are two habitats in this zone, which contain foliose algae, encrusting algae and non-visible epilithic biofilms comprising the cyanobacteria *Aphanocapsa* spp and *Gleocapsa* spp plus macroalgal spores and propagules (Kaehler and Froneman 2002).

II. Assessment of mesograzing effect and set-up

The design assessed the effects of: (1) mesograzers (3 treatments), (2) habitat (2 treatments) and (3) substratum manipulation (2 treatments) in a factorial design with 12 replicates, forming 48 blocks and 144 experimental units altogether. The experiment used a cage random block design with three treatments in each block (a) grazer exclusion, (b) partial fences forming a procedural control, and (c) non-fenced areas marked with four screws at the corners, providing free grazer access, these are termed open controls (Fig 4.1). These treatments were randomly distributed within each block in the upper eulittoral zone. Blocks were separated by 1-20 m. The area of each experimental unit was 0.25 x 0.25 m, and the entire design was repeated in two habitats: ‘open rock’ and ‘tidal pools’ and with two substratum disturbance manipulations. Fences were made of rolled wire mesh (0.5 cm mesh size), forming a cylindrical shape with stop the entrance of mesograzers. The manipulations allowed the inclusion of the influence of encrusting and epilithic algal communities on grazer effects and involved one of two starting conditions: ‘burnt’ (all living material on the rock removed from the substratum using a scraper and butane-propane torch) and ‘non-burnt’ (encrusting algae and epilithic biofilm were not removed). This design provided four independent datasets for two habitats and two manipulation combinations. These conditions were: BOR ‘burnt open rock’, NBOR ‘non-burnt open rock’, Bpool ‘burnt tidal pool’ and NBpool ‘non-burnt tidal pool’ (Fig 4.1). Each condition was analyzed independently, comparing exclusion treatments with procedural and open controls. To study the stability and persistence of grazer effects between years, the condition ‘burnt open rock’, ‘burnt tidal pool’, and ‘non burnt open rock’ were burnt again on the 18th April 2005 and the experiment was repeated for one year. The ‘non burnt tidal pool’ condition could not be repeated during 2005 as I was not able to control the inflow of seawater to some of the pools. The multi factorial structure of the experimental design suggests intuitively the insertion of every factor into a multiple factorial analysis. The factors that would be included are: year, habitat, manipulation (burnt and non burnt), treatment and time. However, the repetition of the experiment during the second year and the difference in sampling dates, as well as the changes on the manipulation non-burnt to burnt in some habitats, made it impossible to test the hypotheses with a single model.

II.1. Levels of resolution

The effects of mesograzers on the algal community were analyzed at three levels of resolution: i. percent cover of species, ii. percent cover of foliose and encrusting functional groups, and iii. algal biomass expressed as the concentration of chlorophyll *a*, the most general measure, involving the entire assemblage. For the first two levels of resolution, digital photographs were taken and the algal cover was estimated using the software Image Tool 3.0.

a. Species: using digital photographs, I estimated the algal cover of foliose and encrusting algal groups which previously were classified by local authorities in algal taxonomy, Prof. J. Bolton and Dr. R. Anderson and Dr. G. Maneveldt for encrusting coralline species.

b. Foliose/encrusting functional groups: using the same digital photographs to determine the cover of species, I estimated the cover of functional groups. The effect of mesograzers at the end of the experiment on algal cover was analyzed by grouping the algal species into the foliose (*Ulva rigida*, *Porphyra capensis* and *Chaetomorpha aerea*) or the encrusting (*Hildenbrandia rubra* and *Spongites yendoi*) functional groups.

c. Concentration of chlorophyll *a* level: three rock chips (approximately 1 cm^2) were collected using a chisel from each experimental unit (432 chips per sample/date) and immediately transported in darkness in insulated cooler boxes to the laboratory where they were individually submerged in 6 ml of cold 80% methanol for 24 hours in darkness. The samples were initially taken every two weeks, later monthly and finally at one and a half month intervals. The concentration of chlorophyll *a* was estimated with a spectrophotometer (Spectrophotometer SHIMADZU UV-1201) using the following formula:

$$[\text{Chl-}a] = (\text{A.V.13}) / \text{a.d}$$

Where A = absorbance at 665 nm – absorbance at 750 nm, V = volume of solvent, 13 = spectrophotometric constant, a = area of the chip (cm^2, measured by image analysis), and d = cell path length (cm). The concentration of chlorophyll *a* was expressed in $\mu g.\ cm^{-2}$.

Univariate analyses were carried out separately for each condition. These comprise repeated measures (RM-ANOVA) for the effect of treatment at each level of resolution. Bonferroni correction was used to correct dependent variables at the level of species (critical value $\alpha = 0.05/5 = 0.01$) and for functional groups (critical values $\alpha = 0.05/2 = 0.025$).

Homogeneity of variance was checked using Cochran's C test. When the homogeneity test failed, I transformed the data using 'ln (x + 1)' for concentration of chlorophyll *a* and 'arcsin(x + 1) for algal cover. Post-hoc multiple means comparisons were performed using Student Newman Keuls (SNK) tests at the $\alpha = 0.05$ significance level.

II.2. Spatial stability between years

In order to determine spatial stability between years, I compared the coincidence of significant results from overall treatment effects of the ANOVA analyses during 2004 and 2005. In addition, I calculated the effect sizes for each block and at every sampling date obtaining the spatiotemporal intensity of grazing effects (see chapter V for definition) using the following formula:

Spatiotemporal intensity during 1 year $= \sum_{K=1}^{N} \frac{(\ln (C/E)_{1k})}{N}$

Where C, represents the cover of concentration of chlorophyll *a* in the open control treatment, while E, represents the cover of concentration of chlorophyll *a* in the exclusion treatment, finally 'ln' represents natural logarithm.

Once I obtained the values of spatiotemporal intensity of grazing effects for each year, I correlated these values i.e. the grazing intensity for each block in 2004 was correlated with intensity for the same block in 2005. A significant positive relationship implies spatial determinism or stasis (see Menge et al. 2005) of microhabitats where the ecological phenomenon is stable, a non-significant relationship implies non-determinism or kinesis, and a negative relationship means an unlikely total change of the conditions of the microhabitats, this is likely to occur only when a disturbance is extremely strong, such as an earthquake.

III. Grazer abundance

Mesograzers and micrograzers were counted using quadrats of 1 m x 1 m and 0.25 m x 0.25 m, respectively. The quadrats were placed in the vicinity of the treatments within the blocks. Quadrats were placed 10 cm from any treatment plot. Each quadrat was set twice in the vicinity of the block in order to obtain two estimates of grazer abundance and to have replication for the randomized block test (see point III. b). During the first experiment, mesograzers were counted on four separate occasions: March 2004 (summer-autumn), June 2004 (winter), November 2004 (spring) and March 2005 (summer-autumn). For the second experiment, mesograzers were counted only for the conditions BOR ‘burnt open rock’, NBOR ’non-burnt open rock’ and Bpool ‘burnt tidal pool’ during June 2005 (winter) and September 2005 (spring).

Micrograzers were sampled in July and December of 2004 and in June and September of 2005.

III.1. Mesograzer abundance by habitat and manipulation

In order to understand the distribution of abundances of the mesograzers in the upper eulittoral zone, a 2-way MANOVA was used to test for differences in abundance as explained by habitats and manipulation. The four sets of data from the 2004 experiment were pooled to obtain a single set of data that was used to represent the variability in grazer abundances among the four different experimental conditions.

III.1.a. Spatial variability of mesograzers among blocks

I counted the number of mesograzers using a quadrat of 1 m x 1 m in the vicinity of each block twice. These two counting of grazer abundance per block allow me to carry out four randomized block 1-way ANOVAs, one for each condition on the abundance of grazers.

III.1.b. Temporal variation of mesograzer abundance by habitat and manipulation during 2004 and 2005

Six samples were taken within the period of 2004-2005 in each condition ‘habitat and manipulation’, these were used to carried out a 1-way RM-ANOVA for each condition, except for ‘non-burnt pool’ (NBpool) during 2005

III.2. Micrograzer analysis

Micrograzers comprised littorinids and juveniles of siphonarid limpets, which were counted using quadrats of 0.25 m x 0.25 m on four occasions, allowing their spatial and temporal variability to be analyzed.

Block spatial analysis was carried out using 1-way MANOVA for each condition to separate the effects on the two variables, i. abundance of littorinids and ii. abundance of juveniles.

Temporal analysis was conducting using two 1-way RM-ANOVA for littorinids and juveniles separately using Bonferroni correction at $\alpha/2 = 0.025$. During the first experiment, four conditions (‘BOR’, ‘NBOR’, ‘Bpool’, ‘NBpool’) were analyzed and their micrograzers were counted, however in the second experiment there were three, not four conditions (‘BOR’,’NBOR’ and ‘Bpool’).

IV. Statistical consideration

Univariate analyses are designed to examine the responses of individual variables, while multivariate analysis is used to examine and characterize changes in the many variables associated with overall community structure. Both techniques are valid and useful for experiments such as this (Anderson and Underwood 1997). The information obtained from grazing manipulation was factorial and involved a dependent temporal factor, although the data went from multivariate at the species level to univariate at the chl *a* level. For multivariate cases, MANOVA and ANOSIM can be considered good choices. The problem with using ANOSIM is that the interpretation is quite complex, especially when there are several variables, factors and an extra temporal factor, while MANOVA requires that the variables be correlated with each other in a particular way called ‘compound symmetry’; this assumption is difficult to find in ecological data (Underwood pers. comm.). Another type of test is PERMANOVA which is a multivariate analysis, so that at the level of species, each variable must be treated individually. In addition, PERMANOVA does also not include temporal dependence in the data (Anderson pers. comm.), therefore it is necessary to run additional programs, which makes the interpretation more complex. For these reasons and for simplicity, I used individual time series univariate analyses (repeated measures ANOVA) with Bonferroni correction in cases of dependency. This analysis allows the incorporation of temporal dependence and the interpretation is simple.

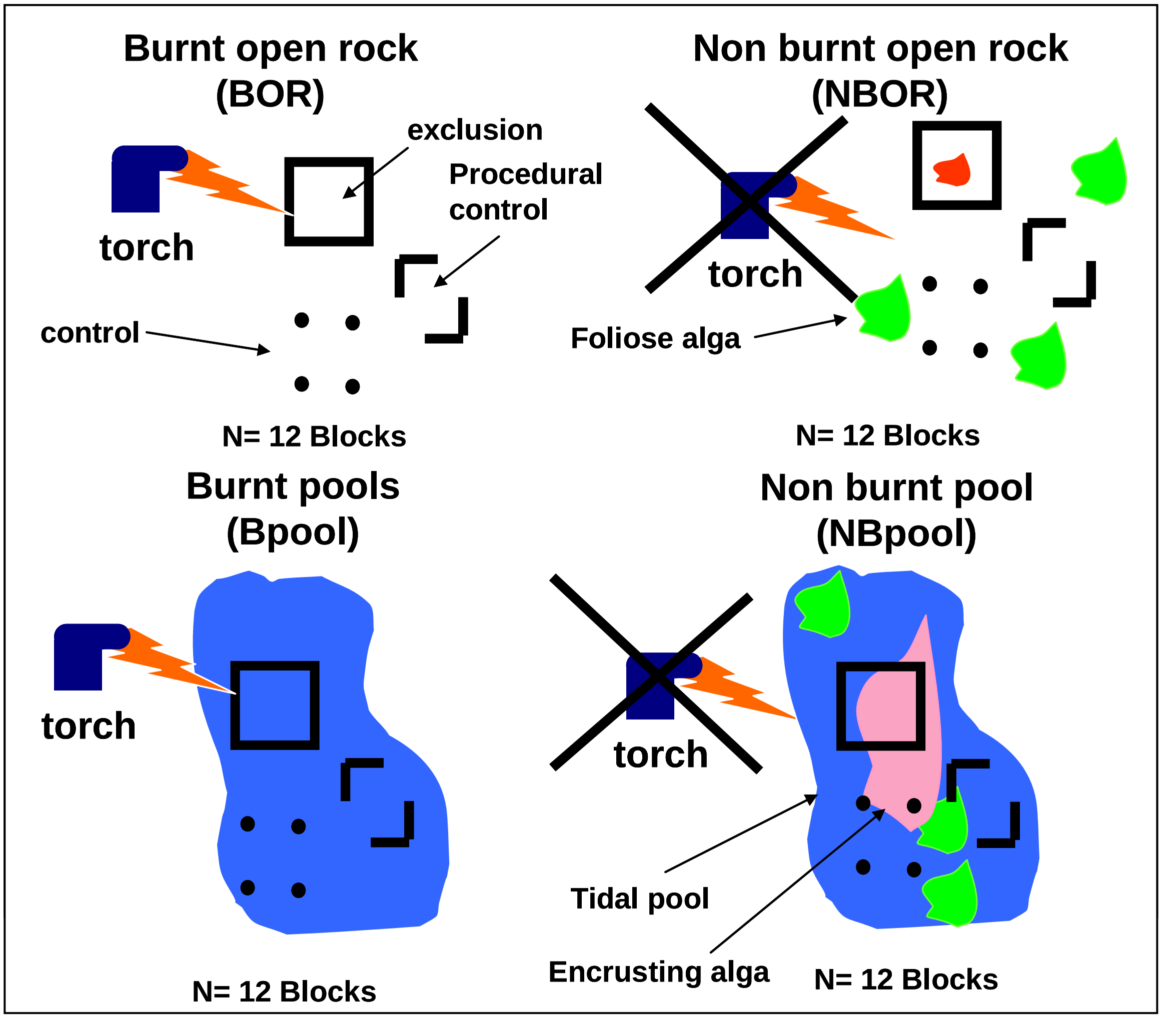

Figure 4.1. Experimental design diagram. The exclusion, procedural control and control treatments were set in a random block design. The experiments were carried out in two habitats in the upper eulittoral zone: 'open rock' and 'tidal pools'. At the same time the substratum was manipulated by burning or not burning the existing algal community, resulting in four conditions: 'burnt open rock' (BOR), 'non-burnt open rock' (NBOR), 'burnt pool' (Bpool) and 'non-burnt pool' (NBpool). The second experiment was repeated for three of the four conditions previously assessed: BOR, NBOR and Bpool.

RESULTS

I. Mesograzer effects on the algal assemblage at different levels of resolution

I.1. The finest level of resolution: species level

The assemblage in the upper eulittoral zone comprised only five species of algae. The foliose alga *Porphyra capensis* inhabits open rock, *Ulva rigida*, *Chaetomorpha aerea* and *Hildenbrandia rubra* inhabit both open rock and tidal pools, and finally *Spongites yendoi* is found only in tidal pools.

I.1.a. Succesional patterns during 2004 and 2005

I.1.a.1. 'Burnt open rock' (BOR) was hardly colonized by algae during 2004. The exclusion treatments were colonized firstly by *Chaetomorpha aerea* (mean cover ± s.d.: 6.2 ± 15 %) and *Porphyra capensis* (6.6 ± 22.1) during May 2004. *Ulva rigida* started to recruit in June (0.8 ± 2.14) and reached a maximum of cover (13 ± 30.9 %) in November 2004 (spring). As *U. rigida* grew, *C. aerea* and *P. capensis* decreased their cover in the exclusion treatments. The controls showed very little colonization (average cover < 5%) by foliose algal species. Consequently, there was no overall grazing effect in the BOR condition (Table 4.1. Fig. 4.2). However, the effect of grazing on *U. rigida* was significant for the interaction 'time x treatment' and for 'time'.

I.1.a.2. 'Burnt open rock' (BOR) showed a similar trend in 2005. The foliose algae *Porphyra capensis* and *Ulva rigida* started to colonize the exclusion treatments in June 2005, with a percentage of cover lower than 5% (*P. capensis* 1.33 ± 3.44 and *U. rigida* 0.66 ± 1.77). *Ulva rigida* started to dominate the exclusion treatments from August 2005 (9.6 ± 28.7%), exhibiting maximum cover during spring (October, 19.5 ± 37.3% and

November, 25 ± 38.9%), while the cover of *P. capensis* was always lower than 5% and *Chaetomorpha aerea* was absent in 2005 (Table 4.2. Fig 4.3). However, the effect of grazing on *U. rigida* was significant for the interaction 'time x treatment' and 'time'.

I.1.b.1. 'Non burnt open rock' (NBOR) during 2004. At the beginning of the experiment the substratum was covered with some spots of the encrusting *Hildenbrandia rubra* and epilithic microalgae. The cover of *H. rubra* varied from 11 to 24% during 2004. The first alga colonizing the exclusion treatments was *Chaetomorpha aerea* with a lower cover (2.63 ± 9.1 %) in April 2004. The grazer effect on *C. aerea* was significant when it reached its greatest cover in June 2004 (19.86 ± 27.11 %. Table 4.3 and Fig. 4.4c). The open controls always exhibited very low cover (< 3 %) of *C. aerea*. In May 2004, the algae *Porphyra capensis* and *Ulva rigida* colonized the exclusions, exhibiting covers of 4.7 ± 14.3 % and 0.08 ± 0.3 % respectively. *U. rigida*, *C. aerea* and *P. capensis* were all significantly affected by overall grazing effect (Table 4.3). *U. rigida* reached its highest levels of cover in November 2004 and March 2005 (24.54 ± 39.9 % and 30.8 ± 40.8 %, respectively). On these two dates the effect of grazing was significant on *U. rigida* (Table 4.3 and Fig. 4.4b), while in June, only *C. aerea* was affected by grazers (Table 4.3 and fig 4.4).

I.1.b.2. 'Non burnt open rock' (NBOR) during 2005. This condition was sterilized of any foliose and encrusting algae from the previous experiment in 2004, therefore this condition changed to 'BOR' in 2005, although I will continue calling it 'NBOR'. Again *Ulva rigida* and *Porphyra capensis* were the only algae colonizing this condition, starting in May for *U. rigida* and June for *P. capensis*. *U. rigida* was affected by grazers and exhibited highest cover in November 2005 and April 2006 (45.1 ± 50.8 % and 21.6 ±

37.9, respectively). *P. capensis* was not affected by grazers, however it showed temporal variability through the year, exhibiting the greatest cover during October 2005 (Table 4.4 and fig 4.5.).

I.1.c.1. ‘Burnt tidal pool’ (Bpool) during 2004. The first algae to colonize were *Ulva rigida* and *Chaetomorpha aerea*, exhibiting covers of 25 ± 45.2 % and 14.7 ± 34.7 %, respectively in April 2004. *C. aerea* was present only for the first month of the experiment, then it was completely replaced by *U. rigida*. *Porphyra capensis* was not found in tidal pools. *U. rigida* was the only species exhibiting an overall grazing effect (Table 4.5 and Fig. 4.6). *Hildenbrandia rubra* exhibited low levels of cover (always lower than 2%). The encrusting alga *Spongites yendoi* started to colonize in August 2004, reaching its maximum cover at the end of the experiment in March 2005 when it reached a cover of 25% in every treatment (Table 4.5 and Fig.4.6e).

I.1.c.2. ’Burnt tidal pool’ (Bpool) during 2005. In this habitat *Ulva rigida* and *Chaetomorpha aerea* were the first algae to colonize, exhibiting covers of 20.8 ± 38.2 % and 41.6 ± 51.5 % respectively in May 2005.These two algae were affected by grazers and exhibited variability in cover through 2005 (Table 4.6). *C. aerea* was affected more by grazers during May 2005. As in 2004, *Porphyra capensis* was not found in tidal pools and *H. rubra* exhibited low levels of cover (always lower than 5 %). S*pongites yendoi* started to colonized in August 2005 again reaching maximum cover at the end of the experiment (March 2006) Table 4.6 and Fig. 4.7).

I.1.d. ‘Non burnt tidal pool’ (NBpool). This condition was dominated by the two encrusting algae, which exhibited patchy distribution among and within tidal pools. The percentage of cover of *Hildenbrandia rubra* varied from 12 to 24 % and for *Spongites* *yendoi* from 10 to 45 % (Fig. 4.8). There were tidal pools containing just one kind of encrusting alga and others exhibiting a mixture of both. This condition showed faster colonization at the beginning the experiment (April 2004) by *U. rigida* and *C. aerea* in the exclusion treatments (0.74 ± 1.8 % and 9.9 ± 25.9 %, respectively). *U. rigida* reached it maximum cover in November 2004 and was the only alga affected by grazers (Table 4.7).

Table 4.1. Burnt open rock (BOR) condition during 2004. Repeated measures ANOVA on each species of algae shows the effect of grazers (treatment effect), time and the interaction of time and treatment. The data were arcsin(square root (x+1)) transformed to achieve homogeneity and normality. * means P < 0.01 and ** P < 0.001.

	Porphyra capensis			***Ulva rigida***			***Chaetomorpha aerea***			***Hildenbrandia rubra***			***Spongites yendoi***		
Factors	**DF**	**MS**	**F**	**DF**	**MS**	**F**	**DF**	**MS**	**F**	**DF**	**MS**	**F**	**DF**	**MS**	**F**
Treatment	**2**	**0.16**	**3.046NS**	**2**	**0.32**	**3.01NS**	**2**	**0.05**	**1.9NS**	**no recruitment**			**no recruitment**		
Error	**33**	**0.06**		**33**	**0.1**		**33**	**0.02**							
Time	**6**	**0.00**	**1.14NS**	**5**	**0.049**	**4.3***	**3**	**0.007**	**1.4NS**						
Time*Treat	**12**	**0.008**	**1.07NS**	**10**	**0.04**	**3.3****	**6**	**0.007**	**1.3NS**						
Error	**198**	**0.007**		**165**	**0.01**			**99**	**0.005**						
Cochran C test		**P < 0.05**			**P < 0.05**			**P > 0.05**							
Treatment	**NS**			**NS**			**NS**								
Time	**NS**			**Sep04=Nov04 > all**			**NS**								
Time*Treat	**NS**			**no logical groups**			**NS**								

Table 4.2. Burnt open rock (BOR) condition during 2005. Repeated measures ANOVA on each species of algae shows the effect of grazers (treatment effect), time and the interaction of time and treatment. The data were arcsin(square root (x+1)) transformed to achieve homogeneity and normality. * means P < 0.01 and ** P < 0.001.

	Porphyra capensis			***Ulva rigida***			***Chaetomorpha aerea***			***Hildenbrandia rubra***			***Spongites yendoi***		
Factors	**DF**	**MS**	**F**	**DF**	**MS**	**F**	**DF**	**MS**	**F**	**DF**	**MS**	**F**	**DF**	**MS**	**F**
Treatment	**2**	**0.07**	**4.06NS**	**2**	**1.2**	**3.5NS**	**no recruitment**			**no recruitment**			**no recruitment**		
Error	**33**	**0.02**		**33**	**0.4**										
Time	**5**	**0.001**	**1.72NS**	**5**	**0.07**	**3.1***									
Time*Treat	**10**	**0.003**	**0.62NS**	**10**	**0.06**	**2.4***									
Error	**165**	**0.005**		**165**	**0.02**										
Cochran C	**P < 0.05**			**P < 0.05**											
Treatment	**NS**			**NS**											
Time	**NS**			**Nov05 =Sept05=Aug05=Jan06 > Jun05**											
Time*Treat	**NS**			**No logical groups**											

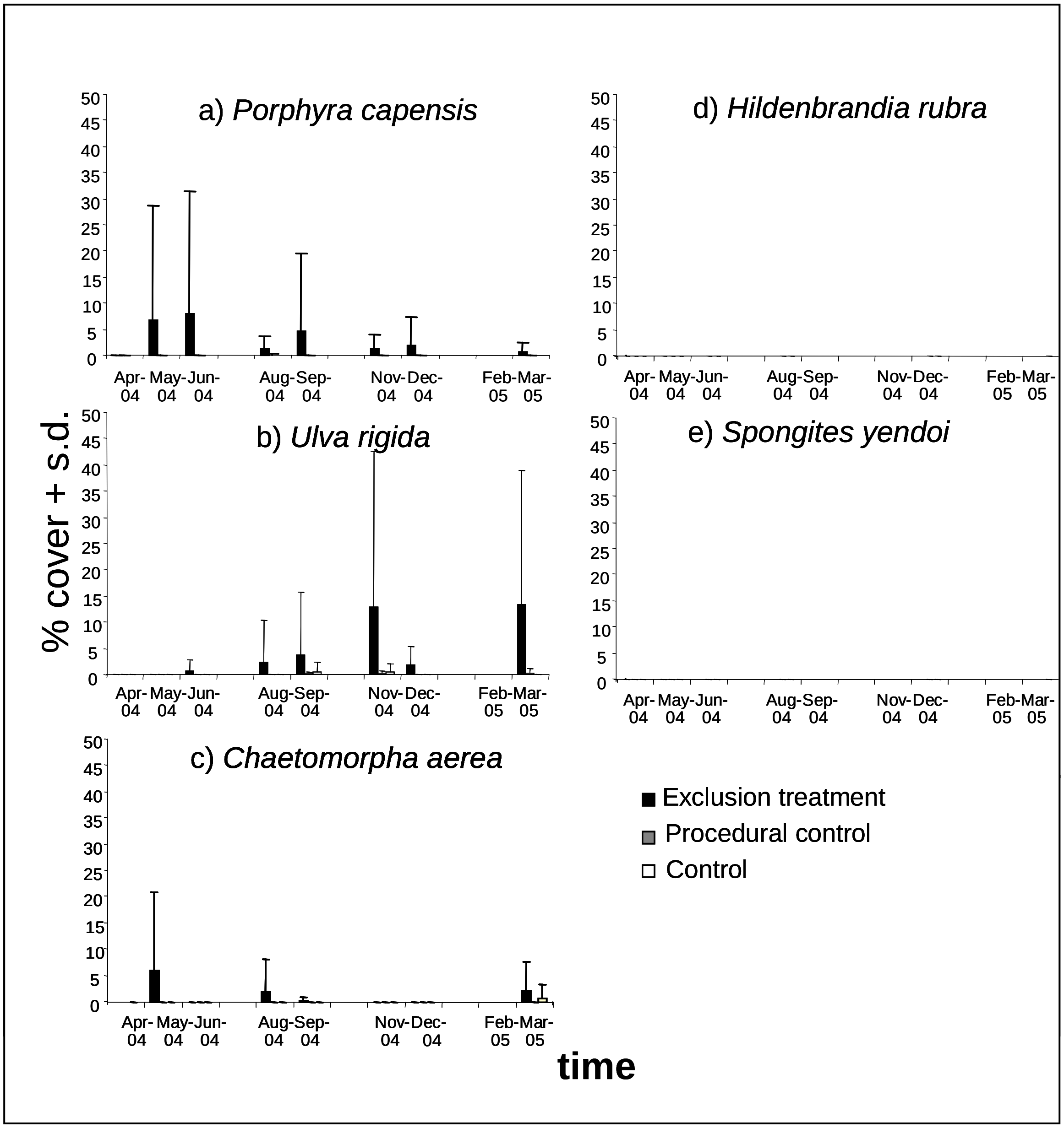

Figure 4.2. Burnt open rock (BOR) condition. Mean of cover + standard deviation of each algal species in the upper eulittoral zone assemblage during the first experiment in 2004. Black, grey and white bars indicate exclusion, procedural control and control treatments, respectively.

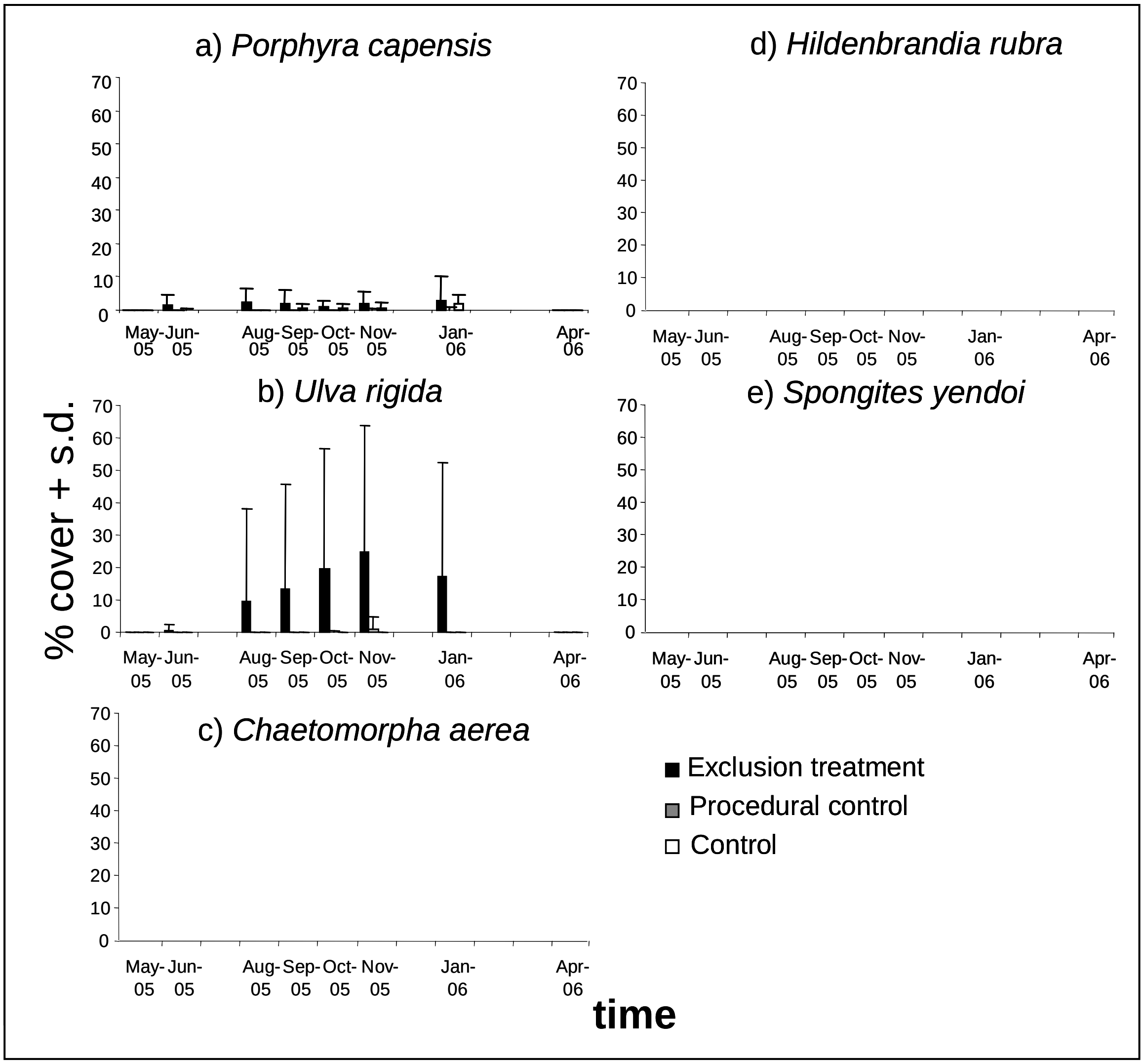

Figure 4.3. Burnt open rock (BOR) condition. Mean of cover + standard deviation of each algal species in the upper eulittoral zone assemblage during the second experiment in 2005. Black, grey and white bars indicate exclusion, procedural control and control treatments, respectively.

Table 4.3. Non burnt open rock (NBOR) condition during 2004. Repeated measures ANOVA on each species of algae shows the effect of grazers (treatment effect), time and the interaction of time and treatment. The data were arcsin(square root (x+1)) transformed to achieve homogeneity and normality. * means P < 0.01 and ** P < 0.001.

	Porphyra capensis			***Ulva rigida***			***Chaetomorpha aerea***			***Hildenbrandia rubra***			***Spongites yendoi***		
Factors	**DF**	**MS**	**F**	**DF**	**MS**	**F**	**DF**	**MS**	**F**	**DF**	**MS**	**F**	**DF**	**MS**	**F**
Treatment	**2**	**0.09**	**10.4****	**2**	**0.63**	**7.2***	**2**	**0.3**	**9.6****	**2**	**0.2**	**0.14NS**	**no recruitment**		
Error	**33**	**0.01**		**33**	**0.09**		**33**	**0.03**		**33**	**1.6**				
Time	**6**	**0.002**	**0.5NS**	**5**	**0.29**	**7.1****	**3**	**0.1**	**4.1****	**7**	**1.8**	**9.7****			
Time*Treat	**12**	**0.004**	**0.8NS**	**10**	**0.15**	**3.7****	**6**	**0.1**	**4.3****	**14**	**0.18**	**0.99NS**			
Error	**198**	**0.005**		**165**	**0.04**		**99**	**0.02**		**210**	**0.08**				
Cochran C test	**P < 0.05**			**P > 0.05**			**P < 0.05**			**P > 0.05**					
Treatment	**T > Pc = c**			**T > Pc = c**			**T > Pc = c**			**NS**					
Time	**NS**			**March05 = Nov04 > all**			**June04 > Sept04>all**			**Nov04> all > March05**					
Time*Treat	**NS**			**Nov04: T > Pc = c** **March05: T > Pc = c**			**June04: T > Pc = c**			**NS**					

Table 4.4. Non burnt open rock (NBOR) condition during 2005. Repeated measures ANOVA on each species of algae shows the effect of grazers (treatment effect), time and the interaction of time and treatment. The data were arcsin (square root (x+1)) transformed to achieve homogeneity and normality. * means P < 0.01 and ** P < 0.001.

	Porphyra capensis			***Ulva rigida***			***Chaetomorpha aerea***			***Hildenbrandia rubra***			***Spongites yendoi***		
Factors	**DF**	**MS**	**F**	**DF**	**MS**	**F**	**DF**	**MS**	**F**	**DF**	**MS**	**F**	**DF**	**MS**	**F**
Treatment	**2**	**0.31**	**3.98NS**	**2**	**3.4**	**5.4***	**no recruitment**			**no recruitment**			**no recruitment**		
Error	**33**	**0.08**		**33**	**0.6**										
Time	**6**	**0.04**	**2.8***	**7**	**0.5**	**6.7****									
Time*Treat	**12**	**0.02**	**1.2NS**	**14**	**0.09**	**1.2NS**									
Error	**198**	**0.01**		**210**	**0.08**										
Cochran C	**P < 0.05**			**P < 0.05**											
Treatment	**NS**			**T > Pc = c**											
Time	**Oct05 = Nov 05 > April 06**			**Nov05 = Jan06 > All**											
Time*Treat	**NS**			**NS**											

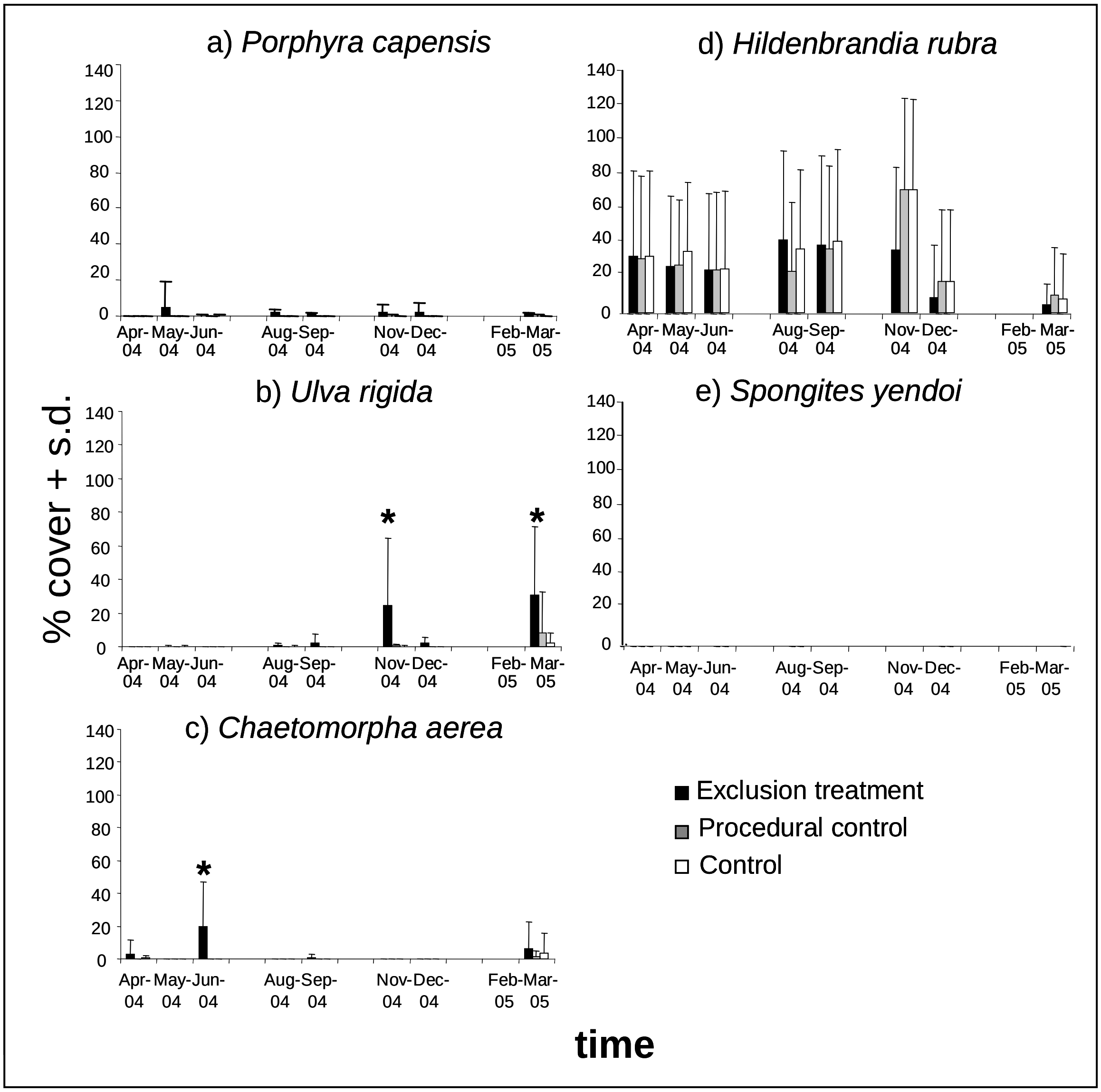

Figure 4.4. Non burnt open rock (NBOR) condition. Mean of cover + standard deviation of each algal species in the upper eulittoral zone assemblage during the first experiment in 2005. Black, grey and white bars indicate exclusion, procedural control and control treatments, respectively. Asterisks indicate the interaction 'Time x Treatment' when the algal cover in the exclusion treatment was higher than the procedural control and control.

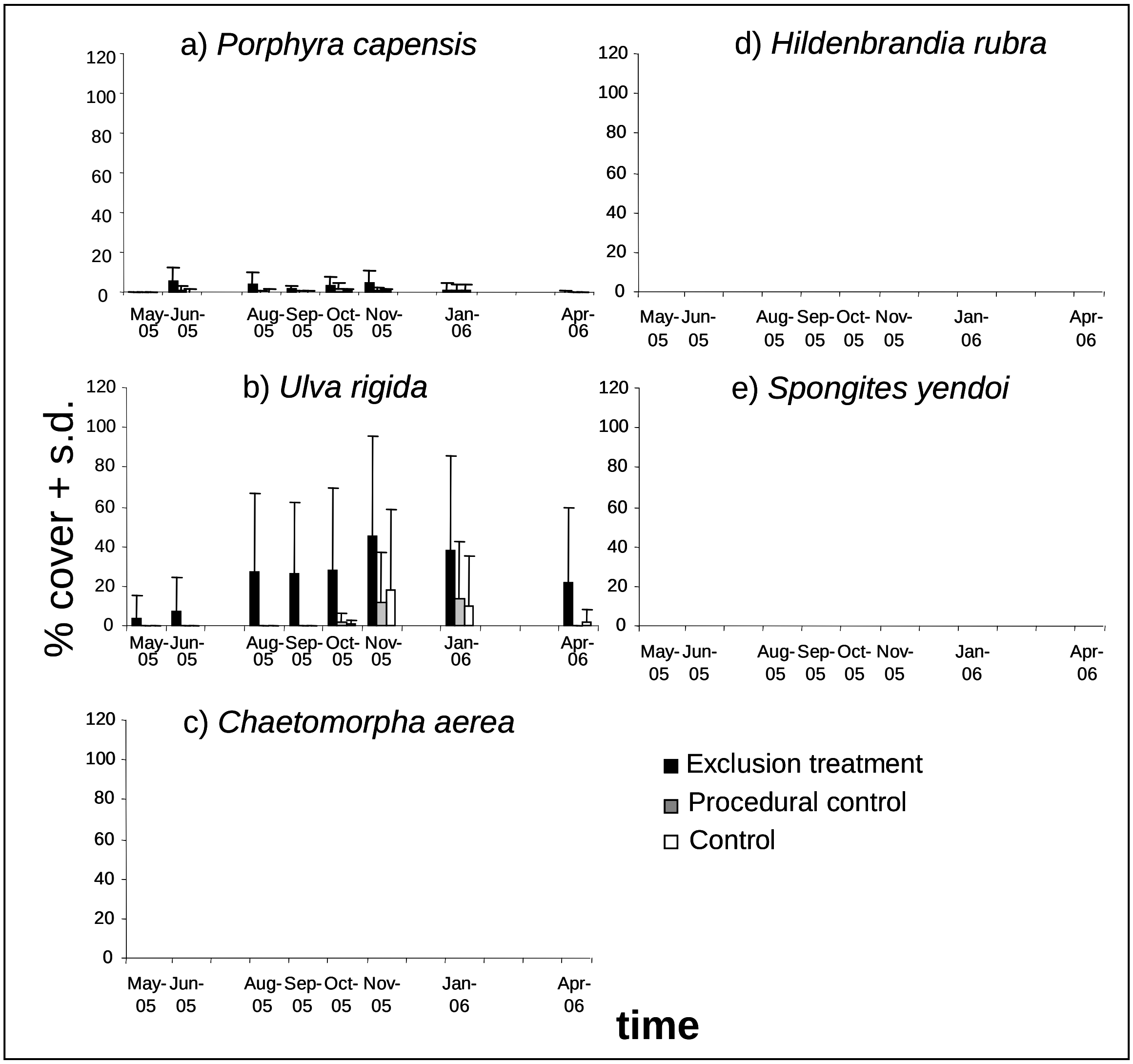

Figure 4.5. Non burnt open rock (NBOR) condition. Mean of cover + standard deviation of each algal species in the upper eulittoral zone assemblage during the second experiment in 2005. Black, grey and white bars indicate exclusion, procedural control and control treatment, respectively.

Table 4.5. Burnt tidal pool (Bpool) condition during 2004. Repeated measures ANOVA on each species of algae shows the effect of grazers (treatment effect), time and the interaction of time and treatment. The data were arcsin(square root(x+1)) transformed to achieve homogeneity and normality. * means P < 0.01 and ** P < 0.001.

	Porphyra capensis			*Ulva rigida*			*Chaetomorpha aerea*			*Hildenbrandia rubra*			*Spongites yendoi*		
Factors	**DF**	**MS**	**F**	**DF**	**MS**	**F**	**DF**	**MS**	**F**	**DF**	**MS**	**F**	**DF**	**MS**	**F**
Treatment	**No recruitment**			**2**	**7.6**	**5.4***	**2**	**0.1**	**0.85NS**	**2**	**0.01**	**0.79NS**	**2**	**0.16**	**0.3NS**
Error				**33**	**1.4**		**33**	**0.13**		**33**	**0.01**		**33**	**0.53**	
Time				**7**	**0.21**	**3.8****				**5**	**0.01**	**3.02NS**	**4**	**0.85**	**17.6****
Time*Treat				**14**	**0.11**	**1.9NS**				**10**	**0.00**	**0.97NS**	**8**	**0.02**	**0.54NS**
Error				**210**	**0.06**					**165**	**0.001**		**132**	**0.04**	
Cochran C test				**P < 0.05**			**P < 0.05**			**P > 0.05**			**P > 0.05**		
Treatment				**T > Pc = c**			**NS**			**NS**			**NS**		
Time				**Nov04>April04=May04=Dec04**			**NS**			**NS**			**March05>Dec04> Nov04>Sep04=Aug04**		
Time*Treat				**NS**			**NS**			**NS**			**NS**		

Table 4.6. Burnt tidal pool (Bpool) condition during 2005. Repeated measures ANOVA on each species of algae shows the effect of grazers (treatment effect), time and the interaction of time and treatment. The data were arcsin(square root(x+1)) transformed to achieve homogeneity and normality. * means P < 0.01 and ** P < 0.001.

	Porphyra capensis			***Ulva rigida***			***Chaetomorpha aerea***			***Hildenbrandia rubra***			***Spongites yendoi***		
Factors	**DF**	**MS**	**F**	**DF**	**MS**	**F**	**DF**	**MS**	**F**	**DF**	**MS**	**F**	**DF**	**MS**	**F**
Treatment	**no recruitment**			**2**	**8.6**	**8.6****	**2**	**0.56**	**2.6NS**	**2**	**0.02**	**1.3NS**	**2**	**0.15**	**0.2NS**
Error				**33**	**1.0**		**33**	**0.21**		**33**	**0.02**		**33**	**0.75**	
Time				**7**	**0.3**	**4.1****	**2**	**0.84**	**7.7****	**4**	**0.01**	**1.8NS**	**5**	**1.22**	**22.54****
Time*Treat				**14**	**0.2**	**2.9****	**4**	**0.38**	**3.5***	**8**	**0.01**	**1.7NS**	**10**	**0.04**	**0.8NS**
Error				**231**	**0.1**		**66**	**0.11**		**132**	**0.00**		**165**	**0.05**	
Cochran C				**P < 0.05**			**P < 0.05**			**P > 0.05**			**P > 0.05**		
Treatment				**T > Pc = c**			**NS**			**NS**			**NS**		
Time				**Oct05 = Nov05 = Jan06 >May05 = April06**			**May05 > all**			**NS**			**Jan06>Nov05>Oct05>Spet05>all**		
Time*Treat				**no logical groups**			**May 05: T > Pc = c**			**NS**			**NS**		

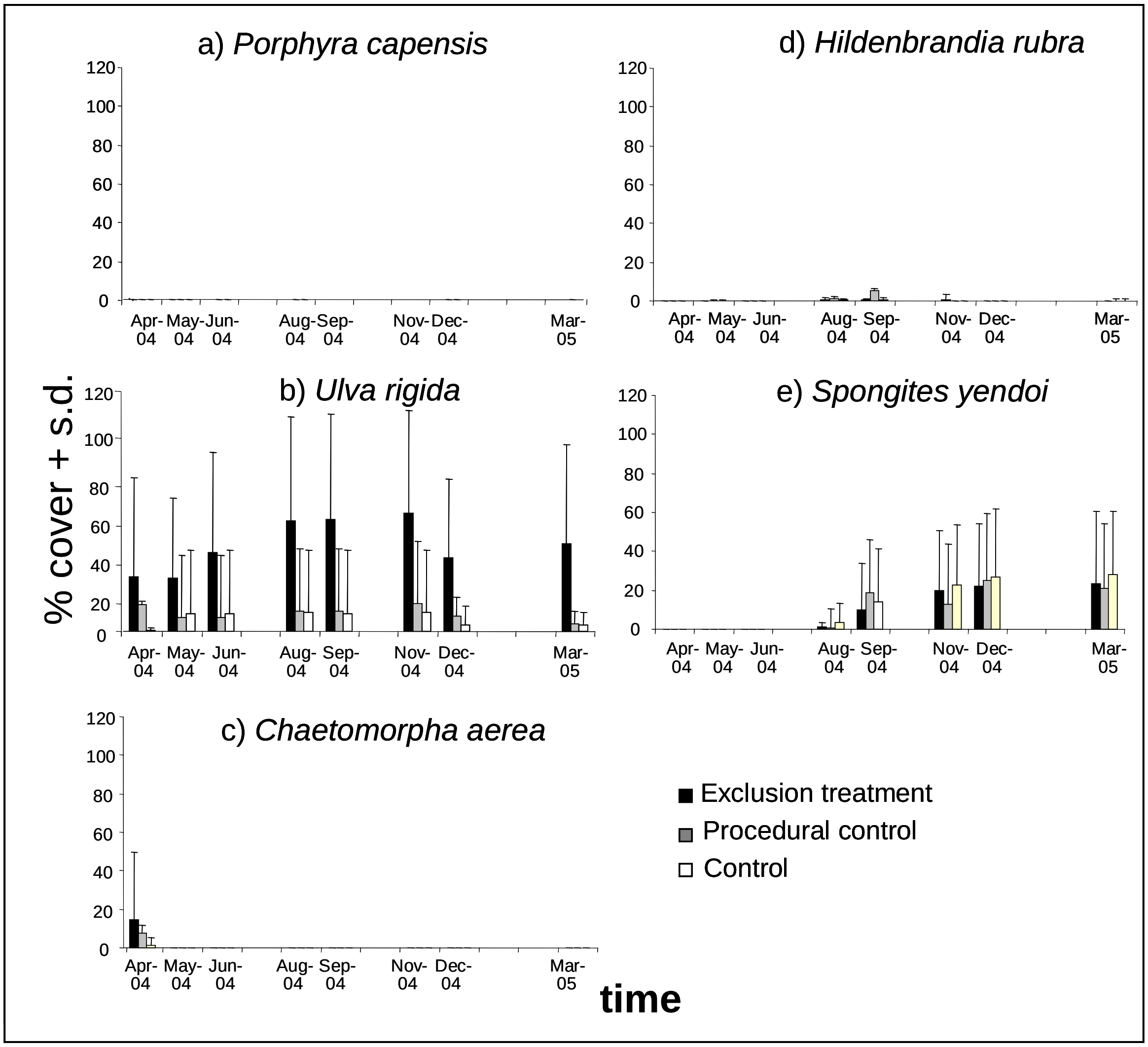

Figure 4.6. Burnt tidal pool (Bpool) condition. Mean of cover + standard deviation of each algal species in the upper eulittoral zone assemblage during the first experiment in 2004. Black, grey and white bars indicate exclusion, procedural control and control treatment, respectively.

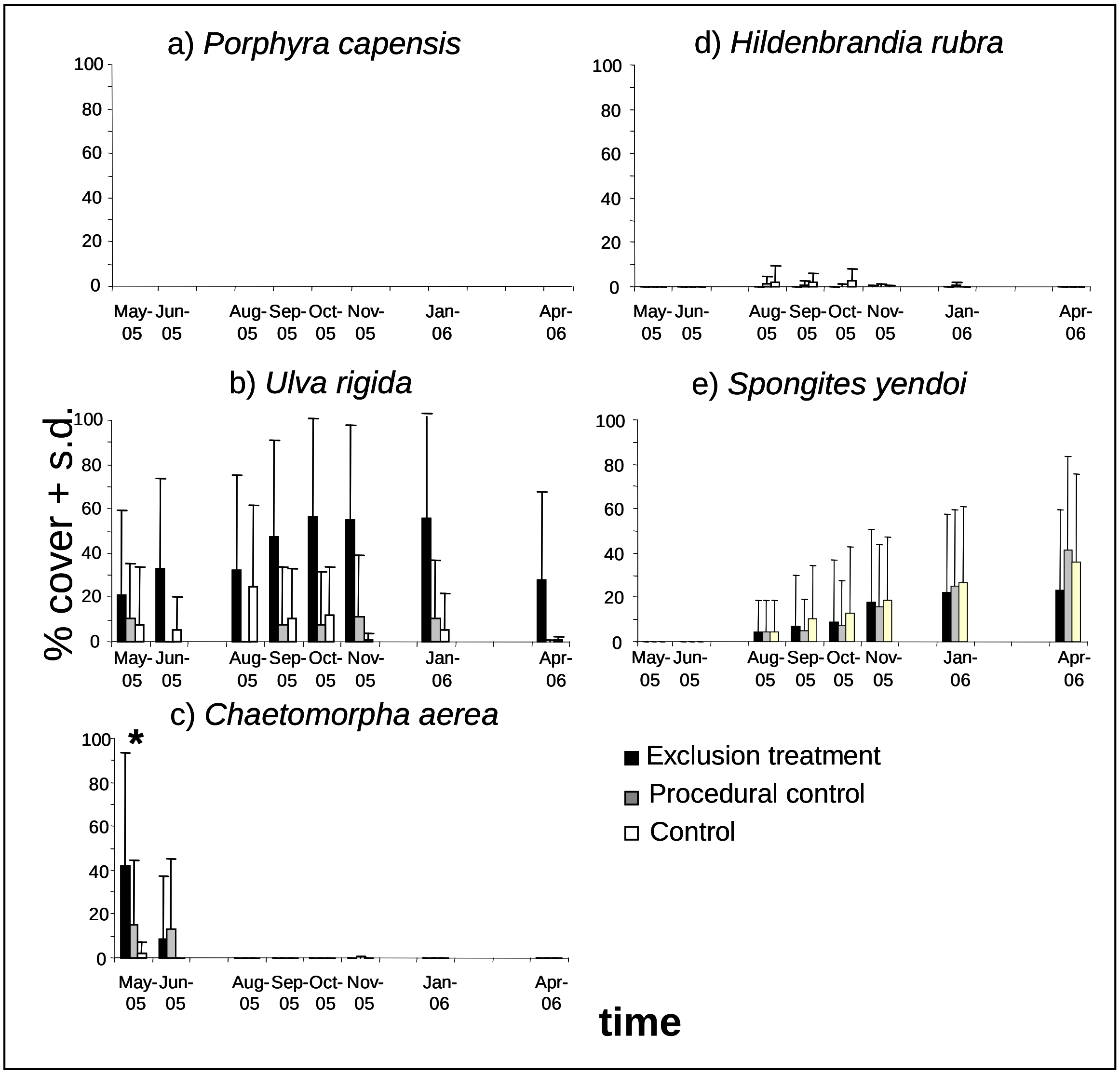

Figure 4.7. Burnt pool (Bpool) condition. Mean of cover + standard deviation of each algal species in the upper eulittoral zone assemblage during the second experiment in 2005. Black, grey and white bars indicate exclusion, procedural control and control treatment, respectively. Asterisks indicate the interaction 'Time x Treatment' when the algal cover in the exclusion treatment was higher than the procedural control and control.

Table 4.7. Non burnt tidal pool (NBpool) condition. Repeated measures ANOVA on each species of algae shows the effect of grazers (treatment effect), time and the interaction of time and treatment. The data were arcsin(square root (x+1)) transformed to achieve homogeneity and normality. * means $P < 0.01$ and ** $P < 0.001$.

	Porphyra capensis			*Ulva rigida*			*Chaetomorpha aerea*			*Hildenbrandia rubra*			*Spongites yendoi*		
Factors	**DF**	**MS**	**F**	**DF**	**MS**	**F**	**DF**	**MS**	**F**	**DF**	**MS**	**F**	**DF**	**MS**	**F**
Treatment		**no recruitment**		**2**	**4.1**	**4.8***	**2**	**0.0**	**0NS**	**2**	**0.14**	**0.09NS**	**2**	**1.5**	**0.8NS**
Error				**33**	**0.9**		**33**	**0.01**		**33**	**1.48**		**33**	**1.8**	
Time				**7**	**0.45**	**7.9****	**3**	**0.01**	**0.8NS**	**7**	**0.02**	**0.96NS**	**7**	**0.4**	**5.2****
Time*Treat				**14**	**0.09**	**1.6NS**	**6**	**0.01**	**0.8NS**	**14**	**0.03**	**1.31NS**	**14**	**0.1**	**1.1NS**
Error				**231**	**0.06**		**99**	**0.09**		**231**	**0.02**		**231**	**0.07**	
Cochran C					**$P > 0.05$**			**$P > 0.05$**			**$P > 0.05$**			**$P > 0.05$**	
Treatment					**T > Pc = c**			**NS**			**NS**			**NS**	
Time					**Nov04> March05=Jun04=Aug04=Sept04>Apr04**			**NS**			**NS**			**Aug04=Sep04=Nov04 < all**	
Time*Treat					**NS**			**NS**			**NS**			**NS**	

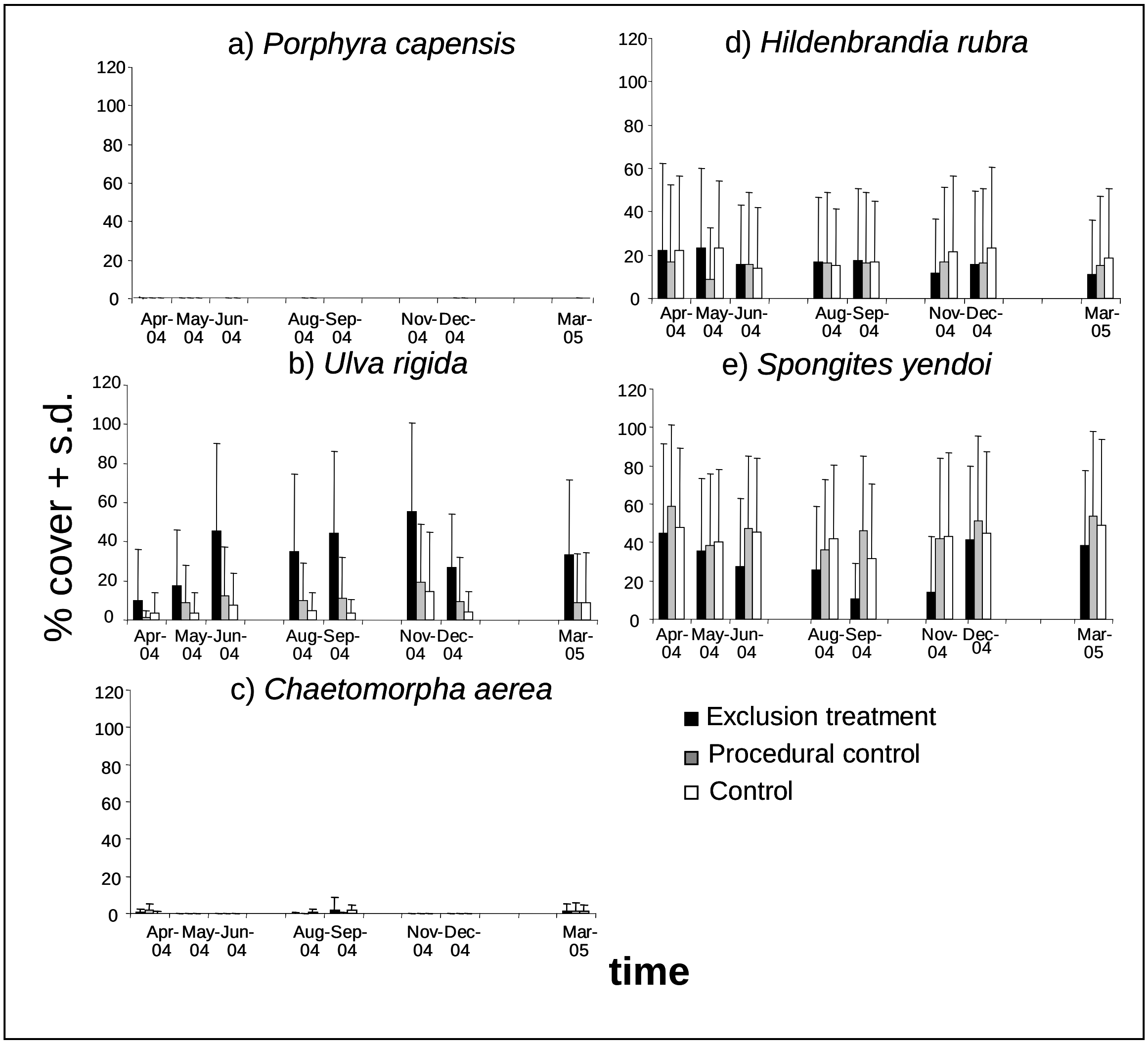

Figure 4.8. Non burnt pool (NBpool) condition. Mean of cover + standard deviation of every algal species in the upper eulittoral zone assemblage during 2004. Black, grey and white bars indicate exclusion, procedural control and control treatment, respectively.

I.2. The functional group level. Comparison of conditions in 2004 and 2005

I.2.a. Burnt open rock (BOR) during 2004 and 2005. There was virtually no colonisation by encrusting algae in either year. The foliose algae started to recruit into the exclusion plots in the second month (May 2004 and June 2005) after the start of each experiment. There were small fluctuations in the percent cover during the year. The maximum level of cover was at the end of the experiment in 2004 (17.1 ± 31.5%) and in spring (October and November) in 2005 (27 ± 38.9%). An overall grazing effect was observed in both years. (Table 4.8. and Fig. 4.9).

I.2.b. Non burnt open rock (NBOR) during 2004 and 2005. Notice here that NBOR 2005 behaves like BOR 2005, due to sterilization of substratum, however I still call it NBOR to differentiate it from the set of blocks belonging to BOR 2005. Foliose algae started to recruit in the first month of each experiment (April 2004 and May 2005). Again, the maximum levels of cover were in late summer for 2004 and spring in 2005 (Table 4.9). Grazers affected foliose algal cover in both experiments (Treatment effect. Table 4.9 and Fig. 4.10), the ‘Time x Treatment’ interaction indicated a treatment effect in 2004, but not in 2005 (Table 4.9). Encrusting algae were present in 2004, but could not recruit the following year, after being removed using a torch in 2005. In November 2004, encrusting algae reached a maximum level of cover (69%, Fig. 4.10).

I.2.c. Burnt pool (Bpool) condition. The foliose algae rapidly colonized some blocks reaching cover inside the cages of 39.7 ± 49.5 with less than 10% in the controls. This was observed in the second week in some tidal pools during both experiments. Again there were two temporal peaks in the foliose algal cover, during spring 2004 (August, September and November, average 50 ± 48%), but with no clear pattern in 2005 (Table

4.10 and Fig. 4.11). An overall grazing effect was observed for foliose algae in both years (Table 4.10).

Encrusting algae started to recruit in August in both experiments (Fig. 4.11). Subsequently, the encrusting algae started to grow until the end of the experiment when they reached highest cover (Table 4.10 and Fig. 4.11).This functional group was not affected by grazers.

I.2.d. Non burnt pool (NBpool) condition tested only in 2004. These tidal pools were dominated by encrusting algae, when the treatments were established. Again the grazers affected the foliose algal group (Table 4.11 and figure 4.12). Foliose and encrusting algae showed temporal variability in the algal cover among sampling dates, with spring showing the maximum values (Table 4.11).

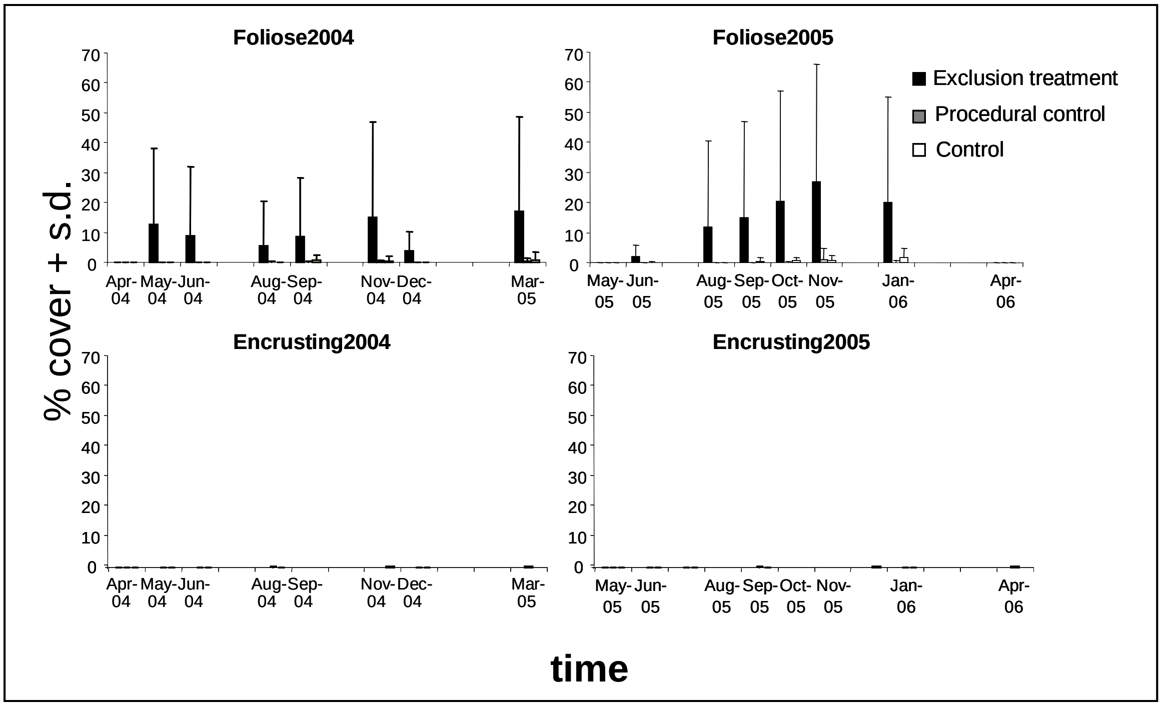

Figure 4.9. Burnt open rock (BOR) condition. Mean of cover + standard deviation of foliose and encrusting algae functional groups in the three treatments during both experiments. Black, grey and white bars indicate exclusion, procedural control and control treatment, respectively.

Table 4.8. Burnt open rock (BOR) condition in 2004 and 2005. Repeated measures ANOVA on the foliose functional group shows the effect of grazers (treatment effect), time and the interaction of time and treatment. All data were arcsin(square root (x+1)) transformed to achieve homogeneity and normality. The level of significance was $\alpha/2 = 0.05/2 = 0.025$. * means $P < 0.025$, ** $P < 0.001$, NS = non-significant.

	Foliose2004			Encrusting2004			Foliose2005			Encrusting2005		
Factors	**DF**	**MS**	**F**	**DF**	**MS**	**F**	**DF**	**MS**	**F**	**DF**	**MS**	**F**
Treatment	2	0.93	4.18*	no recruitment			2	1.7	4.8*	no recruitment		
Error	33	0.22					33	0.36				
Time	6	0.03	2.4*				5	0.1	5.4**			
Time*Treat	12	0.02	1.5NS				10	0.05	2.9**			
Error	198	0.01					165	0.02				
Cochran test	$P < 0.05$						$P < 0.05$					
SNK test												
Treatment	T > Pc = c						T > Pc =c					
Time	March05 > Dec 05						Oct05=Nov05=Jan05>May05=June05=Dec05=April06					
Time*Treat	NS						No logical groups					

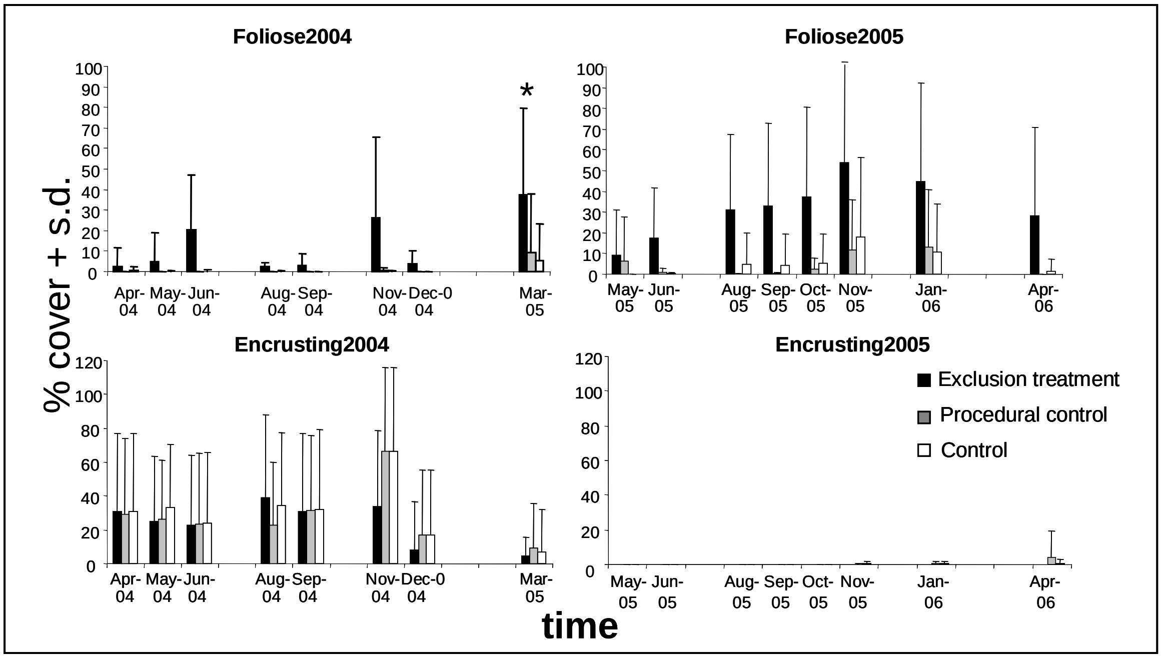

Figure 4.10: Non burnt open rock (NBOR) condition. Mean of cover + standard deviation of foliose and encrusting algae functional groups in the three treatments during both experiments. Black, grey and white bars indicate exclusion, procedural control and control treatment, respectively. Asterisks indicate the interaction 'Time x Treatment' when the algal cover in the exclusion treatment was higher than the procedural control and control.

Table 4.9. Non burnt open rock (NBOR) condition. Repeated measures ANOVA on the foliose functional group shows the effect of grazers (treatment effect), time and the interaction of time and treatment. All data were arcsin(square root (x+1)) transformed to achieve homogeneity and normality. The level of significance was α/2 = 0.05/2 = 0.025. * means P < 0.025, ** P < 0.001, NS = non-significant.

	Foliose2004			**Encrusting2004**			**Foliose2005**			**Encrusting2005**		
Factors	**DF**	**MS**	**F**	**DF**	**MS**	**F**	**DF**	**MS**	**F**	**DF**	**MS**	**F**
Treatment	**2**	**1.6**	**15.2*****	**2**	**0.22**	**0.13NS**	**2**	**4.2**	**7.2***	**no recruitment**		
Error	**33**	**0.1**		**33**	**1.6**		**30**	**0.6**				
Time	**7**	**0.3**	**7.4*****	**7**	**1.8**	**9.7*****	**7**	**0.6**	**9*****			
Time*Treat	**14**	**0.1**	**3.2*****	**14**	**0.2**	**0.98NS**	**14**	**0.1**	**1.6NS**			
Error	**231**	**0.04**		**231**	**0.2**		**210**	**0.07**				
Cochran test	**P < 0.05**			**P > 0.05**			**P < 0.05**					
SNK test												
Treatment	**T > Pc = c**			**NS**			**T > Pc = c**					
Time	**March05 > all**			**Nov04 > all**			**Nov05=Jan06>all**					
Time*Treat	**March05: T > Pc =c**			**NS**			**NS**					

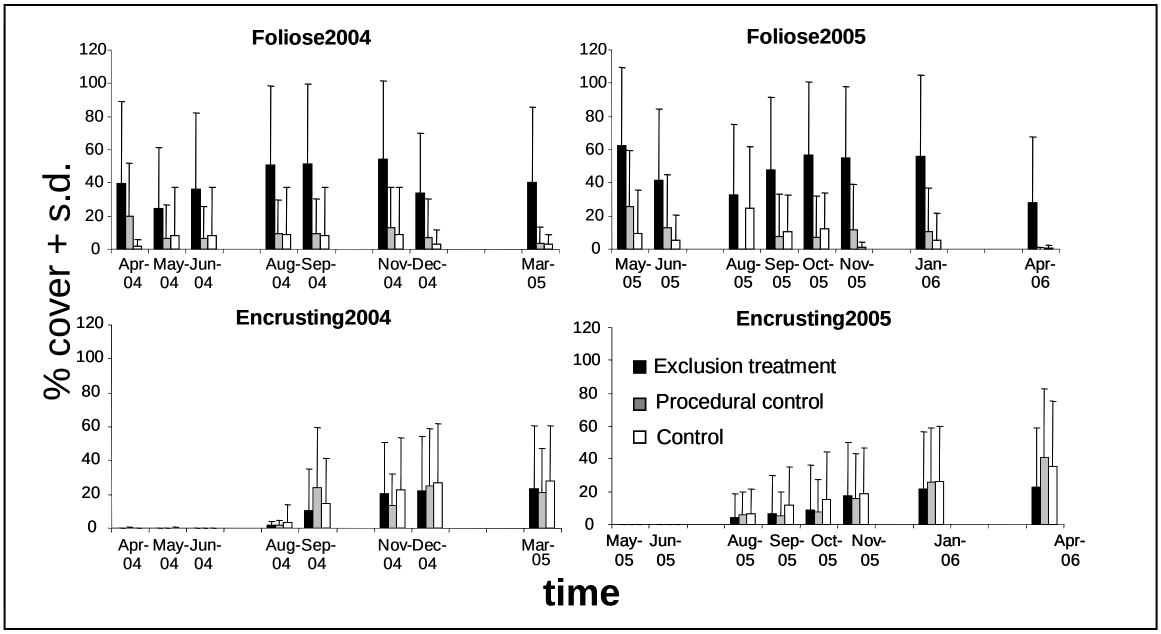

Figure 4.11. Burnt tidal pool (Bpool) condition. Mean of cover + standard deviation of foliose and encrusting algae functional groups in the three treatments during both experiments. Black, grey and white bars indicate exclusion, procedural control and control treatment, respectively.

Table 4.10. Burnt pool (Bpool) condition. Repeated measures ANOVA on the foliose functional group shows the effect of grazers (treatment effect), time and the interaction of time and treatment. All data were arcsin(square root (x+1)) transformed to achieve homogeneity and normality. The level of significance was α/2 = 0.05/2 = 0.025. * means P < 0.025, ** P < 0.001, NS = non-significant.

	Foliose2004			**Encrusting2004**			**Foliose2005**			**Encrusting05**		
Factors	**DF**	**MS**	**F**	**DF**	**MS**	**F**	**DF**	**MS**	**F**	**DF**	**MS**	**F**
Treatment	**2**	**8.2**	**5.46****	**2**	**0.11**	**0.3NS**	**2**	**11**	**10.1****	**2**	**0.28**	**0.4NS**
Error	**33**	**15**		**33**	**0.37**		**33**	**1.1**		**33**	**0.72**	
Time	**7**	**0.2**	**3.5****	**6**	**1.32**	**20.8*****	**7**	**0.3**	**3.3***	**5**	**1.03**	**17.4*****
Time*Treat	**14**	**0.1**	**2.1***	**12**	**0.04**	**0.6NS**	**14**	**0.2**	**1.9***	**10**	**0.03**	**0.59NS**
Error	**231**	**0.05**		**198**	**0.06**		**231**	**0.1**		**165**	**0.06**	
Cochran test	**P < 0.05**			**P > 0.05**			**P < 0.05**			**P > 0.05**		
SNK test												
Treatment	**T > Pc =c**			**NS**			**T > Pc = c**			**NS**		
Time	**Aug04=Sept04=Nov04> all**			**Sept04=Nov04=Dec04=Mar05>all**			**May05,Jun05,Oct05,Jan06>April06**			**Nov05=Jan06=April06>all**		
Time*Treat	**No logical groups†**			**NS**			**No logical groups**			**NS**		

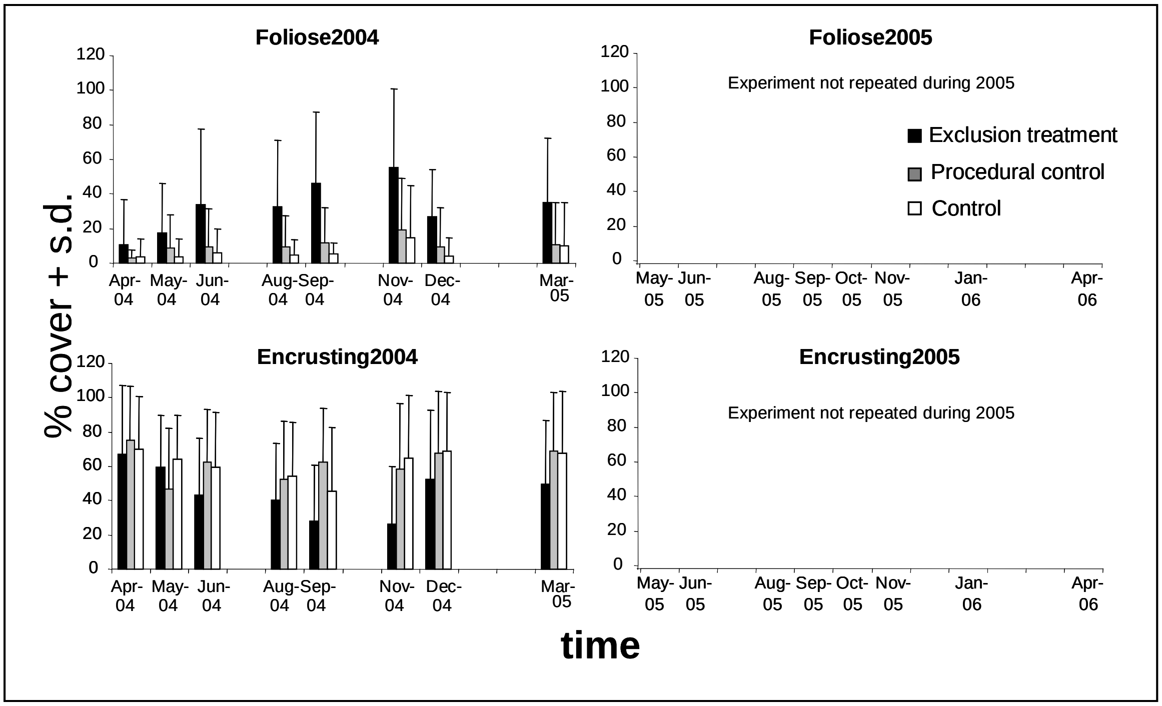

Figure 4.12. Non burnt tidal pool (NBpool) condition. Mean of cover + standard deviation of foliose and encrusting algae functional groups in the three treatments during both experiments. Black, grey and white bars indicate exclusion, procedural control and control treatment, respectively.

Table 4.11. Non burnt pool (NBpool) condition. Repeated measures ANOVA on the foliose functional group shows the effect of grazers (treatment effect), time and the interaction of time and treatment. All data were arcsin(square root (x+1)) transformed to achieve homogeneity and normality. The level of significance was α/2 = 0.05/2 = 0.025. * means $P < 0.025$, ** $P < 0.001$, NS = non-significant.

	Foliose2004			Encrusting2004			Foliose2005			Encrusting2005		
Factors	DF	MS	F	DF	MS	F	DF	MS	F	DF	MS	F
Treatment	2	4	4.8*	2	1.5	1.5NS	experiment not repeated in this condition					
Error	33	0.8		33	1.1							
Time	7	0.4	7***	7	0.5	5.8***						
Time*Treat	14	0.08	1.5NS	14	0.2	1.9NS						
Error	231	0.06		231	0.1							
Cochran test	P < 0.05			P >0.05								
SNK test												
Treatment	T > Pc = c			NS								
Time	Nov04>Sep04>all			April04=Mar05=Dec04>Jun04=Aug04=Sept04=Nov04								
Time*Treat	NS			NS								

I.3. Coarsest level of resolution: chlorophyll *a* concentration. Comparison between experiments in 2004 and 2005

I.3.a. Burnt open rock (BOR) during 2004. Biomass of algae as represented by concentration of chlorophyll *a* was not affected by grazers. However, there was temporal variability, with a peak in the concentration of chlorophyll *a* at the end of the experiment in March 2005 (Table 4.12).

During 2005, algal biomass was affected by grazing (treatment effect: Table 4.13). The factor 'Time' was significant showing a peak in November 2005. (Fig. 4.14).

I.3.b. 'Non burnt open rock' (NBOR) condition. Under this condition, there was a significant treatment effect (Table 4.12). Temporal variability was detected during 2004 with a peak in concentration of chl *a* in July 2004 (Table 4.12) followed by peaks in December 2004 and March 2005 (Table 4.12 and Fig. 4.13).

During 2005, NBOR became a BOR condition. Grazers again affected algal biomass (treatment effect: Table 4.13), with a peak in the concentration of chl *a* in spring (November 2005, table 4.13 and Fig. 4.14).

I.3.c. 'Burnt tidal pool' (Bpool) during 2004. An overall grazing effect was detected, with a peak in the concentration of chlorophyll *a* during July 2004, October 2004 and March 2005 (Table 4.12 and Fig. 4.13).

Again, during 2005 there was an overall grazing effect. Temporal variability was minimal, April 2005 (the beginning of the experiment) had a lower in chl *a* concentration than the rest of the sampling dates (Table 4.13 and Fig. 4.14).

I.3.d. Non-burnt pool (NBpool). Grazers did not affect the concentration of chlorophyll *a*, however temporal variability followed the pattern show in the rest of the conditions, with the greatest concentration of chlorophyll *a* in July 2004. There was a ‘time x treatment’ effect, although the groups were difficult to interpret and did not form any logical temporal pattern.

Table 4.12. The coarsest level of resolution, concentration of chlorophyll *a* in each condition during 2004 Repeated measures ANOVA on each condition shows the effect of grazers (treatment effect), time and the interaction of time and treatment. The data were transformed using Ln (x + 1) to achieve homogeneity. The level of significance was α = 0.05. * means P < 0.05, ** P < 0.01,* P < 0.001, NS = non-significant.**

	Burnt open rock (BOR)			**Non burnt open rock (NBOR)**			**Burnt pool (Bpool)**			**Non burnt pool (NBpool)**		
Factors	**DF**	**MS**	**F**	**DF**	**MS**	**F**	**DF**	**MS**	**F**	**DF**	**MS**	**F**
Treatment	**2**	**3.24**	**3.22NS**	**2**	**10.3**	**17.9*****	**2**	**22.7**	**4.33***	**2**	**13.8**	**2.3NS**
Error	**33**	**1.0**		**33**	**0.57**		**3**	**0.23**		**33**	**6**	
Time	**10**	**5.23**	**22.9*****	**10**	**8.35**	**32.6*****	**10**	**24.9**	**41.12*****	**10**	**17.15**	**31.04*****
Time*Treat	**20**	**0.33**	**1.45NS**	**20**	**0.68**	**2.69*****	**20**	**1.75**	**2.88****	**20**	**1.78**	**3.2*****
Error	**330**	**0.23**		**330**	**0.26**		**330**	**0.6**		**330**	**0.55**	
Cochran test	**P > 0.05**			**P > 0.05**			**P < 0.05**			**P > 0.05**		
Post hoc SNK test												
Treatment	**NS**			**T > Pc = c**			**T > Pc = c**			**NS**		
Time	**Mar05>15April04=1Jul04=1Dec04>all**			**Jul04>Mar05>Dec04>all**			**Jul04>Mar05>Oct04=Aug04>all**			**Jul04>Mar05=May04=15April04>all**		
Time*Treat	**NS**			**No logical groups†**			**No logical groups**			**No logical groups**		

Table 4.13. The coarsest level of resolution, concentration of chlorophyll *a* in each condition during 2005. Repeated measures ANOVA on each condition shows the effect of grazers (treatment effect), time and the interaction of time and treatment. The data were transformed using Ln (x + 1) to achieve homogeneity. The level of significance was α = 0.05. * means P < 0.05, ** P < 0.01, *** P < 0.001, NS = non-significant.

	Burnt open rock (BOR)			**Non burnt open rock (NBOR)**			**Burnt pool (Bpool)**			**Non burnt pool (NBpool)**		
Factors	**DF**	**MS**	**F**	**DF**	**MS**	**F**	**DF**	**MS**	**F**	**DF**	**MS**	**F**
Treatment	**2**	**2.7**	**7.3***	**2**	**5.11**	**5.7***	**2**	**13.29**	**5.94***	**condition not repeated**		
Error	**33**	**0.4**		**30**	**0.89**		**33**	**2.23**				
Time	**7**	**1.39**	**8.9*****	**7**	**2.84**	**10.45*****	**7**	**4.46**	**10.5*****			
Time*Treat	**14**	**0.94**	**6.1*****	**14**	**0.35**	**1.29NS**	**14**	**0.6**	**1.42NS**			
Error	**231**	**0.16**		**210**	**0.27**		**231**	**0.42**				
Cochran test	**P > 0.05**			**P > 0.05**			**P > 0.05**					
Post hoc SNK test												
Treatment	**T > Pc = c**			**T > Pc = c**			**T > Pc = c**					
Time	**Nov05>Jan06=Sept05>all**			**Nov05>Sept05> all**			**All>15April05**					
Time*Treat	**Nov05:T > Pc = c**			**NS**			**NS**					

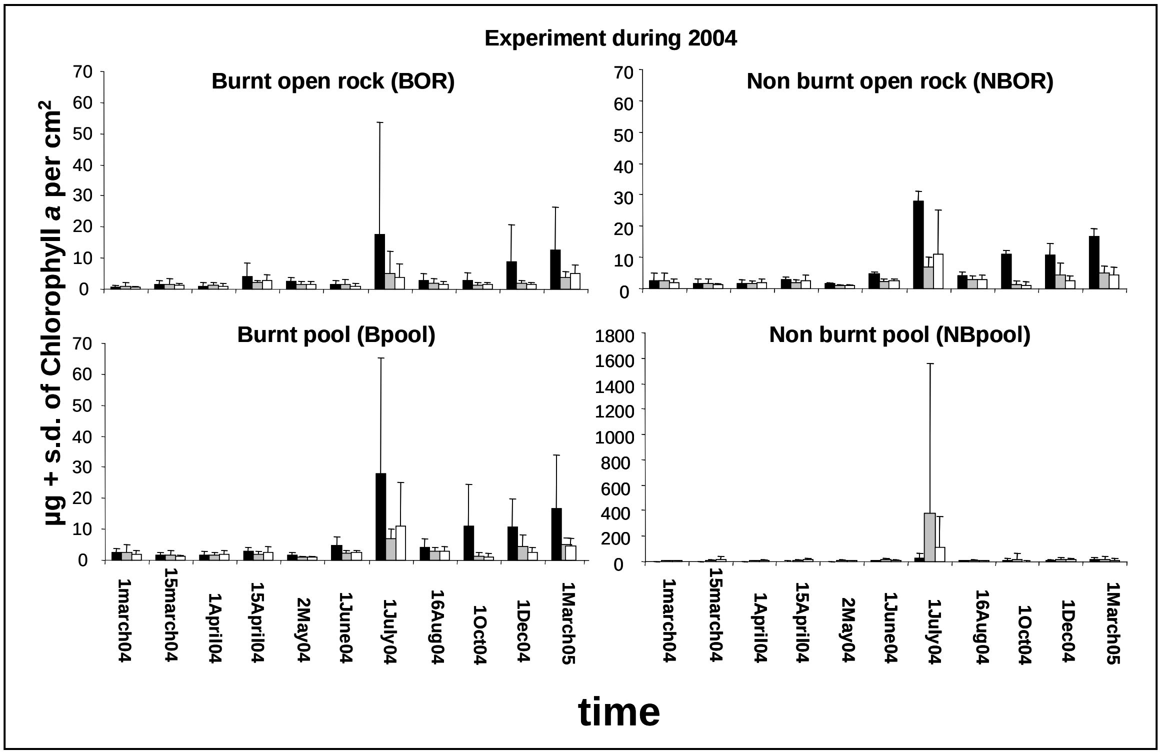

Figure 4.13. Concentration of chlorophyll *a*. Mean of cover + standard deviation of the concentration of chlorophyll *a* in each condition during the first experiment (2004). Black, grey and white bars indicate exclusion, procedural control and control treatment, respectively. Asterisks indicate the interaction 'Time x Treatment' when the algal cover in the exclusion treatment was higher than the procedural control and control.

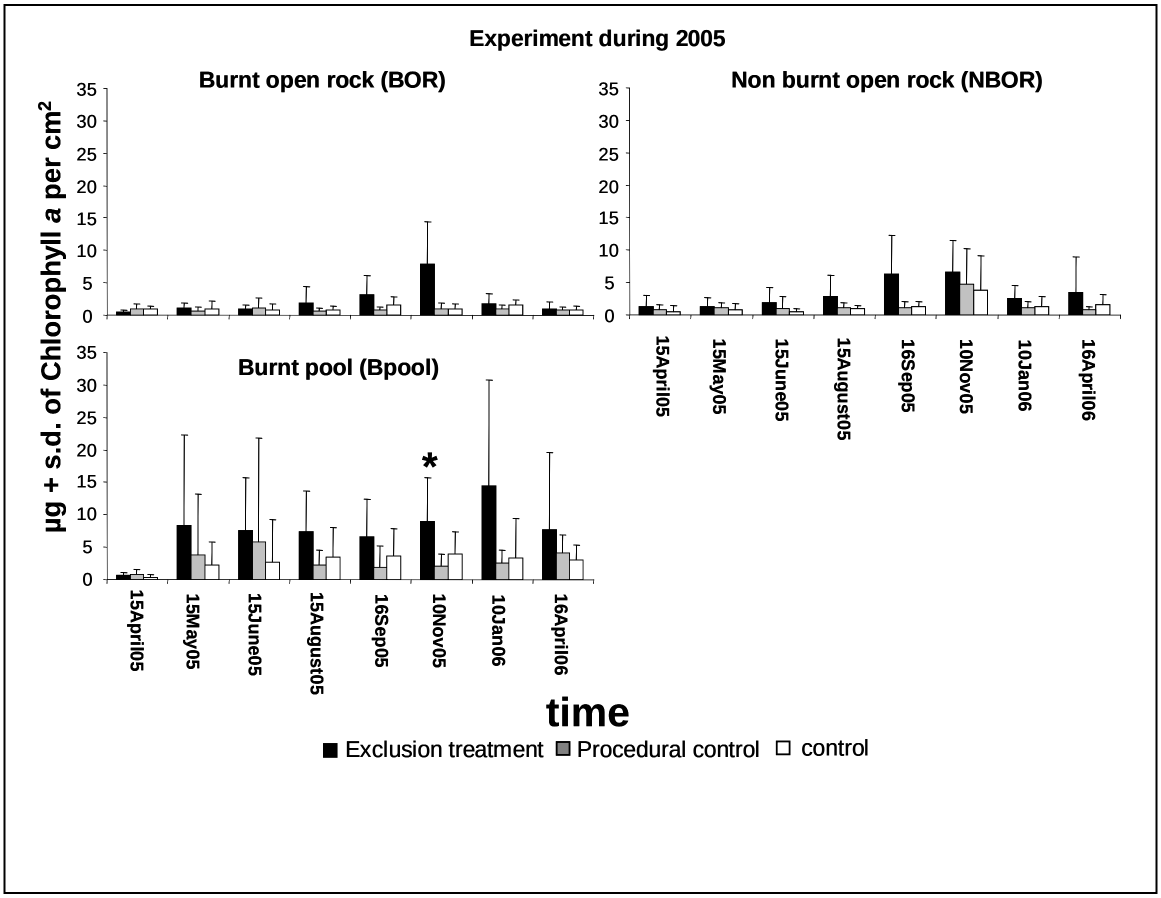

Figure 4.14. Concentration of chlorophyll *a*. Mean of cover + standard deviation of the concentration of chlorophyll *a* in each condition during the second experiment (2005). Black, grey and white bars indicate exclusion, procedural control and control treatment, respectively. Asterisks indicate the interaction 'Time x Treatment' when the algal cover in the exclusion treatment was higher than the procedural control and control.

II. Spatial stability or persistence of mesograzing effects between years

II.1. Spatial stasis or determinism

The experimental design allowed me to study the spatial stability or persistence of grazing effects in the upper eulittoral zone between two consecutive years. Spatial stability is understood as invariant or static positions on the shore where grazing effect is continuously significant. Without varying the position of the plots in the conditions ‘burnt open rock’ BOR, ‘non burnt open rock’ NBOR and ‘burnt tidal pools’, I burnt the treatments after one year. Then I correlated the effect sizes from 2004 and 2005, in order to estimate spatial relationship between one year and another.

At the most specific level of resolution in the BOR condition *Porphyra capensis* showed 60% stability in the effects of mesograzers between years (i.e. $r = 0.6$). The next alga that exhibited spatial persistence between years was *Ulva rigida* in the NBOR and Bpool conditions, with a degree of consistency among blocks of 70% and 82% respectively (Table 4.14).

At the functional group level, foliose algae were found to be consistent in Bpools exhibiting a correlation coefficient of 70% (Table 4.14).

Finally, at the coarsest level of resolution, only BOR exhibited consistency between years with an r value of $r = 0.71$ (71%) (Table 4.14).

Table 4.14. Spatial stability in grazer effects, judged using two criteria: i. spatial correlation of effect sizes and ii. overall grazing effect between both years. Stability was assessed at three levels of resolution. Bold indicates when both conditions are fulfilled to detect spatial stability. At the finest level of resolution (species) * and ** mean P < 0.01 and P < 0.001, respectively. At intermediate (functional groups) level of resolution * and ** mean P < 0.025 and P < 0.001, respectively. Finally at the coarsest level (chlorophyll *a*), * = P < 0.05 and ** < P < 0.001. 'Not possible' means that there were not enough data to carry out the analysis, because of lack of recruitment of certain species. 'yes' or 'no' mean significant or non significant overall grazing effect, in 2004 and 2005. The first row of each result indicates the spatial correlation within blocks and between years and the second the overall grazing effect. Notice 'NBOR 2005' is equivalent to 'BOR' 2005.

Spatial Persistence	BOR 2004 v/s BOR 2005	Bpool 2004 v/s Bpool 2005	NBOR 2004 v/s NBOR 2005
		Specific level of resolution	
Porphyra capensis *Spatial determinism:*	t= ***3.2***$**$ r^2= 60%	not possible	t=1.9NS r^2=55%
Consistence of overall grazing effect 2004 & 2005?	NO: $F_{2,33}$=3NS& NO: $F_{2,33}$=4NS		YES: $F_{2,33}$=10.4$**$ & NO: $F_{2,33}$=4NS
Ulva rigida *Spatial determinism:*	t=2.2NS r^2=56%	**t=3.4$**$ r^2=70%**	**t=4.4 P=0.001 r^2=82%**
Consistence of overall grazing effect 2004 & 2005?	NO: $F_{2,33}$=3NS & NO: $F_{2,33}$=3.5NS	**YES: $F_{2,33}$=5.4$*$&YES: $F_{2,33}$= 8.6$**$**	**YES: $F_{2,33}$=7.2$*$&YES: $F_{2,33}$=5.4$*$**
Chaetomorpha aerea *Spatial determinism:*	not possible	t=1.9 P=0.076 r^2=53%	not possible
Consistence of overall grazing effect 2004 & 2005?		NO: $F_{2,33}$=0.8NS& NO :$F_{2,33}$= 2.6NS	
Hildenbrandia rubra *Spatial determinism:*	not possible	t=1.7 P=0.38 r^2=27%	not possible
Consistence of overall grazing effect 2004 & 2005?		NO: $F_{2,33}$= 0.8NS & NO: $F_{2,33}$= 1.3NS	
Spongites yendoi *Spatial determinism:*	not possible	P=0.1 r^2=48%	not possible
Consistence of overall grazing effect 2004 & 2005?		NO: $F_{2,33}$=0.3NS & NO: $F_{2,33}$= 0.2NS	
		Functional groups	
Foliose *Spatial determinism:*	t=1.7NS r^2=47%	**t=3.1$*$ r^2=70%**	t=2.63NS r^2=66%
Consistence of overall grazing effect 2004 & 2005?	YES: $F_{2,33}$=4.2$*$&YES: $F_{2,33}$= 4.8$*$	**YES: $F_{2,33}$=5.5$**$& YES: $F_{2,33}$= 10.1$**$**	YES:$F_{2,33}$=15.2$***$& YES: $F_{2,33}$=7.2$*$
Encrusting *Spatial determinism:*	not possible	t=2.1NS r^2=54%	not possible
Consistence of overall grazing effect 2004 & 2005?		NO: $F_{2,33}$=0.3NS & NO: $F_{2,33}$= 0.4NS	
		Biomass	
Chlorophyll *a* *Spatial determinism:*	t=3$**$ r^2=71%	t=0.4NS r^2=12%	t=1.2NS r^2=37%
Consistence of overall grazing effect 2004 & 2005?	NO: $F_{2,33}$=3.22NS& YES$F_{2,33}$=7.3$*$	YES: $F_{2,33}$=4.3$*$& YES: $F_{2,33}$=5.9$*$	YES: $F_{2,33}$=18$***$& YES:$F_{2,33}$=5.7$*$

II.2. Consistence in the significance of grazing

Three conditions were assessed for spatial persistence of grazing effects at different levels of resolution, 'burnt open rock', 'burnt tidal pools' and 'non-burnt tidal pools' (Table 4.14). Two criteria were taken into account: i. the spatial determinism or specificity of the grazing effect at each block. This was assessed through a correlation of the intensity of the grazing effect (measured as effect size) between both years using the same blocks. ii. The consistency of statistical significance of the overall grazing effect between years.

Burnt open rock (BOR). *Porphyra capensis* and *Ulva rigida* were the only macroalgae colonizing this condition. Both algae were not affected by grazing in both consecutive years, however only *P. capensis* showed spatial determinism. At the functional level of resolution, the overall grazing effect was significant in both years for foliose algae, but there was no significant spatial relationship in the spatial specificity of grazing effect between years. Finally, at the coarsest level of resolution, overall grazing effect was significant only in 2005, and there was spatial specificity (Table 4.14).

Burnt tidal pool (Bpool). Although four species of algae colonized this habitat, *Ulva rigida* was the most abundant (Table 4.14). The overall grazing effect on this alga was significant in both years and there was also spatial specificity in the grazing effect. At the functional level of resolution, the foliose algal group exhibited an overall grazing effect and spatial dependence, while the encrusting algal group was not affected by grazers and there was no spatial relationship. At the coarsest level of resolution, spatial determinism (condition 1) was not observed, though the overall grazing effect was significant in both years (condition 2).

Non-burnt open rock (NBOR). *Porphyra capensis, Ulva rigida, Chaetomorpha aerea* and *Hildenbrandia rubra* were present during the first experiment in 2004, however when the experiment was repeated and after burning of the rock substrata, only *U. rigida* and *P. capensis* re-colonized this habitat, as was seen on the original burnt open rock plots in both years. *U. rigida* exhibited an overall grazing effect and spatial determinism, while *P. capensis* was affected by grazers only during the first experiment. At the functional level, the overall grazing effect was significant, but the spatial determinism was non-significant. Likewise, at the coarsest level of resolution only the overall grazing effect was significant.

In synthesis, stability was observed in grazing effect on *Ulva rigida* in the NBOR and Bpool, at the level of foliose functional group in Bpool.

III. Grazer community in the upper eulittoral zone in the south coast of Southern Africa

III.1. Composition

The upper eulittoral zone is characterized by two littorinids snails species, *Nodilittorina knysnaensis* and *N. africana,* and ten species of mesograzers. These are siphonarid limpets (*Siphonaria capensis, S. serrata and S. concinna*), other, less abundant limpets (*Nerita polita, Helcion pruinosus*), winkles (*Oxystele tigrina, O. tabularis*), seastars (*Patiriella exigua*), juvenile sea urchins (*Parechinus angulosus*) and the chiton (*Acanthochitona garnoti*), which is nocturnal and rare and was observed only qualitatively in tidal pools.

III.2. Mesograzer abundance, variation by habitat and manipulation

I used data on abundance of grazers pooled across dates during 2004. The substratum manipulations ‘burnt’ and ‘non-burnt’, affected three out of nine species, which preferred ‘non-burnt’ substrata. These were *Patiriella exigua* and the less abundant limpets *Helcion pruinosus* and *Nerita polita* (Table 4.15 and Fig. 4.15A). The abundances of species varied between habitats and were greater in tidal pools than on open rock for *P. exigua, Oxystele tabularis*, *O. tigrina*, *Siphonaria capensis,* S. *concinna* and *H. pruinosus* (Fig. 4.15B). The sea urchin *Parechinus angulosus* and the limpets *S. serrata* and *Nerita polita* were equally abundant in both habitats. The abundance of every species varied among the four conditions represented by the combination of habitat and manipulation (Fig. 4.15C).

Table 4.15. 2-way MANOVA during 2004 showing the effect of the manipulation, habitat and the interaction between both (condition) on the pooled abundances of the mesograzer assemblage. Data were transformed using Ln (x + 1).

Factors	**Wilks**	**F**	**Effect DF**	**Error Df**
Manipulation	**0.62**	**2.44***	**9**	**36**
Habitat	**0.28**	**10.24*****	**9**	**36**
Manip. x Habitat	**0.57**	**2.95****	**9**	**36**

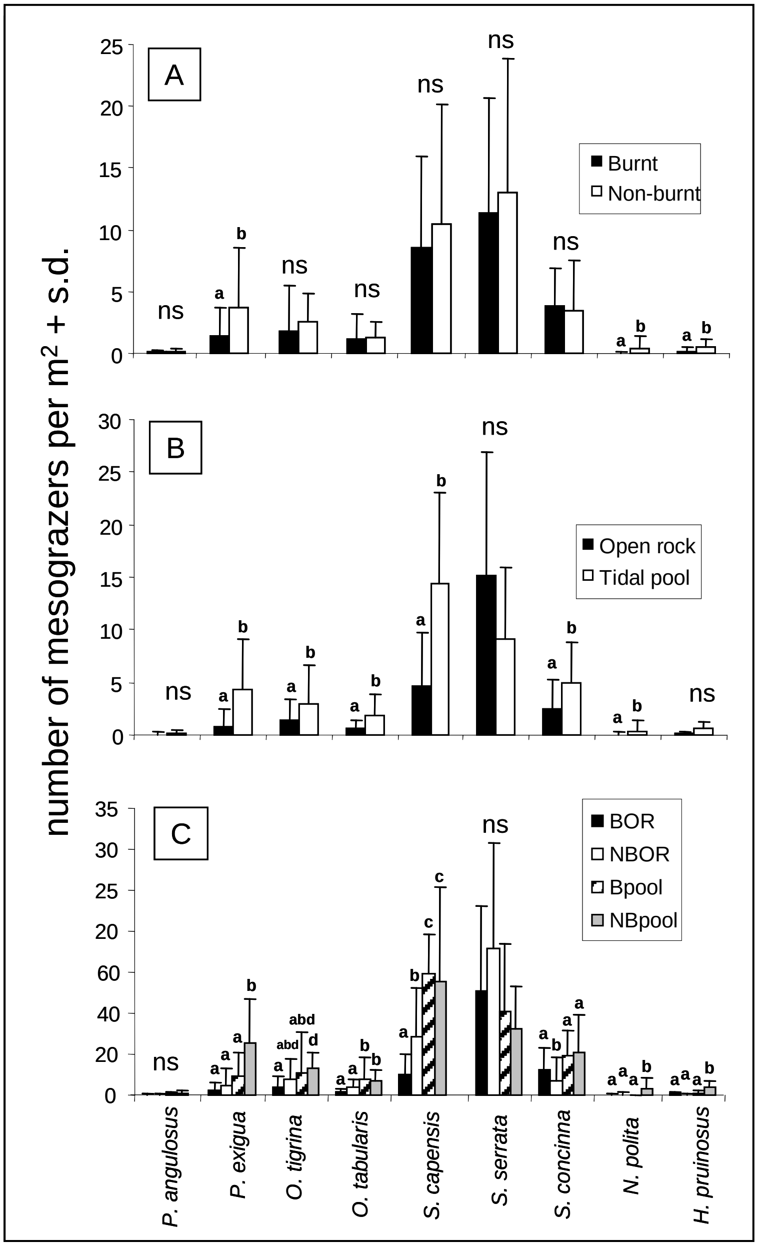

Figure 4.15. Mesograzer assemblages inhabiting the upper eulittoral zone, expressed as numbers of mesograzers per m^2. Results from 2-way MANOVA showing: A. Differences in abundance for each species in the manipulation 'burnt' and 'non-burnt', B. differences in abundance for each species in each habitat and C. differences in abundance among 'burnt open rock' (BOR), 'non burnt open rock' (NBOR), 'burnt tidal pool' (Bpool) and 'non burnt tidal pool' (NBpool) conditions. The letters over the bars indicates the homogeneous groups given by SNK post-hoc test at α = 0.05. NS means non-significant differences.

III.3. Spatial variability of mesograzers among blocks

Mesograzer numbers varied among blocks for ‘burnt open rock’, ‘non-burnt open rock’ and ‘burnt pool’ conditions (Table 4.16). This variability was observed among blocks separated by cm to a few meters. The only condition that exhibited homogenous numbers of mesograzers among blocks was ‘non burnt pool’.

Table 4.16. Individual randomized block 1-way ANOVA analysis of the pooled number of mesograzers at each condition :‘burnt open rock’ (BOR), ‘non-burnt open rock’ (NBOR), ‘burnt tidal pool’ (Bpool) and ‘non-burnt tidal pool’ (NBpool) conditions. Data were transformed using Ln(x + 1).

Conditions	**DF**	**MS**	**F**	**P**
BOR	**11**	**1.97**	**67.6**	**0.0000**
NBOR	**11**	**0.29**	**4.63**	**0.007**
Bpool	**11**	**0.57**	**14.04**	**0.0003**
NBpool	**11**	**0.33**	**1.77**	**0.17**

Post-hoc SNK test P < 0.05

BOR: block number 4 =12 > 8 > 1 = 2 = 3 = 5 = 6 =7 = 9 = 10 = 11

NBOR: block number 4 = 5 = 6 = 9 = 10 = 11= 12 > 1 = 2 = 3 = 7 = 8

Bpool: block number 1 = 2 = 3 = 4 = 5 = 7 > 6 = 9 = 11 = 12 > 10

III.4. Temporal variability of mesograzer densities: comparison between years

Two samples were taken during 2005 (winter and spring), these were compared with the four samples from 2004 using RM-ANOVA in the three conditions that were repeated ‘BOR’, ‘NBOR that changed to BOR’ and ‘Bpool’. The results indicate that the density of mesograzers decreased from March 2005 and remained low until the last sample in September 2005 (Table 4.17).

Table 4.17. 1-way RM-ANOVA on the number of mesograzers (species pooled) with time. The data wer transformed using Ln (x + 1). Cochran's C test indicated homogeneity in the variances (P > 0.05).

Factors	**DF**	**MS**	**F**
Condition	**2**	**10.5**	**2.8NS**
Error	**33**	**3.74**	
Time	**5**	**3.1**	**9.1*****
Time x condition	**10**	**0.22**	**0.65NS**
Error	**165**	**0.339**	
Post-hoc SNK test			
Time: March 04 = June 04 = Nov 04 > March 05 = June 05 = Sept 05			

IV. Micrograzers

IV.1. Variability of micrograzers among blocks

The micrograzers comprised littorinid snails (*Nodilittorina africana* and *N. knysnaensis*) and juveniles of mesograzers (mostly juveniles of siphonarid limpets), with sizes < 1 cm. These two groups exhibited spatial variability among the experimental blocks (Table 4.18).

Table 4.18. Spatial variability among blocks under the different conditions. Four 1-way MANOVAs of were run to test the spatial variability in density of littorinids and juveniles. Data were pooled for both years and were transformed using Ln (x + 1). Cochran's C test indicated homogeneity in the variances (P > 0.05).

conditions	Wilks	F	Effect DF	Error Df	P
BOR	0.011	8.35	22	22	<0000.1
NBOR	0.083	2.47	22	22	0.02
Bpool	0.047	3.62	22	22	0.002
NBpool	0.029	4.8	22	22	0.0002

Post-hoc SNK test

BOR: Littorines block: 2 = 3 = 5 = 6 = 7 = 8 =9 = 10 = 11 > 1 = 4 = 12

Juveniles block: 4 > 5 = 8 = 9 = 11, but 4 = 1 = 2 = 3 = 6 = 7 = 12

NBOR: Littorines block: 1 > 3 = 6, but 1 = 2 = 4 = 5 = 7 = 8 = 9 = 10 =11 = 12

Juveniles block: non-significant

Bpool: Littorines & Juveniles: SNK failed to find differences among blocks

NBpool: Littorines block: 2 = 9 = 12 > 1 = 3 = 4 = 5 = 6 =7 = 8 = 10 = 11

Juveniles block: non-significant

IV.2. Temporal variation of micrograzers

Both components of the micrograzer assemblage exhibited variation explained by time or condition. Juveniles did not exhibit temporal variability in their abundances, while littorinids exhibit temporal variation with July 2004 having the highest abundance. Juveniles exhibited higher abundances in tidal pools, while littorinids numbers were homogeneous among conditions (Table 4.19).

Table 4.19. 1-way RM-ANOVA for A. littorinids and B. juveniles, respectively. Data were transformed using Ln (x + 1) and Bonferroni correction was used at α/2 = 0.05.

A. Littorinid spp (*Nodilittorina africana* and *N. knysnaensis*)		**MS**	**Df**	**F**	**P**	**Post hoc test (SNK)**
Cochran test P > 0.05	**condition**	**17.5**	**2**	**2.24**	**0.13**	
	Error	**7.81**	**33**			
	Time	**20.2**	**3**	**25.13**	**0.0001**	**Jul04>all, Jun05>Dec04=Sep05**
	Time x Condition	**0.38**	**6**	**0.48**	**0.82**	
	Error	**0.8**	**99**			
B. Juveniles (mix juv. of *Siphonaria* spp and other juveniles)		**MS**	**Df**	**F**	**P**	**Post hoc test (SNK)**
Cochran test P > 0.05	**condition**	**20.8**	**2**	**12.4**	**0.0001**	**Bpool>BOR=NBOR**
	Error	**1.68**	**33**			
	Time	**0.62**	**3**	**1.62**	**0.19**	
	Time x Condition	**0.27**	**6**	**0.7**	**0.65**	
	Error	**0.38**	**99**			

DISCUSSION

This study reports on the complex dynamics of variation in grazing effects in the upper eulittoral habitats of open rock and tidal pools. In addition, I analysed the effect of initial conditions and the level of resolution of the algal assemblage on the outcome of grazing.

The detection of grazing effects depends on the availability of alga and their tolerance to survive in harsh conditions in the absence of grazers (grazer exclusion treatment) in the upper eulittoral zone. In this way grazing effect was detected when there were significant differences between exclusion treatments and controls. In contrast, grazing effects were not detected under two conditions: i. when there was no algal recruitment in the exclusion treatment as well as open control treatments and ii. when the same amount of algae was present in both exclusion treatments and controls.

No statistical differences were ever observed between ‘procedural controls’ and ‘controls’ confirming that the experimental fences did not produce artefacts such as shading and/or variability in water movement, that could have affected settlement or growth of algae or passage of grazers in the treatments.

The hypothesis that desiccation is the sole factor structuring the algal assemblages on the high shore was refuted by Kaehler and Froneman (2002) for the south coast of South Africa, when they found that littorinids control microalgal biomass and the recruitment of some foliose macroalgae in the supralittoral zone. As the upper eulittoral zone lies a few meters below the supralittoral zone, a stronger grazing effect was expected as environmental conditions are more benign; and this was the first hypothesis tested.

I.1. Grazing effects at the species level of resolution

The natural condition observed in the ‘open rock’ habitats is to remain devoid of foliose macroalgae, with patches of encrusting *Hildenbrandia rubra* and microalgae species, while ‘tidal pool’ habitats are covered by the encrusting *Spongites yendoi*, *H. rubra* and some patches of *Ulva rigida*. When grazers were excluded in both habitats, a bloom of foliose algae was observed and detected at every level of resolution. This result confirms that grazing is important in the upper eulittoral zone in both open rock and tidal pool habitats, under certain conditions. The absence of foliose algae from ‘open rock’ habitats under natural conditions suggests that mesograzers can control the recruitment of these species by feeding on propagules and spores, but I do not dismiss the effect of desiccation as an important factor interacting with grazing to limit algal distribution. Previous studies on the high shore indicate that desiccation and grazing can control the upward distribution of certain macro and microalgae species in the northern hemisphere (Castenholz 1961, Robles and Cubit 1981, Cubit 1984, Mak and Williams 1999). These studies report a strong grazing effect when conditions are particularly harsh for the algae.

Sterilization of the substratum (burnt condition) at the beginning of the experiment seems to have a strong effect on the outcome of the grazing experiment, explained by a reduction in the recruitment of algae (Jenkins et al. 2001) i.e. no grazing effect. Thus, in this zone I found no overall grazing effect in the ‘burnt open rock’ (BOR) condition during 2004 or 2005. Nevertheless, under non-sterilized conditions (NBOR), a significant overall grazing effect was detected for three of the foliose species studied. When the NBOR experimental plots of 2004 were sterilized for the repeat experiment in 2005, the grazing effect disappeared except for *U. rigida*. Because NBOR 2005 was sterilised, this condition changed to ‘burnt open rock’ BOR, so that the outcome of the experiment should have been similar to the original BOR in 2005, especially as both sets of blocks were inter-dispersed in the same habitat at the same shore height. Nevertheless, BOR 2005 did not exhibit the same grazing effect on *U. rigida* as NBOR 2005. There are two possible explanations for this discrepancy. The first is that, despite interspersion of the two conditions, BOR blocks experienced harsher conditions by chance because their positions. The second is that settlement of *U. rigida* spores was heavier among the NBOR blocks. The latter explanation includes another level of complexity, which is the patchiness of recruitment at small scales. The existence and consequences of this source of variability needs to be explored in another study.

Despite the difference between BOR and NBOR during 2005, sterilization did appear to reduced the ability of the experiment to detect a grazing effect by reducing the recruitment of algae. Interestingly, Madikiza (2005) working in the west coast of South Africa observed the opposite. He noted enhanced recruitment of foliose algae after removal of the epilithic community, which comprised mainly *Hildenbrandia rubra*.

The fact that *Porphyra capensis* did not recruit into tidal pools when grazers were excluded, suggests that this alga does not follow the normal predictions of favouring apparently benign microsites. This alga, *P. capensis* was found only in open rock habitats when grazers were excluded, and even then not in every block, suggesting that a particular combination of factors is required by the alga to inhabit specific microsites. Possibly a low competitive ability can be an adptative force to survive in harsh environments (Sousa 2001, Branch and Menge 2001) or dramatic changes I abiotic factors such as salinity can affect its survival.

The encrusting coralline *Spongites yendoi* also only inhabited one habitat, tidal pools especially bigger ones or more exposed. *Hildenbrandia rubra*, was found in both habitats, but once removed it exhibited very slow recovery; this agrees with reports of low growth rates by Kaehler and Williams (1997,1998) and Forrest et al. (2001). In tidal pools the alga *Ulva rigida* was affected by grazers in both sterilised an in non-sterilised blocks in consecutive years the tidal pools. *Ulva rigida* was observed colonizing both open rock and tidal pools, during the first month in tidal pools and during the second month on open rock, after the start of the experiment in both and conditions, confirming that the benign conditions of tidal pools enhance the primary productivity of certain species (Nielsen 2001, 2003).

In addition, high synchrony in colonization and peaks of abundance was found between years and habitats. The first algae colonizing the open rock habitat were *Porphyra capensis* and *Chaetomorpha aerea* in winter (May 2004 and June 2005). They colonized one month later in 2005, since the experiment started one month later in 2005. These algae were slowly replaced by *Ulva rigida* which started to recruit in June of 2004 and June of 2005. In tidal pools, a similar trend was observed, the first colonizing algae were *U. rigida* and *C. aerea*, and during August of both years *Spongites yendoi* started to recruit and then grew constantly until the end of the experiment. This temporal dynamic in recruitment agrees with previous studies of grazing exclusion which report recruitment of *U. rigida* one month after initiation an of exclusion experiment (Carter and Anderson 1991, Madikiza 2005). Interestingly, Carter and Anderson (1991) initiated the experiment in the same month as the present study but 15 years earlier, and the pattern seems to be the same. In addition, Madikiza (2005), started his experiments on the west coast in May

2004, two month after the present study and again *U. rigida* started to recruit after one, month reaching greater cover if the epilithic community was first removed. This difference can be explained by the more benign eutrophic conditions and lower sea temperatures on the west coast than on the south coast.

I.2. Grazing effects at the functional level of resolution

At the functional level of resolution, an overall grazing effect was observed in three conditions, BOR, NBOR, Bpool in 2004 and 2005, and in ‘non burnt tidal pools’ (NBpool) in 2004. Surprisingly, in the condition BOR, effects were non-significant for all species, but when scaled up to the foliose functional level of resolution, the grazing effect was significant. I interpret this as being due to the addition of individual percentages of cover from different individual species producing a synergistic effect and so changing the outcome of the grazing effect from non-significant to significant.

At the functional level of resolution, temporal patterns (recruitment in winter) were similar to those at the lower level of resolution, however the peaks of recruitment were more diffuse. This is due to the combination of peaks and abundances of a few species rather than a single peak of an individual species, therefore there was a loss of information as I scaled up through the levels of resolution.

The cause of variation in the detection of grazing effects between the species and functional levels of resolutions can be explained by the interactions of the components comprising each level. Therefore, I suggest three possible effects that cause variation with scaling up to a coarser level of resolution:

i. Synergistic effect: a few species that belong to the same functional group are negatively, but not significant by affected by grazers, and when their abundances are pooled into the functional group, the grazing effect becomes significant. This was observed in the burnt open rock (BOR) condition, on moving from the species to the functional level of resolution. Of course, if several components exhibited significant susceptibility to grazers, this effect will be propagated to coarser levels of resolution.

ii. Buffer or antagonistic effect: the set of species affected by grazers within a functional group are in the same proportions as species not affected by grazers. The algae not-affected by grazers can induce a homogenization in the abundances among treatment (resulting in no significant differences among them) at any coarser level of resolution, thus counteracting or buffering the effects of grazing on those species affected by grazers.

iii. Dominant component, if the algal assemblage is sufficiently dominated (in cover/abundance) by one species that is susceptible to grazing, the scaling up the coarser level of resolution, will result in a grazing effect. This was observed in the condition of burnt tidal pools.

I.3. Grazing effects at the coarsest level of resolution

I observed differences in the experimental outcomes when compared to the finer levels of resolution (functional and species level). Grazing was important in 2004 and 2005 for NBOR and Bpool, while burnt open rock (BOR) was the only condition where the grazing effect was non-significant during 2004, though it was significant during 2005. The temporal peaks in algal biomass represented by concentration of chlorophyll *a* were shifted earlier to winter for NBOR, Bpool and NBpool, and to the end of the experiment for BOR 2004. This is in contrast to the functional and species level. In both BOR and NBOR, the maximum concentrations of chlorophyll *a* were found in November 2005.

The difference in outcomes shows that any scaling up to coarser levels can change our perception of the ecological process observed (Allen and Starr 1982, Marquet et al. 2005). This difference can again be explained by synergistic, buffer and dominant effects. The overall grazing effect found on the foliose functional group in the BOR condition was a result of a synergistic effect on particular foliose species, but when looking at chlorophyll *a*, the effect of grazers disappeared during 2004 and re-appeared in 2005. These differences between 2004 and 2005 can be explained by a buffer effect and a dominant component effect, respectively. The absence of any encrusting functional group could not explain this buffer effect, therefore the buffer effect must come from an additional component not considered or not detected in the functional and species level of resolution. This component will have been the epilithic microalgal community (Jenkins et al. 2001), which can be detected at the chlorophyll *a* level and could buffer the effect of foliose algae, which were present at very low cover and with considerable spatial variability within the treatments in open rock habitats.

The dominant component effect was observed in the Bpool condition, when scaled up from the species level to the functional level. In this case, the dominance of *Ulva rigida* and its significant susceptibility to grazing induced a grazing effect at the foliose functional level of resolution. At the level of chlorophyll *a*, grazing was significant, and to get these results, the non-significant effect of encrusting algae was buffered by foliose algae.

The NBOR condition exhibited a change in the initial conditions between 2004 (starting with presence of an epilithic community) and 2005 (starting without an epilithic community). During 2004, synergism was observed in scaling up to the coarsest level (chlorophyll *a*) and during 2005 the dominant effect of *U. rigida* was propagated through each level.

The non-visible microalgal community was not considered at the species and functional levels. Therefore, the variations observed in the outcomes of the overall grazing effect as well as the peaks of maximum concentrations of chlorophyll *a* can be explained by the interaction of these components: interaction within functional groups and interaction between the functional groups and the microalgal community.

II. Spatial stability in grazing effect between years

Disagreements and lack of consensus about the concept of stability have been common in the past 20 years in ecological theory (Sarkar and Plutynski 2008). Steneck and Dethier (1994) referred to the concept of 'stability' as invariability in abundances of functional groups in time. This concept corresponds to the definition of 'constancy' by Pimm (1984). Constancy is the degree of invariance in system properties over a given period of time, while stability refers to the return of the variables comprising the system to a defined equilibrium following a perturbation (Pimm 1984). Additionally, persistence is defined as the ability of a system to remain within defined limits (Pimm 1984, Wu and Loucks 1995). But, Connell and Sousa (1983) used stability and persistence as synonyms. They defined the terms stability/persistence as what Pimm (1984) later referred to 'constancy'. Given these differences in nomenclature I will refer to spatial stability/persistence as the spatially deterministic return to the same level of biotic activity in this case the same magnitude of grazing effects at the same locations, at short/small scales.

A problem related to the stability concept is the assumption of equilibrium and how this equilibrium is perceived at different spatiotemporal scales (Connell and Sousa 1983, Wu and Loucks 1995). In addition, all such the studies are focused on the stability of abundances of species at particular spatiotemporal scales; however it is rare to find studies reporting spatial stability in an ecological interaction and for this reason the stability of grazing effects was studied (but see Navarrete and Berlow 2006). Here I don't pretend to say that the ecosystem is in equilibrium and that it will return to some equilibrium once it is disturbed. However, in the present chapter, I refer to stability of grazing effects as the idea of the return to a defined domain after a disturbance (persistence) in the same positions (determinism).

Therefore I choose two criteria proposed by Connell and Sousa (1983) and Menge et al (2005) to define the stability of a biotic system: 1. Persistence or return to the same level of biological activity after perturbation and 2. stasis or determinism, the stability of the ecological phenomenon must occur in a defined spatiotemporal scale and position.

Here I examined the spatial stability of grazing effects in a harsh environment (upper intertidal) after a disturbance (removal of algae from the substratum in the treatments within blocks), and the stasis/determinism of grazing effects in both habitats and with two substratum manipulations. Spatial stability was experimentally examined using a disturbance which was applied at the beginning of each of two consecutive experiments in different conditions to check if there was a coincidence in the overall grazing effect during both years, while spatial determinism of grazing effects was estimated between years using effect sizes in every block (Menge et al. 2005). If both criteria were significant, this was taken to be an indication of spatial stability.

These relationships between grazing as represented by effect sizes, in 2004 and 2005 at specific microsites within the eulittoral zone indicate that the intensity of the grazing effect at specific sites (blocks) during 2004 is related to the same sites (blocks) during 2005, this is what I have termed ‘spatial determinism, stasis or specificity’. However, the perception of this specificity/determinism in grazing effects was affected by the level of resolution.

The degree of spatial stability differed among conditions. In the BOR condition, the grazing effect was not considered to be stable as there was no match between spatial determinism and persistence between years (0% of the cases analyzed among levels of resolution). However, only *Porphyra capensis* and chlorophyll *a* were spatially deterministic in the same blocks between years. Functional groups did not show spatial determinism in this condition. These differences among levels of resolution can be explained by the same effects that generate variability when one scales up from one level of resolution to another. For example, the buffer effect between *Ulva rigida* and *P. capensis* could obscure spatial determinism at the functional level of resolution. The spatial determinism which appeared again at the level of chlorophyll *a* can be explained by the spatial determinism of the epilithic community.

The Bpool condition, exhibited higher spatial stability, two out seven cases (35% of the cases analyzed among levels of resolution). Spatial determinism and significant grazing effect matched at the specific and functional levels of resolution. First at the level of species, *U. rigida* exhibited spatial stability, as did the foliose functional group, due to a dominant effect. However, the chlorophyll *a* level did not exhibit spatial determinism, most likely because of buffering by the encrusting functional group which did not exhibit spatial stability.

The NBOR condition showed spatial stability only for the alga *U. rigida* (25% of the cases studied among levels of resolution), and not at the coarser levels of resolution: functional groups and chlorophyll *a*. This could result from strong buffer effects by other foliose species.

In conclusion, the theory of stability suggests that even if spatial determinism is absent at the finer level of resolution, it can appear when the components of the system are pooled in a coarser level (synergistic effect) (Steneck and Dethier 1994). Likewise spatial determinism/specificity of grazing can be lost or gained at the functional level depending on the balance between the components comprising the algal assemblage that do or do not exhibit spatial stasis or specificity (buffer effect). When the assemblage exhibits a grazing effect and determinism in a dominant species, the spatial determinism or stasis will be spread throughout the levels of resolution (dominant effect). This framework should apply to for any phenomenon studied at different levels of resolution, the induced variability at each level responds to these three effects: synergism, buffering, and dominance.

Finally, two out of eight cases of stability were found at the level of species, one out of four at the level of functional groups and zero out of three at the level of chlorophyll *a*. These results suggest a low level of spatial stability at coarser levels of resolution in the upper eulitoral zone. This contradicts the expectation that greater levels of stability will be found at coarser levels of resolution (see Steneck and Dethier 1994). Few components from the finer level of resolution, especially in tidal pools were spatially stable. The implications are that at small spatiotemporal scales, only a few specific and functional components can be found to be stable in the tidal pool system, while the other components can have a negative or buffering effect at coarser levels of resolution. This according to the hierarchic-response-stress hypothesis, when there are no agreement among levels of resolution means that the effect of the ecological process is weak (Olsgard et al. 1998). The only stable component was foliose algae, specifically *Ulva rigida*. The spatiotemporal scale was considered adequate, since the spatial stability was estimated as an average for the whole year, rather than at specific times, which can confound results due to natural temporal fluctuations in the algal cover, for example: (i) it has been observed that the cover of foliose seaweeds varies seasonally, appearing in early winter and disappearing in summer, while (ii) fluctuations in the cover of encrusting algal species are due to mortality on hot summer days. All these fluctuation were corrected using effect sizes and repeating the experiment in the following year. I recognize that the assessment of spatial stability was analyzed at a small physical and short temporal scales, and this should be complemented with another study at a longer temporal scale i.e. after five or ten years (Navarrete and Berlow 2006), however small scale spatiotemporal stability is the basis for reconciling short/small scale processes with long/large scale processes.

III. Variability in densities of mesograzers and micrograzers as a source of variation in overall grazing effects

The fact that exclusions of grazers through fences had a positive effect on the colonization of foliose algal groups suggests that mesograzers are important grazers in the upper eulittoral zone. Similar results have been reported by Madikiza (2005) on the west coast of South Africa.

Ten species of mesograzers were observed in the upper eulittoral zone and were responsible for the grazing effects observed under different conditions. Most of the grazers observed feed on fine filamentous algae, foliose algal groups and microalgae, as has been reported for *Siphonaria* spp (Huggett and Griffiths 1986, Hodgson 1999), and *Oxystele* spp (Whittington-Jones 1997). These latter organisms can not feed on encrusting algae since their radula is not adapted to excavate and break the hard substratum comprised of encrusting algal groups (Steneck and Watling 1982). Mesograzers that could have an effect on the encrusting algae were *Acanthochitona garnoti* and *Parechinus angulosus*, however the present experimental design did not detect any negative effect of mesograzers on encrusting species. This is probably due to the small number of these grazers. Although the low numbers of chitons and urchins observed could be due to the measurements being taken during the day, instead of at night when most of the species are active, the fences remained on the shore day and night and should have produced an observable grazing effect.

Mesograzers were more abundant in tidal pools than open rock habitats as tidal pools provide shelter from desiccation and a more constant food supply (Metaxas and Scheibling 1993, Nielsen 2001, 2003).

I manipulated the substratum of these two habitats, by either removing the epilithic algal community or leaving it intact. In this sense I changed the initial conditions of the experiment. Grazers did not distinguish between tidal pools with these two conditions, but in open rock habitats they did. High spatial variability in grazer abundances was observed among blocks in every condition, and the abundance of grazers was greater during 2004 than 2005.

Micrograzers were not excluded during these experiments. These grazers are as abundant as in the supralittoral zone (McQuaid 1981), however the potential effect on the recruitment of macroalgae was unknown in this experiment. I suggest this effect was minimal in open rock and tidal pools habitats since I compared in chapter two treatments where micrograzers were and were not excluded. These treatments did not have an effect on the recruitment of algae. These results contradict the results of Kaehler and Froneman (2002), who reported strong effect of littorinids on the algal community. The only explanation possible to this discrepancy is high inter-annual variation in grazing effects.

IV. Conclusion

Grazing is important in the harsh upper eulittoral zone on the south coast of South Africa. The results showed that tidal pools are more affected by grazers since they are more abundant and larger in this habitat. This strength of the grazing effect changes as the level of resolution of the algal assemblage moves from specific to coarser, due to the interaction of its algal components. Three types of the interactions were identified: synergistic, buffer and dominant effects.

The hypothesis that the spatial pattern of patchiness of grazing effect is spatially invariant or static in the marine ecosystem was investigated in term of spatial stability of grazing interaction. Stability was found to be important, but was dependent on the level of resolution. Stability was a function of spatial determinism and significant grazing effects after disturbance.

Finally, the possibility of unpredictability or chaos at small scales has been refuted in this study. Spatial determinism, in grazing interactions is fixed in particular areas on this rocky shore. However, this concept needs to be tested in other locations and geographical regions and with more complex species assemblages.

CHAPTER V

RELATIONSHIP AMONG FACTORS AFFECTING INTENSITY AND VARIANCE OF GRAZING EFFECTS

INTRODUCTION

I. Concepts

The previous chapter reported the importance of grazing effects at small spatial scales over a period of year. Grazing effects varied among conditions, levels of resolution of the algal assemblage and between years. Significant grazing effects were more likely in tidal pools and in the non burnt open rock condition (NBOR), but not the burnt open rock condition (BOR). However, some degree of stability of the grazing effect was observed if two conditions were fulfilled: spatial determinism/stasis and constancy of grazing effects between years. Again stability varied among levels of resolution. In addition, it was suggested that the spatial distribution of the experimental blocks had consequences for the overall grazing effect.

Every study about grazing ecology reports spatial and temporal variability in the intensity of the grazing effect (e.g. Hawkins and Hartnoll 1983, Vadas 1985, Kaehler and Williams 1998, Boaventura et al. 2002, Coleman et al. 2006, Wai and Williams 2006ab, Freidenburg et al. 2007). Studies that have tried to understand the spatial variability of grazing effect always face a temporal component, e.g. daily patterns of foraging, seasonality, or duration of the experiment (Cubit 1984, Gray and Hodgson 1998). Likewise, studies aimed at understanding the temporal variability of grazing effects are always dependent on the spatial scale used (Hutchinson and Williams 2001, Boaventura et al. 2002, Atalah et al. 2007). From this point of view any ecological phenomenon must be referred to a particular spatial and temporal scale. Therefore, it can be more precise to use the following terms: spatiotemporal and temporospatial, to describe a specific ecological process such as grazing, competition and recruitment. In the case of grazing, the spatiotemporal intensity in the grazing effect refers to the average intensity that occurs in specific places (one block) across time. The second, the temporospatial intensity in the grazing effect is the average intensity at different places (several blocks) at the same time. Often the intensity of the grazing effect is described using an average value, however concepts of spatiotemporal and temporospatial intensity can describe different aspects of the variability such as the variance, i.e. spatiotemporal variance and temporospatial variance (Fig. 5.1).

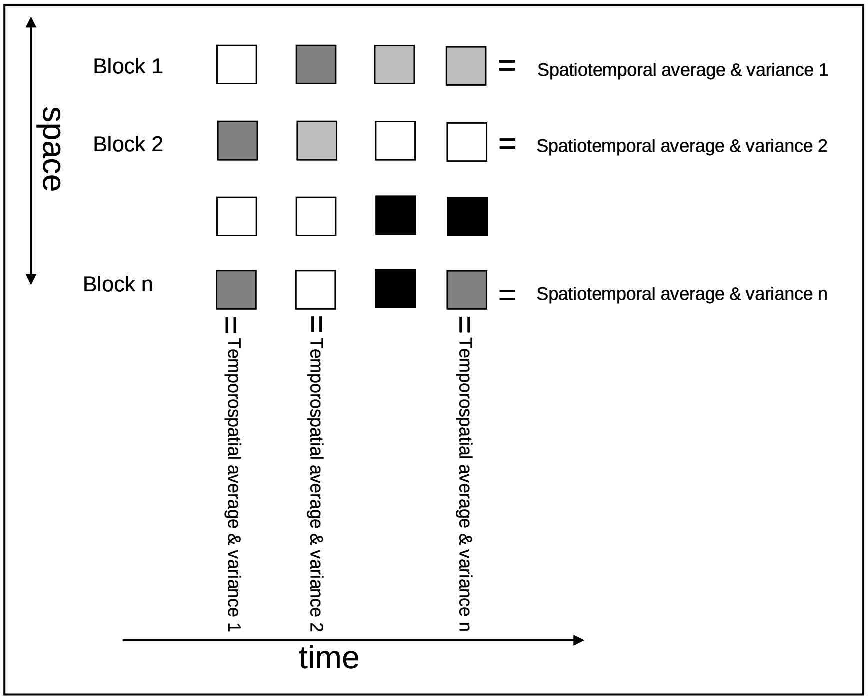

Figure 5.1. Diagram showing how the spatiotemporal and temporospatial intensity and variance are calculated. The average and variance in different blocks across time is called 'spatiotemporal' intensity and variance, while the average and variance among blocks at a particular time is called 'temporospatial' intensity and variance.

It is worth noting that spatiotemporal can be thought as temporal variability in a specific position, this is true for one replicate, however the spatial context is given by the different replicates together. Similarly, temporospatial can be thought as variation in space at one time, but several replicates give again the temporal context that I refer.

II. Factors affecting the spatiotemporal and temporospatial grazing effects

For a grazing effect, and described above, the spatiotemporal intensity and variability can be estimated using the average and variance for each block, pooling the temporal samples. Similarly, the temporospatial intensity and variance can be estimated using the average and variance of in each date from all blocks at each sampling occasion. Thus, spatiotemporal effects generate data from every block or experimental unit, set in different positions within a spatial scale, while the temporospatial gives data from each sampling occasion by averaging the spatial effect (Fig. 5.1). Therefore, it is possible that spatiotemporal and temporospatial intensity and variability are affected by different classes of factors. The factors that induce spatiotemporal variability at small scales can vary from position to position (this implies variation due to spatial coordinates), while the temporospatial effects correspond to the data from each sampling date averaging the spatial arrangement of the blocks. Therefore, factors that can be measured at each spatial position can induce variability in the spatiotemporal effects, such as stress related to desiccation, water movement, emersion time, and topography. As these factors can vary from place to place and at very small scales they are termed ‘microfactors’. On the other hand, the factors affecting the temporospatial grazing effect could be related to weather indices such as air temperature, upwelling events, storms, light regime, sea surface temperature and rainfall, where these factors affect all experimental units (Jenkins et al. 2001, Freidenburg et al. 2007). These factors can vary with time at large spatial scales, but it is difficult to test if they vary at cm to meter scales. Consequently, I will refer to them as 'macrofactors'.

II.1. Microfactors

It seems that in understanding the variability in the effects of intertidal grazing it is first necessary to consider that grazers and algae are exposed to a gradient of desiccation during low tides. As such, grazers have to adapt their foraging time and their return to their refuges according to the tides. Near these refuges, the effects of grazing can be variable depending of the rate of primary production versus the rate of grazing (Williams et al. 2000).

Some of the factors affecting and inducing variability in the spatial structure of intertidal communities are: wave exposure (McQuaid and Branch 1985, Kawamata 1998), topography (Guichard and Bourguet 1998) and tidal dynamics (Denny and Paine 1998). All these factors have also been used to describe grazing at mesoscales of 10 to 100s meters (Harley 2003) and macroscales of 10 to 100s of kilometers (Sanford 1999). However, it is not unknown whether the role of these factors at small scales within a zone is more or less important than at other scales.

a) Water motion: wave exposure is produced by the frequency and height of waves in a determined place. This can vary according to the local morphology e.g. sites protected from waves will increase the desiccation stress for the organisms (Dalhoff et al. 2001, Helmuth et al. 2002). From this point of view, wave exposure works at mesoscales (10 to

100s meters) and macroscales (10 to 100s of kilometers) (Jonsson et al. 2006). However, at small scales (10 to 100s of centimeters), such as within a zone in the intertidal rocky shore, it could be better to refer to differences in water motion, as the level of wave exposure may be the same. Marine ecologists use the term 'water motion' to describe differences in water velocity and acceleration at scales of 10 to 100s of centimeters (Nielsen 2001). At these small, scales water motion has direct effects on adhesion, food availability, oxygen availability, recruitment, settlement of organisms and rates of grazing. For example, for grazers on the low shore, the feeding rate and mobility of the sea urchin *Stongylocentrotus nudus* is negatively affected when the flow rate increases (Kawamata 1998). However, on the west coast of Europe it has been shown that an increase in wave exposure has a positive effect of grazing on fucoid algae (Coleman et al. 2006). Likewise, in the upper eulittoral zone (considered part of the high shore), water movement may have a positive effect on grazing, as this zone is severely stressed by desiccation. In addition, water movement also affects the number of spores and propagules delivered to certain areas of the shore (Underwood 1985, Gaylord 1999). Thus, places with more water motion can experience enhanced primary productivity through the delivery of spores and faster algal growth rates (Freidenbug et al. 2007).

b) Topography: Small scale differences in water movement and velocities are dependent on topographic heterogeneity, which has different components (Guichard and Bourguet 1998), including crevices and cracks, as well as elevation of some parts of the rock. At even smaller scales (10 to 100s µm), rugosity of the rock may also be important, by affecting recruitment (Johnson 1994). The topography can either restrict the movement of grazers, while facilitating the settlement of spores and so reducing the effects of grazing, or vice versa.

c) Emersion time: One of the major of causes of variability in the distribution of animals and plants in the intertidal is the variability of tides among sites. The positions of the upper and lower limits the distribution of marine organisms provide quantifiable biological benchmarks for ecological comparisons through space at meso- and macroscales, however emersion time is only one partial cause of the zonation (Underwood 1978, 1980). The interactions among species is important too (Menge and Branch 2001). At small scales, within a specific zone variation in tides can be described as differences in the times of emersion or inversely inundation time. The distribution of grazers may vary as a result of slight differences in distance from the MLWL, which results in variability in the emersion time or inundation time (see chapter III). Using the same argument, longer emersion times within a zone increase desiccation, this can affect the balance between primary productivity and grazing activity. The time of emersion and distance from the sea are related to the amount of time that algae spend under dry conditions during low tide (McQuaid 1985, Carter and Anderson 1991, Freidenbug et al. 2007).

d) Elevation: The elevation of the substratum can change the emersion regime at local and especially at small scales (Helmuth et al. 2002, Harley and Helmuth 2003). At small scales, differences in the distribution of grazers and algae can be explained by differences in elevation of the substratum, which affects the duration of inundation. These differences in elevation can also create microhabitats where conditions remain wet, increasing algal productivity while rendering them susceptible to both algal recruitment and grazer aggregation (Chapman 1995, Muñoz et al. 2005).

The effects of these factors can be antagonistic, or synergistic. For example, at low tide grazers are often found in crevices, and other microhabitats that are more humid or have more water movement or food availability (Williams 1993). If we consider alga-grazer interactions, the factors mentioned above are related to the avoidance of desiccation. From this point of view, it is not possible to separate the complexity of the factors interacting at microscales. It is possible that two or more of these factors work together synergistically; producing variability in grazer effects (Menge 1991, Chapman 1995, Benedetti-Cecchi et al. 2000, Helmuth and Hofmann 2001, Hutchinson and Williams 2003).

II.2. Macrofactors

On the other hand, the factors affecting the temporospatial variability in grazing effect may be related to large scale weather indices rather than small scales factors acting at specific positions on the shore. Such macrofactors could be air temperature, upwelling events, oceanographic events, storms, seasonality, sea surface temperature and rainfall.

a) Rainfall: Rainfall can stimulate feeding activity in some grazers like littorinids, which become active when they are wet or perceive wet surfaces (Chapman and Underwood 1996).

b) Sea temperature: It has been demonstrated that a decrease in sea temperature can reduce the effects of a keystone predator (Stanford 1999). Evidence that changes in water temperature induce a change in grazing effects has been reported by Jenkins et al. (2001), but only on biofilms estimated as concentration in chlorophyll *a*.

c) Air temperature: Air exposure can affect organisms by inducing physiological stresses and reducing their feeding activity. For example, in the case of the whelk *Nucella ostrina*, on the coast of Oregon, feeding is reduced when air temperature is increased (Dahlhoff et al. 2001, Jenkins et al. 2001).

Ecological theory has not always considered the relationships between macrofactors and microfactors factors and how these relationships are linked to variability in community structure. Recently it has been argued that large-scale climate indices seem to predict ecological processes better than local factors (Hallett et al. 2004). It is possible that macrofactors can modulate microfactors, for example, if air temperature decreases, grazers and algae will tend to survive better in less protected habitats and will not be restricted to refuges, thus increasing the effect of microfactors on patterns of grazing. This would induce spatial variability. On the other hand, macrofactors could diminish the effect of microfactors by creating more benign conditions such as reduced air temperature which would therefore diminish desiccation stress. Bertness and Ewanchuck (2002) examined the linkage between climate and interspecific plant interactions and found that these interactions are linked to climate.

In this chapter, I try to understand the relationships between microfactors and macrofactors at small scales in the upper eulittoral zone and how these factors influence grazing effects. The two habitats and conditions described in chapter IV were analyzed separately. The data on spatiotemporal and temporospatial grazing effects and their variances were extracted from the previous chapter, and the physical factors were monitored *in situ* while the experiment was carried out.

The objectives of this chapter are first to explain how the spatiotemporal intensity and variance of grazing are related to microfactors such as water motion, elevation, emersion time and the density of meso and micrograzers.

Secondly, to understand the role of macrofactors such as sea surface temperature, air temperature and rainfall in shaping the temporospatial intensity and variance of grazing effects.

Thirdly to give insights into the relationship between intensity and variance to understand possible links between micro- and macro factors.

MATERIALS AND METHODS

I. Experiment and formulae

The randomized block design used to assess grazing effects in the upper eulittoral zone described in the previous chapter was used to examine the contribution of micro- and macrofactors to the spatiotemporal and temporospatial grazing effect. In summary, the experiment comprised three treatments: grazing exclusion, partial grazing exclusion and control or open area. These treatments were set in two habitats: open rock and tidal pools. Two manipulations were carried out in each habitat, non-burnt and burnt, in order to contrast grazing effects on the existing algal community and on the recovery of the algal community, respectively. Conditions are referred to as the combination of habitat and manipulation i.e. BOR 'burnt open rock', NBOR 'non-burnt open rock', Bpool 'burnt tidal pool' and NBpool 'non-burnt pool'. The sample size was 12 for each condition.

The experiment was started at the beginning of March 2004 and repeated in exactly the same blocks using the same experimental plots at the beginning of April 2005. Both experiments lasted one year (see previous chapter). In the second experiment the condition 'non- burnt open rock', 'burnt open rock', 'burnt tidal pool' were re-burnt therefore all these conditions change to the category of 'burnt habitats'. However, the condition NBpool 'non-burnt pool' was not re-started as it was impossible to dry out some pools in order to clear the existing algal community properly.

In order to compare the spatiotemporal and temporospatial intensity and variability of grazing effects among conditions, I used effect sizes (Osenberg et al. 1997). I calculated the effect size for each block in each condition pooling the effect sizes for each sample date. Then I calculated the average and variance of this ratio obtaining the spatiotemporal average and variance for one year. These parameters were calculated as the average and variance of the effect sizes of all the blocks across time of the experiment for each condition:

Spatiotemporal intensity = $$\frac{\sum_{K=1}^{N} (\ln (C/E)_{1k})}{N}$$

Spatiotemporal variance = $$\frac{\sum_{K=1}^{N}\left[\frac{\sum_{K=1}^{N} (\ln (C/E)_{1k})}{N} - (\ln (C/E)_{1k})\right]^{2}}{N-1}$$

N is total number of sampling dates (N=7 sampling dates), C is the cover or biomass in the control treatment, E represents the cover or the biomass in the exclusion treatment. K represents a temporal replicate.

The temporospatial intensity and variance was also calculated using effect sizes, calculated using the average and variance of effect sizes of all blocks at each sampling time for each condition:

Temporospatial intensity = $$\frac{\sum_{K=1}^{N} (\ln (C/E)_{k1})}{N}$$

Temporospatial variance = $$\frac{\sum_{K=1}^{N}\left[\frac{\sum_{K=1}^{N} (\ln (C/E)_{k1})}{N} - (\ln (C/E)_{k1})\right]^{2}}{N-1}$$

N is total number of blocks (N=12 blocks), C is the cover or biomass in the control treatment, E represents the cover or the standing stock biomass in the exclusion treatment. K represents a spatial replicate or block.

II. Microfactors affecting spatiotemporal intensity and variance

In order to understand the causes of spatiotemporal intensity and variance among blocks under different conditions, I estimated abiotic and biotic factors that could affect the mosaic of grazing effects. Using multiple regressions, I estimated the contribution of the following factors to the spatiotemporal intensity and variability (Menge 1991):

Grazer abundance: abundances of mesograzers and micrograzers was used and estimated as I described in chapter IV. Four sampling dates in 2004 and three in 2005 for mesograzers, and on two sampling dates in each year for micrograzers.

The following microfactors were determined for each block:

a) Water movement. Using one cement ball anchored in every block by a screw embedded in the cement ball, I estimated the dissolution rate in every block after three days during three spring low tides in each year. The data were expressed as grams lost per day (g. day^{-1}).

b) Inundation time, was estimated during spring tide from the timing of inundation as the tide came up, taking as a reference (time 0) the first block inundated. The measures were ended when the last block was inundated. It was not possible to make this measurement when the tide dropped, as this would have involved more than 12 hours in the field. Measurements were repeated six times using a Stopwatch in each year. The data were expressed in seconds.

c) The elevation of each block was measured using a dumpy level. The reference point was a fixed point in the mid zone. The elevation was expressed in centimeters.

d) The distance from the sea was estimated by marking a line parallel to the direction of the wave approach (derived from aerial photographs). I estimated the perpendicular distance from this line to every block. The distance was expressed in centimeters.

III. Macrofactors affecting the temporospatial intensity and variance

Using multiple regressions, I estimated the contribution of three macrofactors to the temporospatial intensity and variance: air temperature, sea temperature and rainfall. The data were provided by the South African Weather Service SAWS, and were taken daily 20 km south of the experimental location. I estimated monthly sea surface and air temperatures using the daily average for the 30 days before each sampling date. The rainfall was measured every day and expressed in ml, and the average of 30 days prior to each sampling date was used.

IV. Assumptions

Some factors such as topography were not taken into account, because there were minimal differences in topography within the experimental site, however it is not known how much variability can be induced such slight differences.

Some factors that affect spatiotemporal intensity and variability of grazing effects at small scales can exhibit high short term spatial variability. For example, the direction of the waves due to changes in the direction of the wind, oceanographic anomalies, and variability in barometric pressure as well as changes in spring and neap tides. These changes can have consequences for factors such as water movement at small scales or inundation time, but not in factors such as elevation or distance from the sea. For these reasons, measurements of water movement and inundation time should be done at different nested temporal scales e.g. daily, weekly and annual. In this study, however the temporal variability was constrained to three and six times for water movement and inundation time, respectively and I assumed that the linear relationship among temporal scales. I assumed that this sample size was appropriate based on positive correlations between these successive temporal samples ($P < 0.05$ in all cases). This implies that the degree of variability among blocks dates is correlated in time.

Air temperatures, sea surface temperatures and rainfall were chosen as factors rather than upwelling or a storm index because of their ease of measurement and the fact that the data were readily available.

Factors affecting temporospatial variability were measured no more than one month before each sampling date. Here, the assumption was that this period of time was appropriate to temporal changes in grazing effects. This assumption was based on the results of chapter IV, which suggest changes in the spatial patterns of seaweed within one month. There are probably also seasonal and annual changes in these patterns, but they would reduce the sample size and therefore they have not been investigated.

V. Statistical analyses

In order to determine the contribution of each factor to the intensity and variance of grazing effect, I used multiple regression analysis. The criterion to decide which factor is added to the model in order to predict grazing effects was backwards stepwise regression. This approach starts by including all the factors in the multiple regression equation, and then leaves out the factor with the smallest partial correlation. This is carried out through computation of a critical ‘Fs-value’ corresponding to the value when a particular factor significatively decreases R^2. This quantity is known as ‘F-to-remove’. In this way, one by one, independent variables (usually starting with the weakest predictor) are removed, and a new analysis is performed. The results provide the factors with their respective regression coefficients, signifying the degree to which each one, when combined with the others, contributes to predicting the dependent variable. Additionally, positive and negative signs were provided for each significant factor. To run these multiple-regressions the program Statistica 7.0 was used.

The interpretation of the relationship between the dependent variable ‘grazing effects’ and the factors is interpreted upside down, because the intensity of the grazing effects are inverse to the effect size. Therefore, the more negative the value of the effect size, the greater the grazing effect. If any of the factors studied is positively related to the effect size, this means that the factor reduces the grazing effect. The sign of the factors and the variance of grazing effects can be interpreted in the normal way, because the variance does not have negative values.

The P values were corrected using Bonferroni correction for each level of resolution: (1) for the most specific the critical values were estimated at $P < 0.01$ as there were five algal species, (2) at the level of functional groups the critical value was $P < 0.025$ as there were two functional groups, and finally, (3) at coarsest level of resolution $P < 0.05$.

Finally, multiple regression has three requirements or assumptions: i. normality, ii. linear relationship between the independent and dependent variables, iii. homocedasticity and iv. collinearity.

First, multiple regression is robust to violations of normal distribution. Second, the assumption of linearity could have been violated as there were significant differences among treatments that suggested grazing effects, however in those particular cases multiple regression failed to detect this relationship, probably because the relationship between grazing effects and density of grazers is not linear (see discussion). For this reason, the results, predictions and hypothesis are restricted to those which show linear behaviour. Third, I examined the residual distributions of the factors which in most cases showed non-normality and heterocedasticity. This induced an increase in the possibility of Type I errors (Sokal and Rohlf 1995). Finally, collinearity is the result of redundancy of predictors on the variable studied. Two types of effects can be caused by collinearity: i. the inflation of standard errors of the estimated regression slopes, making the overall regression equation significant. ii. Instability in the matrix inversion (a step in the calculation of regression coefficients), this implies that small changes in the data, either adding or deleting one of the predictors, can causes considerable changes in the regression coefficients and signs. Nevertheless, lack of collinearity is very difficult to achieve with real biological data, and the way to deal with it involves the omission of those correlated predictors (Sokal and Rohlf 1995). In the present study I examined a matrix of correlations against the expectations I found low collinearity.

Any violations of these assumptions could lead to spurious relationships between the independent variable and independent factors as the possibility of a Type I error increases. However, I preferred not to transform the data, because effect sizes are already highly deviated values. In order to minimize the effects of Type I errors, I used a conservative approach. The only solution was to set a large ‘F-to-remove’ (F = 11) corresponding to a high ‘P value’ which minimized overestimation of the predictor factors and therefore of Type I errors. I recognize that this approach is far from perfect, but I concluded that it was the only way to deal with the violations of the statistical assumptions. Moreover, this approach yielded interpretable results.

Finally, all the significant results induced either by microfactors and macrofactors were pooled at every level of resolution, and compared using goodness of fit chi-square tests.

RESULTS

A synthesis of the abiotic and biotic microfactors and the three macrofactors in each condition during 2004 and 2005 is shown in Table 5.1.

Before reporting the results, it is necessary to keep in mind that more negative values of the effect size, indicate stronger grazing effects.

I. Microfactors affecting the spatiotemporal intensity and variance

I.1. Finest level of resolution species level

I.1.1.a. Effect of grazing on *Porphyra capensis* in 2004 (Table 5.2)

Different factors explained the spatiotemporal intensity and variance of grazing effects on *P. capensis*:

In the BOR, the physical factors affecting the spatiotemporal intensity of grazing included distance from the sea, inundation time, elevation of the substratum and the density of juvenile grazers. Inundation time was the only factor that diminished the intensity of the grazing effect, therefore it showed a positive relationship in the multiple-regression.

Variance was explained by water movement, distance from the sea, inundation time and elevation. Again, only inundation time decreased the variability, producing a negative sign in the multiple-regression (Table 5.2).

NBOR: none of the physical microfactors affected the spatiotemporal intensity and variance of grazing effect (Table 5.2).

P. capensis did not recruit in pools.

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I.1.1.b. Grazing effect on *Porphyra capensis* in 2005 (Table 5.3)

BOR: inundation time again decreased the intensity of grazing effect, while the variance was not affected by any of the factors studied.

NBOR: water movement increased the grazing intensity, while variance was affected positively by water movement and inundation time and negatively by elevation of substratum.

Again, tidal pools were not colonized by *P. capensis*.

Table 5.1. Average ± SD of microfactors and macrofactors in different conditions, during 2004 and 2005.

Factors	Conditions			
	BOR	NBOR	Bpool	NBpool
microfactors				
Water movement (g)	**4.71 ± 1.6**	**5.3 ± 1**	**5.06 ± 1.24**	**4.57 ± 1.15**
Distance from Sea (cm)	**1145.9 ± 541.52**	**979.42 ± 630.33**	**1127.08 ± 797.21**	**1433. 91 ± 758.3**
Inundation (s)	**2595.19 ± 1023.68**	**1726.05 ± 968.55**	**1880.78 ± 1207.6**	**2030.33 ± 947.89**
Elevation (cm)	**72.38 ± 16.71**	**61.79 ± 9.17**	**68.23 ± 16.06**	**59.47 ± 8.22**
No. mesograzers 2004 (nº.m^{-2})	**41.06 ± 26.53**	**62.33 ± 27.01**	**75.85 ± 34.26**	**91.66 ± 37.16**
No. mesograzers 2005 (nº.m^{-2})	**31.91 ± 29.39**	**49.63 ± 25.55**	**53.58 ± 40.07**	**not repeated**
No. littorinids 2004 (nº. 0.25m^{-2})	**37.02 ± 33.45**	**17.34 ± 15.51**	**13.52 ± 16.44**	**19.75 ± 34.52**
No. littorinids 2005 (nº. 0.25 m^{-2})	**27.25 ± 23.22**	**6.62 ± 7.31**	**4.66 ± 9.82**	**not repeated**
No. juveniles 2004 (nº. 0.25 m^{-2})	**1.69 ± 2.69**	**1.38 ± 0.9**	**7.33 ± 5.1**	**4.84 ± 4.29**
No. juveniles 2005 (nº. 0.25 m^{-2})	**1.33 ± 2.33**	**2.22 ± 3.75**	**6.58 ± 5.91**	**not repeated**
Macrofactors				
Sea surface temperature (ºC)	**2004: 17.01 ± 1.67**	**2005: 17.29 ± 1.16**		
Air temperature (ºC)	**2004: 19.05 ± 2.97**	**2005: 18.6 ± 2.63**		
Rainfall (average mm per month)	**2004: 45 ± 36.7**	**2005: 47.7 ± 42.3**		

Table 5.2. Backward stepwise multiple regression analysis at the species level of resolution for *Porphyra capensis*, representing the percent of contribution of abiotic and biotic microfactors to the spatiotemporal intensity and variance of grazing effects during 2004. Bonferroni correction was used with an $\alpha = 0.05/5 = 0.01$. Values indicate percentage contribution to overall grazing effects. Effects were either positive (+) or negative (-).

Independent variables	**dependent variable**							
	BOR Porphyra		**NBOR Porphyra**		**Bpool Porphyra**		**NBpool Porphyra**	
	Average	**variance**	**average**	**variance**	**average**	**variance**	**average**	**variance**
Water movement	ns	20.2(+)	ns	ns	no recruitment		no recruitment	
Distance from Sea	16.7(-)	16.3(+)	ns	ns				
Inundation	32.3(+)	33.7(-)	ns	ns				
Elevation	27.6(-)	25.1(+)	ns	ns				
No. mesograzers	ns	ns	ns	ns				
No. littorinids	ns	ns	ns	ns				
No. juveniles	19.6(-)	ns	ns	ns				
ANOVA summary								
Source	$F_{5,6} = 53.2$	$F_{5,6} = 52.6$	.	.				
Regression MS	3.12	11.13	.	.				
Residual MS	0.06	0.21	.	.				
P	<0.0001	<0.0001	.	.				
Multiple R^2	0.98	0.98	.	.				

Table 5.3. Backward stepwise multiple regression analysis at the species level of resolution for *Porphyra capensis* representing the percent of contribution of abiotic and biotic microfactors to the spatiotemporal intensity and variance of grazing effects, during 2005. Bonferroni correction was used with an $\alpha = 0.05/5 = 0.01$. Values are in percentages of contribution to overall grazing effects. Effects were either positive (+) or negative (-).

Independent variables	**dependent variable**							
	BOR Porphyra		**NBOR Porphyra**		**Bpool Porphyra**		**NBpool Porphyra**	
	Average	**variance**	**average**	**variance**	**average**	**variance**	**average**	**variance**
Water movement	**ns**	**ns**	**74(-)**	**11.8(+)**	**no recruitment**		**no recruitment**	
Distance from Sea	**ns**	**ns**	**ns**	**ns**				
Inundation	**50(+)**	**ns**	**ns**	**37.8(+)**				
Elevation	**ns**	**ns**	**ns**	**38.4(-)**				
No. mesograzers	**ns**	**ns**	**ns**	**ns**				
No. littorinids	**ns**	**ns**	**ns**	**ns**				
No. juveniles	**ns**	**ns**	**ns**	**ns**				
ANOVA summary								
Source	$F_{1,10} = 10.2$	**.**	$F_{1,9} = 26.6$	$F_{3,7} = 17.6$				
Regression MS	**4.44**	**.**	**5.14**	**10.6**				
Residual MS	**0.43**	**.**	**0.19**	**0.6**				
P	**<0.001**	**.**	**<0.01**	**<0.01**				
Multiple R^2	**0.50**	**.**	**0.74**	**0.6**				

I.1.2.a. Effect of grazing on *Ulva rigida* in 2004 (Table 5.4)

BOR: spatiotemporal intensity was diminished by elevation of the substratum and the density of littorinids, however variance was increased by the densities of juvenile grazers.

NBOR: spatiotemporal intensity was not affected by any of the factors assessed, but the spatiotemporal variance was negatively related to the elevation of the substratum.

Bpool: elevation diminished both the spatiotemporal intensity and variance o the grazing effect.

NBpool: no factors affected spatiotemporal intensity or variance of *U. rigida* under this condition.

I.1.2.b. Grazing effect on *Ulva rigida* in 2005 (Table 5.5)

BOR: water movement and distance from the sea decreased spatiotemporal grazing intensity, while density of mesograzers and littorinids increased the intensity of grazing. The spatiotemporal variance was not affected by any factor assessed.

NBOR: intensity of grazing on *U. rigida* could not be explained by any factor assessed, while the variance was negatively affected by elevation and density of littorinids. The inundation time had a positive effect on the variance.

Bpool: elevation of the substratum decreased the intensity of grazing, while the variance was not affected by any factor assessed.

Table 5.4. Backward stepwise multiple regression analysis at the species level of resolution for *Ulva rigida* representing the percent of contribution of abiotic and biotic microfactors to the spatiotemporal intensity and variance of grazing effects, during 2004. Bonferroni correction was used with an α = 0.05/5 = 0.01. Values are in percentages of contribution to grazing effect. Effects were either positive (+) or negative (-).

Independent variables	**dependent variable**							
	BOR Ulva		**NBOR Ulva**		**Bpool Ulva**		**NBpool Ulva**	
	average	**variance**	**average**	**variance**	**average**	**variance**	**average**	**variance**
Water movement	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**
Distance from Sea	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**
Inundation	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**
Elevation	**44.3(+)**	**ns**	**ns**	**56(-)**	**50.1(+)**	**66(-)**	**ns**	**ns**
No. mesograzers	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**
No. littorinids	**44.9(+)**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**
No. juveniles	**ns**	**56(+)**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**
ANOVA summary								
Source	$F_{2,9} = 37.8$	$F_{1,10} = 12.8$	**.**	$F_{1,10} = 12.8$	$F_{2,9} = 18.3$	$F_{1,10} = 19.8$		
Regression MS	**6.2**	**51.4**	**.**	**72.7**	**25.8**	**56.7**		
Residual MS	**0.16**	**4.0**	**.**	**5.6**	**1.4**	**2.8**		
P	<0.0001	<0.001	**.**	<0.001	<0.001	<0.01		
Multiple R^2	**0.89**	**0.56**	**.**	**0.56**	**0.5**	**0.66**		

Table 5.5. Backward stepwise multiple regression analysis at the species level of resolution for *Ulva rigida* representing the percent of contribution of abiotic and biotic microfactors to the spatiotemporal intensity and variance of grazing effects, during 2005. Bonferroni correction was used with an $\alpha = 0.05/5 = 0.01$. Values are in percentages of contribution to grazing effect. Effects were either positive (+) or negative (-).

Independent variables	**dependent variable**							
	BOR Ulva		**NBOR Ulva**		**Bpool Ulva**		**NBpool Ulva**	
	average	**variance**	**average**	**variance**	**average**	**variance**	**average**	**variance**
Water movement	**13.2(+)**	**ns**	**ns**	**ns**	**ns**	**ns**	**no repeated**	
Distance from Sea	**28.1(+)**	**ns**	**ns**	**ns**	**ns**	**ns**	**.**	**.**
Inundation	**ns**	**ns**	**ns**	**40.9(+)**	**ns**	**ns**	**.**	**.**
Elevation	**ns**	**ns**	**ns**	**41.2(-)**	**70(+)**	**ns**	**.**	**.**
No. mesograzers	**37.2(-)**	**ns**	**ns**	**ns**	**ns**	**ns**	**.**	**.**
No. littorinids	**18.6(-)**	**ns**	**ns**	**6.7(-)**	**ns**	**ns**	**.**	**.**
No. juveniles	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**.**	**.**
ANOVA summary								
Source	**$F_{4,7} = 68.1$**	**.**	**.**	**$F_{3,7} = 17.2$**	**$F_{1,10} = 23.9$**	**.**	**.**	**.**
Regression MS	**7.8**	**.**	**.**	**10.63**	**32.4**	**.**	**.**	**.**
Residual MS	**0.11**	**.**	**.**	**0.6**	**1.35**	**.**	**.**	**.**
P	**<0.0001**	**.**	**.**	**<0.01**	**<0.001**	**.**	**.**	**.**
Multiple R^2	**0.97**	**.**	**.**	**0.88**	**0.7**	**.**	**.**	**.**

I.1.3.a. Effect of grazing on *Chaetomorpha aerea* in 2004 (Table 5.6)

BOR: spatiotemporal intensity was not affected by any of the factors assessed; however the spatiotemporal variance of grazing effect was decreased by inundation time among blocks.

NBOR and Bpool: neither the spatiotemporal intensity nor variance was affected by the factors assessed.

NBpool: water movement and inundation time increased, while the density of mesograzers decreased grazing effects. The variance was not affected by any of these factors.

I.1.3.b. Effect of grazing on *Chaetomorpha aerea* in 2005 (Table 5.7)

The only significant effects were found in the burnt tidal pool (Bpool) condition, where the density of littorinids increased and decreased the intensity and variance, respectively.

Table 5.6. Backward stepwise multiple regression analysis at the species level of resolution for *Chaetomorpha aerea* representing the percent of contribution of abiotic and biotic microfactors to the spatiotemporal intensity and variance of grazing effects, during 2004. Bonferroni correction was used with an $\alpha = 0.05/5 = 0.01$. Values are in percentages of contribution to grazing effect. Effects were either positive (+) or negative (-).

Independent variables	dependent variable							
	BOR Chaetomorpha		NBOR Chaetomorpha		Bpool Chaetomorpha		NBpool Chaetomorpha	
	average	variance	average	variance	average	variance	average	variance
Water movement	ns	ns	ns	ns	ns	ns	31.5(-)	ns
Distance from Sea	ns	ns	ns	ns	ns	ns	ns	ns
Inundation	ns	68(-)	ns	ns	ns	ns	33.3(-)	ns
Elevation	ns	ns	ns	ns	ns	ns	ns	ns
No. mesograzers	ns	ns	ns	ns	ns	ns	29.9(+)	ns
No. littorinids	ns	ns	ns	ns	ns	ns	ns	ns
No. juveniles	ns	ns	ns	ns	ns	ns	ns	ns
ANOVA summary								
Source	.	$F_{1,10} = 21.6$	.	.	.	.	$F_{5,5} = 23.8$	.
Regression MS	.	43.7	.	.	.	.	0.12	.
Residual MS	.	2.02	.	.	.	.	0.005	.
P	.	<0.001	.	.	.	.	<0.001	.
Multiple R^2	.	0.68	.	.	.	.	0.95	.

Table 5.7. Backward stepwise multiple regression analysis at the species representing the percent of contribution of abiotic and biotic microfactors to the spatiotemporal intensity and variance of grazing effects, during 2005. Bonferroni correction was used with an $\alpha = 0.05/5 = 0.01$. Values are in percentages of contribution to grazing effect. Effects were either positive (+) or negative (-).

Independent variables	**dependent variable**							
	BOR Chaetomorpha		**NBOR Chaetomorpha**		**Bpool Chaetomorpha**		**NBpool Chaetomorpha**	
	average	**variance**	**average**	**variance**	**average**	**variance**	**average**	**variance**
Water movement	**no recruitment**		**no recruitment**		**ns**	**ns**	**no repeated**	
Distance from Sea					**ns**	**ns**		
Inundation					**ns**	**ns**		
Elevation					**ns**	**ns**		
No. mesograzers					**ns**	**ns**		
No. littorinids					**63(-)**	**54(-)**		
No. juveniles					**ns**	**ns**		
ANOVA summary								
Source					$F_{1,10} = 17.17$	$F_{1,10} = 12.01$		
Regression MS					**2.24**	**78.6**		
Residual MS					**0.13**	**6.54**		
P					**<0.01**	**<0.01**		
Multiple R^2					**0.63**	**0.54**		

I.1.4.a. Effect of grazing on *Hildenbrandia rubra* in 2004 (Table 5.8)

None of the factors studied affected the spatiotemporal intensity or variance of grazing effect under any condition.

I.1.4.b. Effect of grazing on *Hildenbrandia rubra* in 2005 (Table 5.9)

The only significant effects occurred in burnt tidal pool (Bpool), where density of littorinids decreased the spatiotemporal intensity and increased the variance.

Table 5.8. Backward stepwise multiple regression analysis at the species level of resolution for *Hildenbrandia rubra* representing the percent of contribution of abiotic and biotic microfactors to the spatiotemporal intensity and variance of grazing effects, during 2004. Bonferroni correction was used with an α = 0.05/5 = 0.01. Values are in percentages of contribution to grazing effect. Effects were either positive (+) or negative (-).

Independent variables	dependent variable							
	BOR Hildenbrandia		NBOR Hildenbrandia		Bpool Hildenbrandia		NBpool Hildenbrandia	
	average	variance	average	variance	average	variance	average	variance
Water movement	no recruitment		ns	ns	ns	ns	ns	ns
Distance from Sea			ns	ns	ns	ns	ns	ns
Inundation			ns	ns	ns	ns	ns	ns
Elevation			ns	ns	ns	ns	ns	ns
No. mesograzers			ns	ns	ns	ns	ns	ns
No. littorinids			ns	ns	ns	ns	ns	ns
No. juveniles			ns	ns	ns	ns	ns	ns
ANOVA summary								
Source			.	.	.	.	.	.
Regression MS			.	.	.	.	.	.
Residual MS			.	.	.	.	.	.
P			.	.	.	.	.	.
Multiple R^2			.	.	.	.	.	.

Table 5.9. Backward stepwise multiple regression analysis at the species level of resolution for *Hildenbrandia rubra* representing the percent of contribution of abiotic and biotic microfactors to the spatiotemporal intensity and variance of grazing effects, during 2005. Bonferroni correction was used with an α = 0.05/5 = 0.01. Values are in percentages of contribution to grazing effect. Effects were either positive (+) or negative (-).

Independent variables	dependent variable							
	BOR Hildenbrandia		NBOR Hildenbrandia		Bpool Hildenbrandia		NBpool Hildenbrandia	
	average	variance	average	variance	average	variance	average	variance
Water movement	no recruitment		no recruitment		ns	ns	not repeated	
Distance from Sea					ns	ns		
Inundation					ns	ns		
Elevation					ns	ns		
No. mesograzers					ns	ns		
No. littorinids					89(+)	78(+)		
No. juveniles					ns	ns		
ANOVA summary								
Source					$F_{1,10} = 86.4$	$F_{1,10} = 37$		
Regression MS					3.52	47.9		
Residual MS					0.04	1.29		
P					<0.00001	<0.001		
Multiple R^2					0.89	0.78		

I.1.5.a. Effect of grazing on *Spongites yendoi* in 2004 (Table 5.10)

Spongites yendoi did not recruit in open rock habitats.

Bpool: none of the factors assessed explained the intensity or the variance observed, while in non burnt tidal pool (NBpool) condition, water movement increased the spatiotemporal variance of the grazing effect.

I.1.5.b. Effect of grazing on *Spongites yendoi* in 2005 (Table 5.11)

None of the factors assessed in this study could explain the spatiotemporal intensity or variance of grazing effects.

Table 5.10. Backward stepwise multiple regression analysis at the species level of resolution for *Spongites yendoi* representing the percent of contribution of abiotic and biotic microfactors to the spatiotemporal intensity and variance of grazing effects, during 2004. Bonferroni correction was used with an α = 0.05/5 = 0.01. Values are in percentages of contribution to grazing effect. Effects were either positive (+) or negative (-).

Independent variables	**dependent variable**							
	BOR Spongites		**NBOR Spongites**		**Bpool Spongites**		**NBpool Spongites**	
	average	**variance**	**average**	**variance**	**average**	**variance**	**average**	**variance**
Water movement	**no recruitment**		**no recruitment**		**ns**	**ns**	**ns**	**74(+)**
Distance from Sea					**ns**	**ns**	**ns**	**ns**
Inundation					**ns**	**ns**	**ns**	**ns**
Elevation					**ns**	**ns**	**ns**	**ns**
No. mesograzers					**ns**	**ns**	**ns**	**ns**
No. littorinids					**ns**	**ns**	**ns**	**ns**
No. juveniles					**ns**	**ns**	**ns**	**ns**
ANOVA summary								
Source					.	.	.	**$F_{1,9}$ = 26.7**
Regression MS					.	.	.	**241.2**
Residual MS					.	.	.	**9.03**
P					.	.	.	**<0.0001**
Multiple R^2					.	.	.	**0.74**

Table 5.11. Backward stepwise multiple regression analysis at the species level of resolution for *Spongites yendoi* representing the percent of contribution of abiotic and biotic microfactors to the spatiotemporal intensity and variance of grazing effects, during 2005. Bonferroni correction was used with an $\alpha = 0.05/5 = 0.01$. Values are in percentages of contribution to grazing effect. Effects were either positive (+) or negative (-).

Independent variables	dependent variable							
	BOR Spongites		NBOR Spongites		Bpool Spongites		NBpool Spongites	
	average	variance	average	variance	average	variance	average	variance
Water movement	no recruitment		no recruitment		ns	ns	no repeated	
Distance from Sea					ns	ns	ns	ns
Inundation					ns	ns	ns	ns
Elevation					ns	ns	ns	ns
No. mesograzers					ns	ns	ns	ns
No. littorinids					ns	ns	ns	ns
No. juveniles					ns	ns	ns	ns
ANOVA summary								
Source					.	.	.	.
Regression MS					.	.	.	.
Residual MS					.	.	.	.
P					.	.	.	.
Multiple R^2					.	.	.	.

I.2. Second level of resolution. Functional algal groups

I.2.1.a. Foliose functional group in 2004 (Table 5.12)

BOR: inundation time decreased the spatiotemporal intensity of grazing effects, but reduced the spatiotemporal variance. In addition, the spatiotemporal intensity was increased by the density of juveniles.

NBOR: the intensity and variance were not affected by any of the factors studied.

Bpool: water movement and inundation time decreased the intensity of the grazing effect. None of the factors studied affected the spatiotemporal variance.

NBpool: there were no significant effects.

I.2.1.b. Encrusting functional group in 2004 (Table 5.13)

BOR: there was no recruitment of encrusting algae in this condition.

NBpool: the only significant effect was in the spatiotemporal variance, which was increased by the microfactor water movement.

I.2.2.a. Foliose functional group in 2005 (Table 5.14)

BOR: number of mesograzers increased the mean intensity and variance of spatiotemporal grazing effects.

NBOR: no significant effects.

Bpool: elevation was found to decrease the spatiotemporal intensity of grazing effects, while none of the factors affected the spatiotemporal variance.

I.2.2.b Encrusting functional group in 2005 (Table 5.15)

BOR and NBOR: no recruitment of encrusting algae was observed in these conditions.

Bpool: elevation and density of mesograzers decreased the spatiotemporal variance of grazing effect. None of the factors studied showed an effect on the spatiotemporal intensity.

Table 5.12. Backward stepwise multiple regression analysis at the foliose functional group representing the percent of contribution of abiotic and biotic microfactors to the spatiotemporal intensity and variance of grazing effects, during 2004. Bonferroni correction was used with an α = 0.05/2 = 0.025. Effects were either positive (+) or negative (-).

Independent variables	dependent variable							
	BOR Foliose		NBOR Foliose		Bpool Foliose		NBpool Foliose	
	average	variance	average	variance	average	variance	average	variance
Water movement	ns	ns	ns	ns	32.2(+)	ns	ns	ns
Distance from Sea	ns	ns	ns	ns	ns	ns	ns	ns
Inundation	38(+)	67(-)	ns	ns	48.1(+)	ns	ns	ns
Elevation	ns	ns	ns	ns	ns	ns	ns	ns
No. mesograzers	ns	ns	ns	ns	ns	ns	ns	ns
No. littorinids	ns	ns	ns	ns	ns	ns	ns	ns
No. juveniles	45.8(-)	ns	ns	ns	ns	ns	ns	ns
ANOVA summary								
Source	$F_{2,9} = 24.2$	$F_{1,10} = 20.7$	.	.	$F_{2,9} = 18.2$	.	.	.
Regression MS	14.54	35.7	.	.	30.7	.	.	.
Residual MS	0.6	1.8	.	.	1.7	.	.	.
P	0.001	0.001	.	.	0.0001	.	.	.
Multiple R^2	0.84	0.67	.	.	0.84	.	.	.

Table 5.13. Backward stepwise multiple regression analysis at the encrusting functional group representing the percent of contribution of abiotic and biotic microfactors to the spatiotemporal intensity and variance of grazing effects, during 2004. Bonferroni correction was used with an α = 0.05/2 = 0.025. Effects were either positive (+) or negative (-).

Independent variables	dependent variable							
	BOR encrusting		NBOR encrusting		Bpool encrusting		NBpool encrusting	
	average	variance	average	variance	average	variance	average	variance
Water movement	no recruitment		ns	ns	ns	ns	ns	81(+)
Distance from Sea			ns	ns	ns	ns	ns	ns
Inundation			ns	ns	ns	ns	ns	ns
Elevation			ns	ns	ns	ns	ns	ns
No. mesograzers			ns	ns	ns	ns	ns	ns
No. littorinids			ns	ns	ns	ns	ns	ns
No. juveniles			ns	ns	ns	ns	ns	ns
ANOVA summary								
Source			.	.	.	.	.	$F_{2,9}$ = 19.5
Regression MS			.	.	.	.	.	161.24
Residual MS			.	.	.	.	.	8.26
P			.	.	.	.	.	<0.0001*
Multiple R^2			.	.	.	.	.	0.81

Table 5.14. Backward stepwise multiple regression analysis at the foliose functional group representing the percent of contribution of abiotic and biotic microfactors to the spatiotemporal intensity and variance of grazing effects, during 2005. Bonferroni correction was used with an α = 0.05/2 = 0.025. Effects were either positive (+) or negative (-).

Independent variables	dependent variable							
	BOR Foliose		NBOR Foliose		Bpool Foliose		NBpool Foliose	
	average	variance	average	variance	average	variance	average	variance
Water movement	ns	ns	ns	ns	ns	ns	not repeated	
Distance from Sea	ns	ns	ns	ns	ns	ns		
Inundation	ns	ns	ns	ns	ns	ns		
Elevation	ns	ns	ns	ns	73(+)	ns		
No. mesograzers	81(-)	70(+)	ns	ns	ns	ns		
No. littorinids	ns	ns	ns	ns	ns	ns		
No. juveniles	ns	ns	ns	ns	ns	ns		
ANOVA summary								
Source	$F_{1,10} = 43.9$	$F_{1,10} = 24.3$	.	.	$F_{1,10} = 28$	.	.	.
Regression MS	37.6	102.8	.	.	34.4	.	.	.
Residual MS	0.9	4.22	.	.	1.22	.	.	.
P	<0.0001	<0.0001	.	.	<0.0001	.	.	.
Multiple R^2	0.81	0.7	.	.	0.73	.	.	.

Table 5.15. Backward stepwise multiple regression analysis at the encrusting functional group representing the percent of contribution of abiotic and biotic microfactors to the spatiotemporal intensity and variance of grazing effects, during 2005. Bonferroni correction was used with an α = 0.05/2 = 0.025. Effects were either positive (+) or negative (-).

Independent variables	dependent variable							
	BOR encrusting		NBOR encrusting		Bpool encrusting		NBpool encrusting	
	average	variance	average	variance	average	variance	average	variance
Water movement	no recruitment		no recruitment		ns	ns	not repeated	
Distance from Sea					ns	ns	.	.
Inundation					ns	ns	.	.
Elevation					ns	35.3(-)	.	.
No. mesograzers					ns	27.7(-)	.	.
No. littorinids					ns	ns	.	.
No. juveniles					ns	ns	.	.
ANOVA summary								
Source					.	$F_{2,9} = 7.9$	.	.
Regression MS					.	32.9	.	.
Residual MS					.	4.18	.	.
P					.	0.01	.	.
Multiple R^2					.	0.63	.	.

I.3. Third level of resolution. Chlorophyll *a*

I.3.1. Grazing effects on the chlorophyll *a* in 2004 (Table 5.16)

BOR: the mean spatiotemporal grazing effect was increased by the density of juveniles grazers, with no significant effects on the spatiotemporal variance.

NBOR: neither the spatiotemporal intensity nor variance was explained by the factors analyzed.

Bpool: water movement and elevation decreased the spatiotemporal intensity of grazing effect. At the same time, elevation of substratum increased the spatiotemporal variability of the effect of grazers on the total concentration of chlorophyll *a*.

NBpool: none of the factors analyzed could explain the spatiotemporal intensity, however the distance from the sea decreased the spatiotemporal variability.

I.3.2. Grazing effects on the chlorophyll *a* in 2005 (Table 5.17)

None of the factors studied explained the spatiotemporal intensity and variance in the conditions analyzed (BOR, NBOR and Bpool). NBpool was not repeated during 2005.

Table 5.16. Backward stepwise multiple regression analysis on the coarsest level of resolution representing the percent of contribution of abiotic and biotic microfactors to the spatiotemporal intensity and variance of grazing effects, during 2004. Effects were either positive (+) or negative (-).

Independent variables	dependent variable							
	Chl *a* BOR		Chl *a* NBOR		Chl *a* Bpool		Chl *a* NBpool	
	average	variance	average	variance	average	variance	average	variance
Water movement	ns	ns	ns	ns	40.3(+)	ns	ns	ns
Distance from Sea	ns	ns	ns	ns	ns	ns	ns	33(-)
Inundation	ns	ns	ns	ns	ns	ns	ns	ns
Elevation	ns	ns	ns	ns	47.7(+)	63(+)	ns	ns
No. mesograzers	ns	ns	ns	ns	ns	ns	ns	ns
No. littorinids	ns	ns	ns	ns	ns	ns	ns	ns
No. juveniles	59(-)	ns	ns	ns	ns	ns	ns	ns
ANOVA summary								
Source	$F_{1,10} = 14.9$	.	.	.	$F_{2,,9} = 33.4$	$F_{1,10} = 17.21$	.	$F_{1,10} = 11.4$
Regression MS	3.2	.	.	.	6.34	8.9	.	5.3
Residual MS	0.21	.	.	.	0.19	0.52	.	0.5
P	<0.003	.	.	.	<0.0001	<0.01	.	<0.01
Multiple R^2	0.73	.	.	.	0.88	0.63	.	0.33

Table 5.17. Backward stepwise multiple regression analysis on the coarsest level of resolution representing the percent of contribution of abiotic and biotic microfactors to the spatiotemporal intensity and variance of grazing effects, during 2005. Effects were either positive (+) or negative (-).

Independent variables	**dependent variable**							
	Chl *a* BOR		**Chl *a* NBOR**		**Chl *a* Bpool**		**Chl *a* NBpool**	
	average	**variance**	**average**	**variance**	**average**	**variance**	**average**	**variance**
Water movement	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**not assessed**	
Distance from Sea	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**
Inundation	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**
Elevation	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**
No. mesograzers	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**
No. littorinids	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**
No. juveniles	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**
ANOVA summary								
Source	**.**	**.**	**.**	**.**	**.**	**.**	**.**	**.**
Regression MS	**.**	**.**	**.**	**.**	**.**	**.**	**.**	**.**
Residual MS	**.**	**.**	**.**	**.**	**.**	**.**	**.**	**.**
P	**.**	**.**	**.**	**.**	**.**	**.**	**.**	**.**
Multiple R^2	**.**	**.**	**.**	**.**	**.**	**.**	**.**	**.**

II. Macrofactors affecting temporospatial intensity and variance

II.1. First level of resolution, species level

Only *Ulva rigida* and *Hildenbrandia rubra* showed significant effects on the intensity and variance of grazing effects (Tables 5.21 and 5.25). In 2005 grazing effects on *U. rigida* was decreased in NBOR by air temperature, as was the variance of grazing effects for *H. rubra* in Bpool.

All the other effects were non significant in the multiple regression analyses (Tables 5.18 -5.20, 5.22-5.24, 5.26, 5.27).

II.2. Second level of resolution, functional groups: foliose and encrusting

During the year 2004, none of the factors assessed in the study could explain the temporospatial intensity and variance in grazing effects (Tables 5.28 and 5.29). During 2005 the only significant effect on temporospatial intensity occurred in BOR, where sea surface temperature and air temperature had significant negative and positive effects, respectively. In this condition, the temporospatial variance was positively explained by sea surface temperature (Table 5.30), while no effects were significant for encrusting algal groups (Table 5.29 and 5.31).

II.3. Third level of resolution, biomass represented by chlorophyll *a*

During 2004, several macrofactors were significant in the following conditions: NBOR, Bpool and NBpool.

In NBOR, rainfall increased the temporospatial intensity of the grazing effect (Table 5.32), while decreasing the temporospatial variance. In Bpool, sea surface temperature increased the temporospatial grazing effect (Table 5.32).

In NBpool, sea surface temperature increased both intensity and variance, while air temperature diminished the intensity (Table 5.32).

During 2005, Bpool was the only condition exhibiting predictability in the variability of the temporospatial grazing. The three macrofactors assessed were all significant, sea surface temperature having a positive and rainfall and air temperature a negative effects were found decreasing the temporospatial variance (Table 5.33).

III. Synthesis

The percentage of significant results for grazing effects induced by microfactors and macrofactors varied according to the level of resolution (Table 5.34 and Fig. 5.2). At the species level, 41% of the significant results were produced by microfactors, and only 4.3% by macrofactors (chi-square = 43.4, df = 1, $P < 0.001$).

At the level of functional groups, 38% and 8.3% of the significant result were produced by micro and macrofactors respectively (chi-square = 37.65, df = 1, $P < 0.001$). Finally, at the coarsest level, algal biomass, 29% of the significant results were caused by microfactors and 43% involved macrofactors (chi-square = 9.8, df = 1, $P < 0.001$).

Table 5.18. Backward stepwise multiple regression analysis on different conditions for the alga *Porphyra capensis* representing the contribution of the three macrofactors to temporospatial intensity and variance of grazing effects, in 2004. Bonferroni correction was used with an $\alpha = 0.05/5 = 0.01$. Values are in percentages of contribution to grazing effect. Effects were either positive (+) or negative (-).ns represents non-significant results.

Independent variables	**dependent variable**							
	BOR Porphyra		**NBOR Porphyra**		**Bpool Porphyra**		**NBpool Porphyra**	
	average	**variance**	**average**	**variance**	**average**	**variance**	**average**	**variance**
Sea temperature	**ns**	**ns**	**ns**	**ns**	**no recruitment**		**no recruitment**	
Air temperature	**ns**	**ns**	**ns**	**ns**				
Rainfall	**ns**	**ns**	**ns**	**ns**				
ANOVA summary								
Source	**.**	**.**	**.**	**.**				
Regression MS	**.**	**.**	**.**	**.**				
Residual MS	**.**	**.**	**.**	**.**				
P	**.**	**.**	**.**	**.**				
Multiple R^2	**.**	**.**	**.**	**.**				

Table 5.19. Backward stepwise multiple regression analysis on different conditions for the alga *Porphyra capensis* representing the contribution of the three macrofactors to temporospatial intensity and variance of grazing effects, in 2005. Bonferroni correction was used with an α = 0.05/5 = 0.01. Values are in percentages of contribution to grazing effect. Effects were either positive (+) or negative (-).ns represents non-significant results.

Independent variables	dependent variable							
	BOR Porphyra		NBOR Porphyra		Bpool Porphyra		NBpool Porphyra	
	average	variance	average	variance	average	variance	average	variance
Sea temperature	ns	ns	ns	ns	no recruitment		no recruitment	
Air temperature	ns	ns	ns	ns				
Rainfall	ns	ns	ns	ns				
ANOVA summary								
Source	.	.	.	.				
Regression MS	.	.	.	.				
Residual MS	.	.	.	.				
P	.	.	.	.				
Multiple R^2	.	.	.	.				

Table 5.20. Backward stepwise multiple regression analysis on different conditions for the alga *Ulva rigida* representing the contribution of the three macrofactors to temporospatial intensity and variance of grazing effects, in 2004. Bonferroni correction was used with an α = 0.05/5 = 0.01. Values are in percentages of contribution to grazing effect. Effects were either positive (+) or negative (-).ns represents non-significant results.

Independent variables	**dependent variable**							
	BOR Ulva		**NBOR Ulva**		**Bpool Ulva**		**NBpool Ulva**	
	average	**variance**	**average**	**variance**	**average**	**variance**	**average**	**variance**
Sea temperature	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**
Air temperature	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**
Rainfall	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**
ANOVA summary								
Source	.	.	.	.	.	.	.	.
Regression MS	.	.	.	.	.	.	.	.
Residual MS	.	.	.	.	.	.	.	.
P	.	.	.	.	.	.	.	.
Multiple R^2	.	.	.	.	.	.	.	.

Table 5.21. Backward stepwise multiple regression analysis on different conditions for the alga *Ulva rigida* representing the contribution of the three macrofactors to temporospatial intensity and variance of grazing effects, in 2005. Bonferroni correction was used with an α = 0.05/5 = 0.01. Values are in percentages of contribution to grazing effect. Effects were either positive (+) or negative (-).ns represents non-significant results.

Independent variables	dependent variable							
	BOR Ulva		NBOR Ulva		Bpool Ulva		NBpool Ulva	
	average	variance	average	variance	average	variance	average	variance
Sea temperature	ns	ns	ns	ns	ns	ns	not repeated	
Air temperature	ns	ns	92(+)	ns	ns	ns	.	.
Rainfall	ns	ns	ns	ns	ns	ns	.	.
ANOVA summary								
Source	.	.	$F_{1,3}=39.8$	.	.	.	.	.
Regression MS	.	.	0.48	.	.	.	.	.
Residual MS	.	.	0.01	.	.	.	.	.
P	.	.	0.008	.	.	.	.	.
Multiple R^2	.	.	0.92	.	.	.	.	.

Table 5.22. Backward stepwise multiple regression analysis on different conditions for the alga *Chaetomorpha aerea* representing the contribution of the three macrofactors to temporospatial intensity and variance of grazing effects, in 2004. Bonferroni correction was used with an α = 0.05/5 = 0.01. Values are in percentages of contribution to grazing effect. Effects were either positive (+) or negative (-).ns represents non-significant results.

Independent variables	**dependent variable**							
	BOR Chaetomorpha		**NBOR Chaetomorpha**		**Bpool Chaetomorpha**		**NBpool Chaetomorpha**	
	average	**variance**	**average**	**variance**	**average**	**variance**	**average**	**variance**
Sea temperature	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**
Air temperature	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**
Rainfall	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**
ANOVA summary								
Source	.	.	.	.	.	.	.	.
Regression MS	.	.	.	.	.	.	.	.
Residual MS	.	.	.	.	.	.	.	.
P	.	.	.	.	.	.	.	.
Multiple R^2	.	.	.	.	.	.	.	.

Table 5.23. Backward stepwise multiple regression analysis on different conditions for the alga *Chaetomorpha aerea* representing the contribution of the three macrofactors to temporospatial intensity and variance of grazing effects, in 2005. Bonferroni correction was used with an $\alpha = 0.05/5 = 0.01$. Values are in percentages of contribution to grazing effect. Effects were either positive (+) or negative (-).ns represents non-significant results.

Independent variables	**dependent variable**							
	BOR Chaetomorpha		**NBOR Chaetomorpha**		**Bpool Chaetomorpha**		**NBpool Chaetomorpha**	
	average	**variance**	**average**	**variance**	**average**	**variance**	**average**	**variance**
Sea temperature	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**not repeated**	
Air temperature	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**		
Rainfall	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**		
ANOVA summary								
Source	.	.	.	.	.	.	.	.
Regression MS	.	.	.	.	.	.	.	.
Residual MS	.	.	.	.	.	.	.	.
P	.	.	.	.	.	.	.	.
Multiple R^2	.	.	.	.	.	.	.	.

Table 5.24. Backward stepwise multiple regression analysis on different conditions for the alga *Hildenbrandia rubra* representing the contribution of the three macrofactors to temporospatial intensity and variance of grazing effects, in 2004. Bonferroni correction was used with an α = 0.05/5 = 0.01. Values are in percentages of contribution to grazing effect. Effects were either positive (+) or negative (-).ns represents non-significant results.

Independent variables	**dependent variable**							
	BOR Hildenbrandia		**NBOR Hildenbrandia**		**Bpool Hildenbrandia**		**NBpool Hildenbrandia**	
	average	**variance**	**average**	**variance**	**average**	**variance**	**average**	**variance**
Sea temperature	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**
Air temperature	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**
Rainfall	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**
ANOVA summary								
Source	.	.	.	.	.	.	.	.
Regression MS	.	.	.	.	.	.	.	.
Residual MS	.	.	.	.	.	.	.	.
P	.	.	.	.	.	.	.	.
Multiple R^2	.	.	.	.	.	.	.	.

Table 5.25. Backward stepwise multiple regression analysis on different conditions for the alga *Hildenbrandia rubra* representing the contribution of the three macrofactors to temporospatial intensity and variance of grazing effects, in 2005. Bonferroni correction was used with an $\alpha = 0.05/5 = 0.01$. Values are in percentages of contribution to grazing effect. Effects were either positive (+) or negative (-).ns represents non-significant results.

Independent variables	dependent variable							
	BOR Hildenbrandia		NBOR Hildenbrandia		Bpool Hildenbrandia		NBpool Hildenbrandia	
	average	variance	average	variance	average	variance	average	variance
Sea temperature	ns	ns	ns	ns	ns	ns	no repeated	
Air temperature	ns	ns	ns	ns	ns	98(-)		
Rainfall	ns	ns	ns	ns	ns	ns		
ANOVA summary								
Source	.	.	.	.	.	$F_{1,3}$=155.9	.	.
Regression MS	.	.	.	.	.	14.5	.	.
Residual MS	.	.	.	.	.	0.09	.	.
P	.	.	.	.	.	0.001	.	.
Multiple R^2	.	.	.	.	.	0.98	.	.

Table 5.26. Backward stepwise multiple regression analysis on different conditions for the alga *Spongites yendoi* representing the contribution of the three macrofactors to temporospatial intensity and variance of grazing effects, in 2004. Bonferroni correction was used with an α = 0.05/5 = 0.01. Values are in percentages of contribution to grazing effect. Effects were either positive (+) or negative (-).ns represents non-significant results.

Independent variables	**dependent variable**							
	BOR Spongites		**NBOR Spongites**		**Bpool Spongites**		**NBpool Spongites**	
	Average	**variance**	**average**	**variance**	**average**	**variance**	**average**	**variance**
Sea temperature	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**
Air temperature	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**
Rainfall	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**
ANOVA summary								
Source	.	.	.	.	.	.	.	.
Regression MS	.	.	.	.	.	.	.	.
Residual MS	.	.	.	.	.	.	.	.
P	.	.	.	.	.	.	.	.
Multiple R^2	.	.	.	.	.	.	.	.

Table 5.27. Backward stepwise multiple regression analysis on different conditions for the alga *Spongites yendoi* during 2005 representing the contribution of the three macrofactors to temporospatial intensity and variance of grazing effects, in 2005. Bonferroni correction was used with an α = 0.05/5 = 0.01. Values are in percentages of contribution to grazing effect. Effects were either positive (+) or negative (-).ns represents non-significant results.

Independent variables	**dependent variable**							
	BOR Spongites		**NBOR Spongites**		**Bpool Spongites**		**NBpool Spongites**	
	Average	**variance**	**average**	**variance**	**average**	**variance**	**average**	**variance**
Sea temperature	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**
Air temperature	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**
Rainfall	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**
ANOVA summary								
Source	.	.	.	.	.	.	.	.
Regression MS	.	.	.	.	.	.	.	.
Residual MS	.	.	.	.	.	.	.	.
P	.	.	.	.	.	.	.	.
Multiple R^2	.	.	.	.	.	.	.	.

Table 5.28. Backward stepwise multiple regression analysis at the foliose functional group representing the contribution of the three macrofactors to temporospatial intensity and variance of grazing effects, in 2004. Bonferroni correction was used with an α = 0.05/2 = 0.025. Effects were either positive (+) or negative (-).

Independent variables	**dependent variable**							
	BOR foliose		**NBOR foliose**		**Bpool foliose**		**NBpool foliose**	
	average	**variance**	**average**	**variance**	**average**	**variance**	**average**	**variance**
Sea temperature	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**
Air temperature	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**
Rainfall	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**
ANOVA summary								
Source	.	.	.	.	.	.	.	.
Regression MS	.	.	.	.	.	.	.	.
Residual MS	.	.	.	.	.	.	.	.
P	.	.	.	.	.	.	.	.
Multiple R^2	.	.	.	.	.	.	.	.

Table 5.29. Backward stepwise multiple regression analysis at the encrusting functional group representing the contribution of the three macrofactors to temporospatial intensity and variance of grazing effects, in 2004. Bonferroni correction was used with an α = 0.05/2 = 0.025. Effects were either positive (+) or negative (-).

Independent variables	**dependent variable**							
	BOR encrusting		**NBOR encrusting**		**Bpool encrusting**		**NBpool encrusting**	
	average	**variance**	**average**	**variance**	**average**	**variance**	**average**	**variance**
Sea temperature	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**
Air temperature	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**
Rainfall	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**
ANOVA summary								
Source	.	.	.	.	.	.	.	.
Regression MS	.	.	.	.	.	.	.	.
Residual MS	.	.	.	.	.	.	.	.
P	.	.	.	.	.	.	.	.
Multiple R^2	.	.	.	.	.	.	.	.

Table 5.30. Backward stepwise multiple regression analysis at the foliose functional group representing the contribution of the three macrofactors to temporospatial intensity and variance of grazing effects, in 2005. Bonferroni correction was used with an α = 0.05/2 = 0.025. Effects were either positive (+) or negative (-).

Independent variables	**dependent variable**							
	BOR foliose		**NBOR foliose**		**Bpool foliose**		**NBpool foliose**	
	average	**variance**	**average**	**variance**	**average**	**variance**	**average**	**variance**
Sea temperature	**52.7(+)**	**94(+)**	**ns**	**ns**	**ns**	**ns**	**not repeated**	
Air temperature	**45.9(-)**	**ns**	**ns**	**ns**	**ns**	**ns**	**.**	**.**
Rainfall	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**.**	**.**
ANOVA summary								
Source	**$F_{2,2}$=215.1**	**$F_{1,3}$=52.6**	**.**	**.**	**.**	**.**	**.**	**.**
Regression MS	**0.7**	**59.4**	**.**	**.**	**.**	**.**	**.**	**.**
Residual MS	**0.003**	**1.12**	**.**	**.**	**.**	**.**	**.**	**.**
P	**<0.01**	**<0.01**	**.**	**.**	**.**	**.**	**.**	**.**
Multiple R^2	**0.99**	**0.94**	**.**	**.**	**.**	**.**	**.**	**.**

Table 5.31. Backward stepwise multiple regression analysis at the encrusting functional group representing the contribution of the three macrofactors to temporospatial intensity and variance of grazing effects, in 2005. Bonferroni correction was used with an α = 0.05/2 = 0.025. Effects were either positive (+) or negative (-).

Independent variables	**dependent variable**							
	BOR encrusting		**NBOR encrusting**		**Bpool encrusting**		**NBpool encrusting**	
	average	**variance**	**average**	**variance**	**average**	**variance**	**average**	**variance**
Sea temperature	**no recruitment**		**no recruitment**		**ns**	**ns**	**not repeated**	
Air temperature	**.**	**.**	**.**	**.**	**ns**	**ns**	**.**	**.**
Rainfall	**.**	**.**	**.**	**.**	**ns**	**ns**	**.**	**.**
ANOVA summary								
Source	**.**	**.**	**.**	**.**	**.**	**.**	**.**	**.**
Regression MS	**.**	**.**	**.**	**.**	**.**	**.**	**.**	**.**
Residual MS	**.**	**.**	**.**	**.**	**.**	**.**	**.**	**.**
P	**.**	**.**	**.**	**.**	**.**	**.**	**.**	**.**
Multiple R^2	**.**	**.**	**.**	**.**	**.**	**.**	**.**	**.**

Table 5.32 Backward stepwise multiple regression analysis on the coarsest level of resolution, representing the percent of contribution of the three macrofactors to the temporospatial intensity and variance of grazing effect, during 2004. Effects were either positive (+) or negative (-).

Independent variables	**dependent variable**							
	Chl *a* BOR		**Cho *a* NBOR**		**Chl *a* Bpool**		**Chl *a* NBpool**	
	average	**variance**	**average**	**variance**	**average**	**variance**	**average**	**variance**
Sea temperature	**ns**	**ns**	**ns**	**ns**	**78(-)**	**ns**	**40.8(-)**	**64(+)**
Air temperature	**ns**	**ns**	**ns**	**ns**	**ns**	**ns**	**39.4(+)**	**ns**
Rainfall	**ns**	**ns**	**74(-)**	**64(+)**	**ns**	**ns**	**ns**	**ns**
ANOVA summary								
Source	**.**	**.**	$F_{1,6}$**=17.4**	$F_{1,6}$**= 10.5**	$F_{1,6}$**=21.5**	**.**	$F_{2,5}$**=15.6**	$F_{1,6}$**=10.7**
Regression MS	**.**	**.**	**3.68**	**2.8**	**1.7**	**.**	**1.87**	**5.43**
Residual MS	**.**	**.**	**0.35**	**0.35**	**0.07**	**.**	**0.11**	**0.5**
P	**.**	**.**	**<0.01**	**<0.01**	**<0.01**	**.**	**<0.01**	**<0.01**
Multiple R^2	**.**	**.**	**0.74**	**0.64**	**0.78**	**.**	**0.86**	**0.64**

Table 5.33. Backward stepwise multiple regression analysis on the coarsest level of resolution representing the percent of contribution of the three macrofactors to the temporospatial intensity and variance of grazing effects, during 2005. Effects were either positive (+) or negative (-).

Independent variables	**dependent variable**							
	Chl *a* BOR		**Chl *a* NBOR**		**Chl *a* Bpool**		**Chl *a* NBpool**	
	average	**variance**	**average**	**variance**	**average**	**variance**	**average**	**variance**
Sea temperature	**ns**	**ns**	**ns**	**ns**	**ns**	**45.9(+)**	**not repeated**	
Air temperature	**ns**	**ns**	**ns**	**ns**	**ns**	**22.1(-)**	**.**	**.**
Rainfall	**ns**	**ns**	**ns**	**ns**	**ns**	**30.9(-)**	**.**	**.**
ANOVA summary								
Source	**.**	**.**	**.**	**.**	**.**	**$F_{3,1}$=55283.2**	**.**	**.**
Regression MS	**.**	**.**	**.**	**.**	**.**	**1.74**	**.**	**.**
Residual MS	**.**	**.**	**.**	**.**	**.**	**0.0003**	**.**	**.**
P	**.**	**.**	**.**	**.**	**.**	**<0.01**	**.**	**.**
Multiple R^2	**.**	**.**	**.**	**.**	**.**	**0.99**	**.**	**.**

Table 5.34. Synthesis showing in which conditions spatiotemporal microfactors and temporospatial macrofactors where significant. Ratios indicate how many significant results were found, finally the significant results were counted pooling conditions, years, the intensities and variances and transformed to percentages at every level of resolution.

	Microfactors									**Macrofactors**								
Level of resolution	**BOR**		**NBOR**		**Bpool**		**NBpool**			**BOR**		**NBOR**		**Bpool**		**NBpool**		
	X	**S^2**	**X**	**S^2**	**X**	**S^2**	**X**	**S^2**		**X**	**S^2**	**X**	**S^2**	**X**	**S^2**	**X**	**S^2**	
i) Species																		
2004: *Porphyra capensis*	*	*	ns	ns	no recruitment				= 2/4	ns	ns	ns	ns	no recruitment				= 0/4
2005: *Porphyra capensis*	*	ns	*	*	no recruitment				= 3/4	ns	ns	ns	ns	no recruitment				= 0/4
2004: *Ulva rigida*	*	*	*	*	*	*	ns	ns	= 6/8	ns	ns	ns	ns	ns	ns	ns	ns	= 0/8
2005: *Ulva rigida*	*	ns	ns	*	*	ns	not repeated		= 3/6	ns	ns	*	ns	ns	ns	not repeated		= 1/6
2004: *Chaetomorpha aerea*	ns	*	ns	ns	ns	ns	*	ns	= 2/8	ns	ns	ns	ns	ns	ns	ns	ns	= 0/8
2005: *Chaetomorpha aerea*	no recruitment				*	*	not repeated		= 2/2	no recruitment				ns	ns	not repeated		= 0/2
2004: *Hildenbrandia rubra*	no recruitment		ns	ns	ns	ns	ns	ns	= 0/6	no recruitment		ns	ns	ns	ns	ns	ns	= 0/6
2005: *Hildenbrandia rubra*	no recruitment				*	*	not repeated		= 0/2	no recruitment				ns	*	not repeated		= 1/2
2004: *Spongites yendoi*	no recruitment				ns	ns	ns	*	= 1/4	no recruitment				ns	ns	ns	ns	= 0/4
2005: *Spongites yendoi*	no recruitment				ns	ns	not repeated		= 0/2	no recruitment				ns	ns	not repeated		= 0/2
									Total = 19/46 = 41%									**Total = 2/46 = 4.3%**
ii) Functional groups																		
2004: Foliose	*	*	ns	ns	*	ns	ns	*	= 4/8	ns	ns	ns	ns	ns	ns	ns	ns	= 0/8
2005: Foliose	*	*	ns	ns	*	ns	ns	*	= 4/8	*	*	ns	ns	ns	ns	ns	ns	= 2/8
2004: Encrusting	no recruitment		ns	ns	ns	ns	ns	ns	= 0/6	no recruitment		ns	ns	ns	ns	ns	ns	= 0/6
2005: Encrusting	no recruitment				ns	*	not repeated		= 1/2	no recruitment				ns	ns	not repeated		= 0/2
									Total =9/24 = 37.5%									**Total = 2/24 = 8.3 %**
iii) Biomass																		
2004: Chlorophyll *a*	*	ns	ns	ns	*	*	ns	*	= 4/8	ns	ns	*	*	*	ns	*	*	= 5/8
2005: Chlorophyll *a*	ns	ns	ns	ns	ns	ns	not repeated		= 0/6	ns	ns	ns	ns	ns	*	not repeated		=1/6
									Total =4/14 = 29%									**Total = 6/14 = 43%**

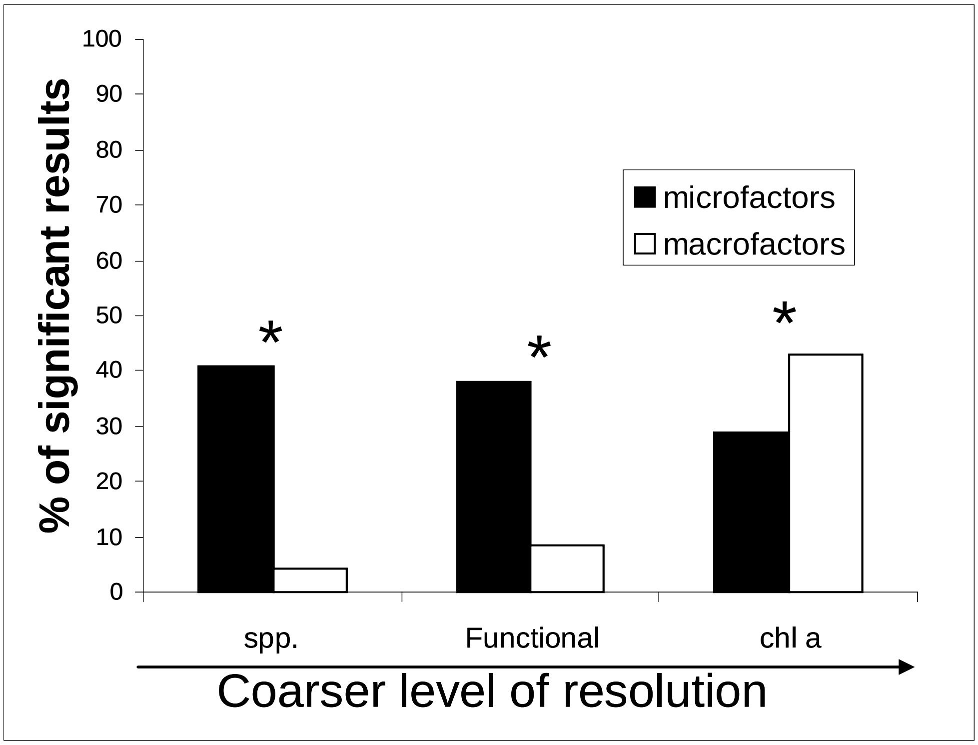

Figure 5.2. Percentage of significant results found at every level of resolution pooling intensity, variance and years. Asterisks indicate significant differences between micro and macrofactors.

DISCUSSION

I. Results synthesis with brief interpretation

Several abiotic and biotic factors were studied in order to understand the variation in outcomes of grazing effects at small scales under different conditions, at different levels of resolution and between years. The goal was to determine which factor or factors influence grazing effects.

Chapter IV addressed the question of whether grazing can be spatially stable in the upper eulittoral zone. This was true at two levels of resolution. First, grazing effects were spatially stable in Bpools and NBOR for *Ulva rigida*, second, at the foliose functional level of resolution, spatial stability was found again in Bpools. One of the goals in this chapter was to determine if the abiotic and biotic factors shaping grazing effect were consistent between years under those conditions in which spatial stability was observed. The only factor explaining the spatial stability of grazing on *U. rigida* was elevation in Bpools. Elevation was important in NBOR in 2004 and 2005 and affected *U. rigida* with two additional factors: density of littorinids and juveniles in 2005. At the foliose functional level of resolution, there was no consistency in the factors explaining this stability. At the functional level, in the first experiment inundation time and water movement were the two important factors, while elevation was important in the second experiment. The conclusion here is that spatial stability can be induced by the same or different combinations of factors. Elevation was important because it can integrate the duration of emergence (inundation time) and extent of temperature fluctuation at small scales, as has reported by Metaxas and Scheibling (1993). The present result agrees with other studies that elevation has been reported as an important factor regulating diversity, richness and abundance across the shore, either on emergent substratum (open rock) (Underwood 1980, Underwood and Jernakoff 1984, Benson 2002, Harley 2003, Harley and Helmuth 2003) or tidal pools (Huggett and Griffiths 1986, Fairweather and Underwood 1991, Metaxas and Scheibling 1993, Bussell et al. 2007).

Interestingly, the main cause determining spatial stability in grazing effects was not density of grazers, as it shown in many experiments in pools in the mid shore (Lubchenco 1982), in the upper eulittoral zone of Nova Scotia (Chapman and Johnson 1990) and in New South Wales (Underwood and Jernakoff 1984, Arrontes and Underwood 1991). This divergence may represent an artefact of non-linearity between the results from grazing manipulation and the linear assumptions of the multiple-regression model (see limitations section below).

The common intuition in ecology is to look for a single factor that explains a specific ecological phenomenon. Here I found the opposite, different conditions and levels of resolution exhibited great variability in the combination of factors predicting grazing effects (including the effects of microfactors and macrofactors acting on the intensity and/or variance together or separately). This agrees with several studies that report interaction of factors predicting ecological processes such as grazing (e.g. Benedetti-Cecchi and Cinelli 1995, Harley 2003, Nielsen 2003). An understanding of how several abiotic factors vary at small scales and induce spatial structure in grazing effects is a central issue to interpret the variability observed on the rocky shores.

The number of microfactors affecting foliose species was larger than for encrusting species. This can be explained by the tolerance to physical and biotic stresses of the encrusting species that makes them largely independent of abiotic factors (Littler and

Littler 1980, Steneck and Dethier 1994). In addition, the combination of factors affecting spatiotemporal grazing effects on algal species varied according to the habitat: tidal pools were less affected by abiotic factors than open rock habitats; however tidal pools were more likely to be affected by biotic factors such as density of grazers, this agrees with other studies done in tidal pools (Metaxas and Scheibling 1993, Nielsen 2001, 2003). In contrast, grazer effects on open rock were more likely to be affected by physical factors related to gradients of desiccation and wave exposure.

II. Limitations of the model

In general, every prediction that comes from multiple regressions can represent a particular state of the spatiotemporal grazing effects at small scales in term of average and variance. The same was observed for the effects of macrofactors on the temporospatial intensity and variance of grazing effects. These microfactors and macrofactors interacted in different combinations to contribute to the prediction of the observed variability in the effects of grazing. However, physical factors dominated the analyses, this agrees with studies done in the high intertidal zone where abiotic factors have more importance than biotic factors (Hawkins and Hartnoll 1983, Cubit 1984, Mak and Williams 1999). It would appear obvious that the main factor inducing variability in grazing effects is the density of grazers, but this was not always sensitive enough to be detected in multiple regressions. For example, the fact that several times mesograzers were not significant predictors of spatiotemporal grazing effects indicates that grazing intensity and density of grazers are not related linearly. Nevertheless, this artefact can be attributed to the idea of linearity in factorial experimental designs. These assume linear relationships between the factor and the response variable. For example, in exclusion experiments, if the exclusion treatment shows more algal biomass than the open grazing access treatment, it is intuitively assumed that there is a linear relationship between grazers and seaweed. However, this relationship can be more complex than linear, affecting the spatial variance (Ruel and Ayres 1999, Benedetti-Cecchi 2000, 2003). In this study, I expected the same negative linear relationship between grazers (mesograzers and/or micrograzers) and the intensity of the grazing effect, since the previous chapter showed significant overall grazing effects in the factorial experiment. However, only a few clear linear relationships were found between density of mesograzers and intensity of grazing, e.g. *Ulva rigida* in 2005 and the foliose functional level of resolution in the burnt open rock condition during 2005. This is one limitation of this study and has been recognized by other authors who have used effect sizes. Coleman et al. (2006) working on the west coast of Europe, found no significant linear relationship between the intensity of grazing represented as effect sizes and the density of limpets, although an overall grazing effect, assessed using experimental exclusions, was significant. Contrary to this, Jara and Moreno (1984) on Chilean coasts, and Benedetti-Cecchi et al. (2005) on the Mediterranean coast, found that the density of limpets linearly reduced the percentage of algal cover. The difference between these two findings could be explained by an artefact due to the use of effect sizes, which transforms a possible linear function into a non-linear relationship (Osenberg et al. 1997).

In the further points III to VI (see below), I propose different models to explain the variability in grazing effects. This was done by categorizing the significant results from microfactor and macrofactor analyses, and reconciling them into a whole model where both types of factors interact. Significant results for the proposed models were extracted using multiple-regression tests, which belong to the category of analyses that contain only additive terms. Additive models do not allow for interactions between predictor variables in a multiplicative way, but they do it in an additive way (Quinn and Keough 2003). The lack of multiplicative interaction can give the impression to ecologists that interactions are only related to multiplicative models, meaning two factors act together in a sequential additive way (similar to ANOVA analyses). Nevertheless, interactions can also be described in an additive way, for example, microfactors ‘A’ and ‘B’ affect the dependent variable, together, but independently, while multiplicative models measure the dependence of the partial regression slope of the variable against ‘A’ on the value of factor ‘B’. Additive and multiplicative interactions are important and are mixed in the multiplicative model, however a problem arises when the variable is contrasted with several multiplicative factors which increase the noise of the prediction through colinearity (Quinn and Keough 2003). Therefore, the only solution is to standardize and check the variables several times until the best adjustment is found, which can produce a non-realistic model. Fitting multiplicative models was not appropriate in this study, due to the large number of factors compared to the sample size (Quinn and Keogh 2003).

III. Differences between micro and macrofactors

Microfactors affected spatiotemporal intensity and variance at the species and functional group levels of resolution, but the proportion of significant results decreased at the level of algal biomass (Table 5.34). In the majority of cases, macrofactors were significant at the coarsest level of resolution and microfactors at the finest level of resolution (Table

5.34). This suggests that macrofactors have a detectable effect on the whole primary producer assemblage as represented by chlorophyll *a*, rather on particular species of the assemblage. This suggests that microfactors influence finer components of the assemblage and macrofactor the coarser ones. It has been proposed that finer components of algal assemblage can vary more than coarser ones (Steneck and Dethier 1994, Carpenter 2002). This has been reported in terms of the relationship between spatial scale and taxonomic levels of resolution, where smaller scale variability matches finer taxonomic levels (Warwick 1988, Underwood and Chapman 1996, Anderson et al. 2005), although there are some exceptions (Cole and Chapman 2007).

IV. Micro and macrofactors among levels of resolution

Although, macrofactors seem to be more effective in predicting effects at coarser levels, they affected finer levels too, together with microfactors. The second conclusion of this study is that either microfactors or macrofactors may affect a given level of resolution e.g. the factors affecting finer levels of resolution may or may not always affect the coarser level of resolution. Thus, as is the case for the problem of small and large scales, outcomes from different level of resolution represent different ecological responses to abiotic and biotic factors (Menge and Olson 1990). As I have shown in this study, common factors affecting different algae can act synergistically and become significant at a coarser level of resolution or factors significant at specific levels can disappear at coarser levels because of the buffer effect of several components which are non-significant. Finally, it is possible to recognize strong effects when a single factor was significant in every level of resolution (number of juveniles in BOR). The significance of microfactors and macrofactors is in agreement with the ‘scaling up framework’ described in the last chapter, where effects of grazers can be modified among levels of resolution through three effects: ‘synergistic’, ‘buffer’ and ‘dominant component’.

The idea of grouping species with similar ecological functions into functional groups simplifies ecological analysis, and this simplification implies a change in the predictability at each level, because the variability among replicates decreases as the level becomes coarser (Ruel and Ayres 1999).

V. Relationship between average and variance

Different conditions showed different factors affecting the average and variance of the grazing effects. Theoretical and empirical studies have shown that mean and the variance can exhibit different types of distribution or behaviours (Ruel and Ayres 1999, Benedetti-Cecchi 2000, 2003), and therefore one of the conclusions of this study is the demonstration that the two parameters can be explained by the same or different factors. Similar and different factors can work together in the following combinations: i) enhance or reduce intensity (represented by the mean grazing effect) but not the variance. This occurs when single microfactor affects every block, reducing or homogeneously increasing the intensity. Therefore, the factor reduces the differences in intensity among blocks, meaning variance diminishes towards zero. ii) Enhance or reduce intensity, but enhance the variance. This implies that the factor affects only a few blocks, which immediately increases the variance. iii) Enhance or reduce intensity and reduce the variance. This implies that the factor acts on the majority of blocks, but acts only very weakly on some, this reduces the variance. iv) No effect on the intensity of the grazing effect, but increases or reduces the variance. This can be explained when each block exhibits the same intensity of grazing effects or a non-linear behaviour, but the spatiotemporal variance differs among blocks so that overall spatiotemporal variance is reduced or enhanced.

It is possible to understand how a factor can increase the intensity of the grazing effect and at the same time decrease its variability. For example, in the upper eulittoral zone of the south coast of South Africa, complexity in microhabitats creates variability in the intensity of grazing effects. However, a benign factor can intensify the grazing effect, e.g. by increasing the time of inundation (decreasing emersion time) or the amount of water movement after low tide in every block. This would reduce the difference between benign and harsh microhabitats, increasing the grazing effect and at the same time decreasing the variance in the intensity among blocks. The opposite effect could be driven by a delay in inundation time and reduction in water movement; this would induce an increase in the difference between benign and harsh blocks. The increase in the harshness in the majority of the blocks results in a reduction of spatiotemporal grazing intensity but also increases the variance in the grazing effect among blocks. I could theoretically exemplify each of four cases of combination between intensity and variance, but I decided to stop here because these cases comprise the same elements and logic. First, there is a complexity given by the substratum which provides benign and harsh microsites, second the species (algae and grazers) distribute themselves according their tolerances to the harshness, and third microfactors can change and modify the quality of particular microsites, changing the strength of the ecological process occurring on those places.

VI. Possible interaction between microfactors

The microfactors measured can be classified as kinetic or static at microscales. Kinetic factors exhibit spatial variability which is a function of time, such as all the physical factors related to gradients of wave exposure at mesoscales; ultimately these are driven by local weather conditions (e.g. winds, change in the barometric pressure) and by season. Inundation time and water movement fit into this category. Biotic factors such as density of meso and micrograzers can be also categorized as kinetic, since these factors can also exhibit spatial and temporal variability. At a given spatial and temporal scale, the same average number of grazers can exert more or less intense grazing pressure depending on the tide, conditions of day or night, or weather conditions which promote moister substrata (Navarrete 1996, Benedetti Cecchi et al. 2005, Morelissen and Harley 2007, Atalah et al. 2007), as well as their own grazing history.

Static factors are related to idiosyncratic features of the topography, such as shape of the substratum (boulders, flat platforms) and within these features elevation and distance from the sea. For static factors, temporal variability tends toward zero. The complexity of grazing effects is created by the interaction of these static and kinetic factors, plus the physiological tolerances of the algae and the local weather. Thus, algae can survive in the harsh upper eulittoral zone where one or more factors work together to create conditions within the physiologically tolerable range for the species, while allowing growth to exceed grazing pressure. Thus, combinations of microfactors and macrofactors can provide more than one solution for the survival of algae.

VII. Interaction between microfactors and macrofactors

In this study microfactors were found to have a stronger influence on grazing effects than macrofactors especially at the level of species. This conclusion is based on the larger number of microfactors than macrofactors that were significant predictors of grazing effects (Table 5.34). The critical microfactors varied with the taxa and the level of resolution. Macrofactors exhibited low variability among levels being non-significant in most cases. Sometimes macrofactors and microfactors were significant at the same time, meaning a possible interaction.

The interaction between macrofactors and microfactors can be described as a hierarchy where macrofactors operating at a larger scale modify the consequences produced by the microfactors, which act at smaller scales. Some examples of this hierarchy are given by Hallett et al. (2004), who reported that large-scale climatic indices predict in a more accurate way ecological processes that operate at smaller scale (mortality of organisms). Similarly, Denny and Paine (1998) proposed that lunar oscillation has effects on tidal regime and that this could change the emersion time, and therefore the distribution of organisms in the intertidal. In addition, Williams and Morrit (1995) reported temporal relativity in the quality of refuges for the high shore grazer *Cellana grata* on coasts of Hong Kong caused by air temperatures. Finally, Sanford (1999) reported that the keystone species *Pisaster ochraceus* is negatively affected by slight decreases in the sea temperature. These studies suggest effects of macrofactors on factors and ecological processes operating at smaller scales. However, in this study micro and macrofactors could in some cases interact. Understanding the interaction as microfactors predictors spatiotemporal grazing effects is already complex, therefore understanding the interactions of macrofactors and microfactors can be even more complex. I suggest a hypothetical model of the interaction between these two types of factors and the consequences for the spatiotemporal intensity and variance of grazing effects. This interaction is driven by three elements: macrofactors, topography and microfactors. Macrofactors are represented by the weather at a particular scale. The topography can be quantified in terms of spatial heterogeneity (see Kostylev et al. 2005 or differences in elevation see chapter III) and, because this heterogeneity is site specific, I will refer to any specific level of heterogeneity as ‘idiosyncratic heterogeneity’. This heterogeneity is given by the structure of the rocky shore: platform, boulders, crevices, gulley etc. Finally, microfactors represent the quantitative characterization of the rocky shore according to various abiotic and biotic factors, as I did in the present chapter. These elements, interact, creating changes in the spatiotemporal intensity and variance of grazing effects. For example, in a system where the spatial heterogeneity is fixed in time (no movement of the substratum), benign macrofactors can act strongly to increase the quality and the availability of shelters for grazing interaction, this will increase the spatiotemporal intensity and reduce the spatiotemporal variance. These three elements can vary in intensity, inducing changes in the spatiotemporal intensity and variance. For this reason in a simplified scheme, I illustrate how the variability in macrofactors affects a specific level of idiosyncratic heterogeneity, and the consequences on the spatiotemporal grazing effect (Fig. 5.3).

VIII. Conclusion

A linear model based on multiple regression analyses was used to predict spatiotemporal and temporospatial grazing effects. The results varied enormously from condition to condition, year to year and through levels of resolution. First, factors predicting grazing effects at finer levels of resolution can change at coarser levels due to a buffering effect of other factors. Only number of juveniles was important in predicting grazing effects in the BOR condition at every level of resolution during 2004. Macrofactors were often significant at the coarsest level of resolution. Spatial stability can be explained by different combinations of factors (in NBOR) or by single factor (in Bpool) at the functional level of resolution. The combination of factors influencing intensity and/or variance of grazing effects can influence the spatial patterns of grazing. If the factor is weak, its effects are thought to affect only some areas of the rocky shore, and therefore it will increase the spatiotemporal variance, but not the intensity. However, if the effect is strong, it will homogenously affect the whole area studied, increasing the spatiotemporal intensity but decreasing the variance. The same hypothetical model was used for the interaction between macro and microfactors. When macrofactors operate weakly, the variability of grazing effects will be driven by microfactors and the idiosyncratic heterogeneity, while if they operate strongly, microfactors will be homogenized and grazing effects will be driven only by macrofactors.

The analytical techniques used here can be considered rudimentary, other statistical-mathematical analyses are necessary and will allow more complex and more realistic understandings of the effects of grazing. However, the present model suggests interesting results which can encourage future ecological models and hypotheses. These are aimed at understanding the effects of large scale factors on small scale ecological processes affected by microfactors (Witman et al. 2004).

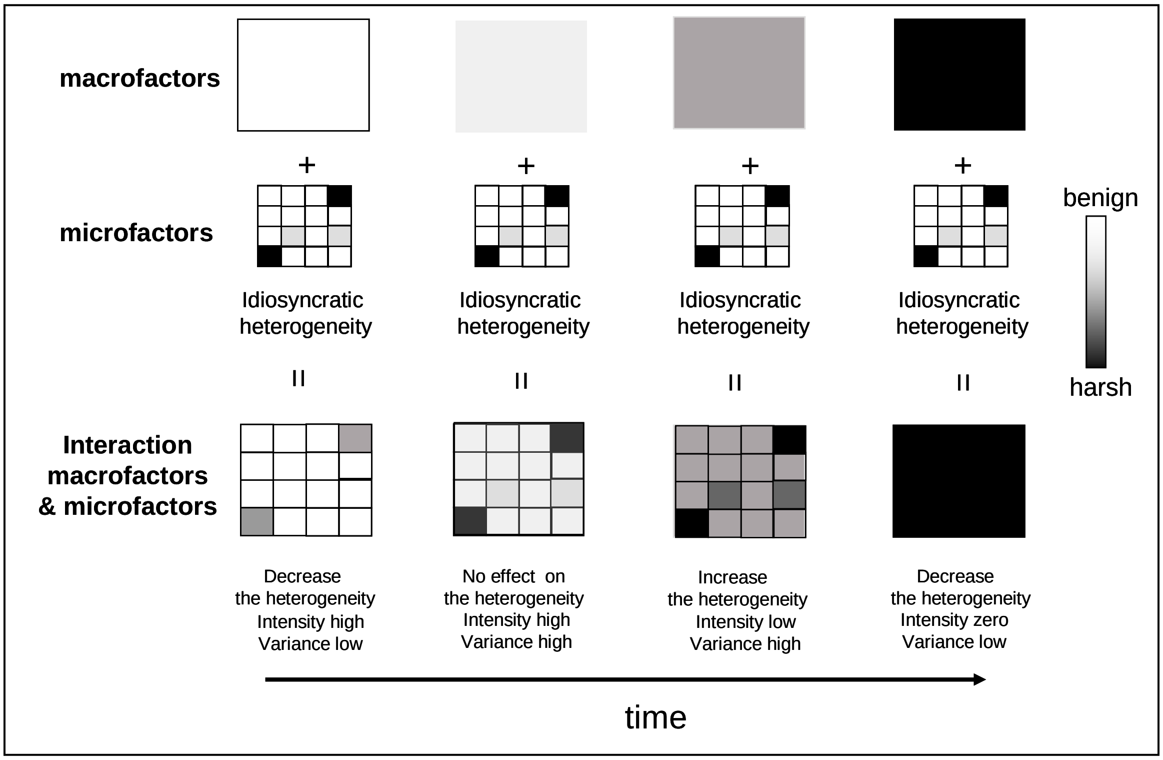

Figure 5.3. Relationship between macrofactors and microfactors. The first row of squares shows a temporal gradient from benign to harsh conditions of any macrofactor. The second row shows a fixed idiosyncratic heterogeneity of any site. The cells that comprise the idiosyncratic heterogeneity reflect the intrinsic variation in conditions for grazing effects induced by microfactors. The third row indicates the possible outcomes of the interaction between macrofactors and microfactors and the consequences for the spatiotemporal intensity and variance of grazing effects.

GENERAL SYNTHESIS

“If a man is offered a fact which goes against his instincts, he will scrutinize it closely, and unless the evidence is overwhelming, he will refuse to believe it. If, on the other hand, he is offered something which affords a reason for acting in accordance to his instincts, he will accept it even on the slightest evidence.”

Bertrand Russell

Recent advances in ecology stress the importance of understanding patterns and processes at different spatial and temporal scales (O'Neill 2001). A major challenge for ecological theory today is to translate the processes and patterns operating at large scales into smaller scales and vice versa. The problem of scale is a problem of resolution, a problem of how the level of detail in which an ecological phenomenon should be described by an observer. I refer to the degree of detail of an ecological phenomenon as 'level of resolution' and this terminology is valid not only for spatiotemporal scales, but also for taxonomic or functional groups and applies to any ecological phenomenon that involves levels of organization. If an ecological process is observed at a fine level of resolution, the parts of this process can be scrutinized and large scale ecological processes can be described as smaller parts at smaller scales, on the assumption that the sum of the parts represents the whole of the larger scale process. This approach analyzing ecology is called 'reductionism' (Keller and Golley 2000), however it is self-evident that the sum of the part does not explain the whole, examples have been demonstrated in terms of spatial scale (Cole and Chapman 2007) and taxonomic level of resolution (Rahel 1990). The opposite extreme view is named holism and assumes that ecological systems operate at a larger scale than their components, so that it is not possible to know and understand the whole organism through the parts interacting at smaller scales. In addition, the holistic assumption is that an ecological system is self-regulating and in equilibrium, where this equilibrium is an emergent property. The 'emergentism' concept represents an intermediate point of view; knowledge of all components it is not critical to an understanding of the whole (Keller and Golley 2000).

The most widely held view these days is that ecological systems are not in equilibrium/stable, therefore the parts/components can explain the whole at large scales. This change of view was derived from disagreement about the meaning of stability (Connell and Sousa 1983, Pimm 1984). However, if we believe that ecological systems do not assume equilibrium/stability, ecology can no longer form the basis of conservation efforts (O'Neill 2001). In this sense, integration between reductionism and holism and among levels of resolution is critical in order to understand ecological phenomena and allow a scientific basis for conservation.

An attempt at integration among levels of resolution gave rise to the hierarchical theory, which is based on the assumption that any ecological process is a system formed by parts, where the parts belong to a lower level of resolution with respect to the whole, which operates at a coarser level of resolution (Allen and Starr 1982). The different levels of resolution may, or may not be connected among themselves, generating either nested or non-nested hierarchies.

Here, I studied grazing as an ecological interaction, trying to understand two of its properties that exhibited hierarchical behaviour: spatial heterogeneity and spatial stability. By definition, grazers remove algae on the rocky shores, by doing this they modify the distribution and abundance of an algal assemblage. Given this, it seems illogical that sometimes one can not observe grazing effects at a particular site. However weak grazing effects on a particular alga can also contribute to the spatial structure of another alga, thus affecting the spatial structure of the whole algal community (Berlow 1999, Freidenbug et al. 2007). I found overall grazing effects decreased the algal abundance on a rocky shore on the south coast of South Africa, under conditions of algal recovery (early succession). This effect was important on the low, upper eulittoral zone and in high shore tidal pools, but was not significant on the midshore in agreement with Whittington-Jones (1997), or in the littoral fringe (high shore). A second experiment across the shore confirmed these findings, however a non-monotonic increase of grazing effects was observed as the distance above the MLWS increased, while at the same time a patchy spatial pattern of grazing effects which changed in time was observed across the shore. Under conditions of non-recovery (late succession), assessing the natural spatial relationship that appears without manipulation between several algal functional groups and grazers, I detected not only a negative relationship between grazers and some foliose functional groups, but also positive relationships, especially between encrusting algae and grazers (Branch et al. 1992, McQuaid and Froneman 1993). Some groups of algae and grazers showed contradictory responses to human exploitation at different sites; these groups were red turfs and red corticated algae. Additionally, these results suggested hierarchical behaviour of spatial scales based on spatial analysis of grazing, which showed a hierarchy of spatial scales of grazing effects on different algal functional groups. It is worth noting that these experiments were analyzed at different levels of resolution of the algal assemblage, functional groups and concentration of chlorophyll *a*. Only in the upper eulittoral zone were all three levels of resolution used, and this showed that the resolution of the algal assemblages affected the significance in the detection of grazing effects.

Complexity in topography at various scales has been recognized in terrestrial (Dale 2000) and marine systems as a source of microhabitats which determine species richness, diversity and patchiness (Kostylev et al. 2005). Burrows and Hawkins (1998) suggested, on the basis of cellular automata models, that on homogenous surfaces, spatial patterns can self-emerge purely as a product of biotic interactions among species. To test to this prediction, I studied two rocky shores with low topographic complexity, where a hierarchy of spatial scales of algae emerged cross-correlated is space to density and biomass of grazers, in this way, the patchiness of grazing can act as equivalent of topographic complexity. Topographic complexity provides alternating areas with benign and harsh conditions for different species of algae, while grazing provides a range of areas with strong or weak grazing pressure, which induces algal recruitment and biomass grazing pressure which induces variability in algal recruitment and biomass on the shore.

An interesting element relevant to the holistic or reductionist perception of the nature of grazing is spatial stability at small scales. The concept of stability has been controversial and involves elements such as: 1. resistance, the capacity to tolerate a disturbance, 2. resilience, the rapidity which the system returns to a previous equilibrium after a perturbation, 3. persistence, the ability of the system to remain within certain boundaries, and 4. variability, the degree of change in a certain period of time (Pimm 1984, Wu and Loucks 1995). These elements commonly refer to how populations of the primary producers (plants, algae) interact with grazer populations so that grazing does not eliminate plant populations, and how a given abundance of plants supports a determined abundance of grazers (Rosenzwig and MacArthur 1963, Noy-Meir 1975, Wu and Loucks 1995). However, the concept of stability has not been applied to the stability of spatial structure in time for an ecological interaction like grazing (Gripenberg and Roslin 2007). Therefore, spatial stability of grazing effects was assessed and defined using two criteria. Burrows and Hawkins (1998) and Menge et al. (2005) addressed the old question of whether spatial patterns (patchiness) are static or dynamic in time. On the basis of theoretical and empirical data, they concluded that spatial pattern can be dynamic (exhibiting a change in the position of the patches), due to disturbances and other factors. If patches of grazing effects are able to return to their original strength of grazing and to the same positions after a disturbance event, then this can be defined as spatial stability. In this context, I found that grazing effects are static in both habitats (tidal pools and open rocks) in the upper eulittoral, after disturbance. However, the degree of stasis or spatial determinism varied according to the level of resolution of the assemblage. Similarly the significance of grazing effects was found to differ among levels of resolution. These divergences among levels of resolution were produced by the relationships among the components at each level resulting in emergent properties. The three levels of resolution used were: species, functional groups and biomass and the relationships identified were synergism, buffering and dominant. According to hierarchical theory (Allen and Starr 1982, O'Neill et al. 1986), an ecological system consists of different levels of resolution/organization, where the levels may or may not exhibit nested relationships. Nested relationships imply that processes are present at every level of resolution. Interestingly, the components of stability, spatial stasis and grazing effects, varied in statistical significance depending on the level of resolution, exhibiting nested properties (synergism and dominant component) from the species to the functional group level and non-nested properties (buffering) from the functional group to the algal biomass level. These non-nested effects were caused by the microalgal community, a component not included at the lower levels of resolution, resulting in emergent non-nested effects (not explained by the parts at the lower level of resolution). The contribution to hierarchical theory is the inclusion of the mix of nested and non-nested relationships between different levels of resolution (Allen and Starr 1982, O'Neill 1986). Therefore, the stability of grazing effects depended on the level of resolution.

Grazing effects can be linearly predicted according to the relationship between micro and macrofactors and 'idiosyncratic heterogeneity'. In this context, the degree of heterogeneity of the rocky shore ('idiosyncratic heterogeneity') generates benign and harsh conditions within which the strength of ecological interactions varies and where complex combinations of microfactors and macrofactors were found to affect the intensity and variance of grazing effects. The intensity and variance of the effects of grazers can be affected by macrofactors, which can influence the quality of the benign and harsh areas (microhabitats) on a rocky shore. This induces spatial patterns in grazing effects, represented as patchiness in the strength of ecological interactions. At the same time the predictability will be affected through a change in the balance of microfactors.

The balance of micro and macrofactors and their effects on the intensity and variance of grazing effects allows us to make predictions about the strength of grazing effects. Finally, microfactors were more sensitive in predicting changes at lower levels of resolution (e.g. species level), while macrofactors (regional scale factors) were more effective at predicting grazing effects at coarse levels of resolution (e.g. concentration of chl *a*). Although stability was observed in grazing effects, this was not explained by the same factors from year to year or among levels of resolution, suggesting that different factors can converge to produce the same strength in an ecological interaction. Therefore, a specific strength and a specific stability point of grazing can be influenced by more than one combination of physical factors.

The conclusion here is that grazing effects are important agents contributing to algal patchiness on the rocky shore through a hierarchy of spatial scales varying from cm to meters. Grazing can behave as a system that exhibits spatial stability and temporal variability that maintains diversity of algae. These two components of spatial heterogeneity and stability were emergent properties of the system studied. Grazing effects and their spatial stability varied according the level of resolution from which the observations were made and this affects predictions of which micro and/or macrofactors are important. Finally, neither reductionist nor holistic are satisfactory. The present study highlights the need to study the ecological systems in a hierarchical way, with special emphasis on understanding the emergent relationships among levels of resolution, this being the only solution to the problem of scaling-up in ecology.

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